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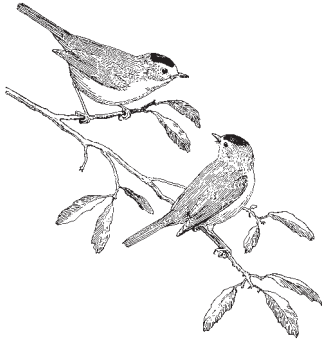
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Satellite tracking reveals age and origin differences in migration ecology of two populations of Broad-winged Hawks (*Buteo platypterus*)

Rebecca A. McCabe,^{1,7*} Laurie J. Goodrich,¹ David R. Barber,¹ Terry L. Master,² Jesse L. Watson,^{3,4} Erin M. Bayne,⁴ Autumn-Lynn Harrison,⁵ Peter P. Marra,⁵ and Keith L. Bildstein⁶

ABSTRACT—Recent conservation plans for long-distance Neotropical migrant birds have emphasized the importance of understanding the ecology and threats facing a species throughout its life cycle, including migration and overwintering periods. To better understand the ecology of Broad-winged Hawks (*Buteo platypterus*) during the nonbreeding period, we followed the movements of 14 hawks from 2 breeding populations during July 2014–April 2019 to their overwintering sites. Three juvenile and 8 adult female Broad-winged Hawks were satellite-tracked from Pennsylvania, USA, and 3 adults (2 females and 1 male) were tracked from Alberta, Canada. We documented pre-migratory movements (post-breeding) of 4 of the 14 individuals. Adults initiated fall migration on $\bar{x} = 25$ August ± 16.38 d and 2 of the 3 juveniles began fall migration on $\bar{x} = 20$ August ± 2 d. Adults had 1–12 ($\bar{x} = 5.0 \pm 3.5$) stopovers in autumn that lasted for 1–24 d and juveniles had 2–5 ($\bar{x} = 3.0 \pm 1.7$) stopovers that lasted 2–51 d. Adults from Pennsylvania spent the overwintering period in Nicaragua, Brazil, Peru, and Colombia ($n = 8$) whereas those from Alberta wintered in Suriname, Venezuela, and Bolivia ($n = 3$). The distance traveled on autumn migration was greater for Alberta birds ($\bar{x} = 10,021 \pm 866$ km, $n = 3$) than for Pennsylvania birds ($\bar{x} = 7,925 \pm 1,631$ km, $n = 8$). Migration distance and overwintering region varied by geographic origin with age but with some overlap between the 2 distinct geographic breeding populations. Broad-winged Hawks appear to follow a hybrid time–energy minimization strategy during fall and spring migrations with (1) energy minimization in North America, and (2) time minimization in Mexico and Central America. Stopover frequency, duration, and migration rate support this hypothesis. Received 11 July 2019. Accepted 18 February 2020.

Key words: pre-migratory movements, raptor, satellite telemetry, stopover, travel rates, wintering areas

Rastreo por satélite revela diferencias en la ecología de dos poblaciones del gavilán *Buteo platypterus* según edad y origen

¹ Acopian Center for Conservation Learning, Hawk Mountain Sanctuary Association, Orwigsburg, PA, USA

² Department of Biological Sciences, East Stroudsburg University, East Stroudsburg, PA, USA

³ HawkWatch International, Salt Lake City, UT, USA

⁴ Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

⁵ Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC, USA

⁶ Blandon, PA, USA

⁷ Current address: Department of Natural Resource Sciences, McGill University, Ste-Anne-de-Bellevue, QC, Canada

* Corresponding author: rebeccamccabe2@gmail.com

RESUMEN (Spanish)—Los planes de conservación recientes para aves migratorias neotropicales de larga distancia han enfatizado la importancia de entender la ecología y amenazas en enfrenta una especie a lo largo de su ciclo de vida, incluidas la migración y el periodo de invernada. Para entender mejor la ecología del gavilán *Buteo platypterus* durante el periodo no-reproductivo, seguimos los movimientos de 14 individuos de 2 poblaciones reproductivas durante julio 2014–abril 2019 a sus sitios de invernada. Tres juveniles y 8 adultos (2 hembras y 1 macho) fueron rastreados desde Pennsylvania, EUA, y 3 adultos (2 hembras y 1 macho) fueron rastreados desde Alberta, Canadá. Documentamos movimientos premigratorios (posreproductivos) de 4 de los 14 individuos. Los adultos iniciaron la migración otoñal en $\bar{x} = 25$ agosto ± 16.38 d y 2 de 3 juveniles comenzaron su migración otoñal en $\bar{x} = 20$ agosto ± 2 d. Los adultos tuvieron 1–12 ($\bar{x} = 5.0 \pm 3.5$) paradas de descanso en otoño que duraron de 1–24 d y los juveniles tuvieron 2–5 ($\bar{x} = 3.0 \pm 1.7$) paradas que duraron 2–51 d. Los adultos de Pennsylvania pasaron el periodo de invernada en Nicaragua, Brasil, Perú y Colombia ($n = 8$) mientras que aquellos de Alberta pasaron el invierno en Surinam, Venezuela y Bolivia ($n = 3$). La distancia de viaje en la migración de otoño fue mayor para las aves de Alberta ($\bar{x} = 10,021 \pm 866$ km, $n = 3$) que para las de Pennsylvania ($\bar{x} = 7,925 \pm 1,631$ km, $n = 8$). La distancia de migración y sitio de invernada variaron por origen geográfico según la edad, aunque con cierto traslape entre las 2 poblaciones reproductivas geográficamente diferentes. Estos gavilanes parecen seguir una estrategia híbrida de minimización de tiempo–energía durante sus migraciones de otoño y primavera con (1) minimización de energía en Norteamérica y (2) minimización de tiempo en México y Centroamérica. La frecuencia y duración de paradas de descanso, y la tasa de migración, apoyan esta hipótesis.

Palabras clave: áreas de invernada, movimientos premigratorios, parada de descanso, rapaz, tasa de traslado, telemetría de satélite

Neotropical migrant birds have been the subject of conservation concern in recent decades due to the many threats occurring throughout the annual cycle, including migration, nonbreeding, and breeding periods (Greenberg and Marra 2005, Sauer et al. 2014, Bayly et al. 2017). The Broad-winged Hawk (*Buteo platypterus*) is a Neotropical migrant that nests in forests of North America and migrates thousands of kilometers to wintering areas in Central and South America (Bildstein 1999, Goodrich and Smith 2008, Goodrich et al. 2014).

