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Authors: Watson, James W., Banasch, Ursula, Byer, Timothy, Svingen, Daniel N., Mccready, Robert, et al.

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FIRST-YEAR MIGRATION AND NATAL REGION FIDELITY OF IMMATURE FERRUGINOUS HAWKS

JAMES W. WATSON¹

Washington Department of Fish and Wildlife, PO Box 43141, Olympia, WA 98504 USA

URSULA BANASCH

Canadian Wildlife Service, 9250 49th Street, Edmonton, AB T6B 1K5 Canada

TIMOTHY BYER

US Forest Service, Thunder Basin National Grassland, 2250 East Richards, Douglas, WY 82633 USA

DANIEL N. SVINGEN²

US Forest Service, Dakota Prairie Grasslands, 2000 Miriam Circle, Bismarck, ND 58501 USA

ROBERT MCCREADY³

The Nature Conservancy, 4889 Eagle Harbor Drive, Bainbridge Island, WA 98110 USA

DAVID HANNI⁴

Bird Conservancy of the Rockies, 230 Cherry Street #150, Fort Collins, CO 80521 USA

RICK GERHARDT

Northwest Wildlife Consultants, Inc., 815 NW 4th Street, Pendleton, OR 97801 USA

ABSTRACT.—From 1999 to 2014 we used satellite telemetry to address knowledge gaps in the migration of juvenile Ferruginous Hawks (*Buteo regalis*) related to their migration independence from adults, migration patterns, and locations of settlement ranges. Nine fledgling hawks migrated independently from their radio-tagged parents, left natal areas at different times and directions, and settled on summer ranges separated from parents by an average of 592 km. Juvenile hawks that we followed through their entire first year ($n=12$) travelled about three times farther and twice as long as adults during annual migrations, and arrived an average of 11 to 38 d later on summer, winter, and spring ranges. Hawks that hatched west of the Continental Divide ($n=14$) migrated northeast in summer to ranges in the northern grasslands and to winter ranges in California and the Great Plains. Hawks that hatched east of the divide ($n=17$) also migrated north to summer ranges, but wintered south from the Central Plains to Mexico. At the end of their first year, hawks ($n=14$) settled on spring ranges within their natal regions, an average of 350 km from their hatch locations. In their third spring, hawks ($n=6$) settled an average of 123 km from hatch locations and two females nested. We ascribe differences in migration distance and timing of juvenile hawks relative to adults to juveniles' inexperience in locating suitable feeding areas and range prospecting independently from parents. Because migration patterns and regional fidelity of juvenile Ferruginous Hawks to settlement ranges were similar to those exhibited by adult hawks, the protection of fossorial prey and their habitats on seasonal ranges that promote survival of adult hawks will afford the same benefits to the juvenile cohorts.

KEY WORDS: *Ferruginous Hawk*; *Buteo regalis*; dispersal; fledgling; migration; range fidelity.

¹ Email address: James.Watson@dfw.wa.gov

² Present address: Fort Pierre Ranger District, 1020 North Deadwood Street, Fort Pierre, SD 57532 USA.

³ Present address: National Wildlife Federation, 1010 Confidence Drive, Longmont, CO 80504 USA.

⁴ Present address: Tennessee Wildlife Resources Agency, 5105 Edmondson Pike, Nashville, TN 37211 USA.

MIGRACIÓN DEL PRIMER AÑO Y FIDELIDAD A LA REGIÓN DE NACIMIENTO DE INDIVIDUOS INMADUROS DE *BUTEO REGALIS*

RESUMEN.—Desde 1999 a 2014 usamos telemetría satelital para responder algunos interrogantes sobre la migración de individuos juveniles de *Buteo regalis* en relación a su migración independiente de los adultos, a los patrones de migración y a la ubicación de las áreas de establecimiento. Nueve volantones migraron independientemente de sus progenitores previamente marcados con radios, dejaron las áreas de nacimiento en diferentes momentos y direcciones, y se establecieron en áreas de verano separadas de los progenitores por un promedio de 592 km. Los juveniles que seguimos a lo largo de todo su primer año de vida ($n = 12$) viajaron aproximadamente tres veces más lejos y el doble de la distancia que los adultos durante las migraciones anuales, y llegaron, en promedio, 11 a 38 d más tarde a las áreas ocupadas en verano, invierno y primavera. Los individuos de *B. regalis* que eclosionaron al oeste de la divisoria continental ($n = 14$) migraron en dirección noreste, en la región de los pastizales del norte, en el verano, y a las áreas de invernada en California y las Grandes Planicies. Los individuos de *B. regalis* que eclosionaron al este de la divisoria continental ($n = 17$) también migraron en dirección norte hacia las áreas de verano, pero invernaron al sur, desde las Grandes Planicies hasta México. Al final de su primer año y durante la primavera, los juveniles de *B. regalis* ($n = 14$) se establecieron dentro de sus regiones de nacimiento a un promedio de 350 km desde donde se produjo la eclosión. En su tercera primavera, los individuos de *B. regalis* ($n = 6$) se establecieron a un promedio de 123 km de las áreas donde se produjo la eclosión y dos hembras anidaron. Nosotros atribuimos que las diferencias en la distancia y el tiempo de migración de los juveniles con respecto a los adultos se debe a la falta de experiencia de los juveniles en localizar áreas adecuadas de alimentación y al hecho de prospectar las áreas independientemente de sus progenitores. Dado que los patrones de migración y la fidelidad regional de los juveniles de *B. regalis* a las áreas de establecimiento fueron similares a los que exhibieron los adultos, la protección de las presas fosoriales y sus hábitats en las áreas ocupadas durante las diferentes estaciones no solo fomenta la supervivencia de ejemplares adultos de *B. regalis* sino que también ofrecería iguales beneficios para las cohortes de juveniles.

