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Source: Journal of Raptor Research, 50(2) : 161-175

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/rapt-50-02-161-175.1>

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USING BANDING AND ENCOUNTER DATA TO INVESTIGATE MOVEMENTS OF RED-TAILED HAWKS IN THE NORTHEASTERN UNITED STATES

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ABSTRACT.—We examined encounter records from 1925 to 2015 for Red-tailed Hawks banded in the northeastern U.S.A. ($n = 1002$) and characterized movement patterns by evaluating straight-line distances, difference in latitude, and directionality between banding and encounter locations. We define “encounter” as any handling of a live banded bird, any recovery (a banded bird found dead), and any resighting (reading and reporting a band number on a live bird without actually handling the bird). The mean direction of all hawk encounters was to the southwest of banding locations but some hawks ranged widely; encounters occurred in 27 states, including some in the Mississippi flyway, and in four Canadian provinces. Hawks banded as nestlings or as hatch-year birds (younger) were encountered at farther distances and across a wider range of latitudes than hawks banded as after-hatch-year (AHY) or after-second-year (ASY; older). Most encounters were of younger hawks. In mid-century, most known mortalities were due to shooting; more recent mortalities were due to collisions with vehicles, buildings, or other objects. Some young hawks apparently dispersed out of their natal areas or began migration by three mo post-fledging, and hawks hatched in the Northeast apparently do not migrate north during their first summer. Hawks banded at higher latitudes were encountered at locations farther south than hawks banded at lower latitudes, substantiating leapfrog migration in this species. Encounter data suggested philopatric tendencies; hawks banded as nestlings and encountered at >46 mo of age were encountered significantly closer to their natal areas than hawks banded as nestlings and encountered <46 mo after banding, and more than 10% of hawks banded as ASY or AHY were encountered after several years in the same 10-minute block in which they were banded. Hawks banded as nestlings and encountered at age >46 mo and >250 km from their natal area were considered long-distance dispersers. Between 1930 and 2010, for all hawks banded during the breeding season or summer and encountered in autumn or winter, the difference between banding latitude and encounter latitude decreased by about 4° , suggesting migratory short-stopping.

KEY WORDS: *Red-tailed Hawk*; *Buteo jamaicensis*; *banding*; *dispersal*; *encounter*; *migration*; *philopatry*.

USO DE DATOS DE ANILLAMIENTO Y DE RECAPTURAS PARA INVESTIGAR LOS MOVIMIENTOS DE BUTEO JAMAICENSIS EN EL NORESTE DE ESTADOS UNIDOS

RESUMEN.—Examinamos los registros de encuentros de *Buteo jamaicensis* durante el periodo 1925–2015 en el noreste de Estados Unidos ($n = 1002$) y caracterizamos los patrones de movimientos evaluando las distancias en línea recta, las diferencias en latitud y la direccionalidad entre el lugar de anillamiento y las localizaciones de los encuentros. Definimos “encuentro” como cualquier manipulación de un ave viva anillada, cualquier recuperación (un ave anillada encontrada muerta) y cualquier re-avistamiento (lectura e informe de un número de anilla en un ave viva sin manipulación del ave). La dirección media de todas los encuentros de *B. jamaicensis* fue hacia el suroeste de las localizaciones de anillamiento, pero algunos individuos realizaron desplazamientos más amplios. Los encuentros acontecieron en 27 estados, incluyendo algunos en la ruta migratoria del Mississippi y en cuatro provincias canadienses. Los *B. jamaicensis* anillados como pollos o como aves de primer año (aves jóvenes) fueron encontrados a distancias más lejanas y a lo largo de un mayor rango de latitudes que aquellos anillados tras el primer año (aves de segundo año, ASA) o después del segundo año (aves de tercer año, ATA; aves de mayor edad). La mayoría de los encuentros fueron con aves jóvenes. A mediados de siglo, la causa de mortalidad más conocida era la muerte por disparos; las causas de mortalidad más recientes fueron colisiones con vehículos, edificaciones u otros objetos. Algunos *B. jamaicensis* jóvenes se dispersaron aparentemente de sus áreas natales o comenzaron a migrar a los tres

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meses de haber dejado el nido, mientras que aquellos que eclosionaron en el noreste no migraron al parecer durante su primer verano. Los *B. jamaicensis* anillados a latitudes mayores fueron encontrados en localizaciones ubicadas más al sur que las de los *B. jamaicensis* anillados a latitudes menores, confirmando la migración “a salto de rana” en esta especie. Los datos de encuentros sugirieron tendencias filopátricas; los *B. jamaicensis* anillados como pollos y encontrados con más de 46 meses de edad fueron hallados significativamente más cerca de sus áreas natales que los *B. jamaicensis* anillados como pollos y encontrados con menos de 46 meses de edad. Más del 10% de los *B. jamaicensis* anillados como ASA y ATA fueron encontrados después de varios años en el mismo bloque de 10 minutos en el que fueron anillados. Los ejemplares anillados como pollos y encontrados a una edad de más de 46 meses y a >250 km de su área natal fueron considerados como individuos dispersivos de larga distancia. Entre los años 1930 y 2010, para todos los *B. jamaicensis* anillados durante la época reproductiva o el verano y encontrados en otoño o invierno, las diferencias entre la latitud de anillamiento y la latitud de recaptura disminuyó cerca de 4°, lo que sugiere una migración de parada corta.

[Traducción del equipo editorial]

Since first used in the early 20th century, scientific bird banding has provided a wealth of information about wild birds, including raptors. Despite some limitations such as regional and temporal bias in recoveries (birds found dead; recoveries are more likely in winter in southern regions, Bildstein and Peterjohn 2012), and changes in recovery rates over the years (i.e., fewer raptors are shot, Newton 1979, Lutmerding et al. 2012), banding and encounter (birds found alive or dead) data have made significant contributions to our understanding of raptor movement ecology. For example, Hoffman et al. (2002) determined that migrating individuals of five raptor species banded at three locations in the intermountain West traveled along three distinct regional flyways. Wood's (2009) analysis of recovery distances of Bald Eagles (*Haliaeetus leucocephalus*) banded as nestlings in Florida suggested a high degree of philopatry and relatively short natal dispersal distances, particularly for male eagles. Goodrich et al. (2012) explored migration patterns and factors associated with migration distances and wintering latitudes of American Kestrels (*F. sparverius*), Sharp-shinned Hawks (*Accipiter striatus*), and Cooper's Hawks (*A. cooperii*) across North America. Faccio et al. (2013) identified differences between males and females in movement patterns, natal dispersal, and survival of Peregrine Falcons (*Falco peregrinus*) banded as nestlings in New England. Compiling results from a long-term study, Bloom et al. (2015) documented northward migration by young Red-tailed Hawks (*Buteo jamaicensis*) banded south of 35° N latitude in the Pacific flyway.

Recognizing the value of conventional banding has been challenging in today's era of modern telemetry technology, but some researchers have argued that banding and encounter data have been largely underused and encouraged renewed examination of these data (Bildstein and Peterjohn 2012, Ralph

2012, Newton 2014). Suggested goals included providing additional knowledge on several aspects of raptor life history and identifying factors influencing population responses to changing environments. For example, multiple decades of banding information can help identify local or regional patterns of change in reproduction or migration with time or in response to climate change (Miller-Rushing et al. 2008, Lehtikoinen et al. 2009).

