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Migratory Connectivity of Red-tailed Hawks (*Buteo jamaicensis*) from Alaska, USA

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ABSTRACT.—A comprehensive perspective on full annual cycle movements and migratory connectivity is essential for assessing population stability and identifying drivers of population change. The Red-tailed Hawk (*Buteo jamaicensis*) is a widespread raptor species that exhibits geographic variation in migration strategies ranging from year-round residence to long-distance migration. Alaska, USA, represents the species' northern- and western-most breeding populations, which have some evidence for short-term population declines since 2011 despite long-term trends suggesting an overall stable to increasing population status range wide. We used GPS transmitters to track the full annual cycle migratory movements of 27 adult Red-tailed Hawks (many of which displayed plumage consistent with the Harlan's subspecies [*B. j. harlani*]) that summered in Alaska. We also present standardized photographs that strengthen our understanding of the plumage diversity present in Alaska. We found weak but significant levels of migratory connectivity (the degree to which migratory individuals remain together between seasons) among all individuals. Overall, Red-tailed Hawks that spent the breeding season in northern Alaska disproportionately migrated longer distances to overwintering locations in the Great Plains, USA, while hawks that spent the breeding season in southern Alaska migrated shorter distances to overwintering locations in southwestern Canada and the western USA. Red-tailed Hawks exhibited earlier breeding arrival within the southern Alaska region compared to northern Alaska as well as substantial regional differences in migratory routing. Improved understanding of migratory connectivity among Alaska's Red-tailed Hawk population may aid biologists in making informed management decisions in the future.

KEY WORDS: *breeding arrival time*; *full annual cycle*; *migration*; *migration distance*; *phenotypic diversity*; *raptor*.

CONECTIVIDAD MIGRATORIA DE *BUTEO JAMAICENSIS* EN ALASKA, EEUU

RESUMEN.—Una perspectiva integral sobre los movimientos durante todo el ciclo anual y la conectividad migratoria es esencial para evaluar la estabilidad poblacional e identificar los factores que impulsan

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los cambios poblacionales. *Buteo jamaicensis* es un ave rapaz ampliamente distribuida que presenta variación geográfica en sus estrategias migratorias en un rango que incluye la residencia sedentaria hasta la migración de larga distancia. Alaska, EEUU, representa las poblaciones reproductoras más septentrionales y occidentales de la especie, las cuales muestran cierta evidencia de declives poblacionales a corto plazo desde 2011, a pesar de que las tendencias a largo plazo sugieren un estado poblacional general estable o en aumento en toda su área de distribución. Utilizamos transmisores GPS para seguir los movimientos migratorios durante todo el ciclo anual de 27 individuos de *B. jamaicensis* (muchos de los cuales presentaban un plumaje consistente con la subespecie *B. j. harlani*) que pasaron el verano en Alaska. También tomamos fotografías estandarizadas que refuerzan nuestra comprensión de la diversidad de plumajes de los individuos de *B. jamaicensis* en Alaska. Encontramos niveles bajos pero significativos de conectividad migratoria (el grado en que los individuos migratorios permanecen juntos entre temporadas) entre todos los individuos. En general, los individuos de *B. jamaicensis* que pasaron la temporada reproductiva en el norte de Alaska migraron desproporcionadamente distancias mayores hacia sus sitios de invernada en las Grandes Llanuras de EE. UU., mientras que los individuos que se reprodujeron en el sur de Alaska migraron distancias menores hacia áreas de invernada en el suroeste de Canadá y el oeste de EEUU. *Buteo jamaicensis* mostró una llegada más temprana de cría en la región del sur de Alaska en comparación con el norte, así como diferencias regionales sustanciales en sus rutas migratorias. Una mejor comprensión de la conectividad migratoria entre las poblaciones de *B. jamaicensis* de Alaska puede ayudar a los biólogos a tomar decisiones de manejo basadas en evidencia en el futuro.

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INTRODUCTION

Many migratory birds spend portions of their annual cycle in ecologically distinct regions that may be separated by thousands of kilometers. Despite this spatial and temporal separation, different portions of the annual cycle can be closely linked (Marra et al. 1998, Norris et al. 2004). For example, carry-over effects accrued during winter can influence pre-breeding migratory timing and even subsequent reproductive success (Norris et al. 2004, Cooper et al. 2015). Understanding how bird populations are linked across the different portions of their annual cycle (i.e., migratory connectivity; Webster et al. 2002) can reveal spatial or temporal patterns of population co-occurrence where selective pressures may have a disproportionate impact on populations. Additionally, survival rates are often lower during migratory portions of the annual cycle (Sillett and Holmes 2002, Klaassen et al. 2014, Buechley et al. 2021), which underscores the importance of understanding full cycle movements and migratory connectivity (Webster et al. 2002, Marra et al. 2015).

The Red-tailed Hawk (*Buteo jamaicensis*) is a widespread raptor (*sensu* McClure et al. 2019) in the order Accipitriformes with a breeding distribution throughout North America, the Caribbean, and Central America (Preston and Beane 2024). Red-tailed Hawks are resident or partial migrants throughout much of their range, but obligate migrants across northern Canada and Alaska, USA (Preston and Beane 2024). Red-tailed Hawk movements and migrations have been previously studied via animal-borne tracking technology (Bloom et al. 2015, Craighead et al. 2016, McCrary et al. 2019, Robinson et al. 2024), which have documented migration strategies ranging from reverse summer migrations in California, USA, populations (Bloom et al. 2015, McCrary et al. 2019) to more typical seasonal migrations from northerly populations within the Rocky Mountain west, USA (Craighead et al. 2016), and in eastern Canada (Robinson et al. 2024).

