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MIGRATION PATTERNS, TIMING, AND SEASONAL DESTINATIONS OF ADULT FERRUGINOUS HAWKS (*BUTEO REGALIS*)

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ABSTRACT.—The Ferruginous Hawk (*Buteo regalis*) is a keystone raptor in arid-land ecosystems in western North America that is experiencing population declines in some regions. Range-wide migration patterns, destinations, and chronology of adult hawks have not been described. Between 1999 and 2014, we captured 69 adult Ferruginous Hawks east and west of the Continental Divide and monitored them ≤ 6 yr with satellite telemetry to document their migration ecology. During a short time ($\bar{x} = 30$ d, $SD = 23$) before migrating, 22% of hawks made brief movements away from territories ($\bar{x} = 211$ km, $SD = 133$) and then returned. Migrating hawks (98% of 89 analyzed patterns) moved across broad fronts using five different strategies in three distinct periods: summer (July–August), fall (September–November), and spring (February–March). Breeding range longitude and latitude strongly influenced ($r = 0.78$) timing of summer migration that was

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directed to focal areas shared by breeding populations of hawks in the Northern Grasslands and Central Plains. Hawks nesting in grasslands from Canada to the Southern Plains demonstrated a strong pattern of southward migration to summer and winter ranges along the east front of the Rocky Mountains to central Mexico. Hawks from shrub-steppes in the Columbia Basin and Great Basin migrated eastward to summer ranges across the Continental Divide to grasslands, then to wintering areas in California and northern Mexico. On average, adult hawks spent 64% of the year away from breeding home ranges and migrated 2376 km (SD = 1165) annually, but differences in migration destinations, distance ($P = 0.048$), and duration ($P < 0.0001$) among populations potentially exposed them to variable levels and types of stressors. Accordingly, conservation of nonbreeding habitats used by Ferruginous Hawks is important for maintaining health of breeding populations; conservation efforts should emphasize protection of fossorial prey and habitats on shared summer ranges and winter ranges in the Mexican grasslands and Central Valley of California.

KEY WORDS: *Ferruginous Hawk*; *Buteo regalis*; dispersal; migration; satellite telemetry; winter ecology.

PATRONES DE MIGRACIÓN, TIEMPOS Y DESTINOS ESTACIONALES DE INDIVIDUOS ADULTOS DE *BUTEO REGALIS*

RESUMEN.—*Buteo regalis* es una rapaz clave en los ecosistemas áridos en el oeste de América del Norte que presenta disminuciones poblacionales en algunas regiones. Todavía no se han descrito los patrones de migración en el área de distribución, los destinos y la cronología de individuos adultos de esta especie. Entre 1999 y 2014 capturamos 69 individuos adultos de *B. regalis* al este y oeste de la Divisoria Continental y los monitoreamos por ≤ 6 años por medio de telemetría satelital para documentar su ecología migratoria. Durante un período breve de tiempo ($\bar{x} = 30$ días, DE = 23) antes del inicio de la migración, el 22% de las *B. regalis* hicieron movimientos breves alejándose de sus territorios ($\bar{x} = 211$ km, DE = 133) y luego regresaron. Los individuos migratorios (98% de 89 patrones analizados) se movieron a lo largo de frentes amplios utilizando estrategias diferentes en tres periodos distintivos: verano (julio-agosto), otoño (septiembre-noviembre) y primavera (febrero-marzo). La latitud y la longitud del área de cría influenciaron significativamente ($r = 0.78$) el inicio de la migración estival con dirección a áreas focales compartidas por poblaciones reproductivas de *B. regalis* de los Pastizales del Norte y de las Planicies Centrales. Los individuos que anidaron en los pastizales desde Canadá hasta las Planicies del sur mostraron un fuerte patrón de migración con dirección sur hacia las áreas de distribución de verano y de invierno a lo largo del frente este de las Montañas Rocosas hasta el centro de México. Los individuos provenientes de estepas arbustivas en la Cuenca de Columbia y la Gran Cuenca migraron con dirección este hacia las distribuciones de verano a lo largo de la Divisoria Continental hasta los pastizales, luego hacia las áreas de invernada en California y el norte de México. En promedio, los individuos adultos permanecieron el 64% del año lejos de las áreas de cría y migraron 2376 km (DE = 1165) anualmente, pero las diferencias entre poblaciones en los destinos, la distancia ($P = 0.048$) y la duración de la migración ($P < 0.0001$) los expuso potencialmente a diferentes tipos y niveles variables de estresores. Por lo tanto, la conservación de los hábitats no reproductivos utilizados por *B. regalis* es importante para mantener la salud de las poblaciones reproductivas de esta especie; los esfuerzos de conservación deberían enfatizar la protección de presas excavadoras de madrigueras y de los hábitats en las distribuciones de verano compartidas en los pastizales de México y en el Valle Central de California.

[Traducción del equipo editorial]

The Ferruginous Hawk (*Buteo regalis*) is closely associated with arid ecosystems from Canada through Mexico east and west of the Continental Divide (Bechard and Schmutz 1995). The largest known nesting populations are in southern Alberta and Wyoming (Ondorff 1993) and as much as 20% of the known wintering area for this species is in Mexico (Bechard and Schmutz 1995). Significant declines in some regional populations of this species have resulted in its national designation as Threat-

ened in Canada, Sensitive in the United States, a Species of Concern in Mexico, and Threatened or Endangered in some provinces and states (Commission for Environmental Cooperation [CEC] 2005).

Range-wide conservation strategies for the Ferruginous Hawk have recognized the need for information on range-wide migration and nonbreeding ecology (Washington Department of Fish and Wildlife [WDFW] 1996, CEC 2005, Collins and Reynolds 2005, Alberta Ferruginous Hawk Recovery

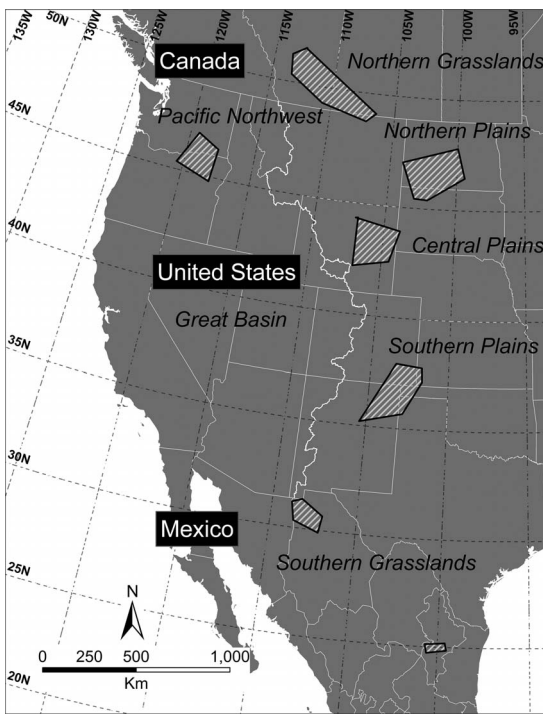


Figure 1. Regions where Ferruginous Hawks were captured and monitored to determine migration patterns and seasonal range use from 1999–2014.

