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NORTHWARD SUMMER MIGRATION OF RED-TAILED HAWKS FLEDGED FROM SOUTHERN LATITUDES

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ABSTRACT.—With a breeding range extending from approximately 68°N in northern Canada to 8°N in Panama, Red-tailed Hawks (*Buteo jamaicensis*) exhibit migrations that vary substantially with latitude. Northern populations are almost completely migratory, middle-latitude populations are partially migratory, and southern populations south of 38°N are considered sedentary. Contrary to the latter widely held belief, we found that many juveniles and young adults from one population below 38°N are also partially migratory. However, unlike most birds in the northern hemisphere that migrate south in autumn, young Red-tailed Hawks from our southwestern California study area migrated north in summer to summering areas as far as 1462 km from their natal nests. Of the 5271 Red-tailed Hawk nestlings we banded in the study area and an additional 189 banded by other researchers, 205 were encountered (found dead or alive or recaptured) outside the study area. We classified 64 encountered hawks as potential migrants, most (69%) of which were encountered to the north of their natal nest (median = 383 km). We found that juveniles and young adults banded south of 35°N in the Pacific Flyway migrated north, whereas those banded north of 40°N migrated south. Sixteen hawks from the study area equipped with satellite transmitters as fledglings migrated north (range 342–24°) in summer, up to 1388 km, and returned to their natal region in autumn of the same year. This pattern was repeated annually until they acquired a mate and territory. Our results showed that many or most young Red-tailed Hawks migrate northward in the summer, and we propose that this pattern may be a response to historical climate changes, seasonal changes in sciurid prey availability, and/or dominance of territorial adults.

KEY WORDS: *Red-tailed Hawk*; Buteo jamaicensis; *banding*; *migration*; *satellite tracking*; *summering area.*

MIGRACIÓN ESTIVAL HACIA EL NORTE DE INDIVIDUOS DE *BUTEO JAMAICENSIS* CRIADOS EN LATITUDES MÁS AUSTRALES

RESUMEN.—Con una distribución reproductiva que se extiende aproximadamente desde los 68°N en el norte de Canadá hasta los 8°N en el sur de Panamá, *Buteo jamaicensis* presenta patrones migratorios que

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varían substancialmente con la latitud. Las poblaciones septentrionales son casi por completo migratorias, las poblaciones de latitudes medias son parcialmente migratorias y las poblaciones meridionales, al sur de los 38°N, son consideradas sedentarias. Contrariamente a esto último, que está ampliamente aceptado, encontramos que muchos individuos juveniles y adultos jóvenes de una población ubicada por debajo de los 38°N son también migrantes parciales. Sin embargo, a diferencia de la mayoría de las aves en el Hemisferio Norte que migran hacia el sur en otoño, los individuos jóvenes de *B. jamaicensis* de nuestra área de estudio ubicada al suroeste de California migraron hacia el norte en verano, a áreas de veraneo ubicadas a distancias tan alejadas como 1462 km de sus áreas natales. De los 5271 individuos de *B. jamaicensis* que anillamos en el área de estudio y de los 189 individuos de la misma especie anillados por otros investigadores, 205 fueron encontrados (muertos, vivos o recapturados) fuera del área de estudio. Clasificamos 64 individuos como migrantes potenciales, la mayoría (69%) de los cuales fueron hallados al norte de sus áreas natales (mediana = 383 km). Encontramos que los individuos juveniles y adultos jóvenes anillados al sur de los 35°N en la vía migratoria del Pacífico migraron hacia el norte, mientras que aquellos individuos anillados al norte de los 40°N migraron hacia el sur. Dieciséis individuos del área de estudio que fueron equipados con transmisores satelitales cuando eran volantones migraron hacia el norte (rango 342–24°) en verano, recorriendo hasta 1388 km, y regresaron a sus regiones natales en el otoño del mismo año. Este patrón se repitió anualmente hasta que estos individuos consiguieron pareja y territorio. Nuestros resultados muestran que muchos o la mayoría de los individuos jóvenes de *B. jamaicensis* migraron hacia el norte en verano. Proponemos que este patrón puede ocurrir en respuesta a cambios climáticos históricos, a cambios estacionales en la disponibilidad de presas de esciúridos y/o a la dominancia de adultos territoriales.

[Traducción del equipo editorial]

Conservation of migratory birds is inherently more complex than for residents. Migrants are subject to the same threats as residents while in their breeding areas, but migrants may encounter a potentially different suite of threats in their nonbreeding areas, and again throughout the migratory pathways they travel twice per year (Senner and Fuller 1989, Sherry and Holmes 1995). Adding further to the challenge of conserving migrants, migratory behavior often varies substantially among populations of the same species; populations may be entirely migratory, partially migratory, or entirely sedentary, and populations from the same breeding area may use different wintering areas (e.g., leap-frog or chain migration; Berthold 2001). Thus, developing effective conservation strategies for migratory species, especially wide-ranging ones, ultimately requires detailed information on the complete annual migration cycle at the species and population level (Faaborg et al. 2010).

The Red-tailed Hawk (*Buteo jamaicensis*) is widespread throughout North America, where it breeds from approximately 68°N in northern Canada to 8°N in Panama. Its migratory behavior is complex, varying by subspecies, geography, topographic features, latitude, and weather. Northern populations (north of approximately 42–44°N) in Alaska, Canada, and the northern continental U.S.A. are almost entirely migratory, with the expected pattern of autumn departure south to their wintering area and return trip north in spring (Steenhof et al. 1984). Northernmost populations tend to begin their migrations earlier than those in the south, apparently in a leapfrog manner (Bent 1937). Populations in middle latitudes (approximately 38–44°N) are partly migratory, with some individuals migrating south during autumn while others remain throughout winter (Brinker and Erdman 1985). Populations farther south (south of 38°N) are considered sedentary (Garrett and Dunn 1981, Brinker and Erdman 1985).

Based on the latitude of southern California (approximately 32.5–35°N), one would predict that hawks from this area would be nonmigratory. However, Robertson (1929) reported the encounter of a single 3-mo-old individual 400 km north of where it was banded as a nestling in southern California and Bloom (1985) noted that a small number of nestlings he banded in southern California were encountered well to the north, as far as Oregon in one case. Although Bloom (1985) suspected these hawks were migrating north, as was known to occur with Bald Eagles (*Haliaeetus leucocephalus*) from Florida (Broley 1947), without additional information (e.g., frequency, timing, movement behavior), the true nature of these northward movements could not be ascertained.