The Red-tailed Hawk is one of North America's most common raptors. Preston and Beane (2009) described various populations as partial short- to intermediate-distance migrants. In autumn, many birds that breed in northern regions (north of approximately 42–44° N) migrate south, remaining away from breeding grounds for 3–5 mo, then returning north in spring (Preston and Beane 2009). Although some northern birds may overwinter near their breeding territories (Lowe 1978), overwintering is more common by hawks breeding in middle latitudes (approximately 38–42° N), where populations are partially migratory (Brinker and Erdman 1985). A species commonly banded in North America, the Red-tailed Hawk has a relatively high encounter rate (4.93%, total encounter reports per total bandings, Lutmerding et al. 2012). In this report, we use encounter data for Red-tailed Hawks banded in the northeastern U.S.A. to investigate patterns of movement and to discuss implications for understanding migration, dispersal, and philopatry in this species.

METHODS

We obtained all encounter data through April 2015 from the U.S.G.S. Bird Banding Laboratory (BBL) for Red-tailed Hawks initially banded in the northeastern U.S.A. (CT, MA, ME, NH, NY, RI, and VT). Following the BBL, we use the term

“encounter” to include any handling of a live banded bird, any recovery (a banded bird found dead), and any resighting (reading and reporting a band number on a live bird without actually handling the bird; Gustafson et al. 1997).

For analysis, we classified the age of each hawk as either nestling (L), hatch-year (HY), after-second-year (ASY) or after-hatch-year (AHY; Gustafson et al. 1997) at the time of banding based on information provided by the bander, assuming that hawks recorded as L, HY, and ASY were correctly aged. Because fewer than 10 individuals were aged as third-year (TY) or after-third-year (ATY), we included these individuals with ASY hawks. We grouped hawks aged as second-year (SY) with those aged as AHY because we assumed these categories to be less precise as reported by banders; combining these categories also improved sample size for analysis. Although studies of various raptor species have identified differences between the sexes in patterns of movement, for example, migration and dispersal distances (Mueller et al. 2000, Goodrich et al. 2012, Facio et al. 2013), we did not include sex as a variable in our analyses. Sex is not easily determined in the field for this species, thus we lacked confidence in this variable when provided; also many records simply lacked this information.

We used available information on the life-history chronology for Red-tailed Hawks in the northeastern U.S.A. (Zeranski and Baptist 1990; Preston and Beane 2009; J. Morrison unpubl. data) to classify all banding and encounter events into one of four periods: spring migration/breeding (March–June), summer (July–September), autumn migration (October–November), and winter (December–February). Migration in this species apparently occurs in a leapfrog manner; autumn migration by individuals from northernmost populations tends to begin earlier than in southern populations (Bent 1937). However, some individuals from northern latitudes remain resident on territories year round; thus, Red-tailed Hawks observed in the northeastern U.S.A. during autumn, winter, or spring may be either residents or migrants from more northern latitudes. We combined the months of March–June into the spring migration/breeding period because of this overlap; hawks resident in the Northeast may begin breeding in early March, while during this same time hawks from more northern populations may continue their migration north to breed in more northern latitudes (Preston and Beane 2009). Finally, when possible, we sought to determine the

cause of mortality associated with recoveries. For analysis, we eliminated all records that had an inappropriate or missing banding date, encounter date, age assignment, or location. We also did not include records that represented bones or band only.

We considered the distance between the banding and encounter location for each hawk to represent a movement by that hawk, although clearly each individual could have traveled to many locations between the banding and encounter events. We described each hawk’s “movement” between banding and encounter locations as a straight-line distance (in km) and in degrees latitude (the difference in the location latitudes reported by the BBL). To investigate directionality of movements represented by distances, we calculated the angle between banding and encounter locations for each hawk (Veness 2015). Then we determined the mean direction of movement for a group of hawks and the value r (range from 0 to 1), which indicates the degree to which observations are clustered around the mean, with a larger r -value indicating greater concentration about the mean. We used Rayleigh’s Z -test for circular uniformity to test the null hypothesis that the directions of movement are uniformly distributed around a circle, and Watson-Williams test to compare directions between groups (Zar 1999).

Most banding and encounter records are stored in the BBL database with a coordinate precision of a 10-minute block (an area of 10 minutes of latitude by 10 minutes of longitude, Gustafson et al. 1997); therefore, when exact recovery locations were unknown, distances between banding and encounter locations were reported as 0. In these instances, we assigned a movement distance of 9.7 km, approximately the distance to the center of the 10-minute block (Bloom et al. 2015). Following Bloom et al. (2015), we considered hawks banded as nestlings and encountered >46 mo after banding to be breeders and those encountered >250 km from their natal nest to be long-distance dispersers; we considered hawks banded as nestlings and encountered at <46 mo of age and >100 km from their natal nest to be migrants. In evaluating philopatric tendencies based on distances moved, we chose 1.4 km to represent the diameter of a Red-tailed Hawk home range (Petersen 1979 and J. Morrison unpubl. data).

For some analyses, we combined hawks banded as L and HY into “younger” and hawks banded as AHY and ASY into “older” hawks. In these analyses we used general linear models (GLM) to examine variation in distances and degrees of latitude moved in

Table 1. Distance and direction between banding and encounter locations for 1002 Red-tailed Hawks banded in the northeastern U.S.A. between 1925 and April 2015. Because most banding and encounter records stored in the BBL database have a coordinate precision of a 10-minute block, exact encounter locations are unknown for hawks reported as encountered in the same block as where they were banded. In these instances, we assigned a movement distance of 9.7 km, approximately the distance to the center of the 10-minute block (Gustafson et al. 1997).

AGE AT BANDING	<i>n</i>	DIFFERENCE IN DEGREES LATITUDE	DISTANCE (km)	DIRECTION (MEAN BEARING) ±SE	<i>r</i>	<i>Z</i>	<i>P</i>
L	8	encountered in same 10' block as banded	9.7 km				
	89	mean 2.7° ± 0.4°, range 1.3° north to 13.0° south of banding latitude	mean 377.3 ± 51.1 km median 111.5 km range 1.5 to 2007.0 km	205.4 ± 8.7°	0.4	19.1	< 0.01
HY	24	encountered in same 10' block as banded	9.7 km				
	617	mean 2.1° ± 0.1°, range 7.3° north to 16.5° south of banding latitude	mean 366.0 ± 14.4 km median 278.5 km range 1.2 to 1885.0 km	208.6 ± 2.9°	0.5	170.3	< 0.01
AHY	24	encountered in same 10' block as banded	9.7 km				
	155	mean 0.6° ± 0.2° range 5.5° north to 10.7° south of banding latitude	mean 185.9 ± 19.6 km median 87.8 km range 1.2 to 1447.0 km	218.8 ± 12.8°	0.5	9.6	< 0.01
ASY	17	encountered in same 10' block as banded	9.7 km				
	68	mean 1.0° ± 0.4°, range 3.3° north to 14.7° south of banding latitude	mean 233.3 ± 45.1 km median 105.0 km range 1.2 to 1680.0 km	161.4 ± 77.7°	0.1	0.3	0.7

relation to age (younger vs. older), encounter decade (1920–2010), and banding latitude (in 1° increments) as categorical explanatory variables. When appropriate, we used weighted regression analysis to account for unequal sample sizes of hawks among categories of latitude or encounter decade (Sokal and Rohlf 1995). Statistical tests were performed using SYSTAT ver. 8.0 (SPSS 1996) and ORIANA (Kovach 2009). We report least-squares means ± 1 SE for all tests including those involving angular data (Kovach 2009). We used $\alpha = 0.05$ as the level of significance for all statistical tests.