In eastern North America, populations of Broad-winged Hawks may be declining, whereas north-central populations appear stable and populations in the West are increasing. For example, Broad-winged Hawks migrating through the western United States increased by 8–20% per site during the 2000s (Crewe et al. 2016), reflecting a possible range expansion occurring in western Canada (Goodrich et al. 2014). In contrast, annual counts of Broad-winged Hawks at eastern hawkwatches in the Atlantic and Appalachian flyways have declined (e.g., 2.3–6.4% from 1990–2000; Farmer et al. 2008), nesting distribution declined in some states (e.g., Wilson et al. 2012), and forest fragmentation or degradation within the breeding or wintering range could be driving declines (e.g., Rappole and McDonald 1994, Robinson and Wilcove 1994). Moreover, because Broad-winged Hawks concentrate in large numbers during migration, they are vulnerable to human persecution (Ellis and Smith 1986, Bildstein 2006). Stressors in one segment of the life cycle could be interacting with and influencing survival in other seasons (e.g., Marra et al. 1998), thus, understanding Broad-winged Hawk migration

ecology and geography could inform conservation and management priorities.

The bulk of continental nesting Broad-winged Hawks converge on the eastern coastal plain of Veracruz, Mexico, each autumn passing through a narrow corridor with near-synchronous timing (Ruelas Inzunza et al. 2010); however, it is not known if subpopulations migrate or winter in different regions south of central Mexico. Species with strong “migratory connectivity” (i.e., connections between breeding and wintering locations of a migratory population; Martell et al. 2001, Webster and Marra 2005) should have distinct wintering areas for birds from different parts of the breeding range (Webster and Marra 2005, Cresswell 2014), and in some species populations from different geographic regions may have different migration routes (e.g., Osprey [*Pandion haliaetus*]; Martell et al. 2001).

Long-distance migrants are thought to follow one of 2 strategies during migration, “time minimization” or “energy minimization” (Alerstam and Lindstrom 1990). Time minimization requires large fuel stores to endure long flights between stops whereas birds following an energy minimization approach fly shorter distances and stop more frequently to refuel. Newton (2008) proposed a third option as a hybrid of the two, with the mode depending on the region or terrain being traversed. Smith et al. (1986) suggested that Broad-winged Hawks and Swainson’s Hawks (*Buteo swainsoni*) might fast during their migration, particularly in Mexico and Central America, indicating they may follow a time minimization strategy. However, telemetry on Swainson’s Hawks revealed they stop and forage regularly during migration with longer stops occurring early in the journey (Kochert et al.

2011), suggesting a hybrid strategy. In addition, Miller et al. (2016) discovered that Golden Eagle (*Aquila chrysaetos*) migratory behavior fell on a continuum of time- and energy-minimization strategies dependent on various factors (i.e., weather, availability of updrafts, soaring conditions, experience). Although Broad-winged Hawks are believed to build up fat prior to migration (Goodrich et al. 2014), it is not known if they fly long distances without stopping or fly shorter distances with frequent stops or perhaps a hybrid strategy similar to Swainson's Hawks. Moreover, birds from different regions may exhibit different migration strategies and distance (e.g., Martell et al. 2001, Airola et al. 2019).

Broad-winged Hawks have been tracked between North and Central/South America in one prior study, however the location data were intermittent and did not provide detail on stopover locations and duration of stay (Haines et al. 2003; i.e., from Maryland and Minnesota, USA, to Brazil and Peru). As stopover quality, availability, and a migrant's ability to refuel can influence survival and breeding success (Newton 2008), a better understanding of Broad-winged Hawk migration patterns, ecology, strategy, and stopover needs is critical to their conservation. Our study is the second study to affix satellite transmitters to Broad-winged Hawks, mainly due to limitations associated with high costs of the telemetry units (>\$3,000 USD/per unit) and transmitter weights that exceeded the 3% body mass recommendation for this species until recent years.

Our specific research questions included: (1) For fall and spring migration, does migration ecology of Broad-winged Hawks—including routes, departure and arrival dates, distance, duration, and migration rate—differ between 2 geographic populations, or between adults and juveniles? (2) Do populations and age classes overwinter in different locations? (3) Does frequency or length of stopovers vary between autumn and spring migration, and/or by latitude? (4) Is initiation of stopover correlated with precipitation?

We hypothesized that hawks would have origin-specific routes and timing (but with autumn migration being longer than spring for all individuals, similar to Haines et al. 2003); that juveniles would have a slower migration rate than adults; that stopover behavior would be similar to that observed for Swainson's Hawks with longer, more frequent

stopovers north of Mexico during fall migration; and stopping to refuel on migration instead of stopping over due to precipitation. In this study, we aimed to scale up previous work to better understand the migration ecology, strategy, and stopover patterns of Broad-winged Hawks from multiple geographic origins and across age classes.

Methods

Study areas

We tracked the migrations of Broad-winged Hawks with satellite transmitters to record full annual cycle movements of individuals representing 2 geographic populations (Pennsylvania and Alberta breeding sites) and 2 age classes (juveniles and adults). Broad-winged Hawks were captured and equipped with satellite tags in Pennsylvania, USA ([40°77'N, -75°59'W], [41°14'N, -75°9'W], and [41°39'N, -79°2'W]) and Alberta, Canada (55°16'N, -113°27'W). All birds, except one from Pennsylvania, were captured on the nesting grounds from June to July 2014 to 2016.

Capture and satellite tracking

We trapped adult birds in Pennsylvania near nests using mist nets, and a mechanical Great Horned Owl (*Bubo virginianus*) and call as a lure (Jacobs 1996, McCloskey and Dewey 1999), and in Alberta using dho-gazas and a live Great Horned Owl (Bloom et al. 1992). Juvenile birds (hatch-year hawks in juvenile plumage) from the Pennsylvania breeding population were captured by climbing the nest tree one week prior to fledging, or trapped using mist nets and a harnessed Rock Pigeon (*Columba livia*; Berger and Hamerstrom 1962) at a raptor-migration banding station in Palmerton, Pennsylvania. Although we do not know the breeding origin of the individual captured during migration, given the location of the banding station on the Appalachian Mountains and the bird's migration path, we assume the bird is a member of the eastern North American breeding population. Therefore, for subsequent analyses, we grouped this individual together with birds captured in Pennsylvania. All birds received a U.S. Geological Survey aluminum leg band and birds caught in Pennsylvania also received 2 plastic color bands for individual identification.

We attached solar-powered Argos satellite 9.5 g platform transmitter terminals (PTTs; Microwave Telemetry, Columbia, Maryland, USA) to 14 Broad-winged Hawks using the backpack harness method and 4–6 mm Teflon ribbons (Bally Ribbon Mills, Bally, Pennsylvania, USA) (Steenhof et al. 2006). All individuals except one adult from Alberta (bird ID #149782) were sexed as female based on their nesting behavior and weight (Mosher and Matray 1974). We deployed satellite tags on individuals that weighed ≥ 380 g to ensure the combined tag and harness weight (approximately 11.5 g) did not exceed 3% of the bird's mass (Murray and Fuller 2000, Barron et al. 2010) for all hawks except the Alberta male. Birds with units transmitting less than 3 months after tag deployment were removed from further analysis.