Team 2009). Previous banding studies have provided insight into winter destinations of hawks originating from grassland breeding areas in Alberta, Saskatchewan, Montana, and North Dakota in the Great Plains south to Mexico (Salt 1939, Gilmer et al. 1985, Schmutz and Fyfe 1987, Houston et al. 1998, Harmata 1981, Harmata et al. 2001). In contrast, juvenile hawks banded west of the Continental Divide at nest sites in Idaho (Thurow et al. 1980), and 11 individuals tracked by satellite telemetry from Idaho and Utah (Schueck et al. 1998) moved widely throughout the west. Investigation of migration patterns and timing is needed to identify shared ranges that are seasonally significant to different populations of breeding hawks and therefore important to conservation. Conversely, understanding timing and use of nonbreeding ranges unique to breeding populations is also important. For species that migrate over large geographic ranges, migration characteristics specific to breeding populations potentially expose them to different types, levels, and timing of habitat and anthropogenic mortality stressors that variably affect individual fitness and

status of source breeding populations (Alerstam and Högstedt 1982, Alves et al. 2012, Klaassen et al. 2013).

In this report, we present results of a 15-yr study of adult Ferruginous Hawks monitored with satellite telemetry to provide baseline migration information that will promote species conservation and facilitate holistic management. Our specific objectives were to: (1) document migration strategies, patterns, and destinations of adult hawks originating from six widely distributed breeding populations; (2) compare migration distance and duration among these populations, as well as the overall duration of the nonbreeding season that may result in different exposure to potential stressors; and (3) describe seasonal migration rate and timing, and test for relationships to geographic coordinates of ranges.

METHODS

We identified seven regions that encompassed multiple study areas where we captured breeding and wintering adult Ferruginous Hawks and radio-tagged them with satellite transmitters (Fig. 1). Study areas were distributed throughout the range of the species in the Pacific Northwest (south-central Washington, north-central Oregon), Northern Grasslands (southern Alberta and Saskatchewan), Northern Plains (Dakota Prairie National Grasslands, North 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). These study areas represent a diversity of nesting habitats in relatively low elevation, flat and rolling terrain (Bechard and Schmutz 1995), where landscapes gradate from grasses (e.g., *Agropyron* spp. and *Bouteloua* spp.) to shrubs (e.g., *Artemisia* spp. and *Atriplex* spp.) often at the periphery of forests such as western juniper (*Juniper occidentalis*). The hawks we studied typically nested in trees or on the ground in rolling landscapes, but on cliffs and creek banks in broken landscapes. We captured wintering hawks in the Southern Grasslands near Janos, Chihuahua, and La Soledad, Nuevo Leon, Mexico. Both areas support significant numbers of wintering Ferruginous Hawks that are attracted to colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) and Mexican prairie dogs (*C. mexicanus*) at the southern extent of their ranges (Trevino-Villarreal 1990, Bak et al. 2001). Hawks captured in Chihuahua provided a sample of

hawks from the sixth breeding population that originated in the Great Basin.

Personnel from agencies, universities, and non-governmental organizations comprised field teams that were assembled to capture hawks in each study area. Our goal was to deploy 70 transmitters on adult hawks and distribute them equally east and west of the Continental Divide. Two experienced team leaders (JWW and UB) oversaw capture and deployment of hawks for safety and consistency. Team members conducted spring surveys in breeding regions to identify occupied nesting territories and potential capture sites. Hawks were captured primarily with live or robotic Great Horned Owl (*Bubo virginianus*) lures and dho-gaza nets (Bloom et al. 1992). We radio-tagged one adult hawk of either sex at each breeding territory. We trapped wintering hawks along roads with bal-chatri traps baited with small rodents (Berger and Mueller 1959).

Captured hawks were weighed, measured (i.e., wing chord, hallux length, bill depth) and banded with USGS tarsal bands. Hawks were sexed based on differences in these morphometric measurements (Harmata 1981) and sex was confirmed for breeding adults by observing their nest attentiveness (females conduct most of the brooding) and food-provisioning activity (males are primary foragers). Hawks were outfitted with two styles of 30-g platform transmitter terminals (PTTs) from Microwave Telemetry Inc., Columbia, MD, USA. Prior to 2005, we deployed battery and solar-powered ARGOS PTTs programmed to transmit fixes 8 hr every 3 d. After 2005 we deployed solar-powered PTTs that transmitted global positioning system (GPS) fixes that transmitted once/hr at 21-hr intervals during daylight. PTTs were attached with "X-attachment" backpacks (Buehler et al. 1995) using 7-mm wide teflon ribbon. Hawks were released at capture locations < 1 hr following capture.

For 35 hawks with PTTs, we analyzed all GPS locational data, with a manufacturer-specified error of ± 22 m (T. Rollins, Microwave Telemetry Inc., pers. comm.). For ARGOS PTTs that were deployed on 34 hawks and provided less-accurate Doppler-generated fixes, we used 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 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. Thirty-eight percent of ARGOS fixes were useable.

For each hawk, each year, we plotted and analyzed fixes to determine the location and timing of movements and associated summer, winter, and breeding ranges using ArcGIS 10.1 (ESRI 2013). We defined *ranges* as collective areas where hawks first became localized after migration as determined from individual analyses. We plotted and interpreted fixes for each annual migration cycle until loss of the PTT signal, expiration of the PTT, or death of the hawk. We did not define time periods to differentiate migration periods *a priori*; rather, we plotted and interpreted each individual's annual movement patterns and summarized these periods for each breeding population. These collective patterns and periods included *premigration*, *summer migration* to summer ranges after the nesting season, *fall migration* to winter ranges, and *spring migration* back to breeding ranges. In premigratory movements, hawks dispersed regionally ≥ 30 km from their breeding territories, but returned to breeding territories for ≥ 1 d before migrating (Todd et al. 2007, Limiñana et al. 2008). In contrast, migration departure was abrupt, flight was strongly directional and at consistent flight speeds (e.g., >20 km/h), and ended at ranges that were disjunct and often >1000 km from hawk breeding territories or seasonal ranges. To determine date and coordinates when hawks first became localized on seasonal ranges, we examined successive fixes in 10-d increments to the point when fixes were <30 km apart, and then evaluated individual fixes to determine the day on which directional movement terminated. When the day of migration 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).