Here we report the results of a long-term study of the migratory behavior from post-fledging to first breeding of Red-tailed Hawks (*Buteo jamaicensis*)

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from southern California. We examined the direction and distance of band encounters from the U.S. Geological Survey (USGS) Bird Banding Laboratory (BBL) of juvenile and young adult Red-tailed Hawks banded as nestlings in southern California and the southern portion of the Pacific Flyway (USGS Bird Banding Laboratory 2010; mainly from the results of our 42-yr of banding in southwestern California) for evidence of migratory behavior. We defined migration as a regularly occurring, long-distance, directional movement from a breeding area to often the same nonbreeding area and back again each year, as opposed to dispersal, which is often random. As further evidence of migration, we compared band encounters from the southern Pacific Flyway with those from higher latitudes where Red-tailed Hawks are considered partially or almost completely migratory. Similarly, we examined band encounters of nestlings banded in other parts of the southern U.S.A. with those from higher latitudes. We also tracked the movements of 16 nestling Red-tailed Hawks from southwestern California via satellite telemetry and compared their movements with band encounter locations. Based on our observations that Red-tailed Hawks in southwestern California are strongly philopatric (Bloom 2011) and that most paired adults in California remain on their territories throughout the year (Fitch et al. 1946, P. Bloom unpubl. data), we predicted that, if it were to occur, migration would be limited to fledglings and juveniles, as with the northward migration of Bald Eagles (Broley 1947, Hunt et al. 1992, Wood 1992, Mabie et al. 1994, Hunt et al. 2009).

METHODS

Study Area and Species. We began our study of Red-tailed Hawks in southwestern California in 1970. Our study area is approximately 6250 km^2 and lies between the cities of Los Angeles and San Diego (Fig. 1); the study area includes portions of Los Angeles, Orange, San Diego, Riverside, and San Bernardino counties. The cities of Riverside and Hemet roughly form the eastern boundary of the study area, and the Pacific Ocean forms the western boundary (33.2°–34.04°N, 116.89°–118.14°W). Elevations range from sea level to 1734 m. Climate is Mediterranean, with comparatively mild winters (daily mean winter range 9.5–11.7°C) and summers (daily mean summer range 21.3–24.1°C); precipitation averages approximately 35 cm/yr, most of which occurs during winter, peaking in February. With a human population of more than four million, much of the study area has been urbanized. Habitats typically used by Red-tailed Hawks in the study area include: oak woodlands characterized by coast live oaks (*Quercus agrifolia*); riparian zones characterized by California sycamores (*Platanus racemosa*) and willows (*Salix* spp.); coastal sage scrub and chaparral characterized by several species of low shrubs including California sagebrush (*Artemisia californica*), California buckwheat (*Eriogonum fasciculatum*), sage (*Salvia* spp.) and chamise (*Adenostoma fasciculatum*); and grasslands of predominantly nonnative bromes (*Bromus* spp.).

Most Red-tailed Hawks in southern California breed for the first time when they are approximately 22–46-mo old (Bloom 2011). Nest building in southern California may begin as early as 1 November, with 1–4 eggs (rarely 5) laid from 1 February to 1 May (Bloom 2011). Incubation is approximately 28 d, and young fledge when 6–7 wk old (late April to late June in southern California; Wiley 1975).

Banding. From approximately 15 March to 1 July each year, we banded Red-tailed Hawks aged 2–9 wk with U.S. Fish and Wildlife Service and USGS aluminum lock-on bands. On 20 October 2010, we obtained from the BBL records for all nestling Red-tailed Hawks banded in North America and all encounter (previously banded bird that has been found dead or alive or recaptured) records for North America through 2009. We considered hawks encountered when <46 mo (approximate age at beginning of fourth calendar year of life) to be nonbreeders, whereas hawks encountered at older than 46 mo were considered breeders. We used 46 mo based on the behavior of an unmated, satellite platform transmitter terminal (PTT)-equipped female that continued to migrate for 4 yr. We considered Red-tailed Hawks encountered >100 km from their natal nest to be migrants because they rarely established territories >100 km from their natal nest (Bloom 2011). Further, the geographical and seasonal movement pattern of PTT-equipped hawks (this study) underscored the likelihood that banded hawks encountered when <46 mo old and >100 km were undertaking similar movements. We did not consider any of the Red-tailed Hawks vagrants because they were all encountered within the species' normal breeding, migratory, or wintering range, as opposed to western Red-shouldered Hawks (*Buteo lineatus elegans*) from the study area that were encountered outside the species' normal range and therefore considered vagrants (Bloom et al. 2011).

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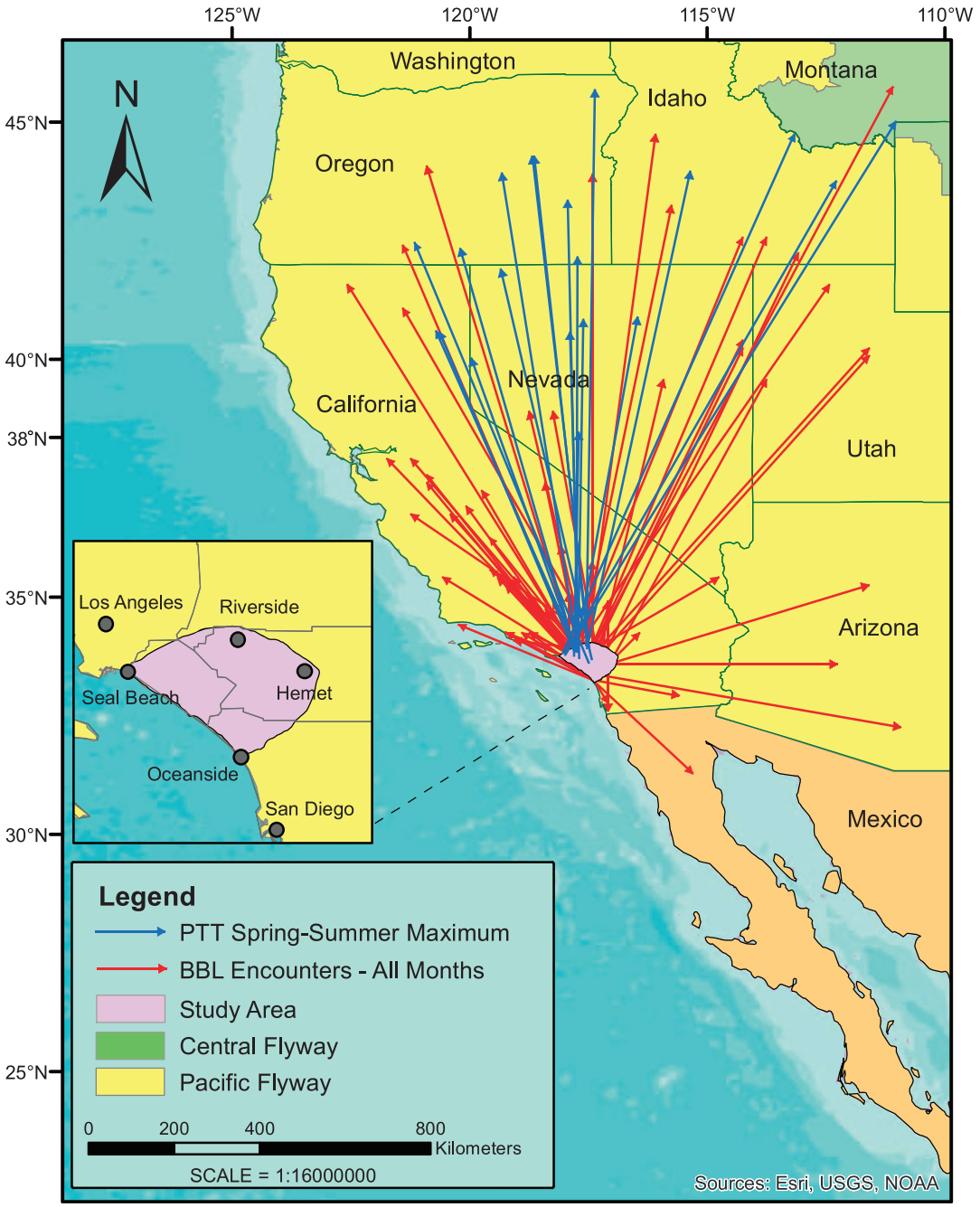


Figure 1. Encounter locations of 64 Red-tailed Hawks banded as nestlings in the study area and encountered >100 km from their natal nest and <46 mo of age, and longest summer distances traveled by 16 Red-tailed Hawks from the study area equipped as fledglings with satellite platform transmitter terminals (PTTs).