[Traducción del equipo editorial]

Juvenile raptors often disperse locally from natal areas when competition for limited resources forces them move to nearby habitats (Bildstein 2006, Morrison and Wood 2009). When juvenile hawks disperse longer distances due to wide spacing or seasonality of habitats, their first-year movements may graduate into migration (Newton 2008). For juvenile migrant raptors, lack of experience and different life needs compared to adult hawks may influence their migration timing and patterns, and locations of settlement areas until the time of their recruitment into nesting populations (Bildstein et al. 1984, Ferrer 1993, Bloom et al. 2015). Different patterns and areas of use may affect age-specific survival and thus be important to conservation needs of immature hawks (Mañosa et al. 1998, McIntyre et al. 2006, Cadahia et al. 2010, Hunt et al. 2017).

In the genus *Buteo*, age-specific differences in timing and range-use patterns of migrant adult and juvenile hawks have been documented for at least two species. Juvenile Red-tailed Hawks (*B. jamaicensis*) preceded adults in autumn migration (Mueller et al. 2000), but migrated later than adults in spring (Mueller et al. 2003). Juvenile Broad-winged Hawks (*B. platypterus*) followed adults during migration (Maransky and Bildstein 2001). Other studies on

Buteo hawks have documented age differences in migration trajectories important to differential distribution and habitat use. Fledgling Red-tailed Hawks in California, USA, for example, dispersed toward the north whereas adults from the same population generally remained sedentary (Bloom et al. 2015). Differences were potentially due to effects of climate change, seasonal prey availability, and adult dominance. In other populations of Red-tailed Hawks, adults remained closer to breeding areas (Preston and Beane 2009) or wintered at different locations (Brinker and Erdman 1985).

The migratory behavior of Ferruginous Hawks (*B. regalis*) is perhaps the least understood of *Buteos* in western North America (Collins and Reynolds 2005, Ng et al. 2017), but recent research documented range-wide migration patterns, timing, and seasonal destinations of adult hawks (Watson et al. 2018). For juvenile Ferruginous Hawks hatched east of the Continental Divide, band recoveries have provided some information about destinations, migration timing, and causes of mortality, and indicate that hawks may migrate independently from parents (Woffinden and Murphy 1983, Schmutz and Fyfe 1987). Other studies suggest juvenile hawks orient randomly during their departure from natal areas

(Salt et al. 1939, Thurow et al. 1980, Gilmer et al. 1985). Information on juvenile hawks hatched west of the divide is limited to band recovery locations (Gossett 1993), and there remain knowledge gaps range-wide about whether juvenile hawks differ from adults in migration routes, locations of settlement ranges, and timing and duration of migration during their first year.

To address these knowledge gaps, we used satellite tracking of juvenile Ferruginous Hawks to gather information about their movements. Our objectives were to: (1) compare juvenile hawks' first migration to their parents' migration in terms of departure timing, directional orientation, and locations of summer ranges; (2) describe migration patterns of juvenile hawks in their first migration and compare migration distance and duration to that previously documented for adult hawks; and (3) document spring settlement locations of juvenile hawks relative to natal areas and document fidelity to summer and winter ranges.

METHODS

Study Areas and Data Collection. From 1999 to 2014, we captured and radio-tagged 54 fledgling Ferruginous Hawks in five regions (Fig. 1). These included the Pacific Northwest (south-central Washington, north-central Oregon), the Northern Grasslands (southern Alberta), Northern Plains (Dakota Prairie National Grasslands, North Dakota and South Dakota), Central Plains (Thunder Basin National Grassland, Wyoming), and Southern Plains (Comanche, Kiowa, and Rita Blanca National Grasslands in Colorado, New Mexico, and Oklahoma, respectively). Study areas were in generally flat and rolling terrain (Ng et al. 2017). Habitats were typically a mix of grasses (e.g., *Agropyron* spp. and *Bouteloua* spp.) and shrubs (e.g., *Artemisia* spp. and *Atriplex* spp.) with western juniper (*Juniper occidentalis*) common in shrub-steppes. Nests were typically in trees or on the ground in relatively flat landscapes, and on cliffs and creek banks in topographically variable landscapes.

We surveyed historical locations of hawk nesting territories provided by wildlife resource agencies in each study region beginning in early spring to identify those occupied by breeding adults; we defined occupied territories as those with two birds at a nest within the territory or at least one adult engaged in territorial defense or nest building. We resurveyed the subset of occupied territories in late spring to identify egg-laying pairs and locations of

