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Northward Migrations of Nonbreeding Bald Eagles from Arizona, USA

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ABSTRACT.—Knowledge of the spatiotemporal patterns of migratory and nonbreeding-season movements by animals is critical for conservation, but can be difficult to obtain if animals move far from known breeding territories and across administrative and country borders. To understand the migratory movements of Bald Eagles (*Haliaeetus leucocephalus*) originating from a demographically closed population in Arizona, USA, we deployed GPS transmitters on 24 juveniles and 2 nonbreeding adult eagles between 2017 and 2023. We identified common migration routes, stopover locations, and migration phenology. Eagles moved north from Arizona during the population's post-breeding period in the boreal spring and summer, and returned south in autumn in advance of the breeding season. Eagles migrated along two primary routes: (1) along the Wasatch Mountains in Utah and extending into the Rocky Mountains of southern Idaho, and (2) through eastern Nevada and along the Rocky Mountains in western and northern Idaho. Stopover locations were frequently near lakes and rivers. Recent fledglings began migration later than older individuals and 15 of 16 of these juveniles that survived until the following breeding season returned to Arizona. The individual that did not return showed evidence of permanent emigration to northern California. Our results contribute to a growing understanding of avian migration routes within the Pacific Flyway and the diverse migration strategies, including northward migration following the breeding season, exhibited across raptor populations. We highlight that explicit studies of juveniles, subadults, and nonbreeding adults are key to understanding avian migration dynamics and identifying opportunities for conservation.

KEY WORDS: *juvenile*; *migration phenology*; *movement ecology*; *northward migration*; *Pacific Flyway*; *satellite tracking*.

MIGRACIONES HACIA EL NORTE DE INDIVIDUOS NO REPRODUCTORES DE *HALIAEETUS LEUCOCEPHALUS* DESDE ARIZONA, EUA

RESUMEN.—El conocimiento de los patrones espaciotemporales de los movimientos migratorios y de la temporada no reproductiva de los animales es fundamental para su conservación, si bien esto puede ser difícil cuando los animales se alejan de los territorios de cría conocidos y cruzan fronteras administrativas y nacionales. Para entender los movimientos migratorios de los individuos de *Haliaeetus leucocephalus* originados a partir de una población demográficamente cerrada en Arizona, EUA, instalamos transmisores GPS en 24 juveniles y 2 adultos no reproductores entre 2017 y 2023. Identificamos rutas comunes de migración, lugares de descanso y la fenología migratoria. Las águilas se movieron hacia el norte desde Arizona durante el período posterior a la reproducción de esta población, en la primavera y el verano boreal, y regresaron al sur en otoño, antes del inicio de la temporada reproductiva. Las águilas migraron a lo largo de dos rutas

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principales: (1) a lo largo de las Montañas Wasatch en Utah, extendiéndose hacia las Montañas Rocosas del sur de Idaho, y (2) a través del este de Nevada y a lo largo de las Montañas Rocosas en el oeste y norte de Idaho. Los lugares de descanso estaban frecuentemente cerca de lagos y ríos. Los volantones más jóvenes comenzaron la migración más tarde que los volantones más viejos, y 15 de 16 de estos juveniles que sobrevivieron hasta la siguiente temporada de cría regresaron a Arizona. El individuo que no regresó mostró evidencia de emigración permanente hacia el norte de California. Nuestros resultados contribuyen a una mejor comprensión de las rutas migratorias de las aves dentro del corredor del Pacífico y de las diversas estrategias migratorias, incluida la migración hacia los polos después de la temporada de cría, exhibidas entre las poblaciones de rapaces. Subrayamos que los estudios explícitos de los juveniles, subadultos y adultos no reproductores son clave para entender la dinámica migratoria de las aves e identificar oportunidades de conservación.

[Traducción del equipo editorial]

INTRODUCTION

Spatiotemporal patterns of movement affect an animal's access to resources and exposure to sources of mortality, and studies of these patterns can provide critical information for conservation planning (Kays et al. 2015). The migratory period is increasingly recognized as a time of high mortality that can have substantial impacts on wildlife population dynamics (Carlisle et al. 2009, Fudickar et al. 2021). Identifying high-use migration corridors and stopover areas can provide insights for targeted management interventions such as the establishment of static or dynamic protected areas, habitat restoration, and barrier removal or circumvention (Shuter et al. 2011).