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Table 1. Mean direction of movement of migrant Red-tailed Hawks by flyway and latitude in which they were banded as nestlings in North America. Insufficient sample size for statistical testing indicated by dashes (---).

	FLYWAY (*n*)			
LATITUDE (°N)	PACIFIC	CENTRAL	MISSISSIPPI	ATLANTIC
30–35	353.3 (76)*	--- (2)	(0)	(0)
35–40	30.8 (11)^{ns}	23.4 (14)^{ns}	227.3 (66)^{ns}	--- (4)
40–45	150.2 (65)*	165.5 (23)*	176.5 (287)*	209.6 (47)*
45–50	146.2 (20)*	151.4 (11)*	171 (11)*	--- (3)
50–55	(0)	136.1 (131)*	(0)	(0)
Total (*n*)	(172)	(181)	(364)	(54)

* Distribution of directions significantly different from uniform (Rayleigh's test, $P < 0.05$).
^{ns} Distribution of directions not significantly different from uniform (Rayleigh's test, $P > 0.05$).

Although encounters of Red-tailed Hawks we banded as nestlings in our study area made up most of data in this analysis, we also examined all BBL records for North America from 1947 (year of earliest encounter in BBL records) through 2009 of Red-tailed Hawks that were banded as nestlings and were later encountered when they were both >100 km from their natal nest and <46 mo of age.

From 1970–2009, we banded 5271 Red-tailed Hawk nestlings in our study area (Fig. 1); an additional 189 were banded in the study area from 1957–2002 by other researchers not associated with this study, for a total of 5460 Red-tailed Hawk nestlings banded in the study area from 1957–2009. Two hundred five of the 5460 (4%) were encountered outside the study area. Sixty-four of the 205 hawks were <46 mo old and were encountered >100 km from their natal nest and were thus considered migrants.

From 1940 through 2009, 31 088 Red-tailed Hawk nestlings were banded in North America (USGS Bird Banding Laboratory 2010). Of these, 1738 (6%) were later encountered (excluding 40 records with errors or incomplete location information). After records were combined with the records of the 64 encounters from our study area and the database corrected for errors and duplicates, we considered that 771 Red-tailed Hawks banded as nestlings in North America were migrants by our definition (i.e., <46 mo and >100 km from natal nest). We grouped locations where migrants were banded into the four major U.S.A. flyways (Pacific, Central, Mississippi, and Atlantic; Table 1) as defined by the BBL. The BBL does not separate birds banded in Canada by flyways, and we therefore classified them according to general boundaries of the four U.S.A. flyways and major topographic features (e.g., Rocky Mountains). Locations of nests where migrants were banded ranged from 31.9–54.4°N, although most (78%) were banded north of 40°N. We then grouped migrants in each flyway in 5° latitude increments from 30–55°N and analyzed directions from natal nest to encounter location in each group (Table 1). We also analyzed directions from 34–42°N in the Pacific Flyway in 2° increments to more finely describe the movements of migrants in that latitudinal zone.

Satellite Platform Transmitter Terminals. From 2004 through 2009, we equipped 26 fledgling (6–10-wk-old) Red-tailed Hawks with backpack-mounted PTTs (17 Doppler PTTs and 9 GPS PTTs; Microwave Telemetry, Columbia, Maryland, U.S.A., and Northstar Science and Technology, Baltimore, Maryland, U.S.A.). All PTTs were solar powered, weighed 23–30 g, and did not exceed 3% of body mass. PTTs were tracked by CLS America Inc. (Lanham, Maryland, U.S.A., a subsidiary of CLS Argos, Toulouse, France). Doppler PTTs were programmed to transmit a 10-hr-on-24-hr-off duty cycle. GPS PTTs were programmed to collect eight GPS locations daily and uplink data every seventh day to Argos. We discontinued data analysis for the last two surviving hawks with functioning PTTs in March 2014.

We based the direction and the distance of migration of PTT-equipped hawks on the straight line between the natal nest and the location of the maximum distance from the nest. We defined the maximum distance as the point at which a hawk started heading back toward its natal region. We defined the natal region for each hawk to be the area within 203 km of the natal nest based on the greatest natal dispersal distance of a banded hawk (Bloom 2011).

Although nestlings were banded throughout the study area, PTT's were deployed in a comparatively small portion of approximately 695 km^2. Territories

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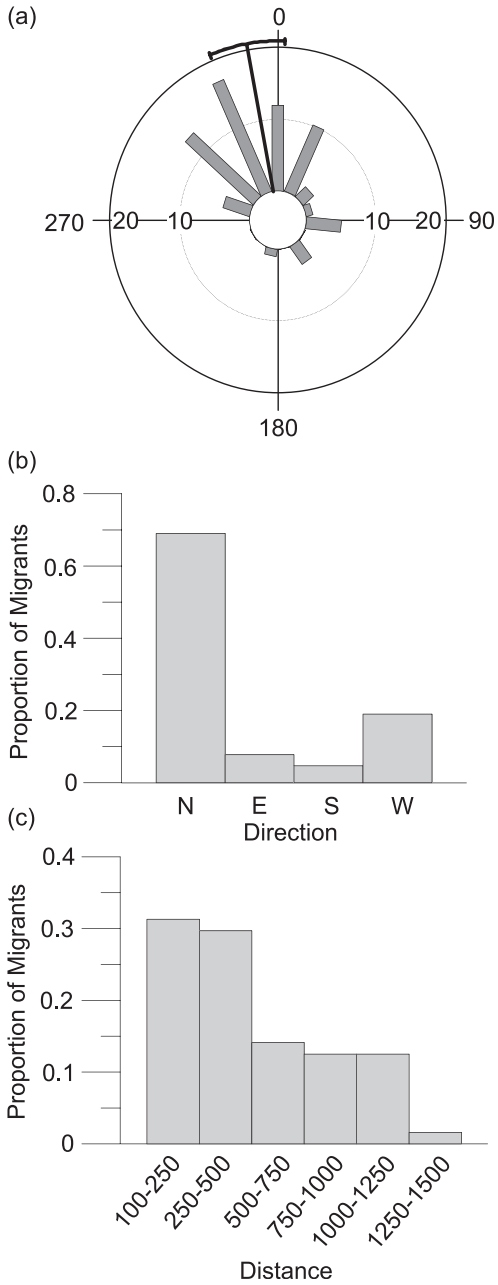