RESULTS

The final dataset used for analysis of encounters of Red-tailed Hawks originally banded in the northeastern U.S.A. included 1002 individual hawks (97 banded as nestlings, 641 as HY, 179 as AHY, and 85 as ASY) and represented the time period 1925 through April 2015. All hawks were banded between 40.5° and 45.0° N; 68% were banded in NY, 19% in MA, 7% in CT, 5% in VT, and <1% each in ME, NH, and RI. Hawks were encountered from within

the same 10-minute block in which they were banded ($n = 91$, 9%, Table 1) up to 2007 km from their banding location. The mean direction of all encounters was to the southwest of banding locations ($208.8 \pm 2.89^\circ$, $r = 0.4$, $Z = 177.7$, $P < 0.01$). Some hawks ranged widely; encounters occurred in 27 states and four Canadian provinces, as far north as Quebec and as far south as Florida (Fig. 1). The spatial distribution of encounters suggested that most hawks remained within the Atlantic flyway, but some inter-flyway movement occurred, as evidenced by encounters recorded in the Mississippi flyway and in Canada (Fig. 2). Unlike findings by Steenhof et al. (1984) and Bloom et al. (2015) for hawks banded in the western U.S.A., none of the hawks in our dataset were encountered in Mexico or Central America.

Overall, younger birds (L and HY, $n = 738$) were encountered at much farther distances relative to their banding locations (367.4 ± 14.1 km) than were older birds (AHY and ASY, $n = 264$, mean 200.7 ± 19.5 km, $t = 6.92$, $P < 0.01$). Younger birds were also encountered across a wider range of

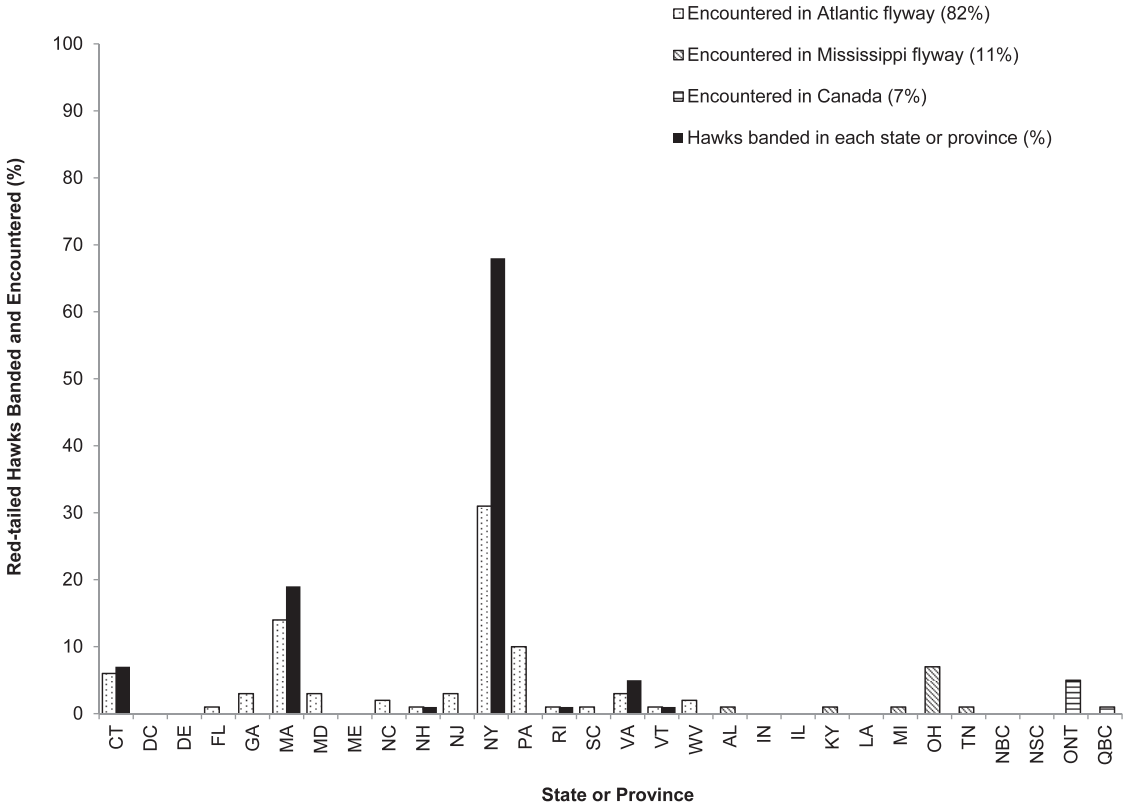


Figure 1. Red-tailed Hawks banded in the northeastern U.S.A. and encountered between 1925 and April 2015 were encountered in 27 states and in four Canadian provinces.

latitudes (across 23.8° , mean $2.2^\circ \pm 0.1^\circ$) than older birds (across 20.0° , mean $0.7^\circ \pm 0.2^\circ$, $t = 6.92$, $P < 0.01$).

Most encounters represented recoveries (78%), and 73% of all recoveries were of younger hawks. Only 1% of encounters represented resightings of live hawks in the field; the other encounters were recapture and either release or removal to captivity (if injured) of a previously banded hawk. For recoveries for which the cause of mortality was known ($n = 325$), 53% were due to collision with a moving object (motor vehicle, train, plane); 14% apparently to an injury of unknown cause; 14% to shooting; 7% to collision with a stationary object (tower, building, fence); 5% apparently to starvation; 4% to being trapped or snared; 3% to disease, poisoning, weather, or attack by a predator; and 1% to entanglement, e.g., in power lines, fishing gear, wire, string, or fence. Through the 1960s, the most common cause of known mortality was shooting; beginning

in the 1990s the primary cause of known mortality was collision with vehicles.

Three hawks were encountered more than 20 yr after banding. One was banded as a nestling in MA in 1981; when captured alive after an injury in 2002, 46 km from its natal nest, it was 20 yr and 8 mo of age. Another was banded as a nestling in CT in 1986, so when it was recovered in CT after being hit by a car 46.3 km from its nest, in 2009, it was 23 yr old. The third hawk was recorded as ASY when banded in 1985, in MA. When recovered in MA in 2008, 13.8 km from where it was banded, this hawk was at least 24 yr old.