Data collection and analyses

Bird locations were calculated using the Doppler shift on transmission frequencies via the Argos Satellite System (Argos 2016) and were recorded with an estimated position error categorized into a location class (Argos 2016). In the first year of study (2014) in Pennsylvania, we programmed tags to transmit on duty cycles of 8 h on and 48 h off ($n = 3$). For all birds captured in 2015 and 2016 ($n = 11$, Alberta and Pennsylvania) we altered transmission cycles to run for 5 h on and 24 h off to acquire more points during migration.

We filtered all location estimates using the hybrid method of the Douglas Argos-filter in Movebank (Douglas et al. 2012). The hybrid method of the Douglas filter used 2 independent methods to filter locations: (1) the first filtering method, called the maximum redundant distance filter, required that locations have at least one other location consecutive in time and redundant in space, which we defined as < 15 km; (2) the second filtering method, called the distance, angle, and rate filter, evaluated movement rates and turning angles among consecutive location estimates (Kochert et al. 2011, Douglas et al. 2012). We defined 90 km hr^{-1} to be the maximum rate of movement (Kochert et al. 2011). Locations that passed the first filter were retained. If distance between consecutive points was > 15 km and the movement rate was $> 90 \text{ km hr}^{-1}$, the second point was filtered. We then filtered the data further by choosing one location per duty cycle using the best location class and if there were any

ties, the location with the most messages was chosen. We analyzed spatial data with ArcGIS 10.2 (ESRI 2011) and calculated the length (distance) between consecutive locations as orthodromes (great circle) navigation.

Migration routes, departure and arrival dates, distance, duration, migration rate, and overwintering locations—We organized Broad-winged Hawk annual movements into 6 categories: pre-migratory movements, fall migration (southward), spring migration (northward), stopover, overwintering, and breeding. Pre-migratory movement was defined as movements toward a secondary site, carried out before migrating from the breeding/natal site and without returning to the nest site (Strandberg et al. 2008, Monti et al. 2018a). Distance traveled during pre-migratory movements was calculated using the most accurate location class per duty cycle (i.e., over 86% of pre-migratory movements were location classes 3s and 2s [most accurate to least accurate 3, 2, 1, 0, A, B]), between successive duty cycles.

We defined the start of fall migration as the first location that was > 32 km (maximum distance Broad-winged Hawks traveled during the breeding season) and south of the breeding site and/or pre-migratory location, and from which the bird continued migrating without backtracking > 32 km per day (Dodge et al. 2014). Fall migration ended and the overwintering period began (Oct–Feb) with the most distant southern location after which all subsequent locations were localized (non-directional movements) and no further migration occurred. Similarly, spring migration began with the first location that was > 32 km and north of an overwintering location, and from which the bird continued migrating without backtracking. For birds that had more than one year of data, we used the first year only to calculate mean and SD of start and end dates for populations and age classes.

To examine the influence of latitude on travel rate we interpolated the date (day and time) that a bird crossed lines of 10° latitude between 50° north and 10° south. We calculated travel rates by using the distance and duration traveled between latitude lines and for the entire one-way journey. Rate of travel was calculated for each bird for each 10° latitude block a bird traveled through for both fall and spring migrations. The travel rate was for a segment of the migration, thus, it included any stopover periods.

Stopover frequency and duration—We defined stopovers as locations where birds spend >24 h during the migratory journey (Strandberg et al. 2008, Kochert et al. 2011, Limiñana et al. 2012, Monti et al. 2018b) to rest, refuel, or as a temporary layover due to weather. Because longer stopovers are hypothesized to be associated with more critical refueling events (Mehlman et al. 2005) we separated stopover durations into long and short stopovers. To calculate mean stopover duration, we summed the stopover days for each individual to get a single value for each bird. The median duration of stopover was 2.5 d for all birds combined ($n = 14$). Mehlman et al. (2005) suggested that “short” stopovers for landbirds would last 2 d or less, thus we defined short stopovers as <3 d and long stopovers as >3 d and compared the proportion of long and short by age class and latitude for both fall and spring migrations.

Some brief stopovers may not have been detected due to data gaps that occurred during fall and spring migration periods. We defined data gaps as a period during migration with no location estimates that spanned ≥ 1 duty cycle. Data gaps for both adults and juveniles averaged 6.37 ± 6.97 d during fall migration and 17.38 ± 18.34 d during spring migration. For the 2014 birds (bird IDs #135757, 135758, and 135760) with 8 h on and 48 h off duty cycles, known stopover locations were >48 h, thus we were unable to identify short stopovers of 24–48 h for these 3 birds. Data gaps often appeared to occur with stopover periods and represented 0–24% of total migration days with mean of 13.8% ($\pm 8.8\%$; $n = 14$) of total migration days per migratory period.

Relationship between stopover initiation and precipitation—To examine if precipitation events influenced stopover initiation we used the Environmental Data Automated Track Annotation System from Movebank.org with the National Centers for Environmental Prediction, North American Regional Reanalysis, for categorical rain days (0 = no rain, 1 = rain) for points in North and Central America to determine if the cause of the stopover was due to precipitation on either the first or second day of the stopover.

Statistical analyses were performed in SYSTAT 13.1 (SYSTAT 2013). To examine differences in migration rate and stopover duration among latitude blocks by region and age we used general

linear models (GLM). To compare the proportion of long and short stopovers by latitude block and to compare stopover initiations under rain and non-rain we used Pearson chi-square. Values reported in the results are means \pm SD, and an α level of 0.05 was used for all statistical tests.

Results

We tracked 14 Broad-winged Hawks, 11 from Pennsylvania, USA, and 3 from Alberta, Canada (Table 1). Of the Broad-winged Hawks from Pennsylvania, 3 individuals were juveniles; 2 tags were deployed on juveniles at the nest and one during fall migration. Of the 14 Broad-winged Hawks studied, (1) one bird’s PTT failed, (2) one lost or removed its transmitter (later re-trapped), (3) one bird was re-trapped on the breeding grounds (summer 2019) and we removed its transmitter due to intermittent signaling, (4) one bird (bird ID #135760) was killed during incubation, presumably by an avian predator after completing fall and spring migration in 2014–2015, (5) 6 birds appeared to have died during migration or the overwintering period as determined by the activity sensor readings from the satellite transmitter downloads and/or lack of return to breeding grounds in subsequent years, and (6) 4 have an unknown status.