We summarized premigration direction metrics with R 3.13 statistical package (R Core Team 2015) using the circular package (Agostinelli and Lund 2013). We used mixed models (PROC MIXED, SAS 9.4, SAS Institute, Inc.) to compare hawk migration metrics among breeding populations and seasonal migration rates, and to compute descriptive statistics. Modeling bird ID as a random effect allowed us to address potential pseudoreplication arising from inclusion of ≥ 2 yr of data for some birds (Hurlbert 1984, Lazic 2010). We do not address the topics of

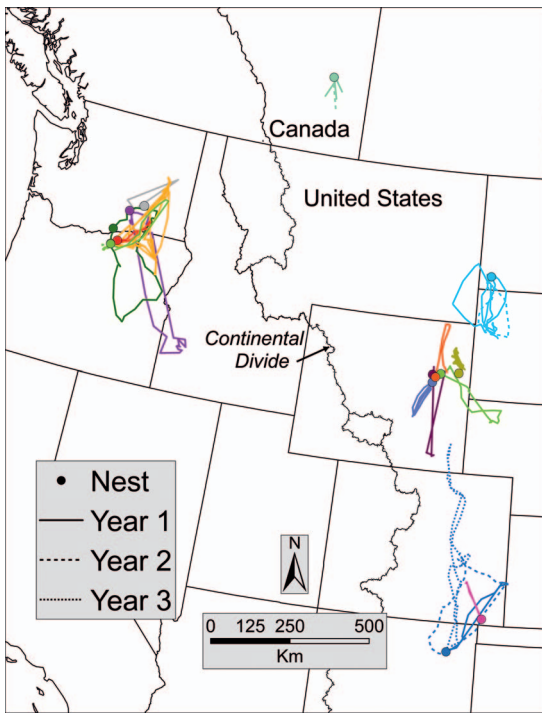


Figure 2. Premigration flights ($n = 20$) of 15 adult Ferruginous Hawks from and to their nests. Matching colors are used to identify an individual's nest location and movements.

individual nomadism and repeatability of migration routes in this paper. We tested one- and two-factor models and used the residual maximum likelihood to calculate parameter values. Normality of variables was confirmed prior to analysis by evaluation of residual plots. Migration speed was computed from hourly sensor data from hawks with GPS PTTs when speed was >4 km/hr (minimum, manufacturer sensor error ± 1.9 km/hr). We used linear regression (PROC REG) to test effects of range latitude and longitude, and sex on departure dates from seasonal ranges. We did not analyze arrival dates for sequential ranges (e.g., departure date from winter range and arrival date on breeding range) because all paired departures and arrivals were highly correlated ($P < 0.0001$). To account for potential pseudoreplication for birds with ≥ 2 yr of data, we averaged departure dates to provide one estimate/bird (Hulbert 1984). We identified collinearity among potential explanatory variables omitting them when the Variable Influence Factor was >2 .

RESULTS

Capture Location and Monitoring Duration. Between 1999 and 2014, we monitored 69 radio-tagged adult Ferruginous Hawks (38 males and 31 females). Thirty-four hawks (50%) nested west of the Continental Divide [Washington ($n = 14$), Oregon ($n = 16$), Arizona ($n = 1$), and Nevada ($n = 3$)] and 35 hawks (50%) nested east of the Continental Divide [Canada ($n = 8$), Dakotas ($n = 6$), Wyoming ($n = 14$), Colorado ($n = 5$), New Mexico ($n = 1$), and Oklahoma ($n = 1$)]. We analyzed data for individual birds ≤ 6 yr post-capture, and the number of hawks monitored each year after they were captured declined from 69, to 41, 27, 12, 7, and 1 as PTTs expired or hawks died.

Premigration. Fifteen hawks (22%) made one to five flights from, and back to their breeding ranges late in the nesting season beginning an average 30 d (SD = 23) prior to migration (Fig. 2). These premigratory flights were linear or loop movements that lasted an average of 15 d (SD = 59) and extended an average distance of 211 km (SD = 133) from breeding ranges before hawks returned. Total distance of premigratory flights calculated from successive fixes averaged 653 km (SD = 709). Direction of departure for premigratory flights from the breeding range was oriented an average of 43° (SD = 16) from the direction they departed in summer migration. Hawks originating east and west of the Continental Divide, in every breeding region and of both sexes, exhibited premigratory flights.

Migration Patterns and Destinations. We analyzed 123 migration patterns, including 55 complete migrations of 41 hawks (breeding range to breeding range). Migration followed one of five patterns with seasonally distinct movements in summer, fall, and spring. In most migrations (72%), hawks migrated to ranges in late summer, then migrated to winter ranges in the fall, and migrated back to breeding ranges in the spring. In 14% of patterns, hawks migrated to one range in late summer that they occupied through winter prior to returning to breeding ranges. In the remaining annual patterns, hawks exhibited stronger fidelity to breeding ranges throughout the year: 6% of the time they migrated to summer ranges, but migrated back to their breeding ranges in fall, 6% of the time they remained on breeding ranges through summer before migrating to winter ranges, and 2% of the time they did not migrate. Hawks that did not migrate or wintered on their breeding ranges nested in Wyoming in 2006–2008 during peak abundance

of black- and white-tailed jack rabbits (*Lepus californicus* and *L. townsendii*) and Nuttall's cottontail rabbits (*Sylvilagus nuttallii*) in 2006–2008 (J. Watson and T. Byer, unpubl. data, G. McKee pers. comm.). When rabbit populations crashed there in 2009, the same hawks did not nest during the breeding season, but wandered up to a few hundred kilometers away from, and back to their breeding ranges every several weeks before migrating to summer and winter ranges.

Seasonal migration patterns of adult Ferruginous Hawks were different east and west of the Continental Divide. Hawks nesting in grasslands from Canada to New Mexico demonstrated a strong southward pattern of migration along a broad front east of the Rocky Mountains (Fig. 3). With the exception of two hawks (6%) that migrated to northeastern Arizona, grassland hawks remained east of the Continental Divide throughout the year. Migration of regional nesting populations of hawks in the grasslands was generally a chain pattern, with northern populations wintering in areas occupied by breeders that also moved southward. Hawks in the Central Plains were the exception, as some birds leap-frogged over the Southern Plains to winter in the Mexican study area at La Soledad (Fig. 3c). No hawk that wintered in the La Soledad study area originated outside the Central Plains. With the exception of hawks from the Southern Plains, individuals from all breeding populations occupied summer ranges in southern Alberta and Saskatchewan. For hawks in the Northern and Central Plains this resulted in northward migration in summer (Fig. 3b, 3c).