Most hawks banded as nestlings (88%) were banded before 1990. Hawks banded as nestlings were encountered from 1 mo to 23 yr after banding at a wide range of distances from their nest and across more than 14° of latitude (Table 1). Fourteen hawks banded as nestlings were encountered within 3 mo of banding, at an average distance of 33.4 ± 15.8 km (range 3.6 to 233.6 km) and in

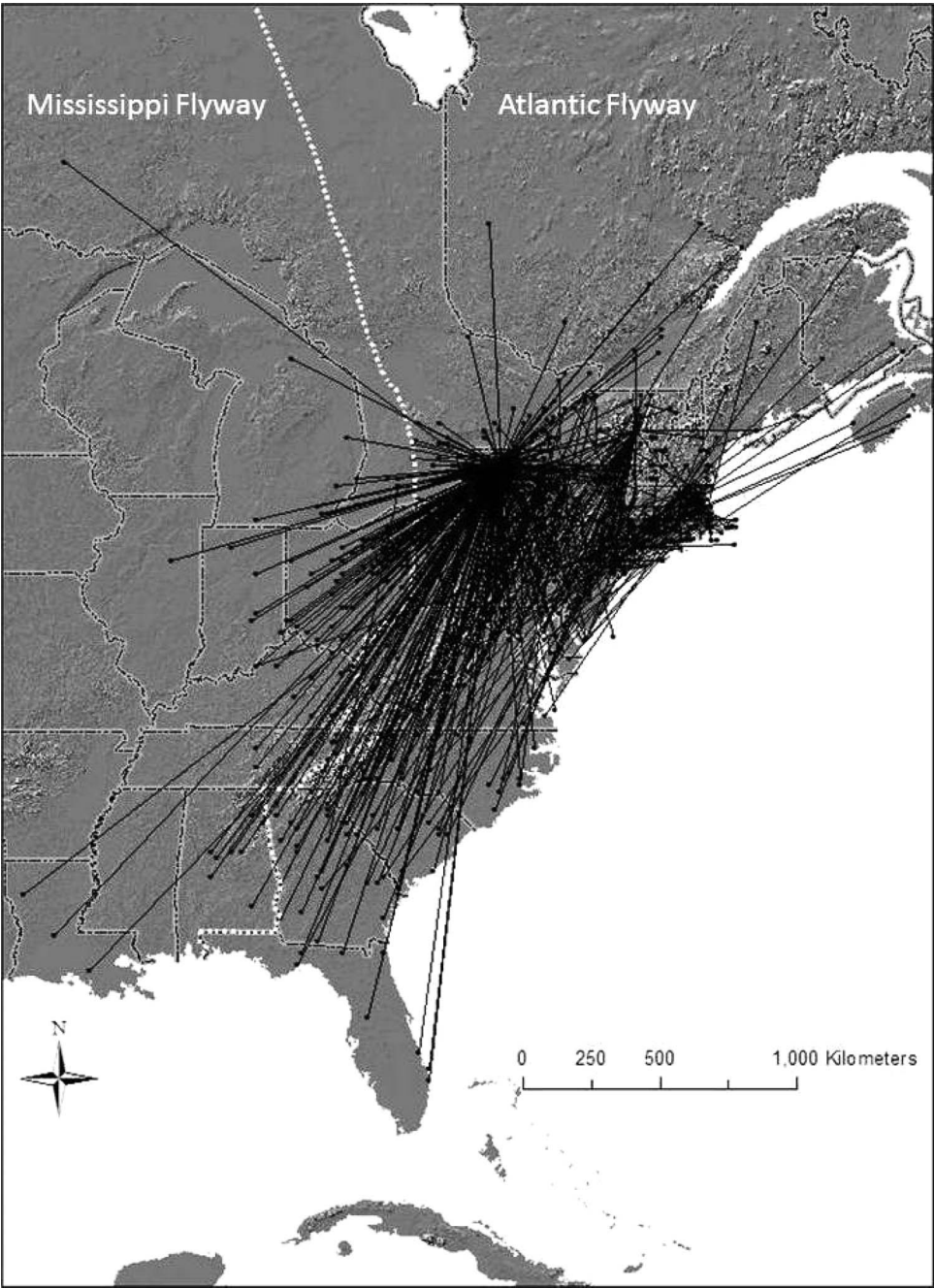


Figure 2. Most encounters of Red-tailed Hawks were recorded in the Atlantic flyway, but some hawks were encountered in the Mississippi flyway and in Canada. The white dotted line is the approximate boundary between the Atlantic and Mississippi flyways (Gustafson et al. 1997).

random directions ($222.5^\circ \pm 34.53^\circ$, $r = 0.2$, $Z = 0.3$, $P = 0.8$) from their natal nest; five of these hawks were encountered in the same 10-minute block in which they were banded. Hawks banded as nestlings and encountered after 3 mo in all seasons ($n = 83$) were encountered farther from their nest (399.9 ± 54.0 km, $t = 6.5$, $P < 0.01$), and mostly in a southwestern direction ($204.7^\circ \pm 8.86^\circ$, $r = 0.5$, $Z = 19.9$, $P < 0.01$, Fig. 3a). Most of these hawks (82%) were encountered in autumn and winter, and records suggested that most mortalities were likely due to starvation or to injuries, perhaps incurred during migration.

Seventeen hawks banded as nestlings were encountered >46 mo after banding so were assumed to be breeders. Three of these hawks were encountered >250 km from their natal area, and thus were considered long-distance dispersers. The remaining 14 hawks were encountered significantly closer (30.0 ± 2.2 km, $t = 6.6$, $P < 0.01$) to their natal area than hawks banded as nestlings and encountered <46 mo after banding (400.7 ± 56.0 km, $n = 80$). Directions to encounter of these 14 hawks did not differ from a uniform distribution ($310.3^\circ \pm 112.6^\circ$, $r = 0.2$, $Z = 0.3$, $P = 0.8$).

Fifty-three percent of hawks banded as nestlings and encountered at <46 mo of age were encountered more than 100 km from their natal area. These hawks were considered migrants and were encountered to the southwest ($207.9^\circ \pm 5.0^\circ$, $r = 0.9$, $Z = 30.4$, $P = 0.0$) and at a mean distance of 742.0 ± 74.2 km from their natal area.

Eleven hawks banded as HY during a breeding season were encountered from 1–7 mo after banding at an average distance of 499.8 ± 130.4 km from their banding location and in a strongly southwestern direction ($219.8 \pm 15.7^\circ$, $r = 0.5$, $Z = 5.1$, $P < 0.01$). Forty-two hawks banded as HY in summer and autumn were encountered at >46 mo of age in a subsequent breeding season. Five were encountered in the same 10-minute block as where they were banded. Twenty-four were encountered >100 km from their banding location and in a southwestern direction ($208.3^\circ \pm 13.8^\circ$, $r = 0.5$, $Z = 7.7$, $P = 0.0$); 19 were encountered >250 km from their banding location. All other hawks banded as HY ranged widely and were encountered in all seasons across almost 24° of latitude and mostly southwest of their banding location (Table 1, Fig. 3b).

Fifty-two hawks were banded as L or as HY during a breeding season or summer and were encountered

during that same summer (i.e., within 3 mo of banding). These hawks were encountered at a mean distance of 184.3 ± 26.0 km from their banding location, and directions to these encounters did not differ from a uniform distribution ($198.8^\circ \pm 17.7^\circ$, $r = 0.1$, $Z = 0.3$, $P = 0.7$).