Migration ecology by population and age class

Pre-migratory movements—Four of the 11 birds from the Pennsylvania breeding population completed pre-migratory movements: 3 adults (bird IDs #135750, 146905, 146904) and one juvenile (bird ID #135760). Dates of departure from the nesting territory ranged between 12 July and 16 August and time spent in pre-migratory areas varied from 7 to 60 d prior to migration initiation. For the 3 adults the initial directional movement was west, with 2 birds then flying north (NW and NE) before moving south. The juvenile Broad-winged Hawk initially moved north (NE then NW) before heading south. Distance of the initial movement from the nesting territory was $\bar{x} = 44.4 \pm 18.2$ km ($n = 4$) and the distance traveled during pre-migratory movements totaled $\bar{x} = 131.8 \pm 73.4$ km ($n = 4$). None of the Alberta birds displayed this behavior and no pre-migratory

Table 1. Start and end dates and distance traveled (km) on both fall and spring migrations for Broad-winged Hawks ($n = 14$) tracked by satellite telemetry in Pennsylvania, USA, and Alberta, Canada, 2014–2019.

Location	Bird ID	Age	Year	Fall migration			Spring migration			
				Start date	End date	Distance traveled (km)	Year	Start date	End date	Distance traveled (km)
Eastern Pennsylvania										
Kempton	135757	Juvenile	2014	22 Aug	22 Nov ^a	5,654.9	—	—	—	—
Kempton	135758	Juvenile	2014	18 Aug	9 Nov ^a	4,384.0	—	—	—	—
New Ringgold	135760	Adult	2014	30 Aug	25 Nov	9,649.7	2015	8 Dec	7 May	9,503.9
Orwigsburg	146902	Adult	2015	23 Aug	17 Oct	6,437.8	—	—	—	—
Dingmans Ferry	146903	Adult	2015	3 Sep ^b	29 Oct	4,853.3	—	—	—	—
Dingmans Ferry	146905	Adult	2015	3 Aug	26 Nov	9,589.7	2016	6 Feb	9 May	8,723.4
	146905		2016	22 Aug	24 Nov	9,035.2	2017	22 Jan	4 May	8,924.6
East Stroudsburg	146904	Adult	2015	11 Sep	1 Nov	7,797.3	2016	23 Dec	26 Apr	8,328.0
Palmerton	146906	Juvenile	2015	18 Sep ^c	19 Jan	5,625.8	2016	14 Apr	10 May	4,745.6
Kempton	146907	Adult	2016	31 Jul	3 Jan	8,764.0	2017	1 Feb ^b	25 Apr	8,717.9
	146907		2017	2 Aug	11 Nov	8,573.4	2018	23 Feb	15 Apr	9,194.8
	146907		2018	1 Sep ^b	4 Dec	8,661.7	2019	17 Feb ^b	25 Apr	8,926.9
Western Pennsylvania										
Clarendon	146909	Adult	2016	26 Jul	31 Oct	7,706.5	2017	26 Feb	16 Apr	7,508.7
	146909		2017	24 Jul	6 Dec	7,708.1	2018	26 Feb	13 Apr	7,629.6
	146909		2018	12 Sep ^b	18 Nov	8,598.9	2019	31 Jan ^b	18 Apr	7,650.3
Bradford	161202	Adult	2016	9 Sep	17 Nov	8,598.9	2017	28 Jan	9 Apr ^a	4,511.4
Alberta										
Northern Alberta	149781	Adult	2015	9 Sep	27 Dec	10,178.2	2016	22 Feb ^b	18 May	9,877.4
Northern Alberta	149782	Adult	2015	5 Sep	27 Nov	10,797.9	—	—	—	—
Lakeland County	149783	Adult	2015	1 Sep	9 Dec	9,087.8	—	—	—	—

^a Last known date before PTT failure or bird mortality.

^b Unknown initial state date, but mid-point date between the last location and the first location after a large data gap.

^c Date when individual was trapped on migration.

movements were documented prior to spring migration.

Fall migration—Fall migration paths for Pennsylvania adult Broad-winged Hawks in general followed the Appalachian Mountains southwest to the southern United States, and then through southeastern Texas, along the Gulf of Mexico south into Central and South America (Fig. 1a). Pennsylvania juveniles used a similar migratory pathway as adults, differing only in southern Mexico where 2 individuals flew farther to the southwest, across the Sierra Madre mountain range toward the Pacific coastal plain before continuing south into Central America (Fig. 1a). In contrast to Pennsylvania hawks, the 3 Alberta adults flew southeast from Alberta into Saskatchewan and into North and South Dakota, and Minnesota south into central Texas and on to the Gulf of Mexico (Fig. 1a).

Adult Pennsylvania Broad-winged Hawks left their breeding localities and began fall migration as early as 26 July ($\bar{x} = 21 \text{ Aug} \pm 17.47 \text{ d}$) and ended their migration as late as 3 January ($\bar{x} = 12$

Nov $\pm 21.98 \text{ d}$; Table 1). Pennsylvania adult birds completed fall migration in $\bar{x} = 82 \pm 42 \text{ d}$ and traveled $\bar{x} = 7,925 \pm 1,631 \text{ km}$ ($n = 8$; Table 1). Two juveniles tracked from nests in Pennsylvania started fall migration on $\bar{x} = 20 \text{ Aug} \pm 2.00 \text{ d}$, and exhibited similar migration duration to adults $\bar{x} = 88 \pm 6 \text{ d}$ (Table 1). Adults from Alberta left their breeding grounds later than Pennsylvania birds ($\bar{x} = 5 \text{ Sep} \pm 3.27 \text{ d}$) and ended fall migration in December ($\bar{x} = 11 \text{ Dec} \pm 12.33 \text{ d}$). However, Alberta adults completed fall migration in $\bar{x} = 90 \pm 11 \text{ d}$, traveling $\bar{x} = 10,021 \pm 866 \text{ km}$, $n = 3$ (Table 1).

