

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

Ruth B. Smith, Timothy D. Meehan and Blair O. Wolf

Smith, R. B., Meehan, T. D. and Wolf, B. O. 2003. Assessing migration patterns of sharp-shinned hawks *Accipiter striatus* using stable-isotope and band encounter analysis. – J. Avian Biol. 34: 387–392.

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 ( $\delta D$ ) to distinguish individuals originating from relatively high and low natal latitudes. We then examined the relationship between feather  $\delta D$  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.

R. B. Smith (correspondence), Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA and HawkWatch International, 1800 South West Temple, Suite 226, Salt Lake City, UT 84115, USA. E-mail: rbsmith@unm.edu. T. D. Meehan and B. O. Wolf, Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

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 (Palmén 1874 in Alerstam and Hedenström 1998) occurs when the latitudinal se-

quence 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).

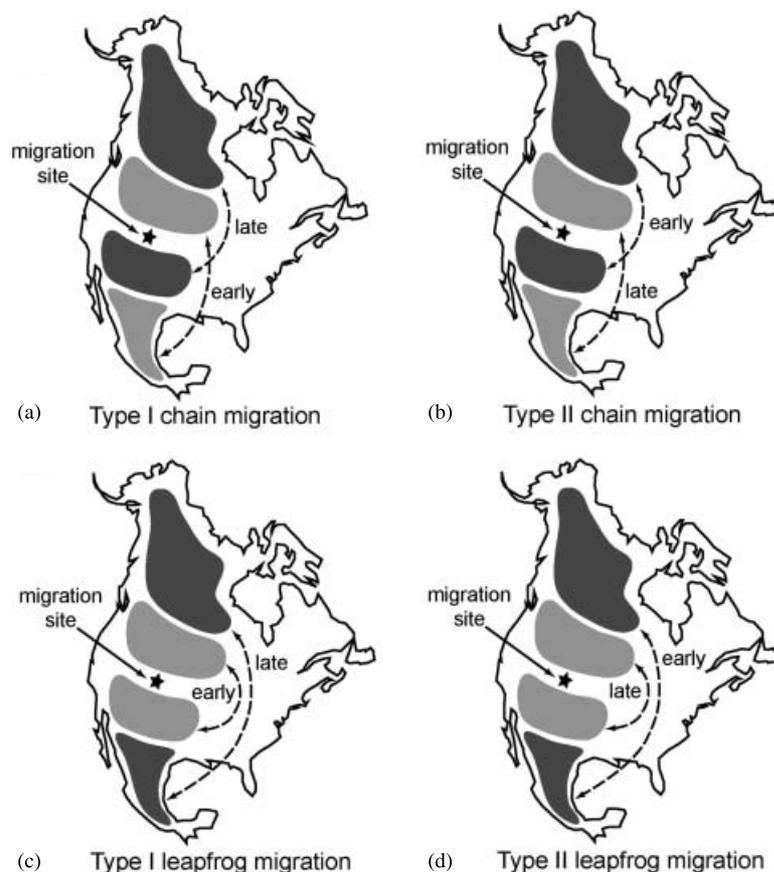


Fig. 1. (a) Type I chain migration, where northern and southern breeding populations keep the same latitudinal sequence on their breeding and wintering grounds. Southern breeding populations pass through migration sites in interior North America before northern breeding populations. (b) Type II chain migration, where northern and southern breeding populations keep the same latitudinal sequence on their breeding and wintering grounds and northern breeding populations pass through migration sites first. (c) Type I leap-frog migration, where northern breeding populations winter further south than southern breeding populations pass through migration sites before northern breeding populations. (d) Type II leap-frog migration, where northern breeding populations winter further south than southern breeding populations and northern breeding populations pass through migration sites first.

