WHAT BANDING TELLS US ABOUT THE MOVEMENT ECOLOGY OF RAPTORS

LAURIE J. GOODRICH,¹ CHRISTOPHER J. FARMER, DAVID R. BARBER, AND KEITH L. BILDSTEIN Hawk Mountain Sanctuary, Acopian Center for Conservation Learning, 410 Summer Valley Road, Orwigsburg, PA 17961 U.S.A.

ABSTRACT.—We examined banding encounter records from 1920 to 2006 for three raptors that are commonly banded in North America: American Kestrel (*Falco sparverius*, 4707 encounters), Sharp-shinned Hawk (*Accipiter striatus*; 5256), and Cooper's Hawk (*A. cooperii*; 3848). We selected birds banded during summer or autumn migration and encountered during winter to investigate movement distances and winter latitudes by sex, age, year banded, banding latitude, and flyway. Female American Kestrels migrated farther than males, but travel distances did not vary by age. Distance moved to wintering sites declined with encounter year for American Kestrels, suggesting that migratory short-stopping may be occurring across North America. Movements of the three species typically showed a chain migration pattern; however, female American Kestrels from the most northern latitudes demonstrated a leapfrog pattern, moving beyond mid-latitude birds to more southerly wintering latitudes. Female American Kestrels and Cooper's Hawks moved farther than males, whereas Sharp-shinned Hawk migration distances did not vary by sex. Hatch-year Sharp-shinned and Cooper's hawks moved farther than after-hatch-year birds, whereas no age difference was observed for American Kestrels. For all three species, northern-latitude birds moved farther than mid- or low-latitude birds, and low-latitude birds appeared to be largely resident. Distances moved also varied by flyway for both accipiters.

KEY WORDS: American Kestrel; Falco sparverius; Cooper's Hawk; Accipiter cooperii; Sharp-shinned Hawk; Accipiter striatus; banding; migration geography; movement ecology; raptors.

LO QUE EL ANILLADO NOS DICE SOBRE LA ECOLOGÍA DEL MOVIMIENTO DE LAS RAPACES

RESUMEN.—Examinamos los registros de encuentro de anillas desde 1920 hasta 2006 para tres rapaces que se anillan comúnmente en América del Norte: Falco sparverius (4707 registros), Accipiter striatus (5256) y A. cooperii (3848). Seleccionamos las aves anilladas durante la migración de verano y otoño y encontradas durante el invierno para investigar las distancias de movimiento y las latitudes de invernada considerando sexo, edad, año de anillado, latitud de anillado y corredor de vuelo. Las hembras de F. sparverius migraron más lejos que los machos, pero las distancias de viaje no variaron con la edad. La distancia recorrida a los sitios de invernada disminuyó con el año de encuentro para F. sparverius, sugiriendo que las paradas migratorias cortas pueden estar sucediendo a lo largo de América del Norte. Los movimientos de las tres especies típicamente mostraron un patrón de migración en cadena; sin embargo, las hembras de F. sparverius de las latitudes más al norte demostraron un patrón de salto de rana, moviéndose más allá que las aves provenientes de latitudes medias hacia latitudes invernales más al sur. Las hembras de F. sparverius y A. cooperii se movieron más lejos que los machos, mientras que las distancias migratorias de Accipiter striatus no variaron según el sexo. Los individuos del primer año de eclosión de A. striatus y A. cooperii se movieron más lejos que las aves de más de un año de eclosión, mientras que no se observaron diferencias de edad para F. sparverius. Para todas estas especies, las aves de latitudes más al norte se movieron más lejos que las aves de latitudes medias o bajas, y las aves de latitudes bajas parecieron ser mayormente residentes. La distancia de movimiento también varió para las dos especies de Accipiter.

[Traducción del equipo editorial]

Banding has been an important tool in studies of the movement ecology of raptors, including their migrations, since the early twentieth century (Clark 1985, Gauthreaux 1985, Schmutz et al. 1991, Hoffman et al. 2002, Smith et al. 2003, Goodrich and Smith 2008). From 1955–2000, 1 022 640 United States Fish and Wildlife Service (USFWS) bands were placed on raptors of 34 species in the United States and Canada (Bildstein 2006). Approximately 3% of banded raptors subsequently were found dead, recaptured, or

¹ Email address: goodrich@hawkmtn.org

resighted (Bildstein 2006). Of the 34 species of North American raptors banded from 1955 to 2000, the four most commonly banded species were the Sharpshinned Hawk (*Accipiter striatus*; 341 718), American Kestrel (*Falco sparverius*; 213 050), Red-tailed Hawk (*Buteo jamaicensis*; 133 770), and Cooper's Hawk (*A. cooperii*; 68 606). Together, these four species made up nearly 75% of all banded raptors in North America (Bildstein 2006).