Pennsylvania adult Broad-winged Hawks exhibited differences in travel rates within 10° latitudinal zones ($F_{4,30} = 15.94$, $P = 0.001$), with the slowest rate ($\bar{x} = 77.62 \pm 28.76 \text{ km d}^{-1}$) at the beginning of migration and the fastest rate ($\bar{x} = 250.78 \pm 68.76 \text{ km d}^{-1}$) in northern Mexico ($30\text{--}20^\circ\text{N}$). Alberta adult travel rates also varied by latitudinal zones ($F_{5,8} = 12.71$, $P = 0.001$), with the slowest rate of travel (20.40 km d^{-1}) toward

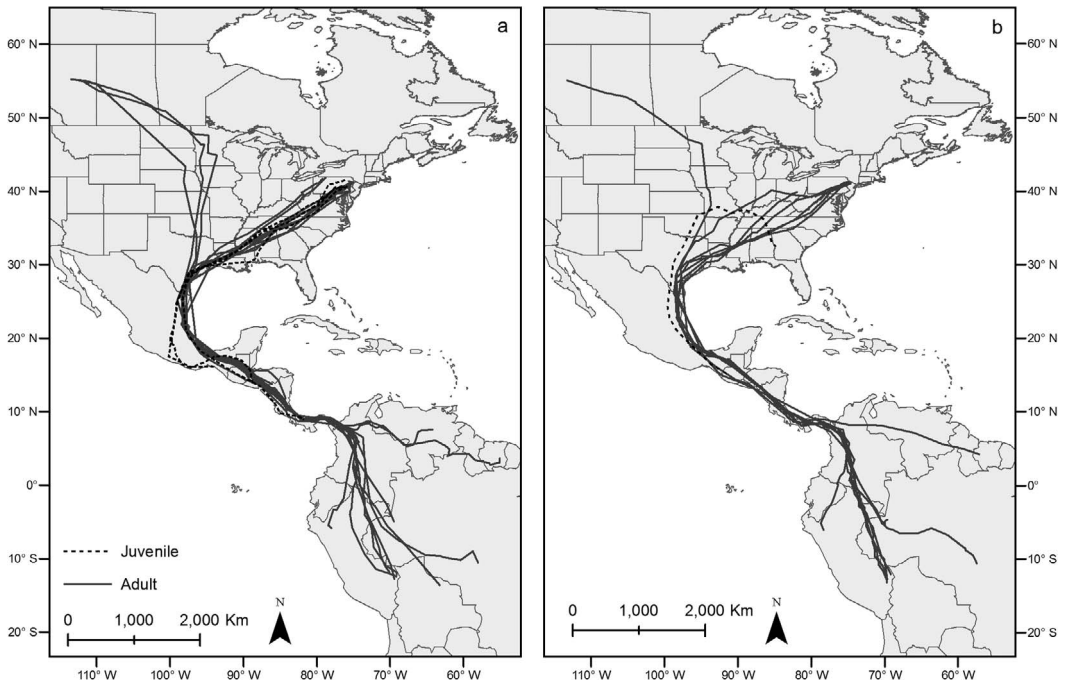


Figure 1. Migratory routes of Broad-winged Hawks from Alberta, Canada, and Pennsylvania, USA, 2014–2017, including (a) fall migrations of 14 individuals (11 adults and 3 juveniles), and (b) return spring migrations of 8 individuals (7 adults and 1 juvenile). Lines indicate unobserved straight-line paths between consecutive transmitter locations using the best location class per duty cycle.

the end of migration (0–10°S) for one bird and the fastest ($\bar{x} = 364.16 \pm 93.34 \text{ km d}^{-1}$) in the southern United States (40–30°N) (Fig. 2). Rate of travel did not differ significantly by latitude block for juvenile Broad-winged Hawks ($F_{2,4} = 0.92$, $P = 0.47$; Fig. 2). Pennsylvania birds flying over the

state of Veracruz, Mexico ($n = 9$), during fall migration, a key bottleneck for Neotropical migrants, all did so within one week of one another (24 Sep–3 Oct). Alberta adults ($n = 3$) flew over the state of Veracruz a few days after Pennsylvania birds (7–10 Oct).

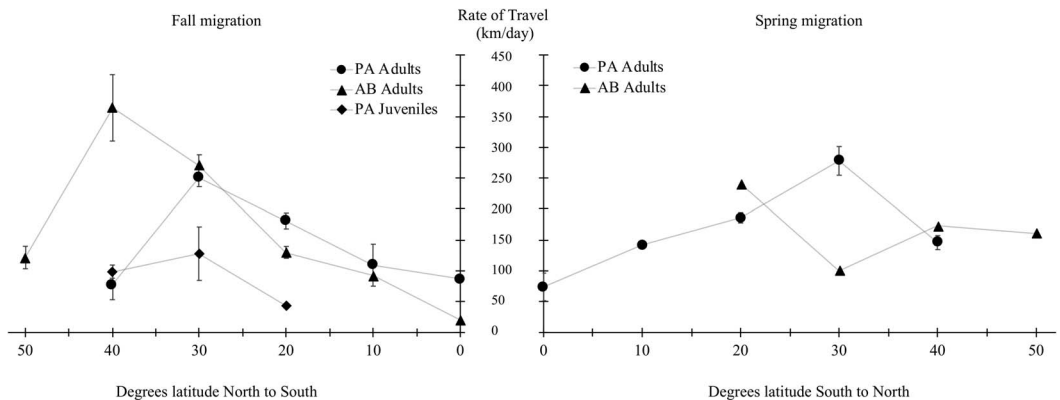


Figure 2. Rates of travel (km/d) for fall migration ($n = 14$) and spring migration ($n = 7$) of Alberta (AB) adults and Pennsylvania (PA) adults and juvenile Broad-winged Hawks for 10° latitudinal zones. Means are depicted with vertical standard error bars.

Spring migration—Adult Broad-winged Hawks ($n = 7$ adults) initiated northward migration during a period of 3 months (Dec–Feb; $\bar{x} = 25 \text{ Jan} \pm 27.78 \text{ d}$) and completed their migration during a narrower time period of about 1.25 months (early Apr to mid-May; $\bar{x} = 28 \text{ Apr} \pm 12.64 \text{ d}$; Table 1). Spring migratory routes were similar to fall migration for both Pennsylvania and Alberta birds (Fig. 1b). One juvenile (bird ID #146906) began its spring migration on 14 April from Guatemala, moving northward along the east coast of Mexico and into Texas, following the same path as the Alberta adult. Instead of continuing north through Missouri as the adult did, this juvenile moved east and then south through Tennessee and into Georgia on 10 May (Fig. 1b). Its signal was lost on 28 May 2016. Pennsylvania adult birds completed spring migration in $\bar{x} = 95 \pm 37 \text{ d}$ and traveled $\bar{x} = 7,882 \pm 1,774 \text{ km}$ ($n = 6$), whereas the one spring migration recorded for the Alberta adult took approximately 86 d to travel 9,877 km (Table 1). Migration duration and distances were similar in spring and fall for both breeding populations.