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 ( $\delta D$ ) found in precipitation vary systematically across North America and show a steadily decreasing  $\delta D$  value from the southeast to the northwest (Hobson and Wassenaar 1997, Araguas-Araguas et al. 2000). The  $\delta D$  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  $\delta D$  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,  $\delta D$  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 1999). 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  $\delta D$  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 Delta<sup>Plus</sup> 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  $\delta D$  values from this analysis were calculated using the following standard model:  $\delta D = [(\text{hydrogen isotope ratio of sample/hydrogen isotope ratio of Vienna Standard Mean Oceanic Water, VSMOW}) - 1] \times 1,000$ .  $\delta D$  values are reported in parts per thousand (‰). The precision of our analyses was  $\delta D \pm 5\text{‰}$  (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  $\delta D$  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  $\delta D$  values of feathers from 120 HY sharp-shinned hawks migrating through the Manzano Mountains. The feather  $\delta D$  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<sup>2</sup>,  $t = -4.47$ ,  $P \leq 0.001$ ) terms. Thus, birds with higher feather  $\delta D$  values (i.e., from relatively lower natal latitudes) passed through the New Mexico banding site earlier in the season than those with lower feather  $\delta D$  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

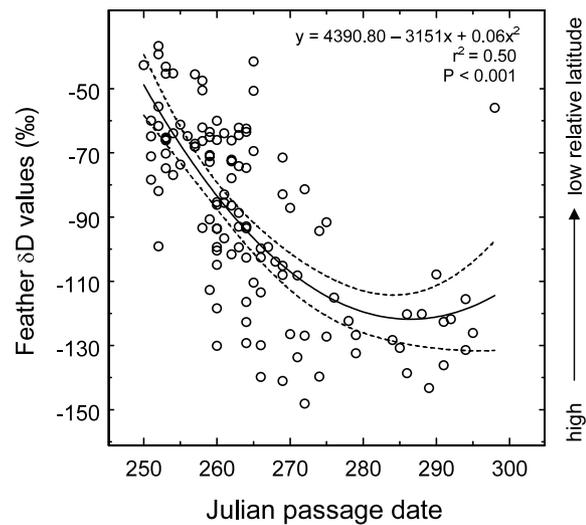


Fig. 2. Feather  $\delta D$  values of HY sharp-shinned hawks relative to their passage date through the Manzano Mountains in New Mexico, USA ( $n = 120$ ). Migrants passing through the Manzano Mountains earlier in the autumn migration season tended to originate from lower latitudes. Migrants passing through the Manzano Mountains later in the season tended to be from higher latitudes. Feather  $\delta D$  values were derived from stable-hydrogen isotope analysis and are reported in parts per thousand (‰). The solid line represents the quadratic relationship, while the dashed lines indicate the 95% confidence interval.

( $n = 19$ ); Minnesota, USA ( $n = 11$ ); Nevada, USA ( $n = 9$ ) and Idaho, USA ( $n = 3$ ). These birds were later encountered on the wintering grounds from  $13.67^\circ$  to  $43.67^\circ$  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.

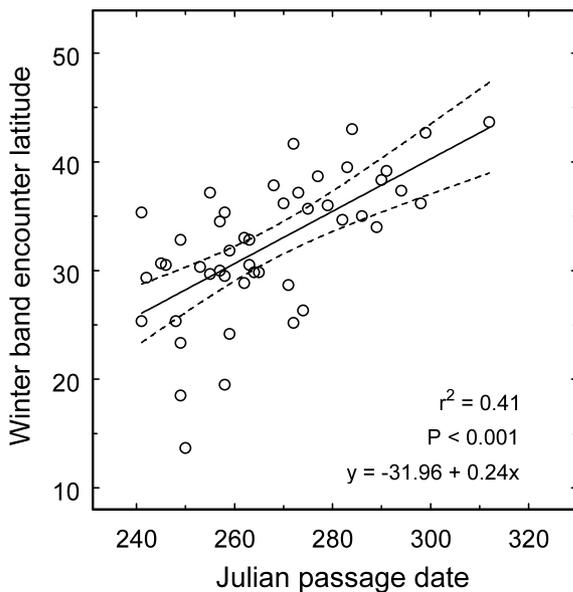


Fig. 3. Band encounter latitudes of HY sharp-shinned hawks on their wintering quarters relative to their passage date through migration banding sites in interior North America. Migrants passing through sites earlier in the season tended to winter furthest south. Birds passing through later in the season, tended to winter further north. Band encounter data ( $n = 47$ ) were obtained from the Bird Banding Lab of the United States Geological Survey and included birds banded as HY birds during their first fall migration and encountered that following winter between the dates of 15 December and 15 February, from the years of 1942 through 2000. The solid line represents the linear relationship, while the dashed lines indicate the 95% confidence interval.