Hawks banded as AHY were encountered mostly to the southwest of their banding location and across more than 16° of latitude (Table 1, Fig. 3c). Eight hawks banded as AHY during a breeding season were encountered during a subsequent breeding season at >46 mo of age; we assumed these hawks were breeders. Five of these hawks were encountered more than 250 km from (301.4 ± 28.1 km) and to the southwest ($292.6^\circ \pm 21.4^\circ$, $r = 0.6$, $Z = 2.6$, $P = 0.07$) of their banding location. The remaining three hawks were encountered an average of 71.4 ± 11.0 km from their banding location, and these encounters did not differ from a uniform distribution ($217.5^\circ \pm 28.9^\circ$, $r = 0.4$, $Z = 1.2$, $P = 0.3$). All other hawks banded as AHY were encountered at an average distance of 186.1 ± 21.7 km and to the southwest of their banding location ($206.2^\circ \pm 14.6^\circ$, $r = 0.3$, $Z = 7.5$, $P = 0.0$), although 28 of these hawks were encountered in the same 10-minute block in which they were banded, eight after more than three yr.

Thirty-eight hawks banded as ASY during a breeding season (28%) were encountered more than one yr after banding, 12 in the same 10-minute block in which they were banded. Twenty hawks banded as ASY during a breeding season were encountered after at least one yr during a subsequent breeding season at an average distance of 148.2 ± 29.5 km and mostly to the southwest of their banding location, but directions to these encounters did not differ from a uniform distribution ($223.6^\circ \pm 25.8^\circ$, $r = 0.1$, $Z = 0.3$, $P = 0.7$, Fig. 3d).

Three hundred seventy-seven hawks (54 L, 261 HY, 42 AHY, and 20 ASY) were banded in the breeding or summer season and encountered outside the 10-minute block in which they were banded in either autumn or winter. We assumed the distance between banding and encounter locations for these hawks represented autumn migratory movements. The GLM revealed influences of age, banding latitude, and encounter decade on distances traveled as measured in degrees latitude between banding and encounter locations (Table 2). Younger hawks (L and HY, $n = 315$) were encountered farther south ($t = 2.9$, $P < 0.01$) and at farther distances ($t = 3.0$, $P < 0.01$) than older hawks (AHY and ASY, $n = 62$; Table 3). Overall movement by all 377 hawks

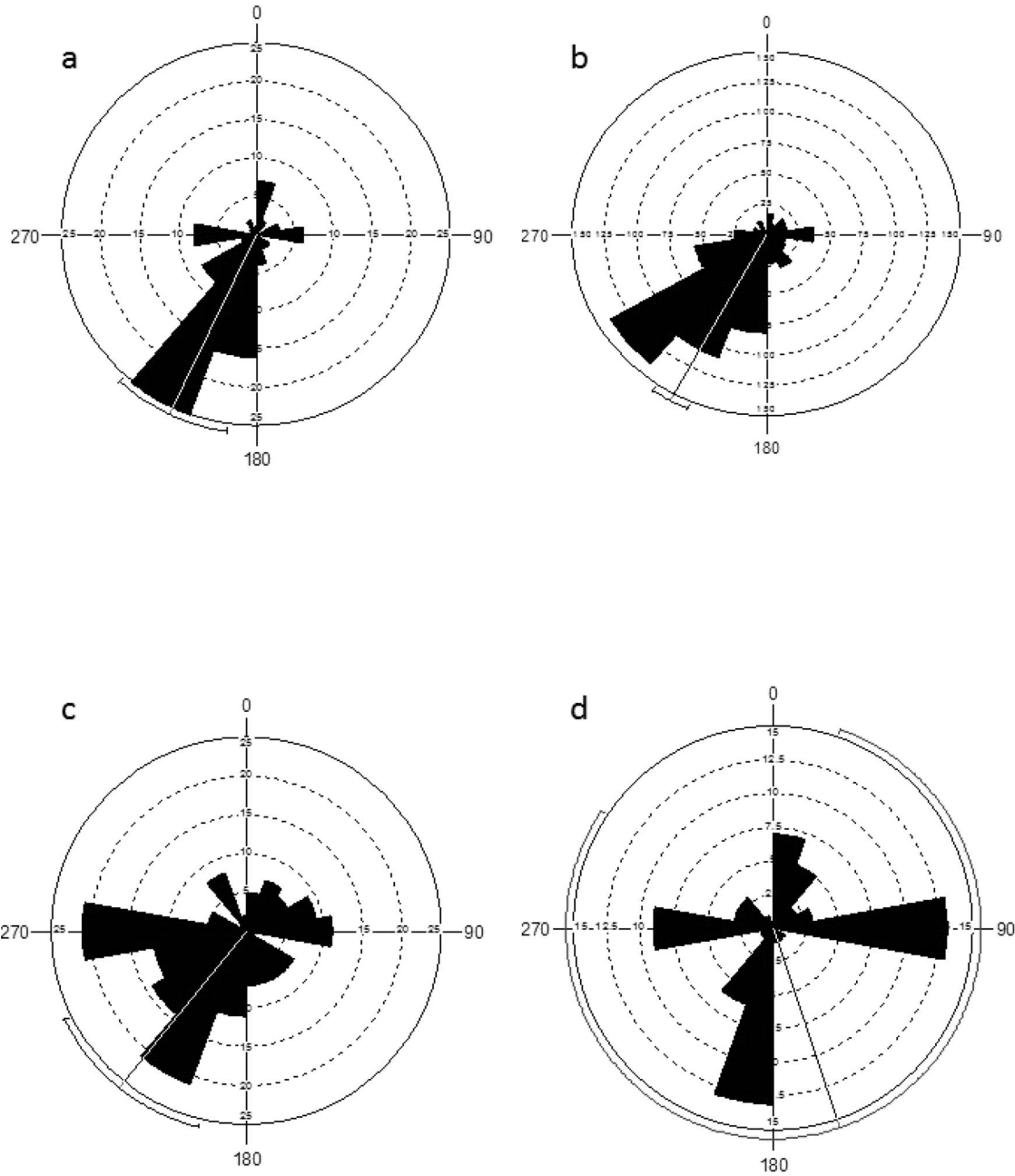


Figure 3. Angular dispersion of movements between banding and encounter locations of Red-tailed Hawks banded as (a) nestlings, (b) HY, (c) AHY, and (d) ASY in the northeastern U.S.A. Each wedge represents 10° of the total circular range, and the length of each wedge (the radius from the center) represents the number of observations falling within that range. The white or black line running from the center to the outer edge of the diagram is the mean angle of the data. The arcs extending to either side of this line represent the 95% confidence limits of the mean.

Table 2. General linear model results evaluating possible relationship between distance between banding and encounter locations (as measured by difference in degrees latitude) and age (younger vs. older), banding latitude (between 40° N and 45° N), and encounter decade (1920–2010) as explanatory variables, for 377 Red-tailed Hawks banded during the breeding season or summer and encountered during autumn or winter. All hawks were banded in the northeastern U.S.A. Banding and encounter events occurred between 1925 and April 2015. Younger hawks are those banded as L or HY ($n = 315$) and older hawks are those banded as AHY and ASY ($n = 62$).