Travel rates differed by 10° latitudinal zones during spring migration for Pennsylvania adult Broad-winged Hawks ($F_{1,28} = 9.27$, $P = 0.05$), with the slowest rates ($\bar{x} = 74.07 \pm 38.74 \text{ km d}^{-1}$) in northern South America ($0\text{--}10^\circ\text{S}$) and the fastest rates ($\bar{x} = 278.09 \pm 52.02 \text{ km d}^{-1}$) in northern Mexico ($20\text{--}30^\circ\text{N}$), similar to fall migration (Fig. 2). For the one Alberta adult that returned north (bird ID #149781), rate of travel was the slowest (100.05 km d^{-1}) in northern Mexico ($20\text{--}30^\circ\text{N}$), and the fastest (241.05 km d^{-1}) at the beginning of spring migration in South America ($20\text{--}10^\circ\text{N}$) (Fig. 2).

Overwintering distribution by population and age class

Broad-winged Hawks from this study spent the overwintering period from southern Mexico south into Bolivia (15°N to 15°S), with the most southerly location being an adult male from Alberta at $15^\circ53'\text{S}$, $61^\circ49'\text{W}$ in Santa Cruz, Bolivia (Fig. 1a, Appendix 1). Pennsylvania and Alberta adults appeared to winter in different regions with Alberta adults wintering in Suriname, Venezuela, and Bolivia, and Pennsylvania adults wintering in Peru, Colombia, and Brazil (Appendix 1). Last known locations for wintering

juveniles occurred farther north compared to adults (i.e., Mexico and Central America). In January 2017, 3 female Broad-winged Hawks (bird IDs #146907, 146905, 161202) from 3 regions in Pennsylvania spent the overwintering period within 46–135 km of one another in southeastern Peru’s Amazon Basin. Three individual hawks were recorded for more than one year (bird IDs #146905, 146907, 146909). These 3 individuals showed high fidelity to wintering sites in South America returning within 50–100 km of their first winter location.

Stopover frequency and duration

We recorded at least one stopover for 13 of the 14 captured Broad-winged Hawks during fall migration. The number of stopovers for adults from Pennsylvania ($\bar{x} = 5.28 \pm 4.11$) and the number of days ($\bar{x} = 3.61 \pm 1.64 \text{ d}$, $n = 7$) spent on stopover during fall migration were similar to the number of stopovers ($\bar{x} = 4.67 \pm 0.58$) and duration ($\bar{x} = 2.54 \pm 2.59 \text{ d}$, $n = 3$) for adults from Alberta (Table 2). Juvenile hawks from Pennsylvania had 2–5 stopovers each that ranged from 2 to 51 d ($\bar{x} = 13.08 \pm 16.43 \text{ d}$, $n = 3$; Table 2).

Five of the 8 birds with spring migrations, all of which were adults, stopped one or more times. Number of stopovers by adults during spring migration (Pennsylvania and Alberta combined; $\bar{x} = 2.50 \pm 3.04$) were less than fall migration (Table 2). No stopover locations were observed along the juvenile’s satellite track, although its transmitter signal was intermittent (i.e., experienced data gaps of >2 weeks). Pennsylvania adults spent $\bar{x} = 2.48 \pm 1.64 \text{ d}$ and only one Alberta adult had spring stopover data (Table 2). Mean stopover duration by adults did not differ between fall and spring migrations (paired t -test = 1.468, $df = 68$, $P = 0.15$).

Most (64%) of Broad-winged Hawk stopovers were less than 3 d (Fig. 3). However, the number of long stopovers ($>3 \text{ d}$) for Pennsylvania and Alberta adults combined were significantly greater during fall vs. spring migration ($\chi^2 = 4.16$, $P = 0.04$, $n = 70$). Fall migration data gaps, periods with no transmission between the unit and satellites, were shorter ($\bar{x} = 6.37 \pm 6.97 \text{ d}$) than spring migration data gaps ($\bar{x} = 16.29 \pm 16.40 \text{ d}$), which could have influenced detection of stopover events during spring migration. Combining both

Table 2. Number of stopovers of satellite-tagged Broad-winged Hawks ($n = 14$) during fall and spring migrations, 2014–2017.

Bird ID	Location of capture	Age	Fall migration				Spring migration			
			Year	# stopovers	Range (d)	Mean duration (d)	Year	# stopovers	Range (d)	Mean duration (d)
135757	Eastern PA	Juvenile	2014	2	3–21	12.0	2015	n/a	–	–
135758	Eastern PA	Juvenile	2014	2	3–16	9.5	2015	n/a	–	–
135760	Eastern PA	Adult	2014	1	2–3	2.5	2015	5	3–9	4.6
146902	Eastern PA	Adult	2015	2	2–15	8.5	2016	n/a	–	–
146903	Eastern PA	Adult	2015	n/a	–	–	2016	n/a	–	–
146905	Eastern PA	Adult	2015	8	2–10	4.4	2016	8	2–6	2.9
146904	Eastern PA	Adult	2015	1	3	3.0	2016	1	4	4.0
146906	Eastern PA	Juvenile	2015	5	2–51	16.4	2016	0	–	–
146907	Eastern PA	Adult	2016	12	2–24	5.2	2017	0	–	–
146909	Western PA	Adult	2016	8	2–10	4.5	2016	0	–	–
161202	Western PA	Adult	2016	4	3–5	4.0	2017	3	3–4	3.7
149781	Alberta	Adult	2015	4	2–5	3.3	2016	3	2–4	3.0
149782	Alberta	Adult	2015	5	2–5	3.0	2016	n/a	–	–
149783	Alberta	Adult	2015	5	2–7	4.4	2016	n/a	–	–

fall and spring migration stopovers, juvenile Broad-winged Hawks had longer stopovers ($\bar{x} = 13.08 \pm 16.43$ d) compared to Pennsylvania adults ($\bar{x} = 3.24 \pm 3.77$ d) ($F_{1,59} = 15.22$, $P = 0.0001$) (Table 2). Stopover duration did not vary

among latitude blocks for adults or juveniles ($P > 0.1$), and the proportion of long and short stopovers did not vary significantly by latitude block during fall or spring migrations for age classes or regions, although sample sizes were