Alaska represents both the northern- and western-most breeding populations of Red-tailed Hawks. Although there have been no published data documenting the migratory behavior of Red-tailed Hawks from Alaska, the state contains a significant portion of the Harlan's subspecies (*B. j. harlani*) population; this distinctive group has a wintering distribution that covers much of the central and western USA (Mindell 1985, Moreno-Contreras et al. 2021, Preston and Beane 2024). Red-tailed Hawks nest in low densities throughout forested regions of Alaska, where at least two subspecies occur: *B. j. harlani* nests across most of the state, while *B. j. alascensis* nests in the Alexander Archipelago of southeastern Alaska where it occurs in very low densities (Gibson and Withrow 2015). This kind of population structure between southeastern and the rest of Alaska is common in many taxa, largely explained by the region's glacial history and the presence of an inter-glacial refugium in the southern islands of the archipelago (Sawyer et al. 2019). How biogeography and the population structure of Red-tailed Hawks in Alaska interact to influence migratory behavior is not well established.

Although the Red-tailed Hawk's International Union for Conservation of Nature (IUCN) Red List threat status is least concern (BirdLife International 2024), any given species' threat status can vary regionally (Rodrigues et al. 2014). Long-term trends based on counts of migrating or wintering individuals suggest stable to increasing Red-tailed Hawk populations at regional and continental scales throughout North America (Farmer et al. 2008, Paprocki et al. 2014, 2017). However, the long-term status of northern migratory populations of Red-tailed Hawks—such as those in Alaska—is less certain because (1) counts of migrating or wintering individuals cannot easily distinguish how trends vary by breeding origin; and (2) long-term breeding season surveys, such as the Breeding Bird Survey (BBS; Hostetler et al. 2023), have low statistical power to detect Red-tailed Hawk trends in places like Alaska due to low densities and poor survey coverage (Dunn et al. 2005). Short-term trends with increased spatial resolution during the breeding season suggest recent population declines in some northern regions that are steeper compared to range-wide estimates. Specifically, eBird data from 2012 through 2022 found a −11.2% change in Alaska versus a −6% range-wide change (Fink et al. 2023). Consequently, an improved understanding of migratory connectivity in Alaska's Red-tailed Hawk population is important because population changes can be driven by factors influencing reproduction and survival throughout different portions of the annual cycle (Norris et al. 2004, Genovart et al. 2024).

We provide the first perspective on full annual cycle movements and migratory connectivity of Red-tailed Hawks that spent the breeding season in Alaska, including an account of their phenotypic diversity within this region. Our objectives were to (1) document spatial patterns in breeding season locations and phenotypic diversity within Alaska; (2) quantify the strength of migratory connectivity within and between breeding season regions in Alaska; and (3) quantify and describe any differences in migratory behavior between regions in Alaska. Given the potential for population structure within Alaska, we expected some level of migratory connectivity and regional differences in migratory behavior among Alaska's Red-tailed Hawks. Alternatively, if there was minimal population structure among Alaska's Red-tailed Hawks, then we expected to find no migratory connectivity and minimal differences in migratory behavior among breeding season regions in Alaska.

METHODS

We trapped and attached solar-powered GPS-PTT (30 g; Microwave Telemetry) or GPS-GSM (19–21 g; Druid Technology or Ecotone Telemetry) transmitters using a backpack-style harness to 27 adult (i.e., after first-cycle) Red-tailed Hawks that spent the breeding season in Alaska. We trapped Red-tailed Hawks throughout the annual cycle including on wintering grounds within the conterminous USA ($n = 17$), along migration routes in Canada ($n = 5$), and near the end of migration in Alaska ($n = 5$) between 2020 and 2024 (Table 1). For wintering and migration captures, we targeted individuals that appeared consistent with the *B. j. harlani* or other migratory phenotypes. For this analysis, we only included the subset of 26 birds that spent the breeding season in Alaska. We programmed transmitters to collect locations at variable temporal intervals ranging from 1 min to 6 hr depending on transmitter voltage. For each hawk, we (1) took a set of standardized photographs to document plumage diversity, (2) determined age at capture using cycle-based terminology (modified from Pyle et al. 2022), and (3) determined sex using molecular methods ($n = 24$; Fridolfsson and Ellegren 1999) or morphometrics ($n = 2$). We used morphometrics from hawks sexed genetically to assign sex to those not genetically sexed (Fig. 1). More detailed methods for photographic documentation and age and sex determination are provided in Robinson et al. (2024).

For all subsequent analyses, we assigned individual hawks to one of two regions within Alaska based on the geographic location of breeding season home ranges (Fig. 2, Table 1). Hawks assigned to the northern region had home ranges north of the Alaska Range within the Intermontane Boreal Level 1 ecoregion, whereas hawks assigned to the southern region had summer home ranges south of the Alaska Range within the Alaska Range Transition and Coastal Rainforests Level 1 ecoregions (Nowacki et al. 2003). The Alaska Range is the dominant geographic feature that bisects the breeding distribution of Red-tailed Hawks in Alaska. Ecoregions north of the Alaska Range are drier with greater seasonal temperature extremes, whereas ecoregions south of the Alaska Range transition to wetter climates with less seasonal temperature fluctuations (Nowacki et al. 2003).