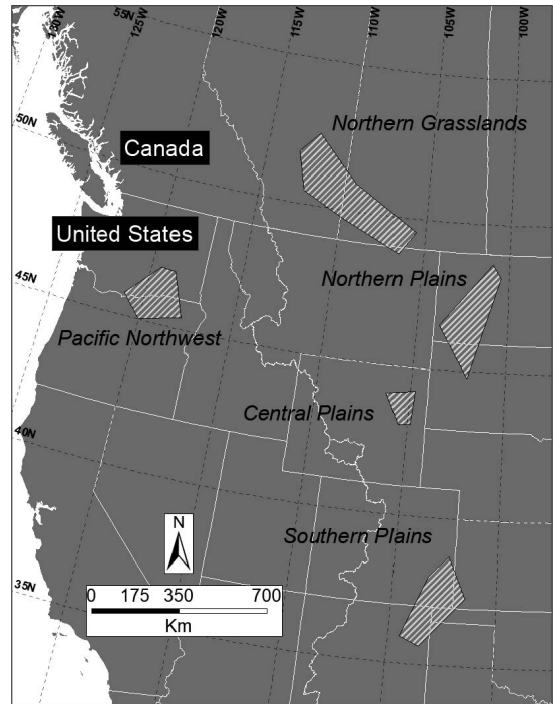


Figure 1. Study areas where juvenile Ferruginous Hawks were captured and radio-tagged at nests to understand their migration behavior from 1999–2014.

used nests where eggs were laid, and again in summer to identify productive nesting territories and estimate ages of nestlings (Moritsch 1985). When nestlings were nearly or completely feathered (50 d post-hatching) we removed the oldest, or most accessible bird from nests or hand-captured them on the ground if they fledged prematurely. Hawks were weighed, measured (i.e., wing chord, hallux length, and bill depth), and banded with USGS bands. Hawks were classified to sex based on differences in these measurements (Harmata 1981).

Each hawk was outfitted with one of two types of 30-g platform transmitter terminals (PTTs; Microwave Telemetry, Columbia, MD). From 1999 to 2005, we deployed battery and solar-powered ARGOS PTTs on 20 hawks. These units provided Doppler-generated fixes for 8 hr every 3 d. We filtered these data with the Douglas Argos-filter Algorithm (<https://alaska.usgs.gov/science/biology/spatial/douglas.html>) that employs hybrid filtering to exclude implausible locations (Douglas et al. 2012). Filtering was set to include fixes with an accuracy ≤ 1.5 km (ARGOS designated classes 3, 2,

and 1 fixes), and exclude auxiliary fixes in classes (0, A, B, and Z) that did not conform to a prescribed maximum movement rate threshold of 100 km/hr and a spatial redundancy threshold of 15 km. This resulted in an average of 127 ± 25 (SE) fixes/bird. After 2005, we deployed solar-powered PTTs on 34 hawks that transmitted global positioning system (GPS) fixes once per hr at 21-hr intervals during daylight. Fixes had a manufacturer specified error of ± 22 m (T. Rollins pers. comm.) and we included all GPS fixes in analyses ($\bar{x} = 2276 \pm 761$ fixes/bird). PTTs were attached to hawks with "X-attachment" backpacks (Buehler et al. 1995) using 7-mm-wide teflon ribbon. Juvenile hawks were returned to nests <1 hr following their capture.

We monitored hawk movements until loss of the PTT signal, expiration of the PTT, or death of the hawk. We plotted and interpreted each individual's annual movement patterns using ArcGIS 10.1 (ESRI 2013). We conducted a cursory examination of plots that revealed a repeated pattern of hawk settlement at local areas, followed by their departure, migration, and resettlement. We identified the most biologically appropriate classification of fixes to capture this pattern. We classified all fixes as either local or migratory and differentiated them by examining successive fixes in 10-d increments. Local fixes were <30 km apart, oriented randomly, and identified settlement locations in seasonal ranges. Migratory fixes were >30 km apart for >1 d, with a strong directional orientation, and indicated consistent flight speed (PTT sensor indicating >20 km/hr). Migration distance was computed as the cumulative distance between each pair of migration fixes for the designated season. When the day of migration initiation could not be determined because it occurred during a non-transmission cycle of ARGOS fixes, we identified the migration day as the median date between the last and first fixes spanning the period in question (i.e., <36 hr from actual time). Because we analyzed birds from ARGOS and GPS data with different accuracy and number of fixes, combining birds resulted in increased imprecision of distance and date estimates. Based on tests done on birds with GPS data sets that also provided simultaneous ARGOS data, we assumed the lower sampling rate of ARGOS data collections (55% of birds tracked in migration) underestimated migration distances by $\leq 14\%$ (J. Watson unpubl. data), resulting in conservative summary estimates.

Analyses. At nine territories where we radio-tagged fledglings and one parent, we calculated and reported the number of days separating juvenile migration and migration of male and female adults, although these data were too sparse (i.e., <30) for statistical comparisons. We computed bearings of juvenile and adult hawks using the bearing calculator in ARCGIS when hawks were 50 km, 150 km, and 500 km from their nest locations and tested for correlations between parents and offspring at each increment using the circular package (Agostinelli and Lund 2013) and the R 3.1.3 statistical package (R Core Team 2015).

We compared migration characteristics of the entire radio-tagged juvenile cohort with that published for adult hawks (Watson et al. 2018) for total annual migration distance and duration, and departure dates from seasonal ranges (converted to Julian day). We categorized local and migratory fixes of adult hawks as we did for juvenile hawks. We pooled distance estimates from birds with ARGOS- and GPS-generated data for all analyses. We used general linear mixed models in SAS (PROC GLIMMIX, SAS 9.4, SAS Institute, Inc.) to test the effect of hawk age (juvenile or adult) on dates, distance, and duration. Models were run with the identity link and parameter values were computed with the residual maximum likelihood. Band number was modeled as a random effect to address potential pseudoreplication arising from inclusion of ≥ 2 yr of migration data for some adults (Hurlbert 1984, Lazic 2010). Normality of variables was confirmed prior to analyses by evaluation of residual plots.