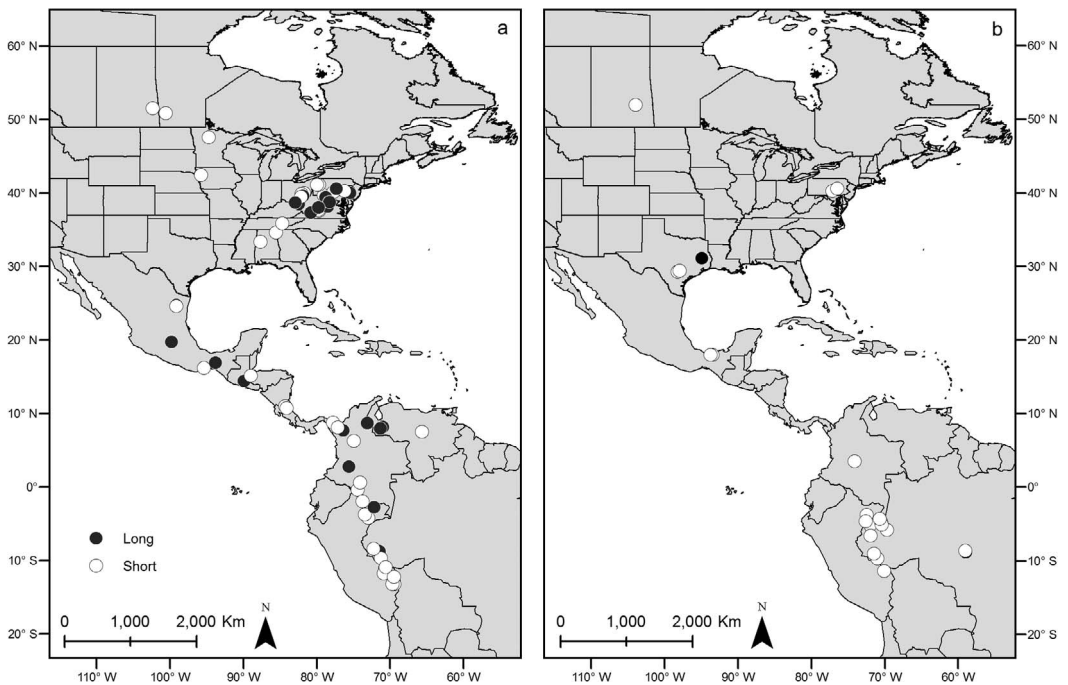


Figure 3. Long (>3 d) and short (<3 d) stopovers for adult and juvenile Broad-winged Hawks during (a) fall and (b) spring migration from 2014 to 2017. Black circles represent long stopovers and white circles represent short stopovers. Based on 13 hawks stopping 59 times on fall migration and 5 hawks stopping 20 times on spring migration.

small ($P > 0.1$). Most stopovers occurred in largely forested regions with at least 2 eastern birds' stopovers occurring in national forests.

Stopover initiation and precipitation

Among both adults and juveniles, and for both fall and spring migrations combined, 30% of the 79 stopovers were associated with rain, whereas 33% were not. Weather data were not available for 37% of the stopovers. Initiation of stopover by Pennsylvania adults was associated with a rain event for 13 of 53 total stopovers (25%), whereas 15 (28%) were not associated with rain events and 25 (47%) had no precipitation data available. Of the 17 Alberta adult stopovers observed, 7 (42%) were initiated on days with rain, 6 (35%) were initiated on non-rainy days, and 4 (23%) had no precipitation data available. Pennsylvania juveniles initiated 4 (44%) of 9 total stopovers on rainy days, whereas 5 stopovers (56%) were initiated on non-rainy days. Stopover duration did not vary between rain-initiated stopovers and stopovers initiated without rain ($P > 0.3$).

Discussion

Pre-migratory movements

Our study is the first to report on pre-migratory movements of Broad-winged Hawks. This behavior has been observed in Ospreys from Sweden who also abandoned the nest site in July to early August when young were still dependent on parents for food (Kjellén et al. 1997). Monti et al. (2018a) documented pre-migratory (fall) movements in 90% of the GPS-tracked adult Ospreys from Corsica, traveling on average 103 km from their nest site, similar to Broad-winged Hawks in our study ($\bar{x} = 132$ km). The early departure, along with distance traveled and number of days spent during pre-migratory movements, may reduce competition for food on the nesting territory. This may allow for greater resource acquisition by young birds (Martell et al. 2001) and be crucial for long-distance migrants who require appropriate fat reserves before moving south (Kjellén et al. 1997). Additional research is needed to discern why some adults displayed this behavior and others did not, and whether males as well as females display this behavior.

Migratory routes

Our study supports previous observations (Smith 1980, Bildstein 2004, 2006; Goodrich et al. 2014) and one telemetry study (Haines et al. 2003) on Broad-winged Hawk migration and reports on new migration pathways that may have been delineated in Mexico, where juveniles crossed the Sierra Madre Occidental mountain range, and in South America, where adults followed the eastern slope of the Andes south to Peru and Brazil.

Similar to Swainson's Hawks and Turkey Vultures (*Cathartes aura*; Kochert et al. 2011, Dodge et al. 2014), Broad-winged Hawks nesting in western Canada and the eastern United States both converged along the Gulf of Mexico and migrated past the River of Raptors watchsite in Veracruz, Mexico (Ruelas Inzunza et al. 2000), during the last week of September and the first 2 weeks of October, coinciding with Haines et al. (2003) and peak migration counts of Broad-winged Hawks at the River of Raptors watchsite (Ruelas Inzunza 2007, Goodrich and Smith 2008). The western Canada birds moved past Veracruz several days later than the eastern birds. The synchronicity could be related to the large flocks they form as they move south (Bildstein 2006, Ruelas Inzunza 2007), and may play a role in the time-minimization strategy they adopt in this region.

Overwintering localities and site fidelity

Fall routes in South America diverged significantly by age and origin with juveniles wintering in Mexico and Central America and adults wintering from Nicaragua south to Bolivia, the most southerly overwintering location from this study and the Haines et al. (2003) study. Although further research is needed to examine questions of migration connectivity in Broad-winged Hawks and other raptors, these data suggest there could be differences in winter range for different nesting populations. Ospreys in North America have shown similar patterns (Kjellén et al. 2001, Martell et al. 2001). However, male and female Swainson's Hawks from the same breeding area used the same region during the overwintering period in 2 studies (Sarasola et al. 2008, Kochert et al. 2011). In contrast, Swainson's Hawks nesting in the Central Valley of California wintered over a wide

geographic area from western Mexico through central South America (Airola et al. 2019).

Overwintering locations of Pennsylvania and Alberta adult Broad-winged Hawks differed, with most of the birds wintering in South America (Appendix 1) in locations similar to those reported in Haines et al. (2003; i.e., Venezuela, Peru, and Brazil). However, Alberta birds spent the overwintering period farther east compared to Pennsylvania birds, similar to interior North American Turkey Vultures (Dodge et al. 2014). The close wintering locations used by 3 Pennsylvania adults in Peru's Amazon Basin suggests this could be an important overwintering area for Broad-winged Hawks. This region, known as Madre de Dios, has protected nature reserves throughout and is almost entirely composed of low-lying Amazon forest, with rich biodiversity and low human population density.