Among the species commonly banded in North America, encounter rates range from 1% for Sharpshinned Hawks to 5% for Red-tailed Hawks (Bildstein 2006). Encounter rates were higher prior to raptor protection, as many banded birds were shot (15–25%; Robbins 1986). Because large carcasses are found more easily than small ones, encounter rates usually depend on the size of the banded bird. Among raptors with a high degree of sexual size dimorphism, encounter rates tend to be higher for females (Clark 1985, Hoffman et al. 2002).

Autumn migration patterns often are characterized as either chain migration, in which populations at different latitudes migrate the same distance southward, thus preserving their latitudinal relationship with one another, or leapfrog migration, in which high-latitude populations migrate farther south than lower-latitude populations, effectively "leaping" over them (Salomonsen 1955, Holmgren and Lunkberg 1993, Berthold 2001, Smith et al. 2003, Newton 2008). In North America, some species of raptors have exhibited migratory shortstopping, a phenomena in which distances traveled south in autumn have declined over time (Duncan 1996, Viverette et al. 1996). Climate change has been hypothesized to cause changes in migration timing and may be affecting migration travel distance for some species (Miller-Rushing et al. 2008, Newton 2008, Niven et al. 2010, Rosenfield et al. 2011).

We studied encounter locations for three of the most commonly banded species in North America for the period 1920–2006: American Kestrel, Sharp-shinned Hawk, and Cooper's Hawk. We focused on winter encounters of American Kestrels banded during summer and Sharp-shinned and Cooper's hawks banded during summer and autumn migration to bolster the sample sizes for the accipiters. Our objectives were to investigate (1) sex- and age-related differences in distances moved between summer and winter ranges; (2) regional differences in migration distances and wintering latitudes, and (3) changes in migration distances and wintering latitudes over time.

Methods

We obtained banding and encounter records for 1920–2006 from the USGS Bird Banding Lab (BBL) in Patuxent, Maryland. Throughout this paper, we refer to any reporting of a previously banded bird as an encounter, encompassing three categories outlined by the BBL (Gustafson et al. 1997): recovery (encounter of a dead bird), return (resighting or recapture in the same 10-min latitude-longitude block as the banding location), and repeat (recapture or resighting in different 10-min block than banding location). We defined four banding seasons corresponding to the life cycle of the birds: summer (11 May-31 August), autumn migration (i.e., outbound; 1 September–30 November), overwintering (hereafter winter; 1 December-9 March), and spring migration (i.e., return; 10 March-10 May). We excluded records where the encounter date was unknown. To investigate differences in migration distances related to longitude, we divided encounters in North America into eastern ($\leq 79^{\circ}W$), central (80– 100° W), and western (>100^{\circ}W) continental regions or "flyways" (Goodrich and Smith 2008). We estimated latitudinal distances traveled between banding and encounter locations (in degrees; accuracy ± 10 min) as the difference in the location latitudes reported by the BBL.

We compared variation in migration distances and wintering latitudes in relation to sex, age, banding latitude, flyway, and encounter year. For both Sharp-shinned Hawks and Cooper's Hawks, sample sizes of birds banded during summer and encountered in winter were small (n = 22 and 293, respectively). Because of this, we included in our analyses for these two accipiters the records of birds banded during autumn migration. We used general linear models (GLM) to examine differences in migration distances and wintering latitudes in relation to age (hatch-year [HY] or after-hatch-year [AHY]), sex, and flyway as categorical explanatory variables, and banding latitude and encounter year as continuous covariates. We also evaluated the interactive influence of age and sex, but did not consider additional interactions in our models due to the modest number of encounters. We used Fisher's least significant difference (LSD) tests to confirm differences among flyways following demonstration of a significant main effect. We considered $P \le 0.05$ indicative of a significant result. We present results as least-squares means \pm SE throughout. We compared movement patterns across North America by grouping data into 5°-latitude blocks based on

banding latitude and designated each block by the lower number of the 5°-latitude block. For example, the "30°-banding block" represented birds banded from 30° to 34.9°N latitude and the "35°banding block" represented birds banded from 35° to 39.9°.