We created maps in ArcGIS Pro 3.4 (Fig. 2) and ggplot2 (v. 3.4.4) in R Version 2023.12.1 + 402 (Fig. 3). We used software from the R Core Team (2023) for all analyses. We included all years for

Table 1. Overview of individual GPS-tracked Red-tailed Hawks summering in Alaska, USA. Figure ID corresponds to individual breeding or nonbreeding season home range locations shown in Figures 2 and 3.

Figure ID	Sex	Age[a]	Morph	Capture Date	Breeding Season Region	Nonbreeding Season Region	Capture State/ Province	Migration Distance (km)	eBird Checklist[b]
1	M[c]	A3C	light	17 Apr 2023	northern	NA	Alberta	NA	S134217889
2	M	A2C	dark	29 Feb 2024	northern	east	Oklahoma	5102	S163357798
3	M	3C	light	26 Feb 2024	northern	east	Oklahoma	5007	S165079759
4	M	A4C	dark	7 Mar 2021	northern	west	Idaho	3112	S82964443
5	F	A3C	dark	26 Feb 2024	northern	east	Oklahoma	4994	S163166664
6	F	A4C	light	18 Jan 2021	northern	east	Kansas	4593	S79519403
7	M	A3C	dark	7 Mar 2024	northern	east	Oklahoma	4688	S164005520
8	F	A5C	dark	20 Feb 2021	northern	east	Kansas	4447	S128229072
9	M	A4C	dark	20 Feb 2021	northern	east	Kansas	4435	S208407458
10	F	A4C	dark	29 Feb 2024	northern	east	Oklahoma	4588	S163357793
11	F	A3C	light	19 Apr 2023	northern	east	Alberta	4561	S134667062
12	F[c]	A3C	dark	27 Feb 2024	northern	east	Oklahoma	4676	S163153780
13	F	A3C	dark	20 Apr 2023	northern	east	Alberta	4229	S134408539
14	M	A4C	dark	20 Mar 2022	northern	east	Kansas	4731	S105843992
15	M	A4C	dark	19 Apr 2023	northern	east	Alberta	4084	S134666666
16	M	A4C	dark	14 Mar 2023	southern	west	Washington	2423	S130927114
17	M	2C	dark	5 Feb 2022	southern	west	Idaho	3289	S102089889
18	M	A3C	dark	19 Apr 2023	southern	east	Alberta	4829	S134666666
19	F	A3C	dark	18 Feb 2022	southern	west	Idaho	2486	S103121702
20	M	4C	dark	18 Dec 2020	southern	west	Utah	3269	S83782823
21	M	3C	light	19 Feb 2023	southern	west	Idaho	1965	S129009243
22	F	A3C	dark	25 Feb 2023	southern	west	Washington	1382	S129643141
A	F	A2C	dark	10 Apr 2022	southern	west	Alaska	2308	NA
B	F	2C	dark	26 Apr 2024	southern	east	Alaska	5303	NA
C	M	A3P	dark	8 Aug 2023	southern	west	Alaska	2560	NA
D	M	A4P	dark	15 Apr 2022	southern	NA	Alaska	NA	NA
E	F	A3C	dark	28 Apr 2023	southern	west	Alaska	3199	NA

[a] Age on capture date; A3P and A4P codes correspond to hawks molting into A3C and A4C plumages, respectively.

[b] At capture location, includes all standardized photographs.

[c] Individuals sexed using morphometrics (see Fig. 1).

individuals that gathered multi-year data in our movement map (Fig. 3) to fully illustrate migratory routing. For individuals with multiple years of tracking data, we selected a single complete fall and spring migration for the calculation of migration metrics (Table 2, Fig. 4). We prioritized the most recent fall and spring migrations for each individual to better account for any potential age (particularly younger adults; Sergio et al. 2014) or transmitter effects (Lamb et al. 2020). We identified breeding and nonbreeding season home ranges for each individual-year for the calculation of migration metrics and defined them as follows: (1) breeding—longest continuously occupied home range within Alaska; and (2) nonbreeding—southernmost home range occupied during the nonbreeding, wintering season (on average November–March; Table 2). Seasonal home ranges were more generally identified as the area within which an individual moved less than 10 km per day in a directional manner for a minimum of seven consecutive days based on visual inspection of movement tracks. We then used a single centroid location within breeding and nonbreeding season home ranges for presentation in figures and calculations of migration distance.

We quantified the strength of migratory connectivity between the most recent breeding- and nonbreeding season locations (i.e., centroids of home ranges) using great-circle distances among individuals during one season of the annual cycle (e.g., breeding) compared to distances among the same individuals during another season of the annual cycle (e.g., nonbreeding). We calculated distance matrices using the "distm" function from the