Figure 2. (a) Directions of movement of Red-tailed Hawks banded as nestlings in the study area and encountered >100 km from the natal nest and <46 mo of age (n = 64). Each bar in the circular histogram represents 24° of the total circular range, and bar length (radius from center) represents number of observations. Mean direction (348°) is shown as the line running from center to outer edge, and arcs extending to either side represent 95% confidence limits. (b) Proportion of banded Red-tailed Hawks encountered in each of the directional quadrants (N = 315–44.9°, E = 45–134.9°, S = 135–224.9°, W = 225–314.9°). Hawks were banded as nestlings in the study area and encountered >100 km from their natal nest and <46 mo of age (n = 64). Distribution of directions was significantly different from a uniform circular distribution (χ^2 = 68.1, df = 3, P <0.0001). (c) Frequency distribution of encounter distances (km) for migrant Red-tailed Hawks banded as nestlings in the study area.

where PTTs were used were selected on the basis of many years of occupancy by Red-tailed Hawks, ease of access to both nest tree and nest, and age of young when PTTs were deployed.

Nestlings and fledglings were sexed by body size, tarsal width, culmen length, and contrasting size and age of siblings. Twenty-four females and two males were fitted with PTTs. Sample size was biased toward females, which are the larger sex (Donohue and Dufty 2006), to reduce any effect that higher PTT weight relative to body mass could potentially have on smaller males; the two males were selected because of their larger size compared to other males.

We used NCSS statistical software (Hintze 2007) to analyze distances and ORIANA (Kovach 2009) to analyze directions. Rayleigh's uniformity test was used to examine distribution of directions, Watson-Williams test was used to compare directions between groups, and Mann-Whitney U-test was used to compare distances and dates between groups. Means are reported ±SD, and we used $\alpha = 0.05$ as the level of significance for statistical tests.

RESULTS

Band Encounters. *Study area: direction, distance and destinations.* Directions of the 64 migrant encounters from the study area (Fig. 2a) deviated significantly from a uniform circular distribution (Rayleigh's test, $Z = 32.2$, $P < 0.001$). Mean direction was 348 ± 48° ($r = 0.71$). Although the Pacific Ocean along the southwestern border of the study area likely affected the distribution, most hawks headed north while very few flew south or east where there was no such limitation to their movements. When compass directions were divided into four quadrants (north = 315–44.9°, east = 45–134.9°, south = 135–224.9°, west = 225–314.9°), we found the proportion of hawks encountered in each quadrant differed significantly from expected (χ^2 = 68.1, df = 3, $P < 0.001$); more migrants

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(69%) headed north from the study area (Fig. 2b), whereas fewer headed east (8%), south (5%), or west (19%).

Median encounter distance of the 64 migrants from the study area was 383 km (mean = 508 ± 360 km, range 104–1462 km); migrants that headed north (median = 570 km, mean = 615 ± 376 km, n = 44) traveled significantly farther than those in the other three directions (median = 196 km, mean = 273 ± 160 km, n = 20; Mann-Whitney U = 199, $P <$ 0.001). Most migrants (63%) were encountered in California (Fig. 1), mainly in the western Mojave Desert, Los Angeles Basin, and Central Valley. Another, smaller group (9%) was spread across the northern Great Basin and Columbia Plateau in northeastern Nevada, northwestern Utah, Oregon, and southern Idaho, which was the same general area where many PTT-equipped hawks traveled (see below). Most migrants (59%) were encountered <500 km from the study area (Fig. 2c); only 14% were encountered >1000 km. One hatch-year (HY) hawk crossed the Continental Divide and was encountered 1462 km from the study area, near Bozeman, Montana (Fig. 1).

Four North American migratory flyways: directions by latitude. Migrants in the Pacific Flyway, including those from the study area, were banded from 31.9°N in southern Arizona to 47.9°N in northern Washington, U.S.A. (Fig. 3). Directions of migrants from 30–35°N (r = 0.59, n = 76), 40–45°N (r = 0.86, n = 65), 45–50°N (r = 0.77, n = 20; Table 1) each deviated significantly from a uniform circular distribution (Rayleigh's test, $P < 0.001$), but those from 35–40°N (r = 0.27, n = 11) did not (P = 0.46). We pooled data from 40–45°N and 45–50°N, which both had means to the southeast (150° and 146°, respectively) and were not significantly different from each other (Watson-Williams test, F = 0.21, P = 0.65). Directions flown by birds banded as nestlings from 40–50°N were mainly (91%) to the south, and the combined mean from 40–50°N was 149 ± 34° (r = 0.84, n = 85). The mean direction from 40–50°N differed significantly from that from 30–35°N (353 ± 59°, n = 76; Watson-Williams test, F = 336, $P <$ 0.001).

We next analyzed directions flown by the 64 migrants banded in the Pacific Flyway from 34–42°N, the general zone between migrants that headed north from their natal nests and those that headed south, in 2° increments to determine more exactly the latitude at which the reversal in direction occurred. Although most migrants (75%) were banded from 40–42°N, and only directions in those latitudes deviated significantly from a uniform circular distribution (Rayleigh's test, Z = 38.3, $P < 0.001$), the general trend was for migrants banded north of 38° to head in a southerly (90–269°) direction (46 of 49 [94%]), whereas those banded south of 38° headed in a northerly (270–89°) direction (12 of 15 [80%]). Thus, the data suggest that the shift in direction of migration from north to south in the Pacific Flyway occurred between approximately 38 and 40°N in northern California and central Nevada and Utah.

Only limited comparisons can be drawn between the Pacific Flyway and the other three flyways because data are severely lacking or completely absent for several latitudes in the other flyways (Table 1). Although the general pattern at higher latitudes (>40°N) was the same across all flyways, with mean directions all to the south (range 136–210°), we were unable to determine if the significant, northward direction from 30–35°N in the Pacific Flyway also occurred in any of the other flyways, because only two migrants in the other flyways in those latitudes were encountered (Table 1). However, distribution of movement directions from 35–40°N in the Mississippi and Central flyways was similar to that at the same latitudes in the Pacific Flyway. As with the Pacific Flyway, there was no statistically distinct migration direction from 35–40°N in either the Mississippi (r = 0.2, Rayleigh's test, Z = 2.61, P = 0.07, n = 66) or Central (r = 0.43, Rayleigh's test, Z = 2.61, P = 0.07, n = 14) flyways, suggesting this could be a transition zone. Although only four migrants from 35–40° in the Atlantic Flyway were encountered, they were all encountered in a northerly direction (range 358–35°) from their natal nests.

Platform Transmitter Terminals. Of the 26 fledgling hawks from the study area we equipped with PTTs, 10 became silent within 2–3 wk and were not included in the analysis. The remaining 16 hawks survived for at least 2 mo (Table 2), with four surviving for >2 yr (31 to >69 mo).