Five of seven hawks that nested in the Northern Grasslands of Canada and one of six hawks from the High Plains in the Dakotas remained on their nesting ranges through late summer and then migrated directly to ranges they occupied throughout winter (Fig. 3a, 3b). Hawks in the Southern Plains also migrated northward in summer, but to relatively close winter ranges in the Central Plains (Fig. 3d). They also wintered just north of their breeding ranges, mixing with hawks that originated from other populations.

In contrast to grassland populations, 88% of adult hawks nesting in shrub-steppes of the Columbia Basin and Great Basin migrated across the Continental Divide during the nonbreeding period (Fig. 4). In summer, hawks nesting in the Columbia Basin migrated northeast or southeast to summer ranges in the southern provinces, northwest Montana, and the Northern and Central Plains, then westward to

the Central Valley of California where 78% of their winter ranges were located (Fig. 4a). Hawks originating in the Great Basin wintered on ranges near Janos, Mexico (Fig. 4b). Because hawks nesting in the Great Basin were initially captured on winter ranges near Janos, Mexico, their annual migration patterns, particularly during winter, may be reflective of only one segment of Ferruginous Hawks from that regional nesting population.

Migration Distance and Duration. Average annual migration distance for hawks within regional breeding populations ranged between 381 km and 2865 km and varied among populations ($F = 2.67$, $P = 0.048$, $n = 41$ hawks). Close proximity of hawks from the Southern Plains and Northern Plains to their wintering areas in the Southern Plains accounted for comparatively shorter average migration distances for these populations (Table 1). Hawks from the same populations spent the least amount of time in migration compared to other populations ($F = 38.45$, $P < 0.0001$, $n = 34$ hawks) that ranged from 25 d to 63 d (Table 1). On average, for all populations, hawks spent 233 d, or 64% of the year away from breeding ranges between summer and spring migration, but the length of the nonbreeding period was different among breeding populations ($F = 492.8$, $P < 0.0001$, $n = 69$ hawks). Hawks from the Northern Grasslands and Plains spent 57% and 59% of the year in migration and on nonbreeding ranges, owing to their extended time on breeding ranges into late summer, and at the other extreme hawks in the Great Basin were away from breeding ranges for 74% of the year (Table 1).

Seasonal Migration Rate and Chronology. Hawks migrated at different daily rates ($F = 46.01$, $P < 0.0001$, $n = 69$ hawks) in summer ($\bar{x} = 116.5$ km/d, $SD = 20.9$), fall ($\bar{x} = 87.0$ km/d, $SD = 22.3$), and spring ($\bar{x} = 122.9$ km/d, $SD = 24.6$). During migration, flight speed averaged 89.9 km/hr ($SD = 16.1$) but did not vary by season ($P = 0.910$). The date hawks migrated in summer varied significantly ($F_{2,26} = 20.17$, $P < 0.0001$, $r = 0.78$) with breeding range longitude ($\beta = -0.74$ SE = 0.50), and latitude ($\beta = 0.58$, SE = 0.77). Strong influence of longitude in timing of migration from breeding ranges in July and August was driven by attraction of hawks to summer ranges in the Northern Grasslands and Central Plains (Fig. 5). That included hawks nesting in the Pacific Northwest and Great Basin that nested farthest west (i.e., at maximum longitudes) and mid-latitudes and departed in mid-July (Table 2). This contrasted with mid-August departure of hawks

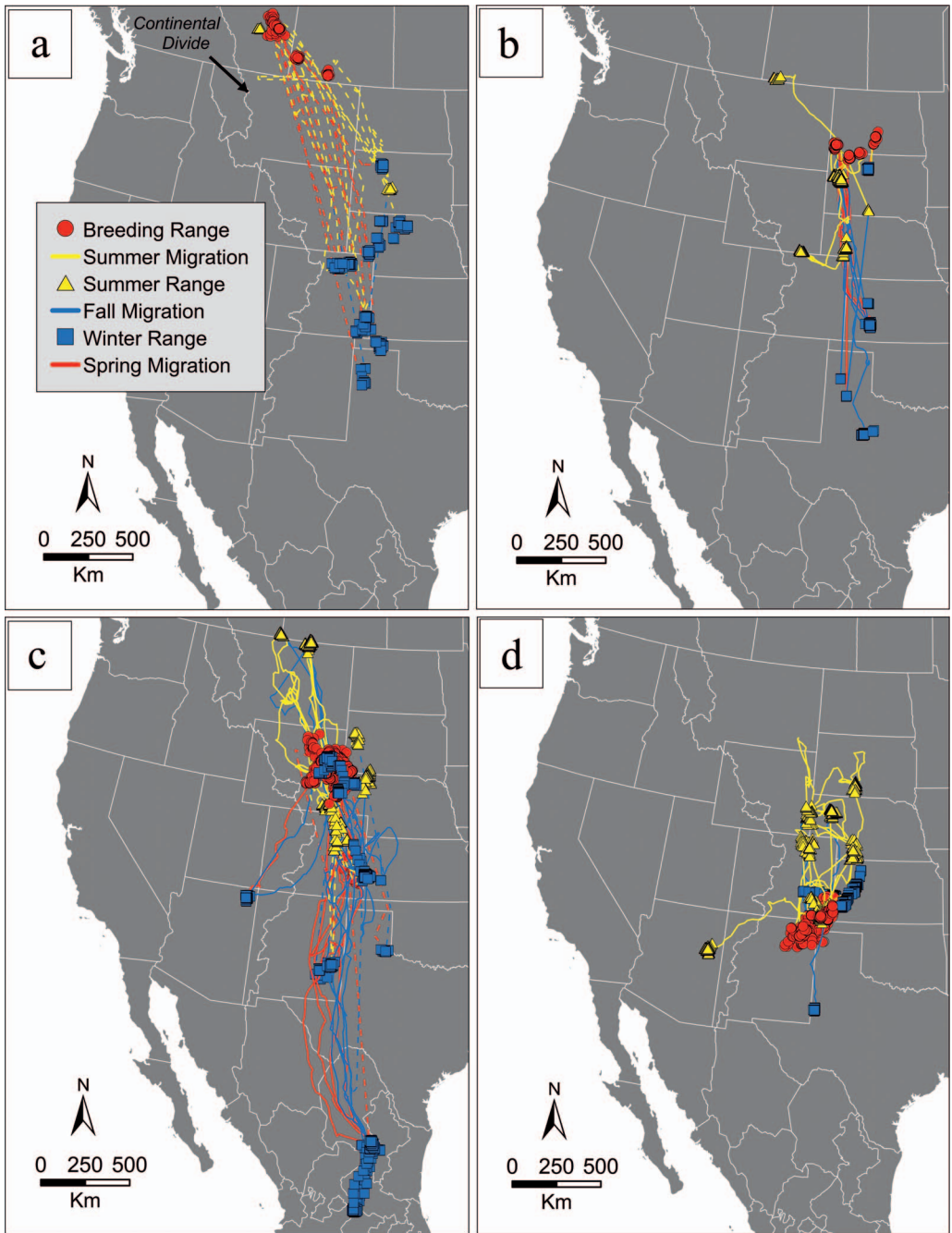


Figure 3. Year-round migration patterns of adult Ferruginous Hawks breeding in four grassland regions east of the Continental Divide and tracked ≤ 6 yr including the (a) Northern Grasslands ($n = 8$), (b) Northern Plains ($n = 6$), (c) Central Plains ($n = 14$), and (d) Southern Plains ($n = 7$). Dotted lines are tracks from birds with ARGOS platform transmitter terminals.