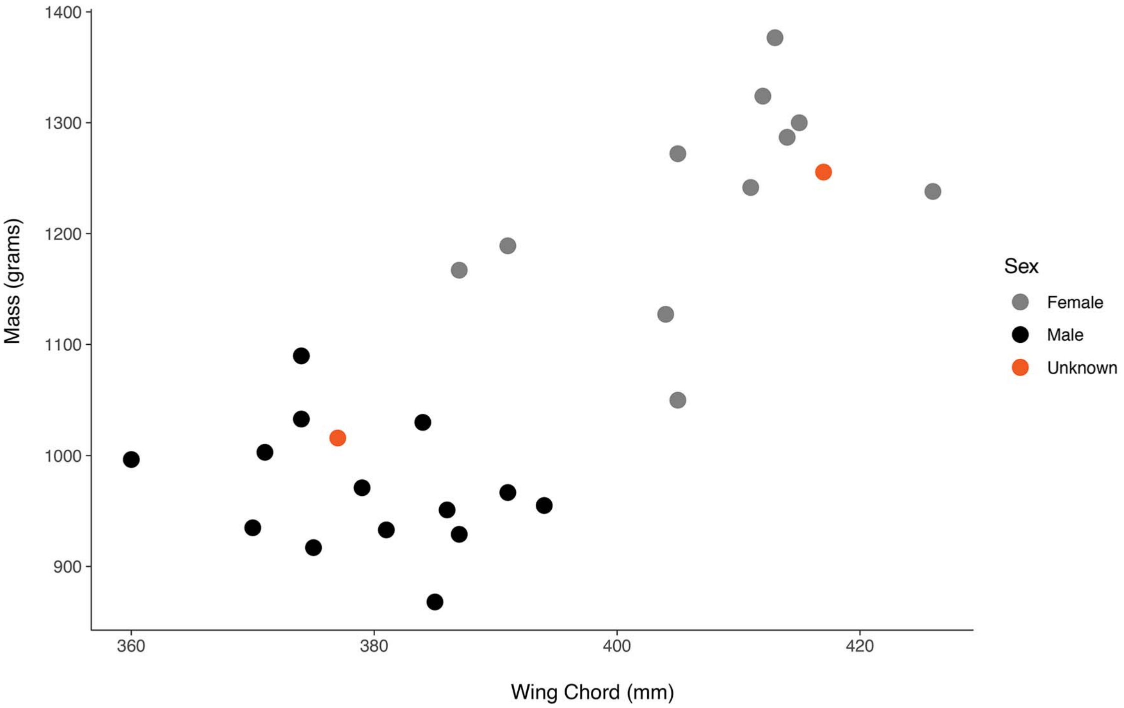

Figure 1. Morphometrics (wing chord and mass) of Alaskan Red-tailed Hawks sexed genetically (male or female) that were used to assign sex to those not sexed genetically (unknown; $n = 2$).

geosphere R package (v. 1.5-20; Hijmans 2024) and migratory connectivity using the nonparametric Mantel test from the *ade4* R package (v. 1.7-22; Dray and Dufour 2007). We calculated Mantel correlation coefficients for all hawks combined (i.e., degree of inter-population mixing) and within each breeding season region (northern or southern; i.e., degree of population spread; *sensu* Finch et al. 2017). Statistical significance of Mantel correlation coefficients was determined by 9999 random permutations.

We calculated migration distance using the straight-line, great-circle distance between breeding and nonbreeding season home range centroids. Migration start dates were defined using the first GPS location at which displacement continuously increased away from breeding or nonbreeding season home ranges (Phipps et al. 2019). Migration end dates were defined using the first GPS location upon arrival to a breeding or nonbreeding season home range. Migration duration was calculated as the difference between migration start and end dates and included time spent at stopovers. We tested for differences in each migration metric by breeding season region (northern or southern Alaska) via the "Anova" function from the *car* R package (v. 3.1-2; Fox and Weisberg 2019) by fitting linear models explaining each migration metric predicted by breeding season region.

RESULTS

We obtained home range locations from 27 GPS-tracked Red-tailed Hawks that spent the breeding season in Alaska including 15 from northern and 12 from southern Alaska regions (Fig. 2, Table 1). All Red-tailed Hawks were aged as adults (i.e., ≥ after first-cycle) at time of capture and included 15 males and 12 females, comprising 22 dark and 5 light morphs (Fig. 2, Table 1). We obtained complete spring migrations from 22 hawks and complete fall migrations from 23 hawks (Fig. 3).

We primarily sampled Red-tailed Hawks ($n = 17$ of 27 captures) from two distinct wintering areas (an eastern and western region), which we found corresponded to two broad breeding season regions within Alaska. Overall, Red-tailed Hawks that spent the breeding season north of the Alaska Range disproportionately migrated from an eastern nonbreeding region ($n = 13$ of 14 individuals) in the Great Plains from Nebraska south to Kansas and

Texas. Conversely, Red-tailed Hawks that spent the breeding season south of the Alaska Range disproportionately migrated from a western nonbreeding region ($n = 9$ of 11 individuals) in the Pacific Northwest (British Columbia, Canada, and Washington, USA) or the Intermountain West (east and south to Montana, Idaho, Utah, and Wyoming; Table 1, Fig. 3). The migratory differences between northern and southern Alaska regions corresponded to low but significant migratory connectivity (rM = 0.283, $n = 25$ individuals, $P = 0.0016$) between breeding and nonbreeding season home ranges among all Red-tailed Hawks from Alaska (i.e., inter-population mixing). Within breeding season regions, we observed high population spread with no migratory connectivity detected among hawks from northern (rM = 0.041, $n = 14$ individuals, $P = 0.305$) or southern (rM = −0.184, $n = 11$ individuals, $P = 0.841$) Alaska. Additionally, two individuals from southern Alaska changed nonbreeding season (i.e., wintering) locations between years (both shifted their home range locations eastward; Fig. 3A), which had a negligible effect on migratory connectivity as we still found low but significant migratory connectivity among all Red-tailed Hawks from Alaska (rM = 0.292, $n = 25$ individuals, $P = 0.0006$), and no migratory connectivity among hawks from southern Alaska (rM = −0.192, $n = 11$ individuals, $P = 0.870$). Within Alaska, we observed no changes to the location of breeding season home ranges between years. We also observed prominent differences in migratory routing between breeding season regions such that hawks from northern Alaska undertook a more easterly migration that was more concentrated, particularly through the Yukon Territory and northeastern British Columbia, Canada (Fig. 3). In contrast, hawks from southern Alaska undertook a more westerly migration that was more dispersed and variable in terms of routing (Fig. 3).