Summer migration: timing, direction, distance, and destinations. The 16 hawks that survived for at least 2 mo fledged from early May to mid-June at 6–7 wk of age, with most fledging in mid-May. Thirteen of the 16 hawks migrated during their first summer (Table 2). Two (47804-1 and 65999-2; Table 2) did not migrate during their first year but did migrate during their second. Hawk 47804-3, the sibling of 65999-2, had also not migrated by 25 August of its first year when it died approximately 40 km northeast of its natal nest. Although 47804-3 may

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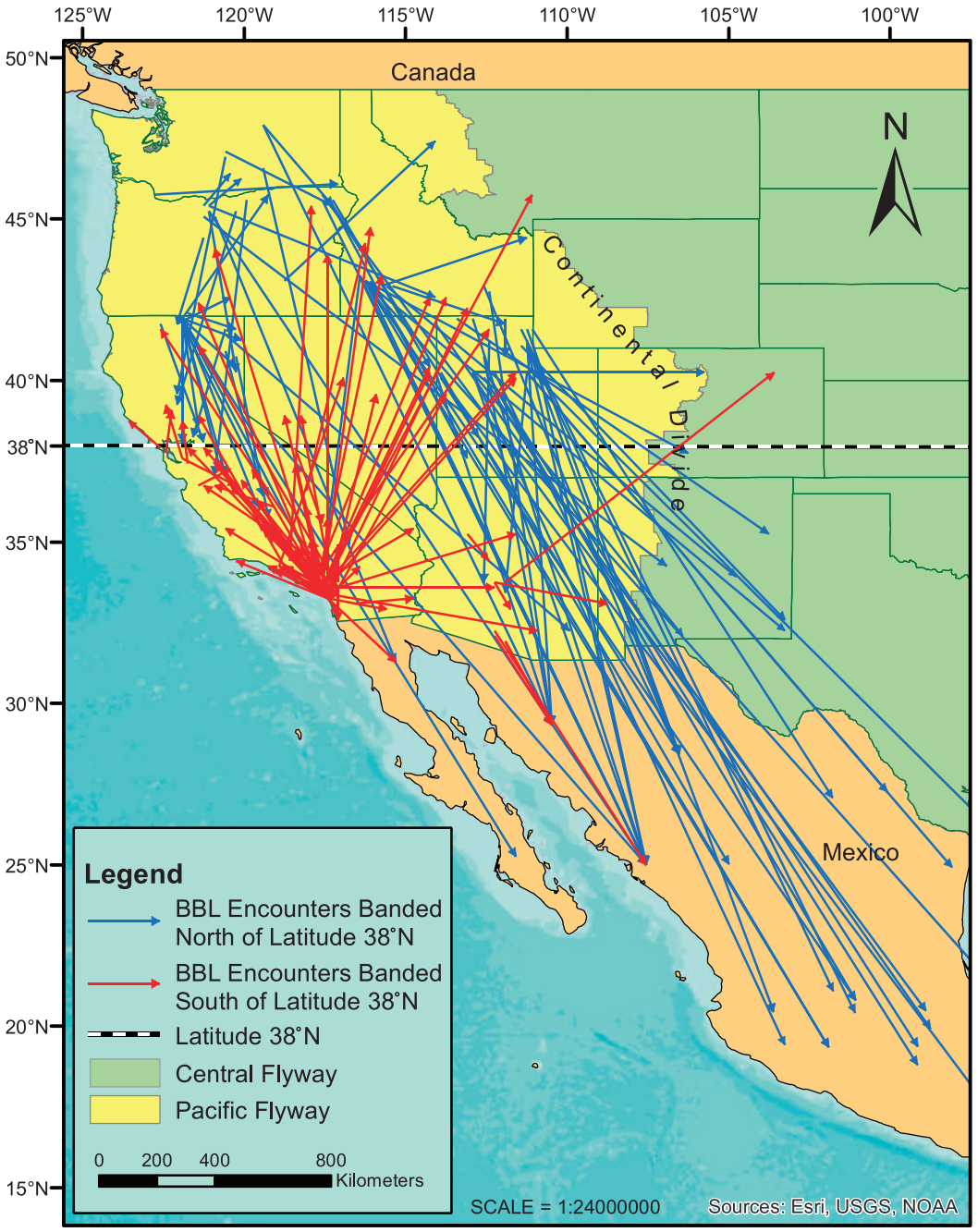


Figure 3. Movements of 173 Red-tailed Hawks banded as nestlings in the Pacific Flyway and encountered >100 km from their natal nest and <46-mo of age.

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Table 2. Timing, distance, and direction of migration of 16 juvenile and young adult (<46 mo) Red-tailed Hawks equipped with platform transmitter terminals (PTT) as fledglings in the study area.

PTT ID[1]	Sex	Date PTT Attached	Initiation of Migration	Maximum Distance (km)	Arrival at Maximum Distance	Direction (degrees)[2]	Arrival at Natal Region
47801-1	F	3 July 2004	4 July 2004	1343	24 July 2004	1	3 September 2004
			6 May 2005	1170	6 August 2005	10	2 September 2005
			2 May 2006	1189	9 August 2006	357	11 October 2006
			18 June 2007	1187	3 July 2007	357	3 November 2007
47803-1	F	4 July 2004	23 July 2004	915	27 July 2004	352	18 September 2004
47804-1	F	14 June 2005	did not migrate				
			14 May 2006				signal lost
47805-1	F	14 May 2005	12 July 2005	977	2 August 2005	348	29 September 2005
			8 June 2006	725	12 July 2006	345	signal lost
65991-1	F	8 May 2006	24 June 2006	1295	18 July 2006	18	15 August 2006
			24 April 2007	1290	3 July 2007	24	signal lost
65992-1	F	8 May 2006	4 July 2006	1388	18 July 2006	24	12 September 2006
			8 May 2007	1223	15 May 2007	23	17 September 2007
65995-1	F	13 May 2006	9 July 2006	1140	20 August 2006	354	1 October 2006
65994-2	M	26 May 2007	28 June 2007				signal lost
65993-3	F	10 July 2007	2 August 2007	797	30 August 2007	342	signal lost
47804-2	F	26 May 2007	3 August 2007	804	21 August 2007	342	1 November 2007
47803-2	F	12 June 2007	24 July 2007	1010	8 August 2007	344	signal lost
65994-3	F	21 June 2008	3 August 2008	932	10 August 2008	0	23 October 2008
			27 July 2009	786	13 September 2009	1	20 September 2009
65999-1	F	21 June 2008	30 July 2008	755	2 August 2008	359	7 October 2008
47801-2	F	16 May 2009	4 July 2009	1069	22 July 2009	1	24 September 2009
65999-2	M	18 June 2009	did not migrate				
			6 August 2010	805	12 September 2010	10	24 October 2010
47804-3	F	19 June 2009	did not migrate				

[1] PTTs were reused when possible.