## Discussion

Our stable isotope analysis indicated that migrants passing through a migration site earlier in the season were from relatively lower natal latitudes than those passing through later in the season. Comparing our feather  $\delta D$  values with a map developed by Wassenaar and Hobson (2001) indicates that early season migrants originated from areas south of the USA/Canada border while those passing through later in the season originated from points further north. Our band encounter analysis indicated that the migrants passing through migration sites earlier in the season wintered further south than those migrating through later in the season. Thus, our results indicate that HY sharp-shinned hawks migrating through interior North America during autumn used a type I chain migration (Fig. 1a). Salomonsen (1955) noted that chain migration is not as common as would be expected, whereas several examples of leap-frog migration have been documented (Swarth 1920, Salomonsen 1955, Boland 1990, Bell 1996). Although it is not fully understood why birds utilize such migration patterns, several hypotheses have been developed to attempt to explain the evolution of chain and leap-frog migration. Here we review two

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  $\delta D$  values (i.e., from relatively higher natal latitudes) were larger than those with higher feather  $\delta D$  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  $\delta D$  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  $\delta D$  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  $\delta D$  values (i.e., from relatively higher natal latitudes) were carrying higher estimated fat loads than those with higher feather  $\delta D$  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 HY 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.

*Acknowledgements* – We thank Keith Bagnall, Wendy Beard, Steve De La Peña, John DeLong, Leigh Greenwood, Carrie Hisaoka, Tuk Jacobson, Jessica Jewell, Denise Johnson, Walt Lehman, Patrick McKann, Bill Ostheimer and Tracey Ostheimer for field assistance. Special thanks to Viorel Atudorei for dedicated assistance in the stable isotope lab. Thanks to the staff of HawkWatch International (HWI) for coordinating research efforts at the Manzano migration research site. We also thank Casey Lott and three anonymous reviewers for their helpful comments on this manuscript. Research was funded by the University of New Mexico and the following HawkWatch International supporters: USDA Forest Service, Cibola National Forest, New Mexico Department of Game and Fish, US Fish and Wildlife Service (Region II), National Fish and Wildlife Foundation, Intel Corporation, New Belgium Brewing Company, Baker & McKenzie Attorneys at Law, Central New Mexico Audubon Society, and HWI members.