We found several significant differences in Red-tailed Hawk migratory behavior between northern and southern regions in Alaska (Table 2, Fig. 4). Red-tailed Hawks that spent the breeding season in the northern region migrated significantly longer distances compared to those in the southern region ($F = 19.2$, df = 1, $P \leq 0.001$). We also found Red-tailed Hawks that spent the breeding season in the northern region arrived at breeding season home ranges significantly later compared to those in the southern region ($F = 6.38$, df = 1, $P = 0.019$). The earlier breeding season arrival by southern birds remained significant even after the removal of an outlier from southeastern Alaska (our southernmost breeding season location; Fig. 2) that arrived 12 d earlier (30 March; Fig. 4C) than any other individual in our sample ($F = 4.56$, df = 1, $P = 0.044$). We found no significant differences between northern and southern regions in all other migration metrics including the timing of nonbreeding season arrival or departure, breeding season departure, or migration duration (both spring and fall; Table 2; Fig. 4). Both fall migration duration ($F = 0.006$, df = 1, $P = 0.937$) and timing of nonbreeding season arrival ($F = 0.501$, df = 1, $P = 0.488$) results were robust to the inclusion of an outlier with an especially protracted fall migration (124 d) leading to a late nonbreeding season arrival (22 January).

DISCUSSION

We documented the first full annual cycle perspective on the migratory movements of Alaska's Red-tailed Hawk population and found substantial differences in migratory behavior between breeding season regions in northern and southern Alaska. Red-tailed Hawks that spent the breeding season in northern Alaska primarily overwintered in the Great Plains of the USA and migrated nearly 1500 km farther than hawks in southern Alaska that primarily overwintered in southwestern Canada and

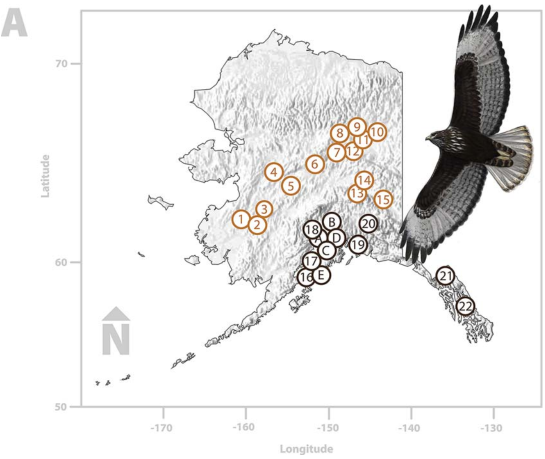

Figure 2. Breeding season home range locations of 27 GPS-tracked Red-tailed Hawks throughout Alaska, USA. Color of breeding season locations corresponds to two regions: northern (orange) and southern (dark brown) Alaska. Locations of home ranges (A) correspond to photos (B) illustrating the plumage diversity present in our sampling of Alaska's Red-tailed Hawk population. Locations with letters A–E correspond to individuals lacking standardized photo documentation. All numbers and letters correspond to individual information in Table 1.

Figure 2. (Continued).