Past animal movement studies have commonly focused on the movement of breeding individuals, often due to difficulty in capturing and resighting juveniles, subadults, and nonbreeding adults (Tanferna et al. 2013, Wolfson et al. 2020). However, these demographic groups often have different survival rates than breeding adults (Harris and Wanless 1995, Newton et al. 2016). For example, juveniles and subadults frequently experience higher mortality than breeding-age individuals, and this differential mortality can have population-level consequences (Gaillard et al. 1998, Altwegg et al. 2005, Votier et al. 2008, Abadi et al. 2017). An understanding of the spatiotemporal patterns and strategies for migration among these demographic groups is needed to identify the ongoing threats to migratory populations.

Billions of birds migrate to and from their breeding and nonbreeding grounds each year (Hahn et al. 2009, Dokter et al. 2018, Newcombe et al. 2019). Within North America, the Pacific Flyway is one of the four major migration routes among birds and broadly describes pathways traveled over land along and west of the Rocky Mountains. Western flyways are historically understudied relative to eastern flyways in North America (Carlisle et al. 2009, Newcombe et al. 2019), although organizations focused on migratory raptors have recorded the migratory movements of raptors in the western United States for decades (Smith and Hoffman 2000). These observations provide valuable information about phenology and population trends and offer opportunities for band resighting. Yet finer resolution tracking studies are still needed to understand full migration cycles, identify important stopover locations, and examine variation among individuals.

Despite the presence of long-term monitoring programs for migratory raptors along the Pacific Flyway, the migration patterns of Bald Eagles (*Haliaeetus leucocephalus*) originating from the southwestern United States remain poorly understood. Within Arizona, there is a growing population of Bald Eagles whose breeding population is thought to be demographically closed and is managed separately from other Bald Eagle populations in the conterminous United States (Allison et al. 2008, Cappello et al. 2024). In contrast to many raptor populations throughout North America and Bald Eagle populations in the northern United States and Canada (Hodges et al. 1987, McClelland et al. 1994, Harmata 2002, Mandernack et al. 2012), these individuals have been observed migrating northward during the population's nonbreeding period and returning south in the boreal fall before the breeding season begins (Hunt et al. 2009). This northward movement during the population's nonbreeding period has been observed in other Bald Eagle populations (band-resight studies: Broley 1947, Mabie et al. 1994; radio telemetry: Hunt et al. 1992b; satellite telemetry: Mojica et al 2008, 2016) and to a limited degree in other raptor species (Bloom et al. 2015, 2017, Friedemann et al. 2020), but generally represents an uncommon movement strategy among migratory birds (Newton 2008, Friedemann et al. 2020). Understanding the movement ecology of individuals from the Arizona Bald Eagle population both enhances knowledge of migratory movements along the Pacific Flyway and provides insights into distinct migration strategies exhibited across a species' range.

We investigated the migratory movements of juvenile, subadult, and nonbreeding adult Bald Eagles from Arizona using data from GPS logging devices collected between 2017 and 2023. Here, we describe the phenology of documented eagle movements, characterize space-use patterns and interannual route fidelity using dynamic Brownian bridge movement models, and examine the habitat characteristics of stopover locations. We predicted that spatial and temporal migration patterns would differ across eagle sex and age classes. Because males are smaller than females (Bortolotti 1984a), they are likely less competitive when pirating or scavenging resources (Hansen 1986) and more agile while hunting (Reynolds 1972, Andersson and Norberg 1981, Pérez-Camacho et al. 2018). We therefore predicted that males may exhibit different migration strategies than females. For example, if males are overall less successful in competing for prey when resources are scare, they may need to travel farther (Wheat et al. 2017) or depart earlier for migration. We also predicted that individuals in their first year would display distinct migration patterns as they develop their flight and hunting skills and become more familiar with the landscape. To further understand the degree to which the Arizona breeding population is demographically closed, we also examined evidence for permanent emigration from Arizona. We consider these results in the broader context of Bald Eagle and raptor migration in North America and their implications for conservation.

METHODS

Study Species. The population of Bald Eagles breeding in Arizona has been monitored statewide annually since 1972 and studied intensively since 1987. It contains an estimated 73 pairs of territorial breeders as of 2022 (Cappello et al. 2024). The highest density of Bald Eagle nesting territories occurs in central Arizona along the Salt, Verde, and Gila Rivers. Bald Eagles also nest along Tonto Creek, the Bill Williams, Agua Fria, San Carlos, and Colorado Rivers, in the White Mountains, and in suburban areas in the Phoenix metropolitan area (McCarty et al. 2022).