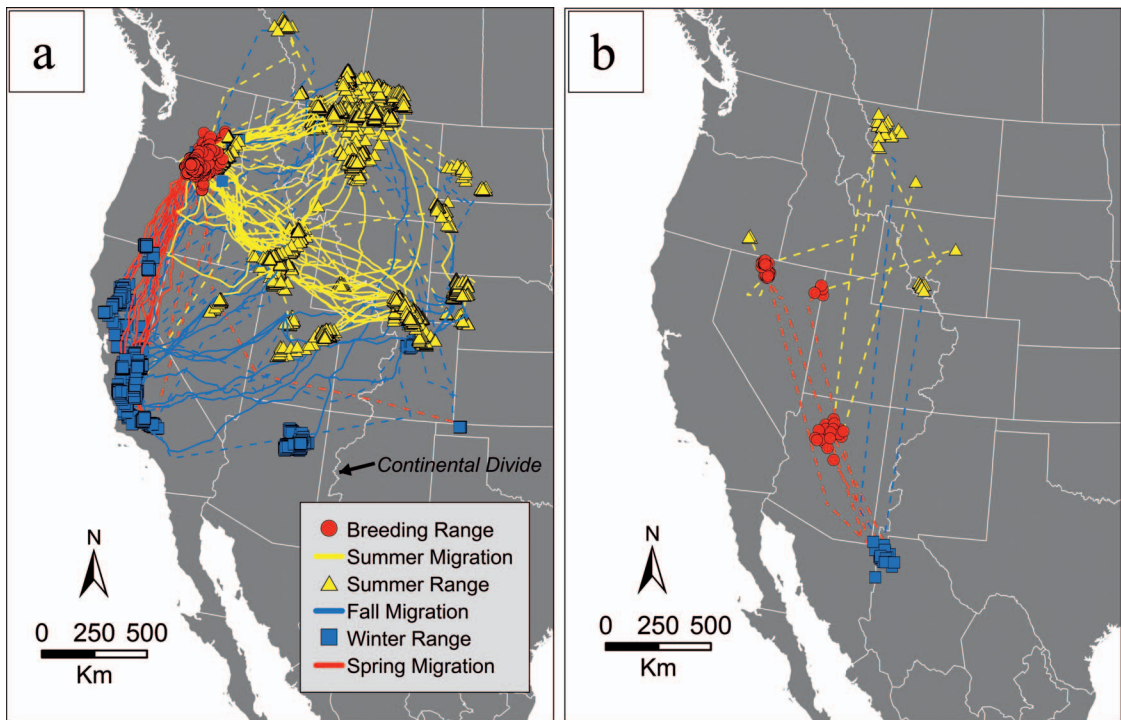


Figure 4. Year-round migration patterns of adult Ferruginous Hawks breeding in shrub-steppes west of the Continental Divide and tracked ≤ 6 yr including the (a) Pacific Northwest ($n=30$) and (b) Great Basin ($n=4$). Hawks that nested in the Great Basin were captured on winter ranges near Janos, Mexico. Dotted lines are tracks from birds with ARGOS platform transmitter terminals.

nesting in the Northern Grasslands and Plains at the minimum longitudes and maximum latitudes (Table 2). We detected no relationship between the date hawks departed for fall migration in September through November (Table 3) and the geographical coordinates of summer ranges or winter ranges ($P =$

0.180). Fall migration resulted in most hawks from shrub-steppes returning westward across the Continental Divide (Fig. 5). Spring migration in February and March from winter to breeding ranges was significantly dependent ($F_{2,35} = 12.19$, $P < 0.0001$, $r = 0.64$) on winter range longitude ($\beta = -0.61$, $SE =$

Table 1. Annual migration characteristics of breeding populations of Ferruginous Hawks in western North America. Summary does not include hawks that did not migrate (2%).

| BREEDING REGION | DISTANCE ^a | | | DURATION ^a | | | TIME AWAY FROM BREEDING TERRITORY ^b | | | |
|---------------------|-----------------------|--------|-----------|-----------------------|------|-----------|--|------|---------|-----------|
| | \bar{x} (km) | SD | No. BIRDS | \bar{x} (d) | SD | No. BIRDS | \bar{x} (d) | SD | % OF Yr | No. BIRDS |
| Southern Plains | 381.1 | 208.1 | 2 | 25.3 | 21.1 | 2 | 241.4 | 26.0 | 66 | 6 |
| Great Basin | 2865.0 | 502.8 | 4 | 62.5 | 52.5 | 2 | 269.6 | 50.1 | 74 | 4 |
| Central Plains | 2157.9 | 950.2 | 9 | 56.5 | 26.4 | 8 | 235.4 | 31.8 | 64 | 15 |
| Pacific Northwest | 2679.6 | 61.1 | 17 | 40.7 | 14.1 | 14 | 229.3 | 31.2 | 63 | 30 |
| Northern Plains | 1019.1 | 946.3 | 2 | 36.3 ^c | | 1 | 214.0 | 63.0 | 59 | 6 |
| Northern Grasslands | 2668.6 | 599.8 | 7 | 61.3 | 14.6 | 7 | 209.0 | 14.4 | 57 | 8 |
| Range-wide | 2376.2 | 1164.6 | 41 | 47.5 | 21.5 | 34 | 233.4 | 39.0 | 64 | 69 |

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

^b Summer migration through spring migration.

^c Individual value rather than mean.