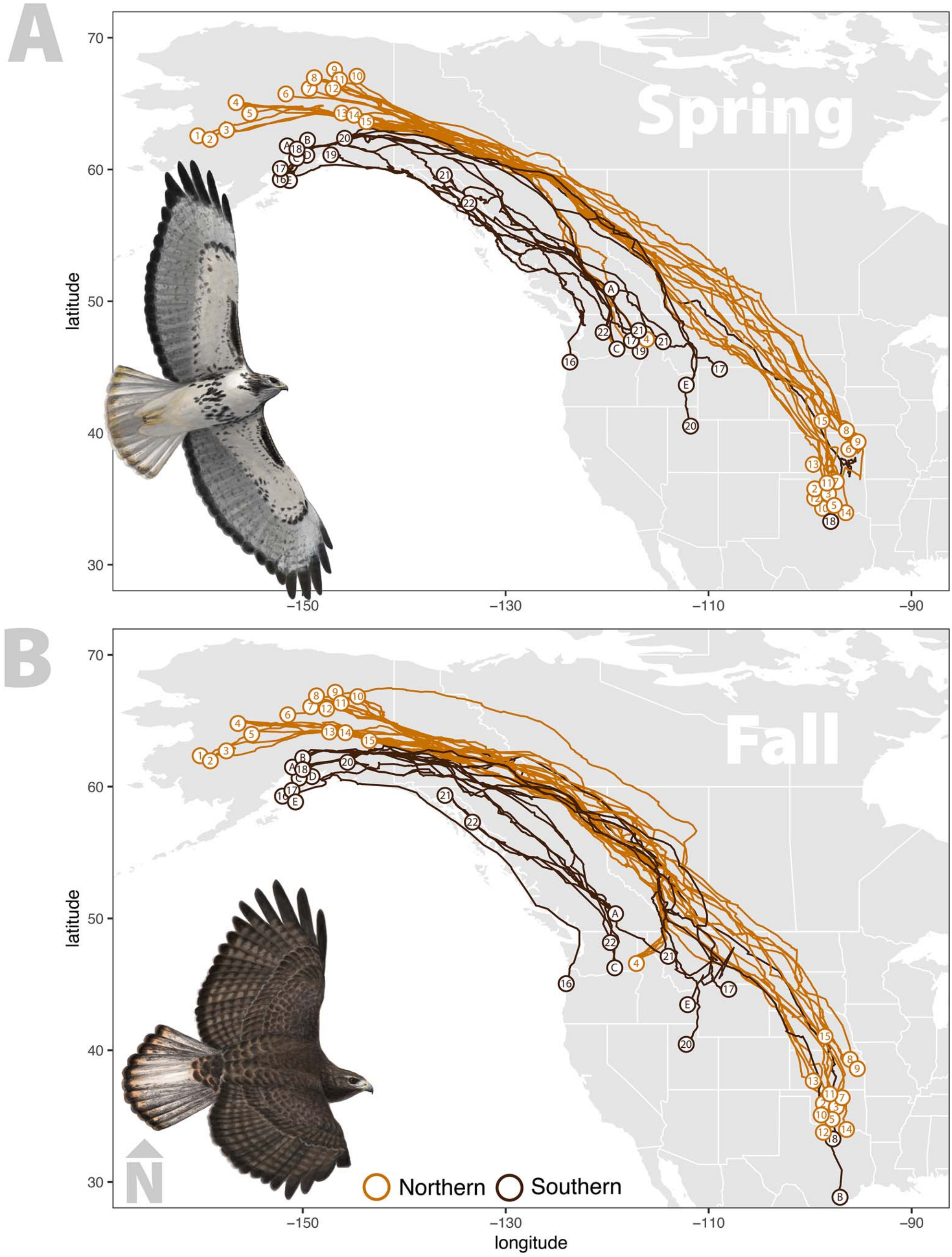

Figure 3. Spring (A) and fall (B) migration tracks for Red-tailed Hawks that spent the breeding season in Alaska, USA. Individuals from northern (orange) and southern (dark brown) regions in Alaska exhibited significant migratory connectivity and overwintered in disparate regions. Map shows all data from all years including multiple migrations from some hawks.

Table 2. Migration summary (distance, phenology, and duration) of Red-tailed Hawk populations in Alaska, USA. Values represent means ± SD (*n* individuals). *P*-values are from ANOVA's testing for differences between populations in Alaska (northern vs. southern) and are bolded if <0.05. Migration distance is the straight-line, great-circle distance between breeding and nonbreeding season home ranges.

		Alaska Population		
Migration Metric	*P*-value	Northern	Southern	All
Migration distance (km)	**0.0002**	4518 ± 495 (14)	3001 ± 1175 (11)	3850 ± 1139 (25)
Winter departure	0.85	23 Mar ± 12 (13)	22 Mar ± 12 (9)	23 Mar ± 12 (22)
Breeding arrival	**0.019**	25 Apr ± 4 (15)	19 Apr ± 9 (10)	23 Apr ± 7 (25)
Spring migration duration (d)	0.33	32 ± 13 (13)	26 ± 16 (9)	30 ± 14 (22)
Breeding departure	0.32	11 Sep ± 13 (15)	16 Sep ± 11 (11)	14 Sep ±13 (26)
Winter arrival	0.90	11 Nov ± 27 (13)	10 Nov ± 15 (10)	10 Nov ± 22 (23)
Fall migration duration (d)	0.51	61 ± 23 (13)	55 ± 15 (10)	58 ± 20 (23)

western USA. Although the northern Alaska breeding population wintered farther south (compared to those from southern Alaska), a pattern consistent with leapfrog migration, Red-tailed Hawks at a broader scale appear to exhibit a chain migration (Newton 2008) pattern because at least some migratory populations from lower latitudes in western North America migrate even farther south to Mexico (Craighead et al. 2016). Although we found a clear separation of migratory routing and wintering locations between hawks that spent the breeding season in two separate regions of Alaska, our sampling was biased toward two disparate wintering areas where most of our captures occurred: an eastern region in the southern Great Plains, USA, and a western region in the Pacific Northwest, USA. This disparate sampling approach may have accentuated differences in migratory behavior between regions (although captures that occurred in southern Alaska generally followed this same disparate nonbreeding pattern). A larger sample of individuals (captured either throughout the entire nonbreeding or the entire breeding season distribution) would likely uncover nuances to the patterns we found. Sampling throughout areas of contact between the northern and southern breeding season regions separated by the Alaska Range would likely strengthen our perspective on the migratory diversity and connectivity among Alaska's Red-tailed Hawk breeding population.