## References

- Alerstam, T. 1990. Bird Migration. – Cambridge University Press, Cambridge.
- Alerstam, T. and Hedenström, A. 1998. The development of bird migration theory. – *J. Avian Biol.* 29: 343–369.
- Araguas-Araguas, L., Froehlich, K. and Rozanski, K. 2000. Deuterium and oxygen-18 isotope composition of precipitation and atmospheric moisture. – *Hydrol. Process.* 14: 1341–1355.
- Bell, C. P. 1996. Seasonality and time allocation as causes of leap-frog migration in the yellow wagtail *Motacilla flava*. – *J. Avian Biol.* 27: 334–342.
- Bildstein, K. L. and Meyer, K. 2000. Sharp-shinned hawk *Accipiter striatus*. – In: Poole, A. and Gill, F. (eds) The Birds of North America. The Birds of North America, Inc.
- Blem, C. R. 1980. The energetics of migration. – In: Gauthreaux Jr., S. A. (ed.) Animal Migration, Orientation, and Navigation. Academic Press, New York, pp. 175–213.
- Bloom, P. H. 1987. Capturing and handling raptors. – In: Pendleton, B. G., Millsap, B. A., Cline, K. W. and Bird, D. M. (eds), Raptor Management Techniques Manual. U.S. National Wildlife Federation, pp. 99–103.
- Boland, J. M. 1990. Leapfrog migration in North American shorebirds: intra- and interspecific examples. – *Condor* 92: 284–290.
- Chamberlain, C. P., Blum, J. D., Holmes, R. T., Feng, X. H., Sherry, T. W. and Graves, G. R. 1997. The use of isotope tracers for identifying populations of migratory birds. – *Oecologia* 109: 132–141.
- DeLong, J. P. and Gessaman, J. A. 2001. A comparison of noninvasive techniques for estimating total body fat in sharp-shinned and Cooper's hawks. – *J. Field Ornithol.* 72: 349–364.
- DeLong, J. P. and Hoffman, S. W. 1999. Differential autumn migration of sharp-shinned and Cooper's hawks in western North America. – *Condor* 101: 674–678.
- Geller, G. A. and Temple, S. A. 1983. Seasonal trends in body condition of juvenile red-tailed hawks during autumn migration. – *Wilson Bull.* 95: 492–495.
- Hobson, K. A., McFarland, K. P., Wassenaar, L. I., Rimmer, C. C. and Goetz, J. E. 2001. Linking breeding and wintering grounds of Bicknell's thrushes using stable isotope analyses of feathers. – *Auk* 118: 16–23.
- Hobson, K. A. and Wassenaar, L. I. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. – *Oecologia* 109: 142–148.
- Hoffman, S. W., Smith, J. P. and Gessaman, J. A. 1990. Size of fall-migrant accipiters from the Goshute Mountains of Nevada. – *J. Field Ornithol.* 61: 201–211.
- Hoffman, S. W., Smith, J. P. and Meehan, T. D. 2002. Breeding grounds, winter ranges, and migratory routes of raptors in the Mountain West. – *J. Raptor Res.* 36: 97–110.
- Holmgren, N. and Lundberg, S. 1993. Despotism and the evolution of migration patterns in birds. – *Ornis Scand.* 24: 103–109.
- Kelly, J. F., Atudorei, V., Sharp, Z. D. and Finch, D. M. 2002. Insights into Wilson's warbler migration from analyses of hydrogen stable-isotope ratios. – *Oecologia* 130: 216–221.
- Kerlinger, P. 1989. Flight strategies of migrating hawks. – University of Chicago Press, Chicago.
- Lott, C. A., Meehan, T. D. and Heath, J. A. 2003. Estimating the latitudinal origins of migratory birds using stable hydrogen and sulfur isotopes in feathers: influence of marine prey base. – *Oecologia* 134: 505–510.
- Lundberg, S. and Alerstam, T. 1986. Bird migration patterns: conditions for stable geographical population segregation. – *J. Theor. Biol.* 123: 403–414.
- Meehan, T. D., Lott, C. A., Sharp, Z. D., Smith, R. B., Rosenfield, R. N., Stewart, A. C. and Murphy, R. K. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's hawks migrating through the Florida Keys. – *Condor* 103: 11–20.
- Pienkowski, M. W., Evans, P. R. and Townshend, D. J. 1985. Leap-frog and other migration patterns of waders: a critique of the Alerstam and Högstedt hypothesis, and some alternatives. – *Ornis Scand.* 16: 61–70.
- Rubenstein, D. R., Chamberlain, C. P., Holmes, R. T., Ayres, M. P., Waldbauer, J. R., Graves, G. R. and Tuross, N. C. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. – *Science* 295: 1062–1065.
- Salomonsen, F. 1955. The evolutionary significance of bird migration. – *Dan. Biol. Medd.* 22.
- Schmutz, J. K., Fyfe, R. W., Banasch, U. and Armbruster, H. 1991. Routes and timing of migration of falcons banded in Canada. – *Wilson Bull.* 103: 44–58.
- Summers, R. W. 1994. The migration patterns of the purple sandpiper (*Calidris maritima*). – *Ostrich* 65: 67–176.
- Swarth, H. 1920. Revision of the avian genus *Paserella* with special reference to the distribution and migration of races in California. – *Univ. California Publ. Zool.* 21: 75–224.
- Wassenaar, L. I. and Hobson, K. A. 2000a. Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. – *Ecol. Appl.* 10: 911–916.
- Wassenaar, L. I. and Hobson, K. A. 2000b. Improved method for determining the stable-hydrogen isotopic composition ( $\delta D$ ) of complex organic materials of environmental interest. – *Environ. Sci. Tech.* 34: 2354–2360.
- Wassenaar, L. I. and Hobson, K. A. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. – *Environ. Sci. Tech.* 35: 1845–1850.
- Wassenaar, L. I. and Hobson, K. A. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratin for use in animal migration studies. – *Isotopes Environ. Health Stud.* 39: 211–217.

(Received 1 August 2002, revised 22 January 2003, accepted 26 January 2003.)