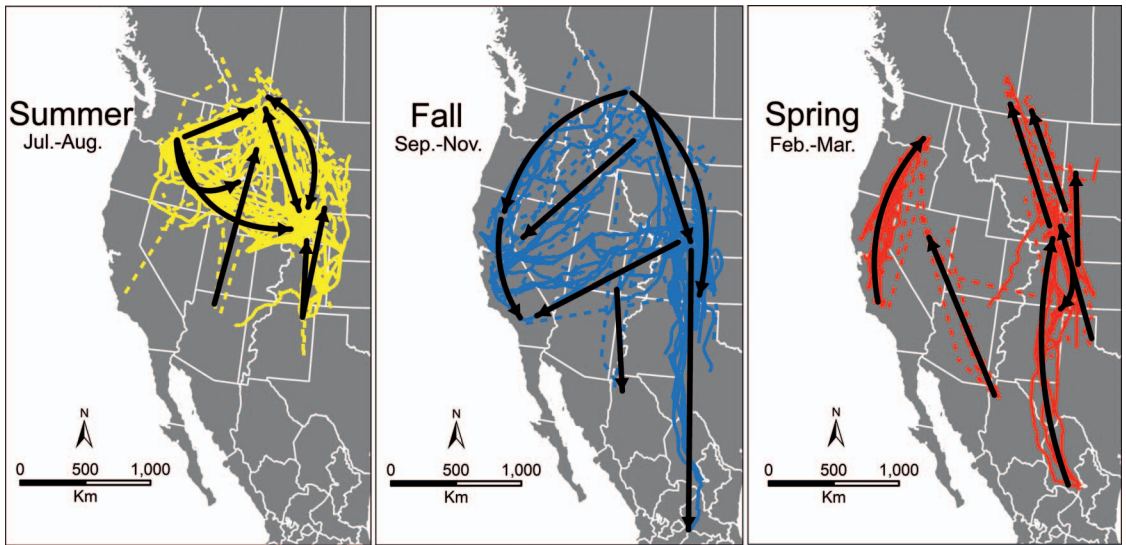


Figure 5. Seasonal migration patterns for Ferruginous Hawks monitored with satellite telemetry ($n = 69$). Arrows represent major flight directions for pooled patterns of individual hawks from global positioning system tracks (solid, colored lines) and ARGOS tracks (dotted lines).

0.19) and breeding latitude ($\beta = 0.29$, $SE = 0.43$). Hawks wintering farthest west (i.e., at maximum longitudes) in California departed in mid-February for breeding ranges in the Pacific Northwest (Fig. 5), whereas most hawks east of the Continental Divide at minimum longitudes departed ranges in early to mid-March (Table 4). Range-wide, the tendency was for hawks to depart later from their winter ranges in spring when they nested at higher latitudes. Although sex did not enter any model, sample sizes were small ($n \leq 5$) except for hawks in the Pacific Northwest. In that population, date of summer departure for female hawks ($n = 9$) was earlier

(sample t -test, $t = 2.09$, $P = 0.046$) than males ($n = 21$) by an average of 19.8 d ($SD = 23.7$).

DISCUSSION

Migration of adult Ferruginous Hawks was partial, although nearly all hawks migrated (98%), and was characterized by diverse strategies that varied by season and across the breeding distribution. Range-wide, this resulted in broad-fronted, complex movements during two-thirds of the year when hawks were away from breeding territories. This facultative migration (Newton 2012) was in stark contrast to obligate migration of congeneric Swainson's hawks (*Buteo swainsoni*) that spend similar time

Table 2. Migration chronology of PTT-tagged Ferruginous Hawks to, and from regional breeding populations in North America.

| BREEDING REGION | LATITUDE °N, LONGITUDE °W ^a | MIGRATION ARRIVAL | | | | MIGRATION DEPARTURE | | | |
|---------------------|---|-------------------|--------|------------------|-----------|---------------------|--------|------------------|-----------|
| | | ̄ DATE | SD (d) | DATE RANGE | No. BIRDS | ̄ DATE | SD (d) | DATE RANGE | No. BIRDS |
| Southern Plains | 36.7, 103.3 | 9 Mar | 14 | 26 Feb to 23 Mar | 2 | 23 Jul | 6 | 6 Jul to 6 Aug | 4 |
| Great Basin | 39.9, 115.6 | 15 Mar | 26 | 30 Jan to 8 Apr | 3 | 21 Jul | 14 | 4 Jul to 9 Aug | 4 |
| Central Plains | 45.5, 105.3 | 21 Mar | 13 | 26 Feb to 10 Apr | 11 | 1 Aug | 14 | 17 Jun to 3 Sep | 8 |
| Pacific Northwest | 45.8, 119.6 | 2 Mar | 11 | 27 Dec to 22 Mar | 14 | 21 Jul | 22 | 5 Jun to 17 Oct | 30 |
| Northern Plains | 46.1, 102.9 | 12 Mar | 10 | 4 Mar to 25 Mar | 2 | 11 Aug | 29 | 23 Jun to 26 Oct | 5 |
| Northern Grasslands | 50.8, 110.6 | 29 Mar | 4 | 24 Mar to 7 Apr | 4 | 23 Aug | 25 | 4 Aug to 22 Oct | 8 |

^a Mean coordinates of hawk capture locations on breeding ranges.

Table 3. Migration chronology of PTT-tagged Ferruginous Hawks to, and from regions they occupied in late summer.

| SUMMER REGION | LATITUDE °N, LONGITUDE °W ^a | MIGRATION ARRIVAL | | | | MIGRATION DEPARTURE | | | |
|---------------------|---|-------------------|-----------|------------------|--------------|---------------------|-----------|------------------|--------------|
| | | \bar{x} DATE | SD (d) | DATE RANGE | No. BIRDS | \bar{x} DATE | SD (d) | DATE RANGE | No. BIRDS |
| Southern Plains | 40.8, 103.8 | 16 Sep | 20 | 14 Aug to 19 Oct | 2 | 13 Oct | 28 | 27 Jul to 30 Dec | 2 |
| Great Basin | 41.6, 112.5 | 10 Aug | 21 | 25 Jul to 26 Aug | 9 | 2 Oct | 37 | 28 Aug to 6 Nov | 7 |
| Central Plains | 41.4, 104.3 | 19 Aug | 36 | 2 Aug to 4 Sep | 20 | 23 Sep | 22 | 8 Sept to 7 Oct | 13 |
| Northern Plains | 44.7, 102.3 | 26 Aug | 22 | 11 Aug to 9 Sep | 10 | 30 Oct | 24 | 8 Oct to 21 Nov | 7 |
| Pacific Northwest | 45.7, 117.6 | 7 Sep | 37 | 8 Aug to 7 Oct | 8 | 23 Oct | 24 | 2 Oct to 14 Nov | 7 |
| Northern Grasslands | 49.0, 110.9 | 28 Jul | 22 | 18 Jul to 6 Aug | 20 | 16 Sep | 21 | 5 Sep to 28 Sep | 18 |

^a Mean coordinates where hawks became localized on summer ranges.

away from breeding ranges but migrate roughly 10 times further, spend about twice as long in migration, with austral movements along relative distinct corridors to well-defined winter ranges (Fuller et al. 1998, Kochert et al. 2011).