VARIABLE	<i>F</i>	df	<i>P</i>
Age	4.1	1	0.04
Banding latitude	3.8	8	< 0.01
Encounter decade	3.1	8	< 0.01

between banding and encounter locations was in a southwestern direction and mean directions did not differ between age groups (Table 3), although movements by older hawks showed greater angular dispersion ($r = 0.4$) than movements by younger hawks ($r = 0.6$). Hawks banded at higher latitudes were encountered at locations farther south than hawks banded at lower latitudes, although for younger hawks, after correcting for unequal sample size among banding latitudes, the regression was not significant (Fig. 4). Older hawks banded below 43° N were encountered at relatively shorter distances as measured in degrees latitude between banding and encounter locations ($0.1^\circ \pm 0.2^\circ$, $n = 24$) than older hawks banded above 43° N ($2.9^\circ \pm 0.7^\circ$, $n = 38$, $t = 4.0$, $P < 0.01$, Fig. 4).

Between 1940 and 2010, distance as measured by the difference between banding latitude and

encounter latitude decreased on average by about 4°, for all hawks banded during the breeding season or summer and encountered in autumn or winter, and the regression was significant ($F_{1,7} = 8.5$, $P = 0.02$, $n = 376$, Fig. 5).

DISCUSSION

Our analyses of hawk encounter data suggest some broad patterns of movements by Red-tailed Hawks banded in the northeastern U.S.A. Movements indicated by encounters in autumn and winter of hawks banded in the breeding season and summer are typical of this species in autumn migration, given its known migration routes as recorded at Hawk Mountain and other hawkwatch sites in the eastern U.S.A. (Holt and Frock 1980, Bednarz et al. 1990, Therrien et al. 2012). However, migratory movements, as indicated by distances between banding and encounter locations, varied substantially with latitude, and this finding was consistent with reports (Bent 1937) that Red-tailed Hawks in the eastern U.S.A. exhibit leapfrog migration. Hawks breeding at higher latitudes may have evolved leapfrog migration to avoid competition in areas already occupied by less migratory southern populations (Berthold 2001, Newton 2008) or perhaps this strategy is a response to increasing human population density and regional changes in land use. For example, northern migrants passing through the heavily urbanized northeastern U.S.A. may be forced to travel farther south to avoid competition with individuals that increasingly remain in their breeding areas all year. Urban areas may provide high quality year-round habitat for some species (Sodhi et al. 1992, Stout et al. 2006),

Table 3. Distance between banding and encounter locations (as measured by difference in degrees latitude and in km) was greater for younger hawks than for older hawks. All hawks were banded during the breeding season or summer in the northeastern U.S.A. and encountered during autumn or winter. Hawks generally were encountered to the southwest of their banding location, but mean directions did not differ between age groups^a. Banding and encounter events occurred between 1925 and April 2015.

AGE AT BANDING	<i>n</i>	DIFFERENCE IN LATITUDE BETWEEN BANDING AND ENCOUNTER		DISTANCE (km) BETWEEN BANDING AND ENCOUNTER	DIRECTION (MEAN BEARING \pm SE)	<i>r</i>	<i>Z</i>	<i>P</i>
Older (AHY + ASY)	62	1.8° \pm 0.5°, range 2.3° north to 14.7° south of banding latitude		mean 297.3 \pm 53.1 km median 105.0 range 1.2 to 1680.0 km	193.3 \pm 12.0°	0.4	10.6	<0.01
Younger (L + HY)	315	3.3° \pm 0.2°, range 3.0° north to 16.5° south of banding latitude		mean 473.0 \pm 24.0 km median 371.0 range 1.5 to 2007.0 km	206.0 \pm 2.9°	0.6	147.4	<0.01

^a Watson–Williams test, $F_{1,420} = 0.1$, $P = 0.7$.

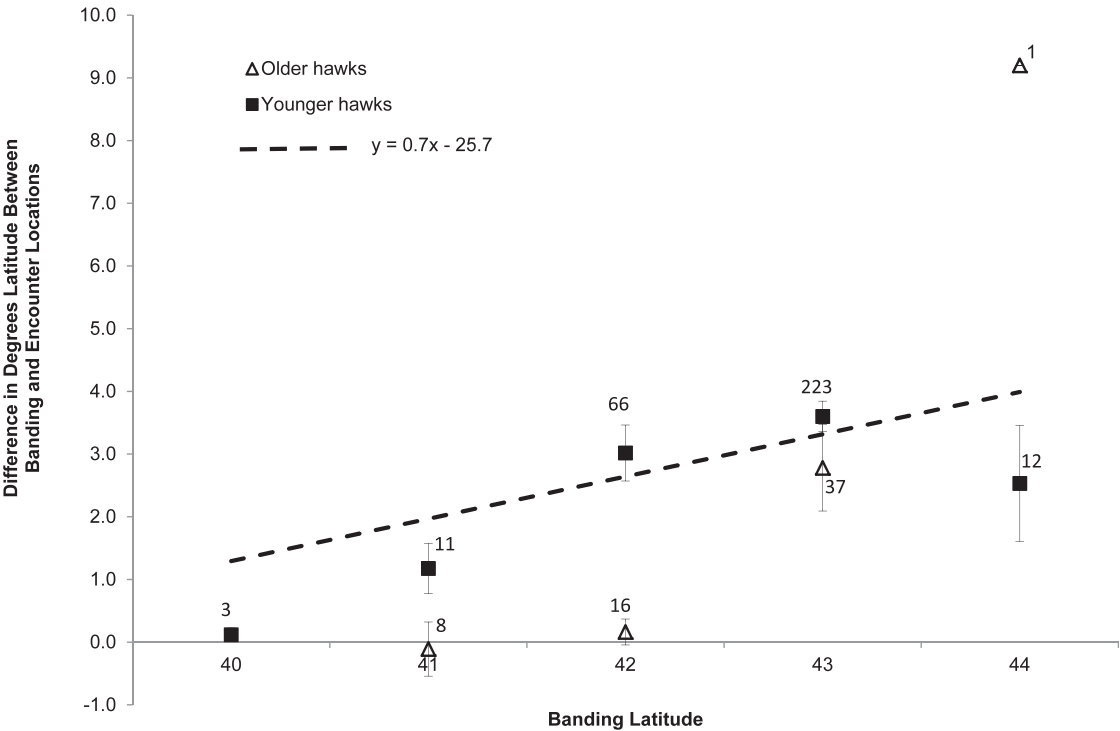


Figure 4. Red-tailed Hawks banded during the breeding season at more northern latitudes were encountered at latitudes farther south than those banded at lower latitudes, although for younger hawks ($n = 315$), after correcting for unequal sample size among banding latitudes, the regression is not significant. Larger positive differences in degrees latitude between banding and encounter locations represent greater movements to the south, from the banding location. Older hawks banded below 43° N ($n = 24$) were encountered relatively closer to their banding latitude than older hawks banded above 43° N ($n = 38$). Numbers adjacent to data points are the numbers of hawks banded in each age class at that latitude.

such that more individuals overwinter in these areas than historically. Telemetry data indicate that many breeding pairs of Red-tailed Hawks in Connecticut remain on their territories year-round (J. Morrison unpubl. data).