In Arizona, breeding Bald Eagles typically court between November and February, lay one to three eggs between late December and mid-March, and rear young in the nest between late January and mid-June (Hunt et al. 1992a). Nestlings fledge when 60–95 d old (Hunt et al. 1992a). Eagles can breed as young as 3 yr old, and Arizona males and females begin breeding, on average, when 5 and 6 yr old, respectively (Allison et al. 2008). The Arizona population also includes nonbreeding adult floaters that make up an estimated 50% (95% Bayesian credible interval = 28–74%) of the adult population (Cappello et al. 2024) and are presumably present in Arizona during the breeding season to prospect for nesting territories and mates.

Data Collection. We deployed cellular-transmitting, solar-powered GPS devices (CTT ES-400, Cellular Tracking Technologies, Rio Grande, New Jersey, USA) on 26 Bald Eagles in Arizona from 2017–2023. GPS tags were backpack-mounted using a nonabrasive Teflon ribbon harness (Bildstein and Bird 2007). We deployed GPS transmitters on 24 nestlings that had not yet fledged ($n = 4$ in 2017, 7 in 2018, 5 in 2019, 3 in 2021, 4 in 2022, 1 in 2023). We deployed GPS tags on nestlings in March or April, toward the end of the breeding season. We classified nestlings with lateral tarsus widths ≥12.5 mm as females and those with measurements <12.5 mm as males (Bortolotti 1984b, Hunt et al. 1992a).

We also deployed GPS transmitters on two adults released from wildlife rehabilitation centers in 2020. One of the adult's GPS tags stopped transmitting <1 mo after the individual's release, and we did not consider those data in our analyses. The other adult (ID #20A01) was a breeding male whose nest at Lynx Lake, Arizona, had two eggs in early 2020. Eagle 20A01 was ousted from his territory during incubation by an intruding Bald Eagle and was rehabilitated to treat related injuries. This eagle was released back to his nesting territory with a GPS transmitter on 31 March 2020, but his nest had since failed. The intruding male established a pair bond with the female, permanently displacing 20A01 from the territory.

We programmed the GPS tags to record a location every 6–900 sec (15 min) while the individual was flying and every 15 min when perching. When a tag stopped transmitting data, we examined the last locations transmitted. If the eagle was clearly moving at the end of data transmission, we considered the tag to have failed. If the eagle had not changed location for 1–3 d, we considered the eagle to have died.

Processing Telemetry Data. We performed all GPS-data processing and statistical analyses in R version 4.3.2 (R Core Team 2023). We first restricted telemetry data to daylight hours between civil dawn and civil dusk using the *suncalc* package (Thieurmel and Elmarhraoui 2022). We then removed obvious outliers (e.g., fixes in the southern and eastern hemispheres, or with highly unlikely step lengths),