Late summer was the season during which Ferruginous Hawks demonstrated the greatest diversity in migration behavior. In fact, had hawks not moved to summer ranges, the proximity of winter and breeding ranges for respective populations suggests fall and spring migration would have been largely latitudinal. Summer ranges in the Northern Grasslands and Central Plains that were shared by breeding populations of hawks west and south of these regions directed summer migration patterns, and resulted in both westward/northward movement orientation and a wide gradient of migration distances/duration among populations. Eighty-eight percent of hawks from the Pacific Northwest migrated across the divide to these ranges and accounted for the strong longitudinal influence on range-wide movements. Their migration was longer

in time and duration than that of hawks from nearby breeding populations in the nearby Northern Grasslands that typically did not migrate in summer. Similarly, hawks breeding in the Southern and Central Plains moved northward shorter distances to these summer ranges or did not migrate during the period of high hare abundance.

These behaviors suggest prey acquisition was the proximate driver for summer migration, a conclusion that was supported by other evidence. For example, overall rate of summer migration for hawks was high and hawks in the Pacific Northwest displayed the greatest urgency to migrate eastward to these summer ranges, with females migrating significantly sooner than males. Two radio-tagged females in this study migrated abruptly after fledging of young, while the adult males continued to provision their young throughout post-fledging before migrating several days later (J. Watson unpubl. data). Earlier departure of females from breeding ranges is found in many migrant raptors and has been attributed to their lack of familiarity

Table 4. Migration chronology of PTT-tagged Ferruginous Hawks to, and from regions they occupied in winter.

| WINTER REGION | LATITUDE °N, LONGITUDE °W ^a | MIGRATION ARRIVAL | | | | MIGRATION DEPARTURE | | | |
|---------------------|---|-------------------|-----------|-------------------|--------------|---------------------|-----------|-------------------|--------------|
| | | \bar{x} DATE | SD (d) | DATE RANGE | No. BIRDS | \bar{x} DATE | SD (d) | DATE RANGE | No. BIRDS |
| Mexico (Nuevo Leon) | 25.0, 100.6 | 27 Oct | 21 | 7 Sep to 16 Dec | 3 | 13 Mar | 6 | 2 Mar to 25 Mar | 4 |
| Mexico (Chihuahua) | 30.8, 108.3 | 17 Nov | 14 | 15 Oct to 20 Dec | 2 | 20 Feb | 26 | 11 Jan to 1 April | 4 |
| Great Basin | 35.4, 108.4 | 26 Oct | 64 | 10 July to 11 Feb | 3 | 13 Mar ^b | | | 1 |
| Southern Plains | 37.0, 101.8 | 20 Oct | 45 | 20 Sep to 17 Nov | 12 | 3 Mar | 7 | 26 Feb to 9 Mar | 11 |
| California | 38.1, 120.9 | 28 Oct | 24 | 15 Oct to 10 Nov | 16 | 19 Feb | 10 | 13 Feb to 24 Feb | 12 |
| Central Plains | 42.1, 104.3 | 26 Sep | 38 | 10 Aug to 12 Nov | 5 | 7 Mar | 11 | 21 Feb to 20 Mar | 5 |
| Northern Plains | 45.2, 101.3 | | | | 0 | 4 Mar | 29 | 1 Mar to 7 Mar | 5 |
| Pacific Northwest | 46.0, 119.3 | 29 Oct | 34 | 22 Aug to 5 Jan | 2 | 28 Feb | 3 | 15 Jan to 13 Apr | 2 |

^a Mean coordinates where hawks became localized on winter ranges.

^b Individual value rather than mean.

with prey on the breeding grounds compared to males that do most of the hunting (Bildstein 2006). Migrant hawks joined breeding hawks in the Northern Grasslands of Canada and Montana and remained there, on average, through late October (Table 3) where Richardson's ground squirrels (*Urocitellus richardsonii*) were abundant on the same ranges (Watson and Pierce 2003). Richardson's ground squirrels are active on Canadian grasslands through late October when the last of the juvenile squirrels enter hibernation (Michener 1992). These summer ranges were high-reward, destination ranges that hawks occupied up to 2 mo, and not staging areas or stopover areas along migration routes where "individuals interrupt their movements and aggregate to feed for up to a week or more, often in anticipation of migration across inhospitable habitats" (Bildstein 2006). Prairie Falcons (*Falco mexicanus*) derived the same benefits from ground squirrel populations in this region after similar, northeasterly, late-summer movements from their breeding ranges in Idaho (Steenhof et al. 2005). The same prey-driven, temporal relationship exists for hawks attracted to prairie dogs (*Cynomys* spp.) on summer ranges in the Central Plains, where these prey are available until they enter torpor due to cold or food stress (Harlow and Frank 2001). Hares and rabbits in the same region may be less reliable as traditional prey because of cyclic abundance as we noted in this study.

Austral, fall migration of Ferruginous Hawks to winter ranges was protracted compared to other migrations. The more casual movement of hawks to southern latitudes was in contrast to the more rapid spring migration northward to breeding territories, which has been described for many birds, including raptors, and most often ascribed to their drive to nest (Bildstein 2006, Newton 2008). The fact that we did not detect any relationships between timing of fall migration and geographic locations of ranges may reflect that the onset of migration was more dependent on localized weather conditions and timing of hibernation of fossorial prey. Average annual snowfall and winter temperatures moderate dramatically east and south of our Southern Plains study area (Fig. 1; 37°N 105°W) and also in interior California (<https://www.ncdc.noaa.gov/cdo-web>). In fall, Ferruginous Hawks in the plains migrated to the edge of this snowline southward to Mexico (Fig. 3, 4). Their use of prairie dog colonies in winter is well-documented in that zone in Colorado (Plumpton and Andersen 1997, 1998), and hawks

winter in the more moderate weather of Texas and New Mexico (Allison et al. 1995, Bak et al. 2001). In the Central Valley in California, California ground squirrels (*Otospermophilus beecheyi*) rarely estivate due to mild conditions (Evans and Holdenried 1943), and this species was very abundant there at several winter locations of radio-tagged hawks (J. Linthicum, M. Smith, J. Pagel, C. Gill, B. Stafford, D. Walker, and G. Hunt pers. comm.).