RESULTS

American Kestrels. From 1920–2006, 632 American Kestrels were banded during summer and subsequently encountered during winter. Of these, 41% (262) were banded in eastern, 40% (255) in central, and 18% (115) in western North America. Twenty (3%) kestrels were recovered south of the United States during winter, 11 (55%) of which were banded north of 45° N latitude.

The GLM revealed significant influences of sex, banding latitude, and encounter year on distance traveled, but migration distances did not vary significantly by flyway or age, and there was no interaction of sex and age (Table 1). Female kestrels migrated 1.5-2 times farther south in winter than did males (Table 2); however, the difference increased among birds banded farther north and was evident only for birds banded above 40°N latitude (Fig. 1). Migration distances declined by an average of 2° of latitude for every 5° reduction in banding latitude; however, it appeared that most birds banded at latitudes below about 35°N moved little (Fig. 1). Western birds moved slightly farther $(3.5 \pm 0.6^{\circ} \text{ latitude})$ than central (3.1 \pm 0.4°) and eastern birds (3.0 \pm 0.4°) but the difference was not significant (Table 1). The distance moved by American Kestrels declined by an estimated 0.35° of latitude per decade or about 3° of latitude over the 86-yr study period.

The GLM revealed significant influences of sex, encounter year, and banding latitude on wintering latitude, but no age or flyway effects, and there was no interaction of sex and age (Table 3). Male kestrels wintered on average about 2° farther north $(39.1 \pm 0.4^{\circ})$ than females $(37.1 \pm 0.5^{\circ})$; however, this difference increased for northern nesting birds and was apparent only for birds banded at or above about 40°N latitude (Fig. 4). Overall, wintering latitudes increased by approximately 3° of latitude for every 5° increase in banding latitude; however, female kestrels banded at or above 45°N latitude actually wintered farther south than females from mid-latitudes (Fig. 4). Consistent with the finding for travel distances, wintering latitudes increased by an estimated 0.35° of latitude per decade.

Sharp-shinned Hawks. From 1920–2006, 1232 Sharp-shinned Hawks were banded in summer or autumn and subsequently encountered during winter. Of these, 39% (562) were banded in eastern, 46% (670) in central, and 15% (217) in western North America. Sixty-five winter encounters (5%) occurred south of the United States.

The GLM indicated a significant main effect for age (Table 1), with AHY birds averaging roughly 40% shorter travel distances (5.6 \pm 0.3°) than HY birds $(9.3 \pm 0.5^{\circ})$. The GLM indicated no significant main effect for sex nor the interaction between age and sex (Table 1). Female HY birds moved nearly twice as far $(10.1 \pm 0.47^{\circ})$ as AHY females $(5.4 \pm 0.29^{\circ})$. Male HY birds also moved farther than AHY birds, but the difference was less than for females (Table 2). Migration distances declined by an average of 3° of latitude for every 5° reduction in banding latitude (Fig. 2), with most birds banded below 30°N latitude showing either no movement or a slight northward shift during winter (Fig. 2). Distance moved did not vary among years (Table 1). Sharp-shinned Hawks banded in the eastern and western flyways moved similar distances south (eastern 6.9 \pm 0.4°; western 6.4 \pm 0.5°), but both moved significantly less than central birds (9.0 \pm 0.4°).

Sharp-shinned Hawk wintering latitudes varied by age, banding latitude, and flyway, but not by sex or encounter year, and there was no interaction of sex and age (Table 3). AHY birds wintered approximately 4° farther north ($36.3 \pm 0.2^{\circ}$) than HY birds ($32.3 \pm 0.4^{\circ}$; Fig. 5). Central-flyway birds wintered farther south ($32.7 \pm 0.3^{\circ}$) than eastern ($35.0 \pm 0.4^{\circ}$) and western birds ($35.2 \pm 0.5^{\circ}$).

Cooper's Hawks. From 1920–2006, 938 Cooper's Hawks were banded during summer or autumn migration and subsequently encountered during winter. Of these, 48% (452) were banded in eastern, 18% (172) in central, and 33% (314) in western North America. Fifty-eight winter encounters (6%) occurred south of the United States.