As a measure of spring range fidelity, we computed the Euclidian distance separating the location of the natal area for each hawk in each successive spring range from hatching until their third year, the age at which they were first capable of breeding. From the same data, we documented whether their spring occupancy of Level III ecoregions changed over time (Omernik and Griffith 2014). We also describe distances separating first- and second-year summer and winter ranges. Sample sizes for comparisons of migration distance, arrival dates on ranges, and distances between seasonal ranges were too small (i.e., <30) for statistical analyses. We summarize sample statistics as $\bar{x} \pm SE$.

RESULTS

Capture Location and Monitoring History. From 1999 to 2014, we radio-tagged 54 fledgling Ferruginous Hawks (34 females and 20 males) in the Pacific

Table 1. Arrival and departure dates of radio-tagged juvenile and adult Ferruginous Hawks from seasonal ranges occupied during the annual cycle throughout western North America. Data for adult hawks were adapted from Watson et al. (2018). Effect of age on date was tested with general linear mixed models.

MIGRATION DEPARTURE OR ARRIVAL	JUVENILE			ADULT			SIGNIFICANCE	
	\bar{x}	SE (d)	<i>n</i>	\bar{x}	SE (d)	<i>n</i>	<i>F</i>	<i>P</i>
Depart nest location	27 July	5	31	28 July	3	60	0.01	0.91
Arrive summer range	15 Aug	5	25	2 Aug	3	48	5.25	0.03
Arrive winter range	13 Nov	10	20	18 Oct	6	45	5.11	0.03
Arrive spring or breeding range	26 April	13	10	19 Mar	6	32	6.94	0.02

Northwest ($n = 27$), Northern Grasslands ($n = 3$), Northern Plains ($n = 10$), Central Plains ($n = 9$), and Southern Plains ($n = 5$) regions (Fig. 1). Twenty-three hawks (43%) died prior to migration and were not used in movement analyses, including four that did not fledge from their nests, and 19 that died an average of 14.9 ± 2.3 d after fledging but had remained on natal ranges. Of the remaining 31 surviving hawks, 17 (32%) were tracked in migration ≤ 1 yr (14 fatalities and three still active when signals lost) and 14 (26%) from 1 to 7 yr.

Adult and Juvenile Association. Nine parents and their offspring migrated independently of each other. On average, radio-tagged adult females ($n = 5$) initiated migration 14.5 ± 6.5 d before their young, whereas adult males ($n = 4$) migrated 9.3 ± 4.2 d after their offspring. All radio-tagged fledglings ($n = 31$) spent an average of 25.8 ± 2.7 d on natal ranges after they fledged and prior to migration. We found no correlations in directional orientation of migration between the nine parent-offspring pairings at distances of 50 km ($r = 0.22$, $P = 0.46$) and 150 km ($r = 0.24$, $P = 0.38$) from nest locations, but these paired correlations approached significance at 500 km ($r = 0.64$, $P = 0.07$). In late summer, eight of nine juvenile hawks that survived summer migration settled on ranges that were separated by an average of 591.8 ± 123.5 km (range = 250–1275 km) from where their radio-tagged parent settled in late summer.

First-year Movement Patterns and Destinations. None of the 31 juvenile hawks we monitored in migration exhibited pre-migration movements. Seasonal migrations were distinguished based on timing of their movements and arrival on ranges (Table 1). There were three patterns of first-year migration for 14 hawks tracked at least 1 yr. Eight birds (57%) made distinct movements to different ranges in summer, fall, and spring. Three hawks (21%) migrated to summer ranges where they remained

through winter until they migrated in spring. Three hawks (21%) did not settle on ranges until winter, and migrated again in spring.

First-year migration patterns were distinct for hawks depending on whether they hatched from the east or west side of the Continental Divide, although during summer some hawks from both sides of the Continental Divide ranged into the Canadian provinces and Mexico (Fig. 2). First-year migration was primarily latitudinal for 17 hawks (10 complete and 7 partial migrations) that hatched east of the Continental Divide (Fig. 2A–C). These birds migrated from the High Plains, Central Plains, and Southern Plains, within the area between southern Canada and northern Mexico during their first year. Three migrants (18%) crossed over the Continental Divide to the west (Fig. 2A, B), but remained ≤ 180 km from the divide. The least-ranging individuals included two hawks from the Central Plains and two hawks from the Southern Plains that remained < 350 km from their natal areas during their first year, respectively. First-year migration patterns of 14 hawks (4 complete and 10 partial migrations) from west of the Continental Divide were more wide-ranging, with a stronger longitudinal pattern (Fig. 2D). Nine hawks (64%) crossed the Continental Divide east to lower elevation ranges along the Rocky Mountain Front, and all but two birds returned west of the divide before the start of their second spring. Three summering hawks from the Pacific Northwest ranged into California where they eventually overwintered.