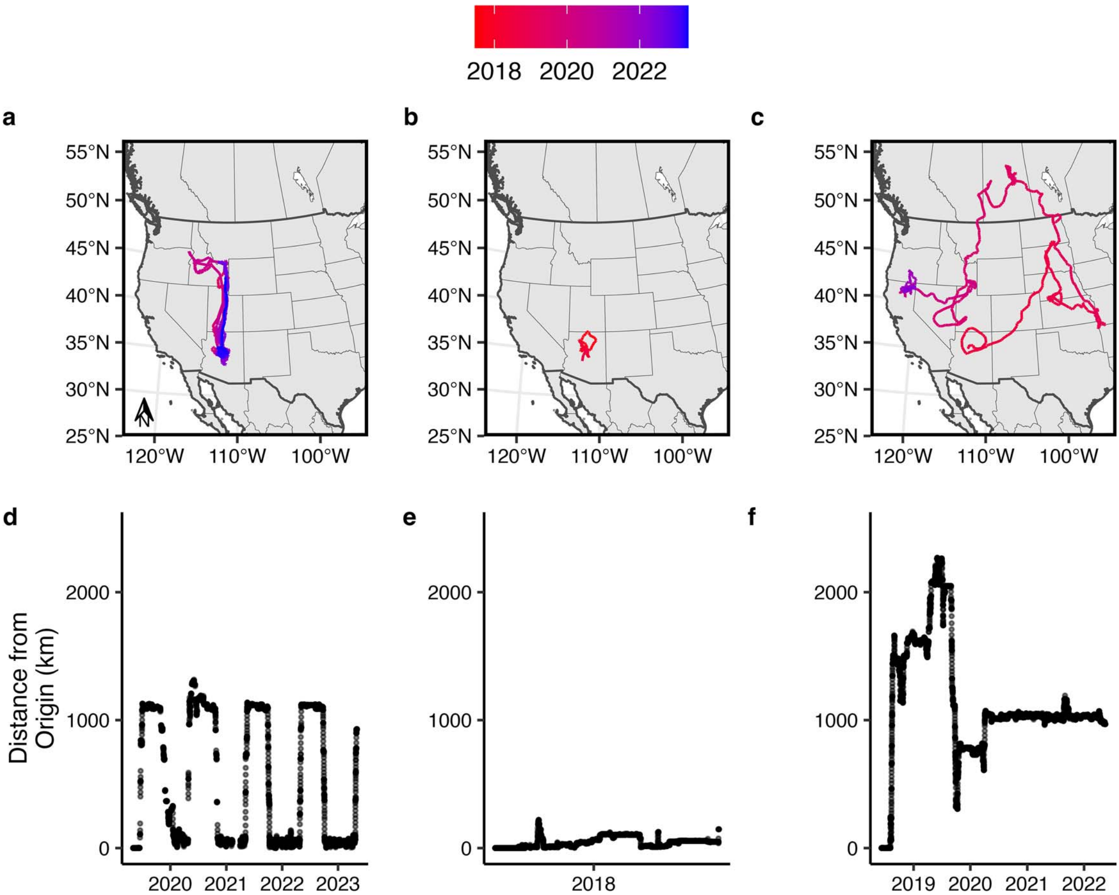

Figure 1. Examples of three movement patterns observed among Bald Eagles originating from Arizona, USA. Panel 1a shows the regular, migratory movements of individual 19J07 between 2019 and 2023. Panel 1d shows 19J07's distance from its origin in Arizona during the same period. Panels 1b and 1e show the movements of individual 17J27, which did not exhibit well-defined migratory behavior. Panels 1c and 1f depict the movement of eagle 18J33, which departed her natal area in summer 2018 and never returned to Arizona before her death in May 2022.

two-dimensional fixes, and fixes where either the horizontal or vertical dilution of precision values were ≥10 (McCabe et al. 2021, Sur et al. 2021, Bergen et al. 2022). Because individual tags had different duty cycles, we resampled the full dataset to give a location every hour (±10 min) between dawn and dusk. We prepared a further filtered dataset to represent only the first post-dawn fix of the day for each eagle. Depending on the analysis, we used either the hourly or daily dataset.

Characterizing Eagle Phenology. To characterize annual-cycle phenology for each eagle and study year (hereafter referred to as "eagle-year"), we used the *adehabitatLT* package to calculate net-squared displacement (NSD) for each individual (Calenge 2006). We plotted the NSD values over time and visually assessed the plots to identify northern-migration start dates and southern-migration end dates for each eagle-year. We then assigned each GPS fix to one of three pheno-phases: (1) post-fledging dependence period, when the individual had fledged but not yet left its natal territory, (2) migration period, defined by the beginning and end of large daily changes in the NSD plots, and (3) breeding season, when the individual returned to Arizona and the NSD plot stabilized at a low value (see Fig. 1d for an example plot). We use the term "breeding season" despite most study individuals being pre-breeders, because their annual return to, and period within, Arizona coincides with the population's breeding season.

To characterize the phenology of important migratory events, we calculated mean migration start and end dates and the mean arrival date at the most distant location during migration (proxy for when movements generally shifted from northward to southward), averaged across individuals. For analyses of farthest-location and migration-end dates, we only included complete migrations (i.e., we excluded migrations during which the eagle died or its transmitter failed). Because some individuals were sampled in more than one year, we calculated the phenology means using intercept-only random-effects models with Gaussian errors, including the phenology metric as the response variable, and eagle ID as a random effect.

Analyzing Phenology and Movement Metrics. We tested for differences in each phenology metric among sex and age classes. We defined age as both a continuous variable ("age") ranging from 0–7 yr and as a binary variable ("age class") with 0 representing recent fledglings aged <1 yr old and 1 representing older eagles. We built separate linear mixed-effects models (LMMs) with Gaussian errors for each combination of phenology and demographic metric, with the phenology metric (departure, farthest location, or return date) as the response variable, sex, age, or age class as the fixed effect, and eagle ID as a random effect. We built all LMMs using the *lme4* package (Bates et al. 2015).