Distance moved to wintering site by Cooper's Hawks varied by age, sex, flyway, and banding latitude, but not by encounter year and there was no significant interaction between age and sex (Table 1). Females moved on average 1° farther south $(3.1 \pm 0.3^{\circ})$ than males $(2.2 \pm 0.4^{\circ};$ Table 2). Distance traveled was greater for western birds compared to eastern and central birds (eastern 1.7 \pm 0.3°; central 2.3 \pm 0.4°; western 3.8 \pm 0.3°). Mean migration distance declined by an average of 1° of

Species and	0	F	df	Р
EXPLANATORY VARIABLE	β			
American Kestrel ¹				
Intercept	43.96	2.32	1,520	0.128
Sex	0.99	11.04	1,520	0.001
Age^2	-0.21	0.50	1,520	0.481
Sex * Age	-0.20	0.44	1,520	0.509
Banding latitude (°)	0.70	86.63	1,520	< 0.001
Flyway ³		0.30	2, 520	0.738
Central	-0.10	0.11	1, 520	0.743
Eastern	-0.19	0.39	1,520	0.539
Encounter year	-0.04	5.79	1,520	0.016
Sharp-shinned Hawk ⁴				
Intercept	23.79	0.52	1, 1211	0.473
Sex	0.32	1.26	1, 1211	0.261
Age^2	-1.85	37.57	1, 1211	< 0.001
Sex * Age	-0.48	2.90	1, 1211	0.089
Banding latitude (°)	0.57	117.42	1, 1211	< 0.001
Flyway ³		14.43	2, 1211	< 0.001
Central	1.53	28.78	1, 1211	< 0.001
Eastern	-0.52	2.71	1, 1211	0.100
Encounter year	-0.02	1.46	1, 1211	0.227
Cooper's Hawk ⁵				
Intercept	41.41	1.80	1,930	0.181
Sex	0.47	4.28	1,930	0.039
Age^2	-0.59	6.81	1,930	0.009
Sex * Age	0.18	0.62	1,930	0.432
Banding latitude (°)	-0.27	36.98	1,930	< 0.001
Flyway ³		15.75	2, 930	< 0.001
Central	-0.29	0.94	1,930	0.334
Eastern	-0.92	15.47	1,930	< 0.001
Encounter year	-0.03	2.60	1,930	0.107

Table 1. General linear model results evaluating relationships between distance traveled (degrees latitude) during autumn migration and various explanatory variables for American Kestrels, Sharp-shinned Hawks, and Cooper's Hawks in North America based on banding and encounter records from 1920–2006.

n = 534 encounters; model $R^2 = 0.42$.

² Hatch-year or after-hatch-year.

³ Western (west of 100°W longitude), central (80–100°W), and eastern (east of 80°W).

4 n = 1219 encounters; model $R^2 = 0.50$.

⁵ n = 938 encounters; model $R^2 = 0.09$.

latitude for every 5° reduction in banding latitude (Table 1, Fig. 3).

DISCUSSION

Wintering latitude for Cooper's Hawks varied by sex, age, banding latitude, and flyway, but not by encounter year and there was no interaction between age and sex (Table 3). Males wintered on average approximately 1° farther north (37.5 \pm 0.3°) than females (36.6 \pm 0.3°; Fig. 6). Western birds (35.8 \pm 0.3°) wintered farther south than central (37.3 \pm 0.4°) and eastern birds (38.0 \pm 0.3°). Banding and wintering latitudes were positively correlated (Fig. 6).

Migration distances of American Kestrels declined across years, indicating the possibility of migratory short-stopping (e.g., Holmgren and Lunkberg 1993). This tends to support the hypothesis that global climate change may reduce migration movements (Berthold 2001). Christmas Bird Count data for North American Rough-legged Hawks (*Buteo lagopus*) also has shown a reduction in migration distance in recent years (Niven et al. 2010). The number of American Kestrels wintering in Pennsylvania Conser-

Species	Sex	HATCH-YEAR		AFTER-HATCH-YEAR	
		$Mean \pm SE$	n	$Mean \pm SE$	n
American Kestrel	Female	5.3 ± 1.27	35	3.4 ± 0.41	201
	Male	2.5 ± 0.73	43	2.2 ± 0.27	249
Sharp-shinned Hawk	Female	11.7 ± 0.61	225	5.1 ± 0.25	688
	Male	11.2 ± 1.2	54	5.7 ± 0.44	252
Cooper's Hawk	Female	3.4 ± 0.52	128	2.7 ± 0.26	465
	Male	2.3 ± 0.57	59	1.3 ± 0.28	286

Table 2. Distances (degrees latitude) moved by age and sex classes for raptors banded during summer (American Kestrel) or summer and autumn migration (Sharp-shinned Hawk and Cooper's Hawk) and encountered in winter in North America from 1920 to 2006.