Range-wide, total distance and duration of first-year migration of 12 hawks from all natal regions was lengthy, ranging between approximately 4900 km and 11,300 km on average, and accounting for 106 d (29%) of the year (Table 2). Summer migration accounted for 43% and 41% of annual migration distance and duration, respectively. Summer movements were complex and multi-directional, and 17

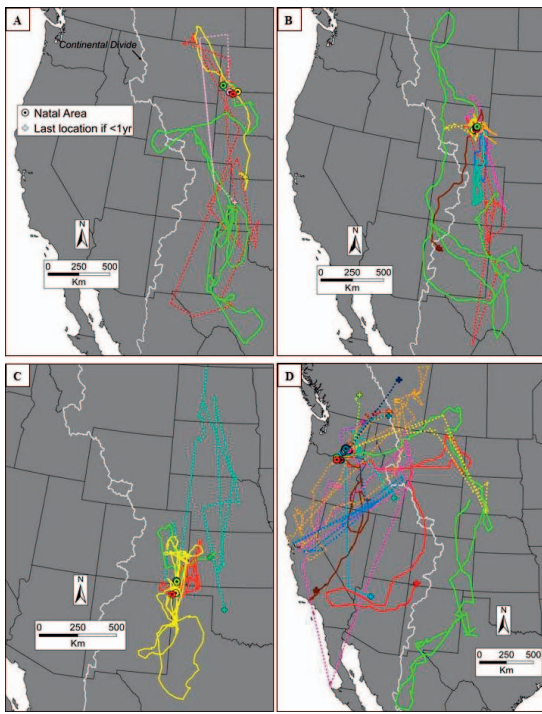


Figure 2. Migration patterns of Ferruginous Hawks tracked during their first-year by satellite telemetry throughout western North America from 1999 to 2014. Patterns are pooled seasonally for hawks from the High Plains ($n = 4$, panel A), Central Plains ($n = 9$, panel B), Southern Plains ($n = 4$, panel C), and Pacific Northwest ($n = 14$, panel D). Dotted lines represent ARGOS tracks and solid lines represent global positioning system tracks.

of 31 hawks (55%) moved back and forth between the same distant locations at least twice. In contrast, fall migration for all fledglings was only southward to winter ranges, whereas spring migration of all hawks was direct and northward.

Table 2. Characteristics of first-year migration of Ferruginous Hawks from their natal ranges to settlement on spring ranges.

NATAL REGION	DISTANCE ^a		DURATION ^a		NO. BIRDS
	\bar{x} (km)	SE	\bar{x} (d)	SE	
Southern Plains	6444.5	3256.5	97.5	60.5	2
Central Plains	4969.2	1324.2	105.6	43.1	5
Pacific Northwest	6078.7	1570.2	88.7	30.6	3
High Plains	11,314.0	217.0	143.5	4.5	2
Range-wide	6549.9	991.4	106.3	20.0	12

^a Pooled measurements from summer, fall, and spring migration.

Age-class Differences in Migration Timing and Distance. Arrival of juvenile hawks on summer ranges ($n = 25$), winter ranges ($n = 20$), and spring ranges ($n = 10$) was progressively later than adults by an average of 13 d, 26 d, and 38 d, respectively (Table 1). On average, during their first year, 12 juvenile hawks migrated 6549.2 ± 991.4 km, significantly farther ($F = 46.50, P < 0.0001$) than adult hawks ($n = 42$) that averaged 2319.1 ± 290.2 km travelled. On average, during their first year, these juvenile hawks migrated for 106.3 ± 20 d longer ($F = 28.53, P < 0.0001$) than adult hawks that migrated for an average of 48.5 ± 10.0 d.

Regional Fidelity. At the end of their first year, juvenile hawks ($n = 14$) settled on spring ranges that were an average of 350.0 ± 92.5 km from their natal areas, and two west-side hawks settled east of the divide (Fig. 3). Six of 14 hawks (43%) spent their second spring in the same ecoregions where their natal areas were located (Fig. 3). In their second year, these hawks settled on fall ranges that were 293.2 ± 96.3 km from their first fall ranges, and subsequently settled on winter ranges that were separated by 146.0 ± 118.4 km from their first winter ranges. In their third spring, six hawks that reached adulthood settled on ranges that were 123.3 ± 35.4 km from their natal ranges and five birds (83%) settled within their natal ecoregions (Fig. 3). Two of these females nested 25 km and 101 km from their natal areas in Wyoming and Oregon, respectively.

DISCUSSION

Ferruginous Hawk fledglings did not exhibit pre-migration movements from natal ranges and there was no association between timing or distances of adults and offspring as they migrated to distant summer ranges. Rather, our results documented differences in migration timing of age classes, with adult females migrating during provisioning of their

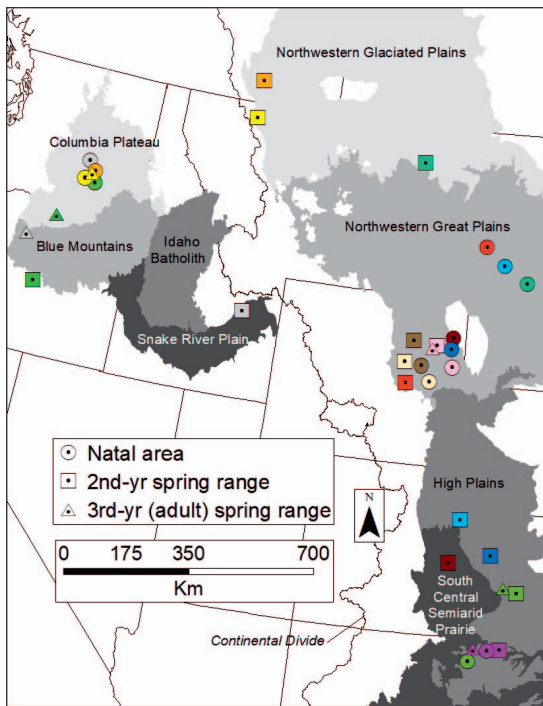


Figure 3. Locations of spring ranges of Ferruginous Hawks in the second ($n = 14$) and third years ($n = 6$) subsequent to their migration from natal areas. Ranges used by the same individual are identified by color. Level III ecoregion designations are from Omernik and Griffith (2014).