Broad-winged Hawks in this study, with more than one year of data, showed high fidelity to their overwintering site. Other studies on raptors such as Rough-legged Hawks (*Buteo lagopus*; Sylvén 1978, McKinley and Mattox 2010), Ferruginous Hawks (*Buteo regalis*; Plumpton and Andersen 1997), Prairie Falcons (*Falco mexicanus*; Steenhof et al. 2005), and American Kestrels (*Falco sparverius*; Hinnebusch et al. 2010), exhibited strict site fidelity to overwintering areas in successive years as well.

Rates of travel

Rates of travel were the fastest between 30°N and 20°N, along the Gulf Coast of Mexico for Pennsylvania Broad-winged Hawks. The strong thermals occurring above the coastal plain of eastern Mexico, and presumably Central America (<200 m above sea level), benefit the migration of many long-distance migrants in this region, providing consistent lift in both spring and autumn (Ruelas Inzunza 2007). Juveniles had a slower rate of travel overall compared to adults, supporting our hypothesis. Maransky and Bildstein (2001) suggested that juvenile Broad-winged Hawks tend to follow adults on their first migration, trailing behind the flock and flying at slower speeds. Rates of travel for the 3 Alberta Broad-winged Hawks differed from Pennsylvania birds by showing faster rates between 40°N and 30°N as they moved south through Kansas, Oklahoma, and Texas during fall migration. Peregrine Falcons (*Falco peregrinus*) and Swainson's

Hawks traveled faster during the middle third of migration when passing the equatorial region (Fuller et al. 1998) instead of earlier in migration as found in Broad-winged Hawks in our study.

Stopover

Stopovers were more frequent during fall migration, with prolonged stopovers occurring primarily at the beginning and end of migration, supporting our hypothesis. Kochert et al. (2011) found a similar pattern in Swainson's Hawks with more prolonged stopovers at the start and end of migration as well as a greater number of stopovers during fall compared to spring migration. Soaring migrants may reduce stopover behavior when passing through Mexico and Central America where they can take advantage of ideal soaring conditions and are traveling in large flocks (Smith et al. 1986, Ruelas Inzunza 2007). The limited number of stopovers by Broad-winged Hawks on spring migration could imply sufficient food supply in the tropics in overwintering areas, thus reducing the need to constantly refuel on spring migration (Alerstam et al. 2006). Conversely, birds migrating to nesting territories may be motivated to migrate quickly to reclaim their nest sites with ample time to raise young (Newton 2008). Finally, we cannot eliminate the possibility that gaps in satellite transmission, which were larger in spring than fall ($\bar{x} = 16.29 \pm 16.40$ d in spring), could have limited our ability to detect stopover events during spring migration. We believe the main cause for data gaps was feathers covering the solar panels on the PTT units and lack of sunlight reaching the solar panels when individuals spent time underneath the forest canopy during the breeding and nonbreeding seasons.

For stopovers with weather data, nearly half were initiated on non-rainy days, suggesting that Broad-winged Hawks are likely stopping to rest and refuel on migration during some of their stopover periods (Kirkley 1991, Bechard et al. 2006), as has been hypothesized for our study and for Osprey and Swainson's Hawks (Kjellén et al. 2001, Kochert et al. 2011, Airola et al. 2019).

Conclusion

Our study of the migration ecology of Broad-winged Hawks has provided important new

insights into the long-distance movements, stopovers, and wintering areas of adult and juvenile Broad-winged Hawks. We documented a shorter fall journey and different overwintering ranges for Pennsylvania juveniles relative to adults. Additional work is needed to verify this pattern; however, it suggests that different conservation strategies may be warranted for the 2 age classes. Moreover, Broad-winged Hawk adults from western Canada wintered in distinctively different regions compared to Pennsylvania, Maryland, and Minnesota telemetered birds (Haines et al. 2003). These results suggest Broad-winged Hawks nesting in distinct regions of their continental range show strong migratory connectivity to different regions of their overwintering range, although some overlap was noted (e.g., Brazil).

In addition, data on migration timing and stopover collected in this study appear to support the hypothesis of a hybrid time and energy minimization migration strategy in Broad-winged Hawks (Alerstam and Lindstrom 1990, Newton 2008). Early migrants follow an energy minimization strategy and switch to a time minimization strategy when thermal strength increases for travel through Mexico and northern Central America (Ruelas Inzunza 2007). Our data suggests young birds may stay with an energy minimization strategy although more data are needed. To further expand our knowledge of migratory connectivity of Broad-winged Hawks, we recommend tracking additional individuals from across the entire breeding range. Both Haines et al. (2003) and this study predominantly tracked females. To fully understand migration movements and conservation threats, both males and additional juveniles need to be tracked to see how migration, stopover, and wintering range vary between age and sex classes and with respect to their breeding geography.

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APPENDIX 1. Wintering locations of Broad-winged Hawks ($n = 14$) equipped with satellite telemetry units from Pennsylvania (PA), USA, and Alberta, Canada. Date and coordinates from the southernmost point of wintering areas.

Bird ID	Year	Location of capture	Age	Country	Coordinates	Date
135757	2014	Eastern PA	Juvenile	Mexico ^a	15°52'N, 93°25'W	22 Nov
135758	2014	Eastern PA	Juvenile	Panama ^a	8°51'N, 81°47'W	9 Nov
135760	2014	Eastern PA	Adult	Brazil	10°42'S, 57°30'W	27 Nov
146902	2015	Eastern PA	Adult	Colombia	5°49'N, 74°14'W	7 Dec
146903	2015	Eastern PA	Adult	Nicaragua	13°40'N, 86°03'W	9 Dec
146905	2015	Eastern PA	Adult	Peru	12°48'S, 68°59'W	29 Nov
	2016			Peru	12°18'S, 68°55'W	27 Nov
146904	2016	Eastern PA	Adult	Brazil	5°22'S, 69°56'W	9 Jan
146906	2016	Eastern PA	Juvenile	El Salvador	13°35'N, 89°15'W	19 Jan
146907	2016	Eastern PA	Adult	Peru	13°16'S, 69°22'W	3 Jan
	2017			Peru	13°15'S, 69°44'W	11 Jan
	2018			Peru	13°37'S, 69°37'W	3 Feb
146909	2016	Western PA	Adult	Peru	6°25'S, 78°5'W	25 Nov
	2017			Peru	6°11'S, 78°19'W	20 Dec
	2018			Peru	6°11'S, 78°20'W	20 Nov
161202	2017	Western PA	Adult	Peru	12°51'S, 69°47'W	25 Jan
149781	2015	Alberta	Adult	Suriname	4°17'N, 54°41'W	30 Dec
149782	2015	Alberta	Adult	Bolivia	15°53'S, 61°49'W	28 Nov
149783	2015	Alberta	Adult	Venezuela	6°52'N, 64°5'W	12 Dec

^a Last known location before PTT failure or bird mortality.