vation Reserve Program grasslands has increased in recent years, also suggesting that migratory shortstopping has increased in this species (Wilson et al. 2010). Band encounters of Sharp-shinned and Cooper's hawks did not show evidence for short-stopping, despite prior research suggesting it may have occurred in some populations of Sharp-shinned Hawks (Duncan 1996, Viverette et al. 1996, Rosenfield et al. 2011). The lack of detectable change may be caused in part by the variation in movement patterns among flyways and because we included autumn migrants in our analyses. In addition, we examined a longer peri-

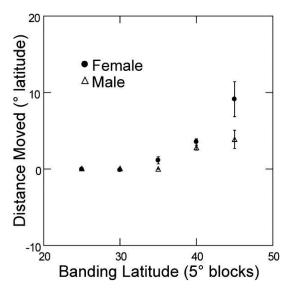


Figure 1. Mean (\pm SE) distance (° latitude) moved southward between summer-banding and winter-encounter locations by male (n = 296) and female (n = 238) American Kestrels banded at different latitudes from 1920 to 2006 (banded birds pooled in 5° blocks; e.g., 20° block includes birds banded at 20–24.9°N latitude).

od than used in other studies where short-stopping was suggested. With a larger sample size, we could have investigated some of the complexities of flyway and year variation more fully. For example, coastal populations in some regions may exhibit less movement than inland populations (e.g., Goodrich and Smith 2008). As the sample of banded birds expands, such differences may more easily be explored.

All three species showed evidence of chain migration. Although migration distance increased with increasing banding latitude, in most cases the relative latitudinal distribution remained similar during winter, simply shifted southward. However, female American Kestrels that summered above 45°N latitude moved much farther and wintered south of mid-latitude birds, exhibiting leapfrog migration. Leapfrog migration has been noted previously for wintering kestrels in the southern latitudes based on stable isotope analyses (Hobson et al. 2009); however, in this study we found that kestrels exhibit a mix of leapfrog and chain migration, depending on their nesting latitude. Moreover, our analyses revealed that only northern-latitude females showed the leapfrog pattern.

A study of Sharp-shinned Hawks in western North America also suggested that hatch-year birds are chain migrants (Smith et al. 2003). The bandencounter data analyzed in this study corroborate this pattern and suggest it extends across age groups and continent-wide for both Sharp-shinned Hawks and Cooper's Hawks. Distance moved was greater for the more northern nesting populations of both accipiters, but not enough to suggest leapfrog migration. It is possible, however, that our inclusion of autumn migrants may cloud this conclusion. Analyses restricted to birds banded on nesting grounds will be useful in further clarifying broad-scale migration patterns in these two species.

Species and				
EXPLANATORY VARIABLE	β	F	df	Р
American Kestrel ¹				
Intercept	-43.90	2.31	1, 520	0.128
Sex	-0.99	11.04	1,520	0.001
Age^2	0.21	0.50	1,520	0.481
Sex * Age	0.20	0.44	1, 520	0.509
Banding latitude (°)	0.30	16.60	1,520	< 0.001
Flyway ³		0.30	2, 520	0.738
Central	0.08	0.11	1,520	0.743
Eastern	0.19	0.38	1,520	0.539
Encounter year	0.04	5.79	1,520	0.016
Sharp-shinned Hawk ⁴				
Intercept	-10.17	0.16	1, 1199	0.724
Sex	-0.33	1.77	1, 1199	0.184
Age	1.96	56.90	1, 1199	< 0.001
Sex * Age	0.35	2.01	1, 1199	0.147
Banding latitude (°)	0.42	87.18	1, 1199	< 0.001
Flyway ³		20.24	2, 1199	< 0.001
Central	-1.55	39.81	1, 1199	< 0.001
Eastern	0.66	5.87	1, 1199	0.016
Encounter year	0.01	0.88	1, 1199	0.349
Cooper's Hawk ⁵				
Intercept	-41.41	1.80	1,930	0.181
Sex	-0.47	4.28	1,930	0.039
Age	0.59	6.81	1,930	0.009
Sex * Age	-0.18	0.62	1,930	0.432
Banding latitude (°)	0.73	264.68	1,930	< 0.001
Flyway ³		15.75	2, 930	< 0.001
Central	0.29	0.94	1,930	0.334
Eastern	0.92	15.47	1,930	< 0.001
Encounter year	0.03	2.60	1,930	0.107

Table 3. General linear model results evaluating relationships between wintering latitude and various explanatory variables for American Kestrels, Sharp-shinned Hawks, and Cooper's Hawks in North America based on banding and encounter records from 1920–2006.

n = 528 encounters; model $R^2 = 0.28$.