Despite biases in our sampling approach, observed differences in migratory routes and destinations between Red-tailed Hawks from northern and southern Alaska suggest the importance of environmental (e.g., geography) or genetic (e.g., evolutionary) factors maintaining differences in migratory behavior between breeding season regions. Environmental factors such as geographic barriers to flight or predictable weather patterns encountered during migration may cause birds to take alternative routes (Eisaguirre et al. 2018) that could influence subsequent routing and migratory destinations. For example, during early fall migration, the presence of the Alaska Range could cause hawks from northern Alaska to take an initially more northeastern migratory trajectory that influences subsequent routing and destinations. Alternatively, genetic factors such as separation during recent glacial cycles, followed by post-Pleistocene expansion and secondary contact (Zink and Gardner 2017, Sawyer et al. 2019, Justen et al. 2024) may explain differing migratory behaviors. Environmental or genetic factors could also explain why we observed a small proportion of birds (3 of 25 individuals) that migrated to opposing breeding or nonbreeding areas (e.g., birds spending the breeding season in southern Alaska but migrating to the eastern nonbreeding season region). Other avian species with widespread breeding season distributions throughout Alaska show broadly similar patterns of migratory connectivity across an east-west continental continuum, including the Tundra Swan (*Cygnus columbianus*; Ely and Meixell 2016), Sandhill Crane (*Antigone canadensis*; Tacha et al. 1984, Petrula and Rothe 2005), and Fox Sparrow (*Passerella iliaca*; Zink 2008, Fraser et al. 2018, Weckstein et al. 2020). Genetic work suggests that the Alaska breeding subspecies (*B. j. harlani*) is more similar to eastern Red-tailed Hawk populations than it is to western populations (Hull et al. 2010) and thus may retain an eastern-oriented ancestral migratory behavior. Although we observed no obvious plumage differences between northern and southern breeding season regions (Fig. 2), their differing migratory behavior may indicate the dominant ancestry for each region (i.e., western ancestry in southern, and eastern ancestry in northern Alaska). More dense sampling paired with genomic analyses across the entire

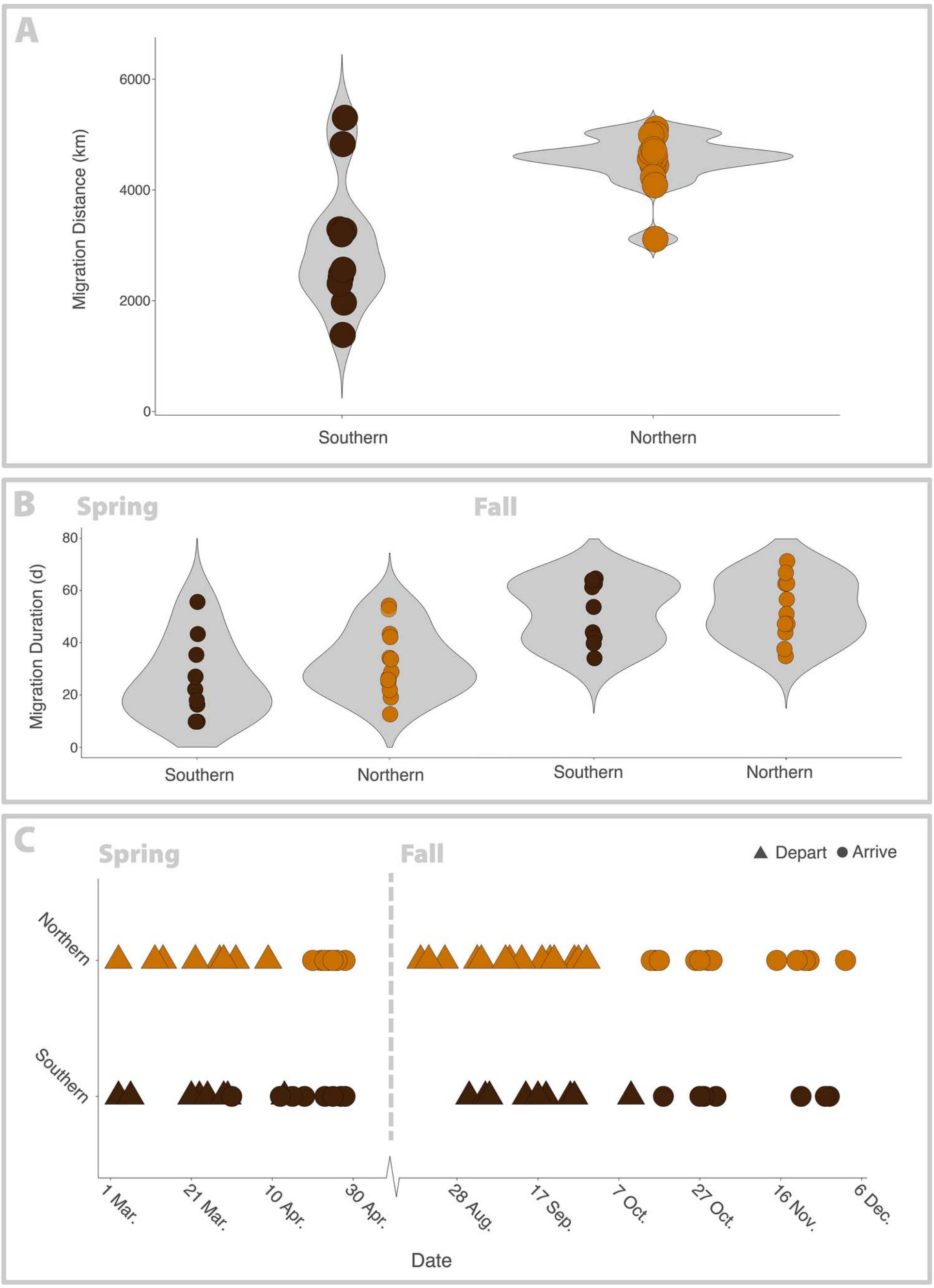

Figure 4. Red-tailed Hawk migration distance (A), duration (B), and phenology (C) among northern (orange) and southern (dark brown) regions in Alaska, USA. Migration distance is the straight-line, great-circle distance between breeding and nonbreeding season home ranges. For presentation purposes, one migration duration (B) and one winter arrival (C) outlier have been omitted from the northern breeding region.

breeding and nonbreeding distribution of Alaska Red-tailed Hawks is needed to assess the potential environmental or genetic basis of our observed differences in migratory behavior.