Analyses of these encounter data suggested age differences in distances moved by Red-tailed Hawks in the northeastern U.S.A., similar to reports for other raptors (Gauthreaux 1985, Goodrich et al. 2012). Overall, younger hawks were encountered at greater distances and over a wider range of latitudes than older hawks. Distances moved by hawks banded as nestlings and as HY within 3 mo of banding may represent natal area movements and nomadic movements made prior to permanent departure from their natal area, movements that are typical of many raptors within their first year (Morrison and Wood 2009). Our analyses also suggested that some young hawks hatched in the Northeast region were already dispersing out of their natal areas or

migrating after only three mo post-fledging. Although many of these hawks were encountered south of their banding location after three mo, some were encountered north of their banding location. Movements represented by encounters of younger hawks in random directions from their banding locations may represent exploration of the larger landscape by these individuals prior to actual migration or prior to settling in a temporary or breeding area (Ferrer 1993). Using recovery data, Adriaensen et al. (1997) found that young Belgian Eurasian Kestrels (*Falco tinnunculus*) showed rapid initial dispersal in all directions (often over more than 500 km). Adriaensen et al. (1997) also reported that recoveries of older kestrels did not show any obvious concentration in any direction and occurred at much shorter distances than recoveries of younger birds. They suggested that older hawks may be more settled and thus migrate less. Other researchers have suggested that younger birds travel farther from

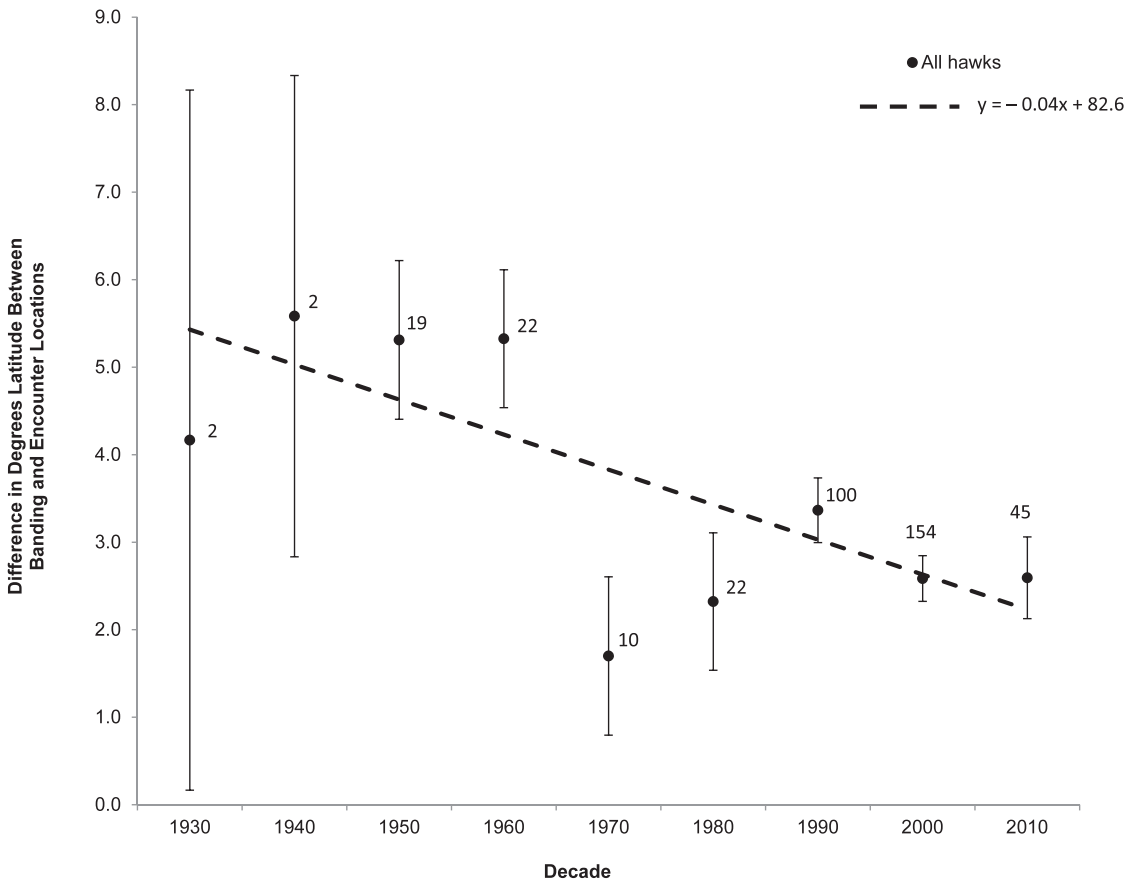


Figure 5. In recent decades, encounters during autumn and winter of Red-tailed Hawks banded during the breeding season in the northeastern U.S.A. ($n = 376$) have occurred at more northerly locations than in past decades. Numbers adjacent to data points are the numbers of hawks banded during each decade. Only one hawk was banded and encountered during the 1920s so it was omitted from this analysis. Larger positive differences in degrees latitude between banding and encounter locations represent greater distances to the south, from the banding location. The slope of the regression is significantly different from 0 ($F_{1,7} = 8.5$, $P = 0.02$).

breeding ranges than adults because adults exclude younger birds from areas near their breeding territories (Mueller et al. 1977).

Contrary to findings by Bloom et al. (2015) that young Red-tailed Hawks fledged in the Pacific Flyway migrate north in summer, encounter data for young hawks banded in the northeastern U.S.A. do not suggest a similar pattern. Fifty-two hawks banded as L or HY in a breeding season and encountered during that same summer were encountered mostly to the south of their banding location. However, our results call into question the origin of hawks banded as HY in these northeastern states in summer or autumn and encountered at >46 mo of age in a subsequent breeding

season >100 km and mostly southwest of their banding location ($n = 24$). Although these individuals may have been hawks that fledged in the northeast region, they also may have been young hawks that migrated north from the southeastern U.S.A. during their first summer, then eventually returned south to breed. Bloom et al. (2015) noted that Red-tailed Hawks rarely establish territories >100 km from their natal nest, so it is unlikely that hawks fledged in the northeast region would breed in more southern latitudes after migrating there. A comprehensive investigation of banding and encounter data for hawks banded in the southern U.S.A. is needed to further address this question.

Our analyses showed that younger hawks made up the largest percentage of recoveries, which was consistent with the pattern that young raptors tend to have higher mortality rates than adults (Harmata et al. 1999, García Dios 2004). Also consistent with other reports (Newton 1979, Adriaensen et al. 1997, Faccio et al. 2013), we found that instances of mortality due to shooting for hawks in our dataset were relatively low compared to other causes and that, since the 1960s, shooting appears to have declined as a major cause of hawk mortality. Instead, we found that most hawk mortalities in recent decades were due to anthropogenic factors, primarily collision with vehicles and other objects, as has been reported by others (Lutmerding et al. 2012).