² Hatch-year or after-hatch-year.

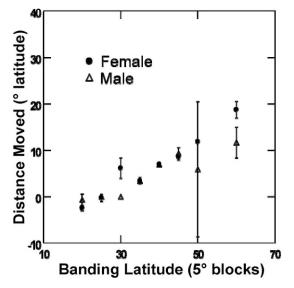
³ Western (west of 100°W longitude), central (80-100°W), and eastern (east of 80°W).

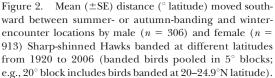
4 n = 1200 encounters; model $R^2 = 0.14$.

5 n = 938 encounters; model $R^2 = 0.26$.

In all three species, adults migrated shorter distances and wintered farther north than immature birds. Although age differences in migration distance have been reported previously in raptors (Clark 1985, Gauthreaux 1985), our results showed that agerelated differential migration was much stronger among Sharp-shinned Hawks than among Cooper's Hawks, and that at best only a weak effect (statistically nonsignificant) was found among American Kestrels. Previous researchers have hypothesized that immature birds move farther south from northern summer ranges than adults, because adults exclude juveniles from areas closer to breeding latitudes (Mueller et al. 1977, Kjellén 1990). If this hypothesis is true, the difference observed here suggests that exclusion probabilities may vary among species.

The extent of seasonal movement varied across the continent for all three species, but patterns differed. Western-flyway birds moved farther in American Kestrels and Cooper's Hawks, although the difference was not significant for the American Kestrel. In contrast to the Cooper's Hawk, Sharp-





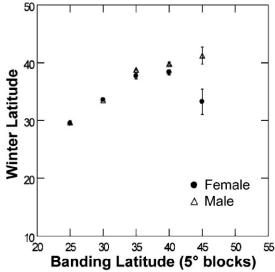
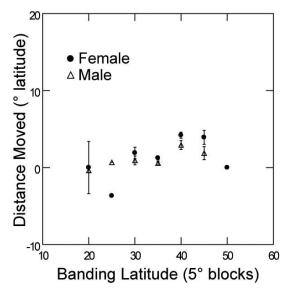


Figure 4. Mean (\pm SE) latitude of winter recoveries for male (n = 296) and female (n = 238) American Kestrels banded during summer at different latitudes from 1920 to 2006 (banded birds pooled in 5° blocks; e.g., 20° block includes birds banded at 20–24.9° latitude).



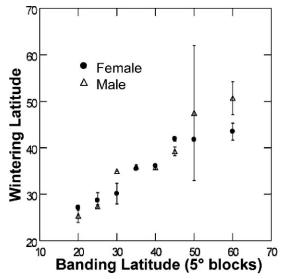


Figure 3. Mean (\pm SE) distances (° latitude) moved southward between summer- or autumn-banding and winter-encounter locations by male (n = 345) and female (n = 593) Cooper's Hawks banded at different latitudes from 1920 to 2006 (banded birds pooled in 5° blocks; e.g., 20° block includes birds banded at 20–24.9° latitude).

Figure 5. Mean (\pm SE) latitude of winter recoveries (1920–2006) for male (n = 306) and female (n = 913) Sharp-shinned Hawks banded during summer or autumn migration at different latitudes from 1920 to 2006 (banded birds pooled in 5° blocks; e.g., 20° block includes birds banded at 20–24.9° latitude).

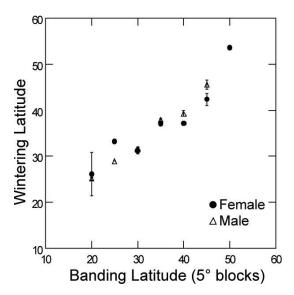


Figure 6. Mean (\pm SE) latitude of winter recoveries for male (n = 345) and female (n = 593) Cooper's Hawks banded during summer or autumn migration at different latitudes from 1920 to 2006 (banded birds pooled in 5° blocks; e.g., 20° block includes birds banded at 20– 24.9° latitude).

shinned Hawks from the central flyway moved farther than eastern and western Sharp-shinned Hawks. The complex patterns observed could be due in part to the differences in species' ranges (Rosenfield and Evans 1980, Bildstein and Meyer 2000, Smallwood and Bird 2002) and how we pooled the data into three flyways. In the west, coastal birds often migrate shorter distances compared with inland-nesting birds (Goodrich and Smith 2008). Harsher winters and climate conditions found in interior North America compared to eastern North America (Brown and Lomolino 1998) may drive interior birds from both the western and central portions of the continent to move earlier and farther than in the east (Goodrich and Smith 2008). The availability of the Meso-American land corridor to southbound central and western migrants also allows central and western birds to migrate farther without crossing water compared to birds in the east. A finer division of flyways may further illuminate regional differences in distance traveled.