Our results strengthen our understanding of the broad plumage diversity present in Alaska because breeding season locations were located throughout the species distribution within the state. Although we sampled hawks with predominantly *B. j. harlani* phenotypes (e.g., tails with variably mottled dark banding or spotting and sometimes extensively white or gray), we also sampled several other individuals that did not match the typical description of *B. j. harlani* (e.g., individuals 2, 7, 9, 10, and 22 from Fig. 2; Preston and Beane 2024). The presence of individuals with plumage inconsistent with the *B. j. harlani* phenotype suggests that, although *B. j. harlani* represents the dominant phenotype throughout Alaska, there is likely gene flow from neighboring taxa. In many cases it is difficult to determine if phenotypes inconsistent with the *B. j. harlani* phenotype—which itself is extremely variable—represent different subspecies, introgression from other subspecies, or unrecognized natural variation within *B. j. harlani.* Red-tailed Hawks in Alaska may represent as many as four distinct subspecies (*B. j. abieticola*, *alascensis*, *calurus*, and *harlani*; Preston and Beane 2024); however a population genetic perspective as well as a full systematic review of the species is still needed and would help confirm the presence of other subspecies within Alaska.

Although our sampling effort was strongly focused on selecting *B. j. harlani* and birds with other plumage types that are also associated with migratory subspecies, it was largely naive to an individual's breeding origin because (1) ~80% of sampled hawks were captured outside of Alaska during the nonbreeding season and (2) the *B. j. harlani* breeding distribution extends well beyond Alaska into northwest Canada (Preston and Beane 2024). However, most of our captures occurred during the stationary nonbreeding season in two disparate regions in the southern Great Plains and Pacific Northwest of the USA. Consequently, our sampling certainly underestimates the overall phenotypic and migratory diversity present in Alaska. Our data particularly under-represent phenotypic and migratory diversity from southeastern Alaska ($n = 2$), the region thought to primarily contain subspecies *B. j. alascensis* (or perhaps *B. j. calurus*; Preston and Beane 2024). Future work should prioritize the tracking of Red-tailed Hawks from southeastern Alaska as migratory behavior in this region may be particularly distinct because of lower latitudes and more temperate climates.

Compared to a more southerly breeding population of migratory Red-tailed Hawks from the conterminous western USA (Craighead et al. 2016), hawks from Alaska migrated longer straight-line distances (3850 vs. 2160 km), departed nonbreeding locations later (23 March vs. 17 March), arrived to breeding season locations later (23 April vs. 8 April), departed breeding season locations earlier (14 September vs. 13 October), and had similar arrival to nonbreeding locations (10 November vs. 5 November). Additionally, both spring (30 d vs. 22 d) and especially fall migrations (58 d vs. 23 d) were longer in duration. Importantly, later arrival to and earlier departure from breeding season areas corresponds to a population-level average of ~42 fewer days spent in breeding season areas for Alaskan migrants compared to migrants from more southerly breeding migratory populations (Craighead et al. 2016). We found a similar pattern within Alaska as the northern region arrived at breeding season locations ~6 d later but departed on fall migration earlier and spent on average 11 fewer days at breeding season locations compared to the southern Alaska region. Past inter- and intraspecific studies have found some support for reduced breeding area residency times among long-distance migrants (Winger and Pegan 2021, Buij et al. 2024). Reduced breeding area residency time among Red-tailed Hawk populations migrating greater distances suggests greater temporal constraints on breeding, which may increase their susceptibility to carry-over effects that can influence pre-breeding (i.e., spring) migratory timing and subsequent reproductive success (Norris et al. 2004, Cooper et al. 2015). Hawks from Alaska also spent considerably more time migrating, with a particularly protracted fall migration, compared to other populations (Craighead et al. 2016). Survival rates during migration are often lower than other portions of the annual cycle (Sillett and Holmes 2002, Klaassen et al. 2014, Buechley et al. 2021), which could mean increased mortality risk among Alaskan migrants compared to other populations. However, reduced survival associated with long-distance migration could be offset by increased survival at stationary breeding or nonbreeding season locations.

A comprehensive perspective on full annual cycle movements and migratory connectivity is essential for assessing population stability and pinpointing drivers of population change (Knight et al. 2021, Lewis et al. 2023). For instance, species or populations exhibiting more restricted seasonal ranges are more likely to exhibit population declines (Gilroy et al. 2016), suggesting those with stronger migratory connectivity may be sensitive to spatially distinct selective pressures throughout the annual cycle (Genovart et al. 2024). We found that the Alaskan population of Red-tailed

Hawks exhibited weak but significant migratory connectivity. Yet, because we only quantified connectivity for one part of this species' broad North American range, our estimates of connectivity are incomplete. Future work should attempt to integrate multiple data types (e.g., GPS-tracking, banding, genetic, and abundance data) across the species entire migratory range to give a more robust and holistic picture of connectivity (Hostetler et al. 2025). Despite our relatively limited geographic scope, we identified spatially distinct seasonal ranges and migration routes among long-distance migratory Red-tailed Hawks from Alaska that have experienced short-term population declines since 2011 (Fink et al. 2023). If short-term population declines continue, our migratory connectivity analysis has revealed spatial and temporal patterns of co-occurrence that will help identify where and when drivers of population change occur. Ultimately, our improved understanding of migratory connectivity among Alaska's Red-tailed Hawk population may aid state and provincial biologists in making informed management decisions.

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