Raptors tend to exhibit philopatry. Many studies have documented that young raptors initially explore, but ultimately return, close to their natal region when they reach breeding age (Ferrer 1993, García Dios 2004, Bloom et al. 2015). Adult raptors often exhibit strong fidelity to an area or even to a territory (Newton 1993, Forero et al. 1999, Jiménez-Franco 2013). Our analyses reveal similar patterns and suggest philopatric tendencies for at least some Red-tailed Hawks in the northeastern U.S.A. Fourteen hawks banded as nestlings and encountered at >46 mo of age were encountered significantly closer to their natal area than hawks banded as nestlings and encountered <46 mo after banding. Overall, 12.5% of older hawks and 1% of younger hawks were encountered, after several yr, in the same 10-minute block in which they were banded. Although these hawks may have traveled some distance between banding and encounter, their eventual encounter in a familiar area suggests philopatry by these individuals. Encounters of the three oldest hawks 20 yr or more after banding and all within 50 km of their banding location also suggest philopatry, at least to the northeast region. Shields (1982) suggested that philopatric individuals were those that dispersed <10 home-range diameters. In our analyses, we used 1.4 km as the diameter of a Red-tailed Hawk home range and 9.7 km to represent distance moved for hawks encountered in the same 10-minute block in which they were banded. Using these criteria, hawks encountered after at least one yr in the same 10-minute block in which they were banded displayed philopatric tendencies under Shields' (1982) definition. Philopatry to the natal or breeding area may be particularly important for hawks in highly urbanized areas such as the northeastern U.S.A., where continued urbanization and land-use change

may be reducing overall habitat available to Red-tailed Hawks. Migratory hawks would likely benefit from returning to a familiar area or even territory, where the distribution of local resources, potential mates, and predators may be known. Philopatric individuals may be able to locate suitable habitat quickly and efficiently, thus enjoying higher fitness (Davis and Stamps 2004).

Alternatively, climate change, increasing hawk populations, expanding urbanization, and other factors may favor individual hawks remaining in a familiar area year-round. Whereas older hawks encountered after several years in the same block in which they were banded may have migrated and returned to a familiar area, they also may have been territorial adults that did not migrate away but remained on their territory throughout the year. Telemetry data indicate that at least one member of 11 breeding pairs of Red-tailed Hawks in Connecticut remains on their territory year-round (J. Morrison unpubl. data).

Twenty-two hawks (three banded as nestlings, 15 as AHY, and four as ASY) were banded in the Northeast during a breeding season then encountered during a subsequent breeding season at >46 mo of age and >250 km from their banding location, suggesting that these individuals were long-distance dispersers. Although it was not known if these individuals were breeding when encountered, the fact that these encounters occurred when these individuals were of breeding age and during a breeding season suggests that is a likely possibility (Bloom et al. 2011).

Our results suggest that the difference between banding latitude and encounter latitude of hawks assumed to be in autumn migration has decreased by about 4° over the past six decades. Other studies have reported similar findings, suggesting that some raptors are not moving as far, during migration, in recent decades. Wilson et al. (2010) found that the number of American Kestrels wintering in Pennsylvania Conservation Reserve Program grasslands has increased in recent years. Goodrich et al. (2012) reported that the distance moved to wintering sites declined with encounter year for American Kestrels. Such "short-stopping" and other changes in migration patterns may reflect responses to climate change, which may affect prey availability, for example (Duncan 1996, Viverette et al. 1996, Niven et al. 2010). Similarly, Christmas Bird Counts in the past several decades have reflected higher numbers of some migratory species, including the Red-tailed Hawk, in the eastern U.S.A. (Anonymous 2015).

However, Breeding Bird Survey data indicate positive trends in Red-tailed Hawk populations all along the eastern seaboard between 2003 and 2013 (Sauer 2013). In addition, it is commonly known that during the past four decades, the overall number of encounter reports has increased (Lutmerding et al. 2012). Thus, it is not clear whether more encounters of these hawks at higher latitudes during autumn and winter reflect short-stopping, greater numbers of people birding or otherwise available to encounter hawks, or an increase in the study of these birds and corresponding increase in the number of birds banded, which has occurred most notably since the 1980s.

We acknowledge that the assumptions of equal and constant probability of encounter across regions or seasons, and for each age class are likely violated, and that this may complicate interpretation of encounters with respect to short-stopping, for example. Nevertheless, our investigation of patterns revealed by encounters of Red-tailed Hawks banded in the northeastern U.S.A. does indicate that many individuals originating in this region migrate to the south and west, that young hawks, in particular, range widely, and that at least some hawks exhibit philopatric tendencies to their natal area, supporting observations (J. Morrison unpubl. data) that some individuals do not migrate, but instead remain on or near a particular area year-round. Finally, although the breeding status of hawks encountered locally or elsewhere in a breeding season is unknown, movements revealed by these encounters may represent natal or breeding dispersal, and for some hawks, long-distance dispersal. Successful reproduction by hawks at encounter locations distant from their banding location would suggest at least some gene flow among Red-tailed Hawk populations within the eastern U.S.A. and perhaps even across flyways.

Although modern telemetry technology has greatly expanded scientists' ability to understand the movement ecology of raptors, this new technology has not replaced conventional banding, which remains an essential tool for both population biologists and ecologists studying raptor movements (Bildstein and Peterjohn 2012, Ralph 2012, Newton 2014). Information about raptor dispersal, migratory routes, settling and wintering areas, and causes of mortality is vital for understanding factors affecting species outside breeding areas, such as habitat loss, environmental contamination, or human interference. With contributions of citizen science adding

to our understanding of avian ecology, people should be encouraged to report all encounters of banded raptors, whether recoveries or resightings. Particularly for species with large numbers of banding and encounter records, much can be learned as more encounters are reported, statistical tools for analyzing banding and recovery data continue to be improved, and these data are combined with data from other techniques (e.g., Smith et al. 2003, Boulet et al. 2006, Robinson et al. 2014). Also of interest from our analyses is that these banding and encounter data suggest that few, if any, studies that included banding of Red-tailed Hawk nestlings have been done since the 1990s in the northeastern U.S.A. Although much is known about basic nesting biology in this species, researchers should be encouraged to include banding nestlings of this species, when possible, to further our knowledge of reproductive success, survival, and movements of this common raptor.

ACKNOWLEDGMENTS

We are indebted to the numerous raptor banders throughout the northeastern U.S.A. who have banded Red-tailed Hawks over the past seven decades, particularly those whose data make up more than 5% of our total dataset: the many Braddock Bay Raptor Research banders under the permit of E. Brooks at the Braddock Bay Bird Observatory; K. Griffith; J. Newhouse; D. Olmstead, and M. Olmstead. We are grateful to D. Bystrak and the Bird Banding Laboratory for providing the banding and encounter data. We thank K. Bildstein for lively discussions associated with our analyses, L. Goodrich, P. Bloom, and W. Stout for constructive comments on drafts of this report, and I. Gottlieb, K. Pias, C. Wells, F. Thomas, and N. Sell for assistance with trapping and banding Red-tailed Hawks in Hartford, CT. This study was supported by a faculty/student research grant to JLM provided by Trinity College. JLM banded Red-tailed Hawks in CT under her federal (#22800) and CT state (#0210001) permits.

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Received 4 February 2015; accepted 2 December 2015