The ecological significance of the premigratory movements that were exhibited by 22% of hawks is unclear. The movements may reflect the pressing drive for hawks to reach summer ranges with ephemeral prey availability, a theory supported by the similar orientation of these movements and their eventual summer migration. Premigratory movements were not regionally specific, and included range-wide birds of both sexes that were successful and unsuccessful breeders (J. Watson unpubl. data), so the trigger that caused hawks to return to their breeding territories was unclear. We suspect return movements may relate to body condition and poor prey conditions in premigration ranges, but other factors related to weather conditions or persisting hormonal influence may have affected migratory urgency. During premigration, juvenile Burrowing Owls (*Athene cunicularia*) in poorer quality habitat dispersed shorter distances and some owls returned to their nest area (Todd et al. 2007), and progressive premigratory movements of Montagu's Harriers (*Circus pygargus*) were possibly affected by their body condition, among other factors (Limiñana et al. 2008).

Our baseline information on annual phenology and distribution patterns of Ferruginous Hawk migration is likely to shift with climate change (Žalakevičius 2012, Jaffré et al. 2013). For Ferruginous Hawks, warmer winter and spring temperatures (Cutforth et al. 1999) may result in advanced spring migration in response to earlier emergence of fossorial mammals (Shank and Bayne 2015), potentially increasing competition for nest territories and reducing nesting success (Heath et al. 2012, Shank and Bayne 2015). We suspect earlier migration of hawks in summer may also result when seed-bearing vegetation dries out sooner, with corresponding estivation of fossorial mammals. In the grasslands, there may be northward shifts in ground squirrel distribution (Shank and Bayne 2015) and a contraction of prairie dog range (Stapp et al. 2004, Lunt et al. 2013). Range contraction could be particularly devastating to prey populations that are geograph-

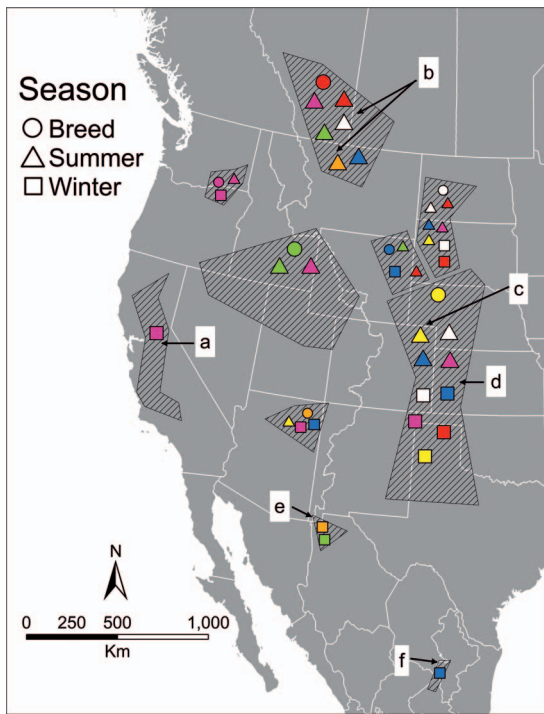


Figure 6. Seasonal structure of the Ferruginous Hawk metapopulation identifying areas (shaded polygons) important to conservation including (a) winter habitat in the Central Valley of California, (b) summer habitat in the Northern Grasslands, (c) summer habitat in the Central Plains, (d) winter habitat in the Southern Plains, (e) winter habitat in northern Mexico, and (f) winter habitat in central Mexico. Colors are unique to each breeding population and allow tracking of individual breeding populations through seasons (pink = Pacific Northwest; red = Northern Grasslands; white = Northern Plains; blue = Central Plains; yellow = Southern Plains; green = Great Basin; and orange = south of Great Basin).

ically isolated and habitat-limited, such as the La Soledad population of Mexican prairie dogs (*Cynomys mexicanus*), and the large population of wintering Ferruginous Hawks that depend on them (Scott-Morales et al. 2004). Distributional shifts from climate change may also be elevational, because migration timing and location of Ferruginous Hawks in the Snake River Plain in Idaho appear to be regulated by the timing of estivation of Richardson's ground squirrels at different elevations (Thurow et al. 1980, Gerstell and Trost 1995).

Conservation Implications. Fitness of migratory birds, and thus their population levels, are increasingly understood to be derived from conditions on

wintering areas and migration, and not solely on breeding-range conditions (Newton 2006, Holmes et al. 1993, Alves et al. 2012). Most birds share a common need after breeding to rebuild fitness lost during nesting, molt, and migration (Jehl 1997, Newton 2004, 2006). For migratory Ferruginous Hawks that spend most of the year on nonbreeding ranges, this need underscores the importance of protection of prey and habitats on these ranges in order to benefit their source breeding populations. This includes maintaining abundance and quality of fossorial prey, which may be affected by recreational shooting and lead exposure (Allison et al. 1995, Knopper et al. 2006, Pauli and Buskirk 2007), use of rodenticides (Schmutz et al. 1989, Proulx 2011, Vyas et al. 2017) and sylvatic plague (Seery and Matiatos 2000). Because we found that migrating Ferruginous Hawks did not follow well-defined corridors, the effects of proposed windpower development on migrant and wintering hawks can best be addressed by recognizing the critical importance of prairie dog towns and ground squirrel colonies in key areas (specified below). Breeding populations of hawks that originate west of the Continental Divide and migrate farther, longer, and more widely may be more at risk than eastern populations due to greater potential exposure to direct anthropogenic threats and the cumulative effects of reduced prey and quality of nonbreeding habitats.

Prioritized protection of landscapes that provide nonbreeding habitats for multiple breeding populations of hawks may be the most beneficial to the species, and will require international cooperation (CEC 2005). These include the summer ranges in the southern Canadian provinces, northern Montana, and the western Dakotas that are critical sources of ground squirrels for nearly all hawks from the Pacific Northwest and individuals from all breeding populations (Fig. 6). In winter, the most important habitats to the metapopulation are in colonies of black-tailed prairie dog (*Cynomys ludovicianus*) in the Southern Plains, particularly <150 km from the Colorado and Kansas border through the Texas panhandle (Fig. 6). Conversely, unique representation of some breeding populations on winter ranges has more direct conservation implications for these populations and also provides the opportunity to assess their status and trends through winter surveys (e.g., Garrison 1990, Pandolfino et al. 2011). This includes the Central Valley of California, which supported nearly all wintering Ferruginous Hawks from the Pacific Northwest, prairie dog colonies in the Janos study

area, which supported wintering hawks from the Great Basin, and the La Soledad study area, which supported hawks from the Central Plains (Fig. 6). Refinement of migration patterns and nonbreeding range delineation for Ferruginous Hawks nesting in southern Canada and the Great Basin that we described could be improved through additional studies that employ GPS telemetry.

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