[2] Maximum distance and direction measured by a straight line from natal nest.

have migrated if it had survived, it had not done so by the time that the other hawks had reached their maximum distance for their first migration (18 July–21 August; Table 2; all dates are ±1–4 d due to transmitter duty cycle and transmission quality). Those hawks that migrated in their first year generally remained in their natal region for approximately 4–10 wk after fledging, although one remained for 14 wk. Estimated date of initiation of migration in the first year ranged from 24 June–3 August (Table 2; mean = 13 July ± 14 d, n = 13), and estimated age at initiation of first-year migration ranged from 55–110 d (mean = 90 ± 14 d).

Seven of the 16 hawks survived >1 yr with functioning PTTs, and all seven initiated migration in their second year, including the two hawks that did not migrate in their first year (Table 2); one of the seven (47801-1) also migrated in its third and fourth year. Initiation dates of second-year and subsequent migrations were earlier (n = 9, range 4–63 d) when compared to the same hawk's first year migration (which was constrained by fledging date), and mean date of initiation of second-year and subsequent migrations (2 June ± 38 d, n = 9, range 24 April–6 August) was significantly earlier than for first-year migrations (Mann-Whitney U = 23, P = 0.009). The three initiation dates of 47801-1 were all earlier than its first-year migration (Table 2).

All first-year and subsequent summer migrations of PTT-equipped hawks were in a northerly direction (n = 20, range 342–24°) from the study area (Fig. 1). The mean straight-line direction of 12 of the 13 first-year migrants from their natal nest to their maximum distance was 357 ± 13° (range 342–24°). Directions deviated significantly from a uniform circular distribution (Rayleigh test, Z = 11.42, $P < 0.001$) and were strongly (r = 0.98) concentrated around the mean. The direction of one

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other hawk (65994-2; Table 2) in its first year was 0°, but we did not include it in the analysis because it died before we could determine if it had reached its maximum distance at 520 km north of its natal nest. Mean direction from the natal nest in subsequent years was 5.9 ± 12.6° (n = 8, r = 0.98, range 342–24°), and directions deviated significantly from a uniform circular distribution (Rayleigh test, Z = 7.6, P < 0.001). One other hawk (47804-1; Table 2) also traveled north (359°) in its second year, but we did not include it in the analysis because it died on migration 291 km north of its natal nest. Mean direction in subsequent years was not significantly different from that of first-year migrations (Watson-Williams test, F = 2.1, P = 0.16), and the pooled mean of all directions was 0.6 ± 13.4° (n = 20, r = 0.97).

The pooled mean direction of PTT-equipped hawks was similar to that for encounters of hawks banded in the study area (0.6 and 348°, respectively), and the means were not significantly different (Watson-Williams test, F = 1.7, P = 0.2). However, encounters of banded hawks (Fig. 1, 3) were more widely dispersed than those of PTT-equipped hawks (r = 0.71 vs. 0.97; Fig. 1), and three banded hawks were encountered east of the study area in Arizona, whereas none of the PTT-equipped hawks were recorded there. Encounters of banded hawks were also more frequently oriented to the northwest of the study area and west of the Sierra Nevada Mountains compared to PTT-equipped hawks, which remained mainly east of the Sierra Nevada Mountains.

Maximum distance locations of most (82%) PTT-equipped hawks were in the Great Basin Desert and Columbia Plateau, including portions of northeastern California, northern Nevada, eastern Oregon, and southeastern Idaho (Fig. 1). Two crossed the Continental Divide into the Rocky Mountains of southwestern Montana, and one of them summered in Yellowstone National Park (Fig. 1). Mean maximum distance was similar for first-year (n = 12) and subsequent (n = 8) migrations (1035 vs. 1046 km), and the pooled mean for all maximum distances was 1040 ± 217 km (n = 20). Mean date of arrival at the maximum distance from the natal nest for first-year migrants was 4 August ± 14 d (n = 12, range 18 July–30 August) and 25 July ± 40 d (n = 8, range 15 May–12 September) for subsequent migrations; the means were not significantly different (Mann-Whitney U = 39, P = 0.49). The period between initiation of migration and the arrival at the location of the maximum distance was highly variable for both first-year (mean = 18 ± 11 d, range 3–42 d) and subsequent (mean = 50 ± 34 d, range 7–99 d) migrations, with that for first-year migrants being significantly shorter in duration (Mann-Whitney U = 19, P = 0.03).

The pooled maximum distance mean for PTT-equipped hawks was significantly greater (Mann-Whitney U = 163, P < 0.001, n = 20) than the maximum distance mean for banded hawks encountered north of the study area (mean = 615 ± 376 km, n = 44). Encounter distances of banded hawks may be underestimates, however, because some hawks may still have been migrating north when they were encountered or may have reached their maximum distance and begun migrating south.

Late summer–autumn migration: timing, direction, distance, and destinations. Ten of the 12 first-year migrants returned to their natal region in southern California later the same year; the other two hawks either died or their transmitters failed before they reached their natal region (Table 2). Return dates of first-year migrants ranged from 15 August–1 November (mean = 25 September ± 23 d, n = 10), whereas return dates for subsequent migrations ranged from 2 September–3 November (mean = 3 October ± 24 d, n = 6).

Behavior of the 10 first-year migrants after they returned to their natal region was variable. Seven of the 10 remained within their natal region until they migrated north the following summer. After first passing through their natal region, three of the 10 continued south into Baja California, Mexico, with one traveling 560 km south of its natal nest. However, all three hawks returned to their natal regions after remaining in Baja for only 2–10 d.

Four PTT-equipped hawks, three females and one male, survived >2 yr (31 to >69 mo) with functioning PTTs, and all four achieved adult plumage. Two of the three females, 47801-1 and 65992-1 (Table 2), died of electrocution within their natal regions at 44 and 45 mo of age, respectively, but the other female (65994-3) and single male (65999-2) were on their breeding territories with functioning PTTs in March 2014 when we ended data analysis for this study. Three of the four hawks ceased migrating after forming pair bonds in southern California. Female 65992-1 formed a pair bond after completing two annual migrations and did not migrate in either of the next 2 yr. Female 65994-3 also ceased migrating after completing two annual migrations and forming a pair bond. Male 65999-2 did not migrate in his first year, but did in the second, after which he formed a pair bond and ceased migrating. In contrast, the other

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female that was electrocuted, 47801-1, never formed a pair bond or built a nest after completing four annual migrations (Table 2).

DISCUSSION

Based on both banding and satellite telemetry data, we found that all juvenile PTT-equipped Red-tailed Hawks and many banded juvenile and young adults (<46 mo of age) from the southern portion of the Pacific Flyway regularly migrate north to summering areas as far as 1462 km from their natal nests and return to their natal regions in late summer–autumn of the same year where they remain for the winter. In contrast, the median distance for band encounters of older (>46 mo of age) adults from the study area was 21.3 km, and directions were randomly distributed (Bloom 2011). Although we originally predicted migration would be limited to fledglings and juveniles, at least some young adult Red-tailed Hawks continued migrating north and returning to their natal region each year until they acquired a mate and territory, after which they apparently ceased migrating altogether. Three of the four PTT-equipped hawks that survived >2 yr formed pair bonds in their natal regions and ceased migrating. The remaining hawk never formed a pair bond and continued to migrate for 4 yr until she died at 45 mo of age after returning to her natal region.