Patterns of migration also varied among the three species, with Sharp-shinned Hawks moving farthest to wintering sites. Cooper's Hawks moved the shortest distance of the three raptors. Across all three species, birds banded at latitudes south of 35°N showed little movement, suggesting these populations may be largely resident. Differences between sexes within each species were most apparent at higher latitudes. In the accipiters, lower latitude birds ($<25^{\circ}$) may have shown a slight northward winter movement. Southern populations moving northward during the nonbreeding season has been documented in other raptors, including western Red-tailed Hawks (*Buteo jamaicensis*; Bloom 1985) and Bald Eagles (*Haliaeetus leucocephalus*; Buehler 2000).

Inclusion of accipiters banded on autumn migration compromised our ability to interpret differences within and among species. This inclusion may have biased our analyses because breeding latitude was unknown for these individuals. We suggest that banding data for species with a small breedingseason sample size may not be well suited to answering questions about migratory connectivity or migration distances. Despite this, the long time-series of banding records available in North America provides unique opportunities for assessing temporal changes in migration behavior in these and other species, particularly for species where banding occurs regularly on the breeding grounds.

The American Kestrel typifies a species that is easily banded during the breeding season and is therefore well suited to analyses of migratory connectivity and migration distance using banding data. Average migration distances in this species differed between males and females, with males staying closer to breeding latitudes than females. This supported the suggestion (Smallwood and Bird 2002) that males generally winter closer to the breeding grounds than females in this species. The decrease in movement across the years studied deserves further monitoring and research in the future. Further research on raptor band-recovery data may prove useful in understanding how climate change may affect migration patterns through time.

Acknowledgments

This paper would not have been possible without the long-term diligent efforts of numerous raptor banders throughout North America. We thank them as well as the USGS Bird Banding Lab for making banding data available for this analysis and for sponsoring the banding symposium at the 2010 Raptor Research Foundation conference in Fort Collins, Colorado. This paper was greatly improved by comments from J. Smith and an anonymous reviewer. This is Hawk Mountain Sanctuary Contribution to Conservation Science Number 208.

LITERATURE CITED

BERTHOLD, P. 2001. Bird migration: a general study, Second Ed. Oxford Univ. Press, Oxford, U.K.

- BILDSTEIN, K.L. 2006. Migrating raptors of the world: their ecology and conservation. Cornell Univ. Press, Ithaca, NY U.S.A.
 - AND K. MEYER. 2000. Sharp-shinned Hawk (Accipiter striatus). In A. Poole [ED.], The birds of North America online, No. 482. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/ bna/species/482 (last accessed 12 October 2011).
- BLOOM, P. 1985. Raptor movements in California. Pages 313–324 *in* M. Harwood [ED.], Proceedings of Hawk Migration Conference I. Hawk Migration Association of North America, Lynchburg, VA U.S.A.
- BROWN, J.H. AND M.V. LOMOLINO. 1998. Biogeography, Second Ed. Sinauer Associates, Inc., Sunderland, MA U.S.A.
- BUEHLER, D.A. 2000. Bald Eagle (*Haliaeetus leucocephalus*). In A. Poole [ED.], The birds of North America online, No. 506. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu.bnaproxy.birds.cornell. edu/bna/species/506 (last accessed 12 October 2011).
- CLARK, W.S. 1985. The migrating Sharp-shinned Hawk at Cape May Point: banding and recovery results. Pages 137–148 *in* M. Harwood [ED.], Proceedings of Hawk Migration Conference IV. Hawk Migration Association of North America, Lynchburg, VA U.S.A.
- DUNCAN, C.D. 1996. Changes in winter abundance of Sharp-shinned Hawks, Accipiter striatus, in New England. Journal of Field Ornithology 67:254–262.
- GAUTHREAUX, S.A. 1985. Differential migration of raptors: the importance of age and sex. Pages 99–106 in M. Harwood [ED.], Proceedings of Hawk Migration Conference IV. Hawk Migration Association of North America, Lynchburg, VA U.S.A.
- GOODRICH, L.J. AND J.P. SMITH. 2008. Raptor migration in North America. Pages 37–150 *in* K.L. Bildstein, J.P. Smith, E. Ruelas Inzunza, and R.R. Veit [EDS.], State of North America's birds of prey. Series in Ornithology No. 3. Nuttall Ornithological Club, Cambridge, MA U.S.A., and American Ornithologists' Union, Washington, DC U.S.A.
- GUSTAFSON, M.E., J. HILDENBRAND, AND L. METRAS. 1997. The North American bird banding manual. Version 1.0. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD U.S.A. http://www.pwrc.usgs.gov/ bbl/manual/manual.htm (last accessed 21 October 2010).
- HOBSON, K.A., S.H. DEMENT, S.L. VAN WILGENBURG, AND L.I. WASSENAAR. 2009. Origins of American Kestrels wintering at two southern U.S. sites: an investigation using stable isotope (δD, δ¹⁸O) methods. *Journal of Raptor Research* 43:325–337.
- HOFFMAN, S.W., J.P. SMITH, AND T.D. MEEHAN. 2002. Breeding grounds, winter ranges, and migratory routes of raptors in the mountain west. *Journal of Raptor Research* 36:97–110.