To further examine the relationship between sex, age, and migratory movements, we built additional LMMs with the following response variables: z-scored maximum distance from origin reached during migration, maximum latitude reached during migration, and cumulative distance traveled during migration. We calculated cumulative distance by summing the distances between hourly GPS fixes each day from dawn to dusk and dividing the total by the number of days of the migration period. As above, we built separate LMMs for each movement response and predictor variable (sex, age, age class) and included eagle ID as a random effect. For all analyses, unless indicated otherwise, we present means ± SD or parameter estimates with 95% confidence intervals (CIs) as summary statistics.

Migration Routes. To identify high-use migration routes, we estimated an occurrence distribution (OD) of study eagles using dynamic Brownian bridge movement models (dBBMMs). These continuous-time models estimate a probability density surface describing the potential location of an individual at any given point in time along an imperfectly sampled movement path (Alston et al. 2022). The OD is estimated using the location of observed start and end points, the time elapsed between the start and end locations, and the speed of the individual (Bullard 1991, Horne et al. 2007).

We built the dBBMMs using the *move* package in R (Kranstauber et al. 2012; 2023) and included the hourly fixes between the migration start and end dates for each eagle-year. Following Mojica et al. (2016), we used a window size of 19 (odd integer closest to the maximum number of fixes per day [20]) and a margin of 9 (odd integer, roughly half of the window size). We set output resolution to 10 × 10-km pixels and error to 30 m, based on the root-mean-square user equivalent range error estimated from GPS fixes of pre-fledglings (i.e., calibration data) using the *ctmm* package (Fleming et al. 2020, Fleming and Calabrese 2023). We built a separate model for each eagle-year. For eagles with multiple years of migration records, we combined their OD surfaces to derive one surface per eagle. To do this, we first identified the fifth quantile of occurrence probability values and removed pixels below that threshold. Next, we weighted each surface by multiplying each pixel by the total number of records during that migration period for that eagle (Palm et al. 2015). We then summed the weighted surfaces for each individual and rescaled the pixel values such that the pixels summed to 1 (Palm et al. 2015). Once we had one OD for each study eagle, we repeated the weighting and scaling process to derive one population-level probability density surface. Last, we binned each nonzero pixel of the final surface into 10 equal-area bins, with 10 representing pixels with the highest probability of use (top 10%), and 1 representing the lowest (Morris et al. 2016).

We measured the fidelity of individual eagles to their previous migration routes using the 95% OD surfaces from above. Using individuals for which we had more than one complete migration period, we calculated the percent overlap of migration routes in consecutive years of tracking (e.g., tracking yr 1 and 2, yr 2 and 3, yr 3 and 4) by overlaying the 95% OD surfaces and tallying the number of pixels that overlapped between years. To calculate the percent overlap, we divided the number of overlapping pixels by the total number of nonzero pixels in both years, subtracting the area of overlap so as not to double-count the overlapped area.

To test the hypothesis that individuals would show higher within-individual fidelity than across-individual fidelity, we simulated a distribution of 95% OD overlap values under the null hypothesis that eagles do not display intra-individual fidelity to migration routes and stopover locations over multiple years. If the null hypothesis were true (for example, if all eagles move north and generally select habitat with water, but do not return to specific features or pathways as they become familiar with the landscape), we expect intra-individual overlap values to fall to within the distribution of the null model. To simulate the null model, we used the same steps as above to calculate the overlap between every pairwise combination of complete eagle migrations, excluding combinations where the individual was paired with itself. We then compared the median, middle 50%, and middle 95% of overlap values from the null model with the overlap values from the multi-year, individual analyses.

Stopovers. To identify Bald Eagle stopover locations during migration, we calculated the distances between daily locations for each eagle. When the distance between consecutive daily locations was less than 20 km, we considered that day to be a stopover. We selected 20 km based on the distances between points that fell along stable (i.e., flat or unchanging) section of the NSD plots. We determined the duration of each stopover and calculated the number and proportion of migratory days that the individual was at a stopover. To visualize important stopover locations, we mapped and examined the locations of stopovers that lasted for ≥10 d. Because the eagles were highly mobile and frequently used multiple long-duration stopover locations during the summer, we use the term "stopover" for each location rather than labeling certain areas as representing "nonbreeding grounds" or "nonbreeding territories."