fledged young and adult males migrating after juveniles migrated. Timing of nest desertion by adult females was consistent with a strategy that best promoted their own fitness and survival of their offspring (Kelly and Kennedy 1993). Migratory independence of juvenile hawks from parents contrasted with the parental dependence juvenile swans, geese, and cranes exhibit in learning migratory routes (Ellis et al. 2003). The fact that the distance and direction juvenile hawks migrated to their first summer ranges was different from those of their parents provided no phenotypical evidence for heritable control of navigation to specific locations (Berthold and Helbig 1992). If migration tracks were heritable, we would expect 50% of the hawks to show migration similar to adults because we only radio-tagged one adult at each paired nest. Nevertheless, many juvenile hawks from most breeding populations in our study arrived at the same Northern Grasslands and High Plains in summer

where adult Ferruginous Hawks are attracted to large populations of Richardson's ground squirrels (*Urocitellus richardsonii*) each fall (Watson et al. 2018). Ferruginous Hawks are prey specialists, favoring medium-sized fossorial mammals and lagomorphs (Ng et al. 2017). Random directional movements from natal ranges to locate these distant ranges would be maladaptive, so must involve other mechanisms for navigation such as habitat recognition or flight-following of unrelated hawks, as discussed below.

Four hawks exhibited localized dispersal that involved gradual and progressive movements from nest locations (Salt 1939, Thurow et al. 1980, Gilmer et al. 1985) that may also have been related to localized prey, rather than distant prey abundance. Two of these hawks were hatched within the Central Plains of Wyoming in 2006, when there was localized peak abundance of black-tailed and white-tailed jack rabbits (*Lepus californicus* and *L. townsendi*) and cottontail rabbits (*Sylvilagus nuttalli*; J. Watson and T. Byer unpubl. data, G. McKee pers. comm.) that reduced migration of adult hawks in the same population (Watson et al. 2018). The other two juvenile hawks exhibiting dispersal movements were hatched in the Southern Plains, which is an important wintering area for Ferruginous Hawks from many nesting populations in part because of reduced snow cover that improves access to prey (Watson et al. 2018); this area may have afforded similar benefits to locally fledged juvenile hawks.

Compared to adult hawks, juvenile hawks had delayed arrival on seasonal ranges, and travelled about three times farther and twice as long during annual migration. Extensive summer movements of juvenile hawks significantly contributed to these differences and may reflect the inexperience of juvenile birds in locating favorable feeding areas. For juvenile Ferruginous Hawks that migrate independently from parents, the probability of encountering other experienced individuals and thereby reducing time and distance required to arrive at seasonal ranges is probably lower than for obligate migrants like Broad-winged Hawks, where juvenile hawks join flocks that migrate along traditional flight lines (Maransky and Bildstein 2001). Indeed, there are comparatively low annual counts of Ferruginous Hawks at major hawkwatch sites (Smith et al. 2008). In Idaho, Taylor and Trost (1985) attributed an unusually high concentration of immature Ferruginous Hawks in late summer to prevailing winds that funneled birds to an area with abundant ground

squirrels. Age-related differences in migration for other raptor species are thought to result from wind drift or atmospheric conditions that hinder juvenile raptors from navigating to traditional locations (Bildstein et al. 1984, Hoffman and Darrow 1992, Håke et al. 2003) or from the lesser navigation abilities of juveniles (Mueller et al. 2003, Thorup et al. 2003).

A benefit of relatively long durations and distances traversed by juvenile hawks, particularly in summer, is that their movements allowed them to prospect for feeding ranges for reference during future migrations (i.e., their movements were also exploratory and not driven solely by food acquisition; Bennetts and Kitchens 2000). This explanation is supported by the fact that several hawks moved more than once between the same distant ranges in their first year. Adult Ferruginous Hawks have comparatively lower repeated annual use of summer migration routes and settlement ranges compared to other seasons (J. Watson unpubl. data), suggesting summer exploration may be important to both age classes of Ferruginous Hawks. For other raptors that migrate long distances, strategies may differ between juveniles and adults of the same species (Maransky and Bildstein 2001, Håke et al. 2003). Juvenile Red-tailed Hawks migrated from California whereas adult hawks from the same populations were generally nonmigratory, possibly a result of climate change, seasonal prey availability, and adult dominance (Bloom et al. 2015).

Migration patterns for juvenile hawks mirrored those of adults from the same populations (Watson et al. 2018), including similarly low crossover of juvenile and adult birds from east to west (12% and 6%, respectively), but high crossover west to east of the Continental Divide (60% and 88%). Gossett (1993) calculated an east-to-west crossover of 4% based on 18 of 435 band recoveries for Ferruginous Hawks, but only 28% crossover west to east (28 of 102 band recoveries), a result which may have been affected by comparatively lower sample size. It is noteworthy that Schmutz and Fyfe (1987) found band recoveries of juvenile hawks fledged from the provinces southward ($n = 80$) distributed more westerly and closer to the Rocky Mountain Front than hawks that fledged in North Dakota and were tracked through band recoveries ($n = 40$). This is not unlike the more-westerly patterns we found for hawks fledged from the Central Plains vs. the Northern and Southern Plains and

suggestive of broad, longitudinal corridors for hawks migrating southward east of the Rocky Mountain Front.