- HOLMGREN, N. AND S. LUNKBERG. 1993. Despotic behaviour and the evolution of migration patterns in birds. *Ornis Scandinavia* 24:103–109.
- KJELLÉN, N. 1990. Sex and age ratios in migrating and wintering rapors in Skåne, southern Sweden. Var Fagelvärld 49:211–220.
- MILLER-RUSHING, A.J., T.L. LLOYD-EVANS, R.B. PRIMACK, AND P. SATZINGER. 2008. Bird migration times, climate change, and changing populations sizes. *Global Change Biology* 14:1959–1972.
- MUELLER, H.C., D.D. BERGER, AND G. ALLEZ. 1977. The periodic invasion of goshawks. *Auk* 95:652–663.
- NEWTON, I. 2008. The migration ecology of birds. Academic Press, London, U.K.
- NIVEN, D., G.S. BUTCHER, AND G.T. BANCROFT. 2010. Northward shifts in early winter abundance. *American Birds* 63:10–15.
- ROBBINS, C.S. 1986. Conservation of migratory raptors: an overview based on 50 yr of raptor banding. Pages 26–34 *in* S.E. Senner, C.M. White, and J.R. Parrish [EDS.], Raptor conservation in the next 50 yr. Raptor Research Report No. 5. Raptor Research Foundation, Provo, UT U.S.A.
- ROSENFIELD, R.N. AND D.L. EVANS. 1980. Migration incidence and sequence of age and sex classes of the Sharp-shinned Hawk. *Loon* 52:66–69.
- , D. LAMERS, D.L. EVANS, M. EVANS, AND J.A. CAVA. 2011. Shift to later timing by autumnal migrating Sharp-shinned Hawks. *Wilson Journal of Ornithology* 123:154–158.
- SALOMONSEN, F. 1955. The evolutionary significance of bird migration. *Biologiske Meddelelser* 22:1–62.
- SCHMUTZ, J.K., R.W. FYFE, U. BANASCH, AND H. ARMBRUSTER. 1991. Routes and timing of migration of falcons banded in Canada. *Wilson Bulletin* 103:44–58.
- SMALLWOOD, J.A. AND D.M. BIRD. 2002. American Kestrel (*Falco sparverius*). In A. Poole [ED.], The birds of North America online, No. 602. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu. bnaproxy.birds.cornell.edu/bna/species/602 (last accessed 12 October 2011).
- SMITH, R.B., T.D. MEEHAN, AND B.O. WOLF. 2003. Assessing migration patterns of Sharp-shinned Hawks Accipiter striatus using stable-isotope and band encounter analysis. Journal of Avian Biology 34:387–392.
- VIVERETTE, C.B., S. STRUVE, L.J. GOODRICH, AND K.L. BILDSTEIN. 1996. Decreases in migrating Sharp-shinned Hawks at traditional raptor-migration watchsites in eastern North America. Auk 113:32–40.
- WILSON, A., M. BRITTINGHAM, AND G. GROVE. 2010. Association of wintering raptors with Conservation Reserve Enhancement Program grasslands in Pennsylvania. *Journal of Field Ornithology* 81:361–372.

Received 22 February 2011; accepted 11 October 2011 Associate Editor: Jeff P. Smith