To characterize the habitat characteristics of prominent stopover locations, we extracted and examined the proportion of land cover within 1195-m-radius circular buffers around each daily GPS point during a ≥10-d stopover. We used the 30-m resolution 2021 National Land Cover Database (NLCD; Homer et al. 2012) to extract land cover values. We chose 1195 m as the buffer radius because it represented the median distance eagles traveled between consecutive daily fixes during a stopover. We combined NLCD classes into the following categories: shrub (class 52), forest (classes 41, 42, 43), herbaceous (class 71), wetland (classes 90, 95), urban (classes 21, 22, 23, 24), open water (class 11), pasture (class 81), and agriculture (class 82). Because the NLCD covers only the United States, we excluded stopover locations in Canada and Mexico for the habitat analyses.

RESULTS

Each of the 24 tagged nestlings fledged, survived the post-fledging dependency period, and departed from its natal site. Seven of these individuals died during the study (five during their first year), eight had GPS transmitters that were assumed to have failed (five during their first year), and nine were alive and transmitting locations in August 2023 when we downloaded data for the current analyses. No individuals tagged as nestlings became breeders during the tracking study. The adult male (eagle 20A01) did not breed during the 3 yr that we tracked him, having been ousted from his nesting territory during incubation, shortly before receiving a GPS tag. However, subsequent to our data compilation for this report, this eagle found a new mate, built a new nest, and established a new breeding territory at Watson Lake, AZ.

Movement Patterns. Most individuals exhibited migratory behavior, wherein they made regular seasonal movements. Twenty-four of 25 individuals, including the tagged adult, made obvious departures from their natal or banding area in the spring or summer after receiving their GPS tag (Fig. 1a, 1d; Supplemental Material Fig. S1–S7). One individual (eagle 17J27), tagged in 2017, remained within 225 km of its natal nest (i.e., within north-central Arizona, with a 1-d excursion into southern Utah) until its death on 5 September 2018. During the 443 d that this individual was tracked, it showed no obvious pattern of seasonal movement (Fig. 1b, 1e). We excluded this eagle from analyses of migration routes and stopover locations.

Eagle migrations were generally characterized by eagles traveling north in the boreal spring and south in the boreal fall. The eagles frequently began migration with rapid and direct movements from Arizona until reaching a northern terminus, at which point their movements became less extensive and less directional. Eagles moved between various stopover locations throughout the summer and returned to Arizona in the fall after several days of rapid movements to the south (Fig. 1a, 1d, S1–S7).

Of the 16 fledglings and one adult that survived their first migratory phase after tagging and retained functioning GPS tags, all but one fledgling returned to Arizona the following breeding season (Fig. 1a–1c, S1–S7). Three first-year eagles that returned to Arizona during the breeding season (eagles 18J08, 22J07, and 22J08) spent a substantial portion of that season in northern Mexico. Eagle 18J08 survived an additional year to the following breeding season (age 2) and remained in Arizona during that time.

The surviving fledgling (eagle 18J33) that never returned to Arizona during this study appeared to have emigrated to northern California (Fig. 1c, 1f). Hatched near Cataract Lake in Kaibab National Forest in 2018, this female eagle fledged prematurely, was rescued and rehabilitated for 6 d at Liberty

Wildlife Rehabilitation Center, was returned to her nest on 8 June, and dispersed from her natal site on 10 August 2018. She then undertook a long movement phase, initially traveling through Colorado, Nebraska, South Dakota, North Dakota, Kansas, Missouri, Arkansas, and Oklahoma (Fig. 1c). By April 2019, she had moved north into Manitoba, Saskatchewan, and Alberta before moving south through Montana, Idaho, Utah, and Nevada. Then, in 2020, she moved west to northern California and spent the next 3 yr in areas around Shasta-Trinity National Forest, Modoc National Forest, and the South Warner Wilderness (Fig. 1c). This eagle died by electrocution in May 2022 (K. Rogers, California Department of Fish and Wildlife, pers. comm.) at 4 yr old and was not known to have a nesting territory. Because she did not exhibit well-defined migratory periods, we excluded this eagle from further analyses of migration routes and stopover locations.