Conservation Implications. Movements of juvenile Ferruginous Hawks throughout western North America may expose them to a variety of mortality sources such as shooting and electrocution (Gossett 1993), wind-energy development (Kolar and Bechard 2016), and secondary poisoning from rodenticides (Vyas et al. 2017). For prey specialists like this species (Ng et al. 2017), these effects may be exacerbated if quality of habitat and associated prey are reduced along migration routes or on winter areas, forcing birds to migrate farther or across a wider area in their first year (Newton 2004, Norris and Taylor 2006, Norris and Marra 2007). This is particularly important for juvenile hawks in shrub-dominated habitats from west of the Continental Divide that, like adult hawks, migrated farther, longer, and more widely than those in eastern populations and may be more at risk where quality of prey and nonbreeding habitats are compromised (Watson et al. 2018). We did not identify areas unique to juvenile hawks and potentially important to first-year survival (Mellone et al. 2013, Bloom et al. 2015). Thus, protection of fossorial prey and their habitats on summer and winter ranges that promotes survival of adult hawks (Watson et al. 2018) will afford the same benefits to the juvenile cohorts.

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LITERATURE CITED

- Agostinelli, C., and U. Lund (2013). R package 'circular': circular statistics (version 0.4–7). <https://r-forge.r-project.org/projects/circular/>.
- Bennetts, R. E., and W. M. Kitchens (2000). Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? *Oikos* 91:459–467.
- Berthold, P., and A. J. Helbig (1992). The genetics of bird migration: stimulus, timing, and direction. *Ibis* 123:35–40.
- Bildstein, K. L. (2006). *Migrating Raptors of the World: Their Ecology and Conservation*. Cornell University Press, Ithaca, NY, USA.
- Bildstein, K. L., W. S. Clark, D. L. Evans, M. Field, L. Soucy, and E. Henckel (1984). Sex and age differences in fall migration of Northern Harriers. *Journal of Field Ornithology* 55:143–150.
- Bloom, P. H., M. D. McCrary, J. M. Scott, J. M. Papp, K. J. Sernka, S. E. Thomas, J. W. Kidd, E. H. Henckel, J. L. Henckel, and M. J. Gibson (2015). Northward summer migration of Red-Tailed Hawks fledged from southern latitudes. *Journal of Raptor Research* 49:1–17.
- Brinker, D. F., and T. C. Erdman (1985). Characteristics of autumn Red-tailed Hawk migration through Wisconsin. *Proceedings of the Hawk Migration Conference* 4:107–136.
- Buehler, D. A., J. D. Fraser, M. R. Fuller, L. S. McAllister, and J. K. D. Seegar (1995). Captive and field-tested radio transmitter attachments for Bald Eagles. *Journal of Field Ornithology* 66:173–180.
- Cadahia, L., P. López-López, V. Urios, and J. J. Negro (2010). Satellite telemetry reveals individual variation in juvenile Bonelli's Eagle dispersal areas. *European Journal of Wildlife Research* 56:923–930.
- Collins, C. P., and T. D. Reynolds (2005). *Ferruginous Hawk (Buteo regalis): A Technical Conservation Assessment*. USDA Forest Service, Rocky Mountain Region, Lakewood, CO, USA. <http://www.fs.fed.us/r2/projects/scp/assessments/ferruginoushawk.pdf>.
- Douglas, D. C., R. Weinzierl, S. C. Davidson, R. Kays, M. Wikelski, and G. Bohrer (2012). Moderating Argos location errors in animal tracking data. *Methods in Ecology and Evolution* 3:999–1007.
- Ellis, D. H., W. J. Sladen, W. A. Lishman, K. R. Clegg, J. W. Duff, G. F. Gee, and J. L. Lewis (2003). Motorised migrations: the future or mere fantasy? *BioScience* 53:260–264.
- ESRI (2013). *ArcGIS Desktop Online Help: Release 10.1*. Environmental Systems Research Institute, Redlands, CA, USA.
- Ferrer, M. (1993). Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* 135:132–138.
- Gilmer, D. S., D. L. Evans, P. M. Konrad, and R. E. Steward (1985). Recoveries of Ferruginous Hawks banded in south-central North Dakota. *Journal of Field Ornithology* 56:184–187.
- Gossett, D. N. (1993). *Studies of Ferruginous Hawk biology*. M.S. thesis. Boise State University, Boise, ID, USA.
- Håke, M., N. Kjellén, and T. Alerstam (2003). Age-dependent migration strategy in Honey Buzzards *Pernis apivorus* tracked by satellite. *Oikos* 103:385–396.
- Harmata, A. (1981). Recoveries of Ferruginous Hawks banded in Colorado. *North American Bird Bander* 6:144–147.
- Hoffman, S. W., and H. Darrow (1992). Migration of diurnal raptors from the Florida Keys into the West Indies. *Hawk Migration Studies* 17:7–24.
- Hunt, G. W., D. J. Wiens, P. R. Law, M. R. Fuller, T. L. Hunt, D. E. Driscoll, and R. E. Jackman (2017). Quantifying the demographic cost of human-related mortality to a raptor population. *PloS ONE* 12:e0172232. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0172232>.
- Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Kelly, E. J., and P. L. Kennedy (1993). A dynamic state variable model of mate desertion in Cooper's Hawks. *Ecology* 74:351–366.
- Kolar, P. S., and M. J. Bechard (2016). Wind energy, nest success, and post-fledging survival of *Buteo* hawks. *Journal of Wildlife Management* 80:1242–1255.
- Lazic, S. E. (2010). The problem of pseudoreplication in neuroscientific studies: is it affecting your analysis? *BMC Neuroscience* 11:5.
- Mañosa, S., J. Real, and J. Codina (1998). Selection of settlement areas by juvenile Bonelli's Eagle in Catalonia. *Journal of Raptor Research* 32:208–214.
- Maransky, B. P., and K. L. Bildstein (2001). Follow your elders: age-related differences in the migration behavior of Broad-winged Hawks at Hawk Mountain Sanctuary, Pennsylvania. *Wilson Bulletin* 113:350–353.
- McIntyre, C. L., M. W. Collopy, and M. S. Lindberg (2006). Survival probability and mortality of migratory juvenile Golden Eagles from interior Alaska. *Journal of Wildlife Management* 70:717–722.
- Mellone, U., P. López-López, R. Liminana, G. Piasevoli, and V. Urios (2013). The trans-equatorial loop migration system of Eleonora's Falcon: differences in migration patterns between age classes, regions, and seasons. *Journal of Avian Biology* 44:417–426.