In the Pacific Flyway, this northward summer migration by juveniles and young adults was generally limited to hawks hatched at latitudes south of 35°N, and contrasts sharply with that of migrant hawks banded north of 40°N, which were mostly (91%) encountered south of their natal nests; data suggest the N–S transition zone in the Pacific Flyway is at approximately 38°N. We found that migrants originating from north of 40°N in each of the other three major flyways of North America were also mostly (87%) encountered to the south of their natal nests, but we were unable to determine if migrants from the southern portion of the other flyways migrate north after the breeding season because of the almost complete absence of encounters of migrants banded south of 35°N. The lack of a clear direction from 35–40°N in the both the Central and Mississippi flyways, however, suggests that northward summer migration may not be limited to the Pacific Flyway.

Migration routes of PTT-equipped hawks from southern California differed somewhat from band encounters. Several banded hawks were encountered northwest of the study area along the central coast and throughout the Central Valley of California, and three from the study area were encountered to the east in Arizona. However, none of the PTT-equipped hawks travelled in those areas. One hawk from the study area was also encountered to the south in Baja, but this hawk may have continued heading south after first returning to its natal region from the north as did three PTT-equipped hawks that also traveled to Baja for a short period of time after returning from the north. Although the reasons are unclear, one possible explanation for the difference between band encounters and PTT data may be that PTT-equipped hawks were all from the same, comparatively small, 695-km^2 portion of the study area, whereas encounters were of nestlings banded over the entire study area.

Post-fledging, northerly migration has also been well documented in Bald Eagles. Fledgling and subadult Bald Eagles in several, mainly lower latitude areas of the U.S.A. (Florida [Broley 1947, Wood 1992, Millsap et al. 2004, Mojica et al. 2008], California [Hunt et al. 1992, Jenkins et al. 1999, Linthicum et al. 2007], Texas [Mabie et al. 1994], and Arizona [Hunt et al. 2009]) migrate as far as 2403 km (Wood 1992) north of their natal regions during summer.

Although differing from Red-tailed Hawks and Bald Eagles in that their complete migration consists of a broad loop, many adult female Prairie Falcons (*Falco mexicanus*) migrated several hundred km northeast from their nesting area in southwestern Idaho to summering areas in the northern U.S.A. and central Canada. After remaining in their summering areas for 1–4 mo, they migrated almost due south to their wintering areas and finally moved northwest in spring to their breeding areas (Steenhof et al. 2005).

Considering the high rate of mortality that raptors may incur during migration (Klaassen et al. 2014), the northward summer migration of juvenile and young adult Red-tailed Hawks clearly must have survival value. Natural selection should select for both the decision to migrate and the migratory route that optimizes the potential for individuals to survive and breed. Understanding why and where birds move is an important part of their conservation, particularly as it relates to protecting breeding habitat and wintering habitat, assuming they are different. This raises an interesting question: why do juvenile and young adult Red-tailed Hawks perform a northward summer migration from an area of relatively mild Mediterranean climate into or across the Mo-

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jave and Great Basin deserts in summer? Although other factors such as seasonal weather changes and increased day length likely play a role, we hypothesize the primary reasons are historical climate changes, seasonal changes in prey availability, and intraspecific competition and territoriality.

Cox (1985) theorized that partial migration may evolve in a resident species when climate change results in favorable conditions along one or more of the borders of its range. During the Last Glacial Maximum (LGM; approximately 17 000–18 000 BP [Pielou 1991, Booth et al. 2003]), the southern extent of the Cordilleran Ice Sheet reached northern Washington, Idaho, and Montana (approximately 47°N; Booth et al. 2003). However, periglacial effects, which may have extended as far south as 40°N (Steadman 2005) corresponding with the southern boundary of the summering area of PTT-equipped hawks in this study, would likely have made much of the area uninhabitable. The receding of the ice sheet after the LGM and subsequent colonization (or recolonization) by small mammals opened up just such a favorable area for Red-tailed Hawks as described by Cox (1985), which may have been an important factor in the evolution of northward summer migration from more southern latitudes.

The northward direction of migration was also likely influenced by postglacial climate changes that occurred to the south and east. While climate in the summering area was moderating after the LGM, the region south and east of the study area was becoming increasingly drier and hotter, culminating approximately 8000 BP (Mead et al. 2010) in the harsh, xeric conditions that characterize the Mojave and Sonoran deserts today. Depending on elevation and latitude, July mean maximum temperatures in these areas are frequently >40°C (Sellers et al. 1985). Prey species diversity also declined in these areas (based on fossil records; Goodwin and Reynolds 1989, Mead et al. 2010).

Importance of sciurids in the diet of Red-tailed Hawks in the western U.S.A. has been well documented (Fitch et al. 1946, Janes 1984, MacLaren et al. 1988, Steenhof and Kochert 1988). California ground squirrels (*Otospermophilus beecheyi*) are the primary prey of Red-tailed Hawks in much of California where the two species co-occur (Fitch et al. 1946) including the study area (P. Bloom unpubl. data), and until recently, were the only sciurid in the study area. Gray squirrels (*Sciurus griseus*) and fox squirrels (*S. niger*) now also occur in the study area; however, they only occur in a few areas at this time and have not been found as prey remains in Red-tailed Hawk nests (P. Bloom unpubl. data). In central California, California ground squirrels made up 50–61% of both individual prey numbers and biomass of the diet of Red-tailed Hawks, and juvenile squirrels (after they emerged) made up a disproportionately higher proportion than adults (Fitch et al. 1946). However, major reductions in California ground squirrel abundance and aboveground activity occur during the summer months. As temperatures increase, both juvenile and adult squirrels may spend only a few hours aboveground each day (Fitch 1948), and many adults estivate, remaining underground until September (Fitch 1948, Linsdale 1946, Tomich 1962), which may in part explain the northward summer migration of juvenile and young adult Red-tailed Hawks. As suggested by Dingle and Drake (2007), ''Migration can be viewed as an adaptation specific to arenas in which changes in habitat quality in different regions occur asynchronously so that movement allows a succession of temporary resources to be exploited as they arise.''

Sciurid diversity in the summering area, where as many as 27 species occur, contrasts sharply with the study area, where only three species occur (Reid 2006). And while California ground squirrels' aboveground abundance and activity are declining in the study area in early summer, juvenile squirrels in many areas to the north are only beginning to emerge, and continue to emerge at different locations and elevations throughout much of the summer (Knopf and Balph 1977, Bronson 1980, Murie and Harris 1982). For example, juvenile golden-mantled ground squirrels (*Callospermophilus lateralis*) emerge from late June to early August depending on snow cover and elevation (Bronson 1980). Thus, migrant Red-tailed Hawks from the south would encounter a diverse sciurid prey assemblage across many habitats and elevations throughout the summer and early fall.