Migration Phenology. Recent fledglings departed from their natal territory and began spring migration as early as 5 May and as late as 1 August (Fig. 2, Table 1). The average date of fledgling departure across all years was 19 June ± 19.4 d ($n = 22$ fledglings). Fledgling age at departure averaged 18.4 ± 1.9 wk (range 13.9 to 22.4 wk, $n = 23$), and the duration of post-fledging dependence periods averaged 51.2 ± 13.5 d (range = 19–75 d, $n = 22$). After-first-year (AFY) eagles migrated, on average, 9 d earlier than recent fledglings ($\beta = -9.35$, 95% CI: −14.20, −4.59, $n = 47$ departures; Table 1) and their movement phenology was less synchronous. Across all years, AFY eagles began spring migration as early as 10 April and as late as 30 May (Fig. 2), with an average departure date of 2 May (95% CI = 24 April–9 May, $n = 25$ departures). AFY eagles also reached their maximum distance from Arizona, on average, 34 d earlier than recent fledglings ($\beta = -33.94$, 95% CI: −62.65, −5.75, $n = 29$ complete migrations; Table 1). The mean date of maximum distance from origin was 12 July (95% CI = 4 July–20 August) for AFY eagles and 16 August (95% CI = 3–28 August) for recent fledglings (Fig. 2). AFY individuals were also less synchronous in their migratory phenology than recent fledglings, reaching their maximum distances from Arizona across a range of dates (23 April–20 September) that was more than twice as broad as for recent fledglings (4 July–16 September; Fig. 2).

Southward return dates did not vary significantly with age or age class (Table 1), and we therefore grouped all individuals to calculate summary metrics. The average return date for southward migrations in the boreal fall was 30 October (95% CI = 29 September–3 December, $n = 29$ migrations), with the observed end dates ranging from 27 August of the current calendar year to 23 April of the following calendar year. Males and females did not differ in their migration phenology (Table 1).

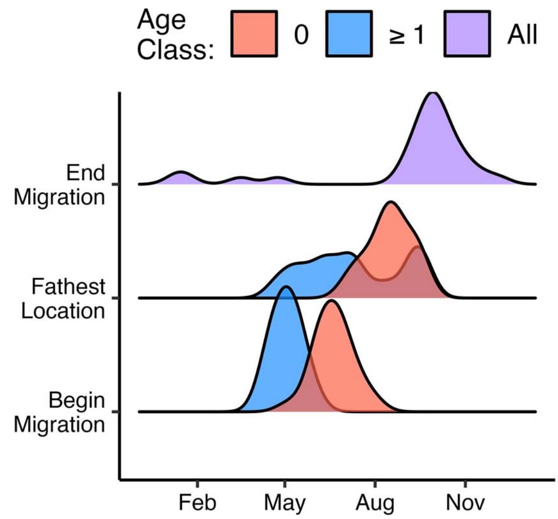

Figure 2. Density plots showing the annual migration phenology of Bald Eagles originating in Arizona, USA. Migratory events shown are (1) dates of departure for northern migration (begin migration), (2) the dates when individuals reached the maximum distance from their banding location (farthest location), and (3) the dates when individuals ended their southern migration in the boreal fall (end migration). When linear regressions estimated a significant difference between the phenology of first-year (age 0) and after-first-year (age ≥1) eagles, we plotted separate density curves for the two groups.

Migration phenology varied across years and individuals. In general, however, few tagged eagles were present in Arizona during July and August, whereas eagles were most commonly in Arizona during January, February, and March (Fig. S8–S10).

Migration Routes and Movement Metrics. The dBBMM results illustrated two primary migration routes for Arizona Bald Eagles. Eagles most commonly moved along the Wasatch Mountains through central Utah and the Rocky Mountains in southern Idaho (Fig. 3). The second most apparent route was concentrated in western Utah, eastern Nevada, and the Rocky Mountains in western and northern Idaho. A third, less pronounced route appeared along the Rocky Mountains, through Colorado and Wyoming. In addition, 10 eagles traveled to areas in the Pacific Northwest, including Oregon, Washington, USA, and British Columbia, Canada.

Table 1. Model outputs from linear mixed effects models testing for a relationship between phenology, movement metrics, age (continuous 0–7 yr), age class (binary, first year [FY] and after first year [AFY], and sex. Estimates whose 95% confidence intervals (CI) do not cross zero are highlighted with bold text.