- Moritsch, M. Q. (1985). Photographic Guide for Aging Nestling Ferruginous Hawks. Bureau of Land Management, Boise, ID, USA.
- Morrison, J. L., and P. B. Wood (2009). Broadening our approaches to studying dispersal in raptors. *Journal of Raptor Research* 43:81–89.
- Mueller, H. C., D. D. Berger, and N. S. Mueller (2003). Age and sex differences in the timing of spring migration of hawks and falcons. *Wilson Bulletin* 115:321–324.
- Mueller, H. C., N. S. Mueller, D. D. Berger, G. Allez, W. Robichaud, and J. L. Kaspar (2000). Age and sex differences in the timing of fall migration of hawks and falcons. *Wilson Bulletin* 112:214–224.
- Newton, I. (2004). Population limitation in migrants. *Ibis* 146:197–226.
- Newton, I. (2008). *Migration Ecology of Birds*. Academic Press, San Diego, CA, USA.
- Ng, J., M. D. Giovanni, M. J. Bechard, J. K. Schmutz, and P. Pyle (2017). Ferruginous Hawk (*Buteo regalis*). In *The Birds of North America* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsna.org/Species-Account/bna/species/ferhaw>.
- Norris, D. R., and P. P. Marra (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* 109:535–547.
- Norris, D. R., and C. M. Taylor (2006). Predicting the consequences of carry-over effects for migratory populations. *Biology Letters* 2:148–151.
- Omernik, J. M., and G. E. Griffith (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environmental Management* 54:1249–1266. <http://dx.doi.org/10.1007/s00267-014-0364-1>.
- Preston, C. R., and R. D. Beane (2009). Red-tailed Hawk (*Buteo jamaicensis*), version 2.0. In *The Birds of North America* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bna.52>.
- R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Salt, W. R. (1939). Notes on recoveries of banded Ferruginous Rough-legged Hawks (*Buteo regalis*). *Bird-Banding* 10:80–84.
- Schmutz, J. K., and R. W. Fyfe (1987). Migration and mortality of Alberta Ferruginous Hawks. *The Condor* 89:169–174.
- Smith, J. P., C. J. Farmer, S. W. Hoffman, G. S. Kaltenecker, K. Z. Woodruff, and P. F. Sherrington (2008). Trends in autumn counts of migratory raptors in western North America. In *State of North America's Birds of Prey* (K. L. Bildstein, J. P. Smith, E. R. Inzunza, and R. R. Veit, Editors). The Nuttall Ornithological Club and The American Ornithologists' Union. Fayetteville, AR, USA. pp. 217–251.
- Taylor, D. M., and C. H. Trost (1985). Fall raptor concentration on Henry's Lake Flats. *Raptor Research* 19:143–144.
- Thorup, K., T. Alerstam, M. Håke, and N. Kjellén (2003). Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270:S8–S11.
- Thurrow, T. L., C. M. White, R. P. Howard, and J. F. Sullivan (1980). *Raptor Ecology of Raft River Valley, Idaho*. US Department of Energy Report EGG-2054. Idaho Falls, ID, USA.
- Vyas, N. B., F. Kuncir, and C. C. Clinton (2017). Influence of poisoned prey on foraging behavior of Ferruginous Hawks. *American Midland Naturalist* 177:75–83.
- Watson, J. W., U. Banasch, T. Byer, D. N. Svingen, R. McCready, M. A. Cruz, D. Hanni, A. LaFon, and R. Gerhardt (2018). Migration patterns, timing, and seasonal destinations of adult Ferruginous Hawks (*Buteo regalis*). *Journal of Raptor Research* 52:267–281.
- Woffinden, N. D., and J. R. Murphy (1983). Ferruginous Hawk postfledging activities. *North American Bird Bander* 8:94–96.

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