Although approximately seven sciurid species occur in the deserts to the east and south of the study area (Reid 2006) as compared to only three in the study area, the harsh, xeric conditions and extreme summer temperatures and estivation or restricted aboveground activity of squirrels in those areas may constitute a substantial impediment to young Red-tailed Hawks from southwestern California. As evidenced by band encounters (Steenhof et al. 1984, Hoffman et al. 2002), not until autumn, when Red-tailed Hawks from northern populations are migrating south, are temperatures apparently mild

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enough or prey abundant enough aboveground that southern deserts can support migrants.

Seasonal shifts in prey availability in the natal and summering areas have also been suggested as an important factor in the northward summer migration of Bald Eagles and Prairie Falcons. Young eagles from northern California migrate north in July and August when carrion fish become less abundant in their natal region; these birds summer in British Columbia where carrion salmon (*Oncorhynchus* spp.) are abundant from late July–October (Hunt et al. 1992). Reduced prey availability that often occurs in their natal region during summer is also likely an important factor in the northward migration of young eagles from Florida (Wood 1992). Steenhof et al. (2005) suggested Prairie Falcons move northeast post-breeding in response to reduced prey availability on their breeding grounds in summer due to estivation of their main prey, Piute ground squirrels (*Urocitellus mollis*), an event that coincides with the emergence of Richardson's ground squirrels (*U. richardsoni*) in the falcon's summering area. Piute ground squirrels begin estivation in late May in southwestern Idaho and are almost completely absent from the surface by early July. Conversely, juvenile Richardson's ground squirrels begin to emerge in May and are active through September (Steenhof et al. 2005).

Competitive dominance over limited resources such as food during the nonbreeding season has been suggested as being an important selective agent in the evolution of partial migration (Gauthreaux 1978). In reference to partial migrants, Lack (1968) suggested that inexperienced juveniles are disadvantaged when competing with territorial adults, and indeed, the migratory portion of the populations of most partial migrant species is made up of young and inexperienced individuals (Gauthreaux 1983). Thus, our findings that juvenile and young adult hawks make up the migratory portion of the population, and that they apparently cease migrating once they acquire a mate and a territory, suggest intraspecific dominance may also be an important factor in the evolution of northward summer migration. Young hawks that have not found a territory likely face intense competition from resident adults, which are highly territorial (Preston and Bean 2009). Adding further to the competitive pressure on young hawks is the high density of territorial adults that occurs in much of California. The highest breeding density of Red-tailed Hawks reported for North America (1.3 pairs/km^2) was in central California, where Fitch et al. (1946) believed the available habitat was saturated. In contrast, densities of breeding adults in the summering area of the PTT-equipped hawks are substantially lower (southwestern Montana, 0.12 pairs/km^2 (Johnson 1975); northern Utah, 0.08 pairs/km^2 (Bosakowski et al. 1996).

We are only aware of one raptor species outside of North America, the Lesser Kestrel (*Falco naumanni*), that may exhibit a regular northward summer migration. Many fledglings and some adult kestrels in Spain (Olea 2001) and Portugal (Catry et al. 2011) move up to 700 km northward in summer possibly to exploit high concentrations of grasshoppers that occur later in the year in northern Spain as suggested by Olea (2001). However, additional banding encounters and more detailed observations of radio-tagged individuals are needed to determine if these northward movements are regular migration or dispersal. Banded individuals of several other European raptors, including Eurasian Kestrels (*Falco tinnunculus*; Schifferli 1965), Common Buzzards (*Buteo buteo*; Olsson 1958), and Ospreys (*Pandion haliaetus*; Osterlöf 1977), are also sometimes encountered north of their natal region, but without additional study, it is unclear whether their movements reflect dispersal or migration.

Conservation Implications and Research Needs. More than 20 research and conservation-oriented raptor migration watchsites have been established in western North America (Goodrich and Smith 2008) to monitor movements and abundance of predominantly southbound migrating raptors in autumn (Bildstein et al. 2008). Observations at watchsites have yielded valuable information on raptor flight mechanics (Kerlinger 1989, Zalles and Bildstein 2000), geographic distribution of raptor migration (Bildstein 2006), and influence of weather (Goodrich and Smith 2008) and climate change (Buskirk 2012) on raptor migration. Watchsite data have also been used to analyze population trends of several raptors including Red-tailed Hawks (e.g., Bednarz et al. 1990, Hoffman and Smith 2003, Smith et al. 2008). However, meaningful application of watchsite migration counts to our understanding of trends in raptor abundance requires information on locations of source populations (Hoffman and Smith 2003). It is assumed that counts in autumn reflect trends in populations north of watchsites, but it is now apparent that a portion of Red-tailed Hawks observed in autumn at western U.S.A. watchsites may actually be from more southern populations that are returning south

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after having already completed a northbound migration. Thus, watchsite counts may also reflect the status of populations to the south, at least in the Pacific Flyway. Our study identifies the need for long-term research involving banding of large numbers of nestlings or alternatively, satellite tracking of a much smaller subset.

Over 250 commercial wind farms have been constructed in the western U.S.A., and many more are planned (OpenEI 2012). Raptors are among the species most vulnerable to collisions with wind turbines, and levels of raptor mortality at some large wind farms are a concern (Erickson et al. 2001, Barrios and Rodríguez 2004, Smallwood and Thelander 2008). Although more passerines are often killed, collisions with wind turbines may be of greater importance to raptors because they are longer-lived, have lower productivity, and mature later (Kuvlesky et al. 2007). Red-tailed Hawks, in particular, suffer some of the highest mortality rates of any raptor at some wind farms (Erickson et al. 2001) with approximately 190 killed annually at the Altamont Pass Wind Resources area in northern California (Smallwood and Thelander 2008). It is important that we understand the implications of collision mortality at the population level, which requires information on locations and population dynamics of source populations (Drewitt and Langston 2008). Based on results of our study, it can no longer be assumed that source populations for migrating Red-tailed Hawks are always to the north of wind farms in temperate regions.

From mid-August through mid-September, mainly juvenile Red-tailed Hawks have been observed flying northward at a watchsite in northeastern Wisconsin, and some individuals that were banded as nestlings in southern Wisconsin have been recaptured at the same watchsite (Brinker and Erdman 1985). Although more information is needed to determine if the Red-tailed Hawks moving north in late summer in Wisconsin are migrants, these observations suggest young Red-tailed Hawks from regions other than the southern Pacific Flyway may migrate north as well. Data are particularly lacking for the southern portion of the Red-tailed Hawk's range. When we examined all BBL records for North America, we found that, other than in the Pacific Flyway, only two migrant hawks banded as nestlings south of 35°N have been encountered. To further our understanding of this type of migration and how it evolved, future research should focus on equipping nestlings from across the southern latitudes of North America with PTTs. Of particular interest would be Red-tailed Hawks fledged from Mexico. Considering differences in diet between Red-tailed Hawks and Bald Eagles, it also seems plausible that individuals of other North American raptor species with ranges south of 35°N may also exhibit northward migrations to exploit summer food resources. These data could prove important when evaluating the effect of climate change on species with alternative migration patterns.

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