Response Category	Response	Fixed Effect	Estimate	SE	2.5% CI	97.5% CI	Number of Migrations (*n*)
Phenology metrics	Date of departure (begin migration)	**Age**	**−9.350**	**4.745**	**−14.198**	**−4.595**	**47**
		Age class (AFY effect)	**−47.825**	**4.882**	**−57.382**	**−38.269**	
		Sex (male effect)	5.098	8.607	−11.751	21.948	
	Date of reaching maximum migration distance	**Age**	**−9.617**	**4.245**	**−18.023**	**−1.305**	**29**
		Age class (AFY effect)	**−33.936**	**14.328**	**−62.655**	**−5.747**	
		Sex (male effect)	10.991	17.965	−25.513	46.451	
	Date of return (end migration)	Age	−6.485	5.686	−17.863	4.734	29
		Age class (AFY effect)	−10.078	15.263	−42.421	20.005	
		Sex (male effect)	−56.385	31.784	−118.501	5.291	
Movement metrics	Maximum distance from origin	**Age**	**−0.245**	**0.109**	**−0.467**	**−0.005**	**29**
		Age class (AFY effect)	−0.565	0.338	−1.249	0.097	
		Sex (male effect)	0.320	0.496	−0.642	1.312	
	Maximum latitude during migration	Age	−0.799	0.425	−1.682	0.217	29
		Age class (AFY effect)	−1.625	1.287	−4.147	0.998	
		Sex (male effect)	1.760	1.916	−1.952	5.589	
	Cumulative distance during migration	**Age**	**−4.294**	**1.547**	**−7.325**	**−1.251**	**29**
		Age class (AFY effect)	**−14.721**	**3.800**	**−23.104**	**−7.288**	
		Sex (male effect)	8.577	8.338	−7.584	25.029	

Eagles generally remained west of 107° W longitude (i.e., the Great Plains), except for female 18J33 who never returned to Arizona (Fig. 1c). Among complete migrations, the highest latitude an eagle reached was 52.36469°N (male eagle 21J06; Fig. S5). This individual was tagged in 2021 and traveled through Utah, Idaho, Oregon, Washington, and to the coast of British Columbia before returning to Arizona (Fig. S5). The mean maximum latitude reached by tracked eagles was 45.11270°N ± SD = 2.23° ($n = 29$ complete migrations by 16 eagles) and did not differ across age or sex classes (Table 1).

The mean distance between daily locations during migration of 24 eagles varied from 3.1 ± 1.2 km on stopover days ($n = 5612$ d) and 102.0 ± 8.1 km on movement days ($n = 1305$ d). With stopover and movement days pooled, the mean daily travel distance was 25.5 ± 7.1 km ($n = 6917$ d).

The farthest an individual moved from its natal nest or banding site (for the adult) was 2465 km (bird 21J06; Fig. S5). Recent fledglings flew farther from their origin location ($\beta = -0.565$, 95% CI: –1.249, 0.097, $n = 29$ complete migrations) and traveled greater cumulative distances ($\beta = -14.721$, 95% CI: −23.104, −7.288, $n = 29$ complete migrations) than older individuals (Table 1). The mean maximum distance traveled was 1429 ± 484 km for recent fledglings ($n = 15$ complete migrations) and 1153 ± 90 km for AFY eagles ($n = 14$ complete migrations). The mean cumulative distance traveled was 5369 ± 2658 km for fledglings (average rate of 47 km/d, $n = 15$ complete migrations) and 4877 ± 2122 km for AFY eagles (29 km/d, $n = 14$ complete migrations). The movement metrics of male and female eagles did not differ significantly (Table 1).

We tracked five recent fledglings and one adult for more than one full migration period. Spatial overlap among migrations routes traveled in consecutive years by the same eagle averaged 31.8 ± 15.5% (range = 9.1–61.2%; Fig. 4). Between eagles, under our null hypothesis that eagles showed no intra-individual tendency toward overlapping migration routes, the mean percent overlap was 12.5 ± 9.6% (range = 0–49.9%, $n = 383$; Fig. 4). This across-individual mean is lower than the within-individual mean, but we note that several within-individual overlap values fell within the 95% CI of the null model (0–33.1%). Notably, five of six overlap values between the first and second year of tracking overlapped with the null model, whereas all three overlap values between the third and fourth year were above the upper CI of the null model distribution. Adult 20A01 carried a transmitter for three full migrations when 5–7 yr old and displayed higher

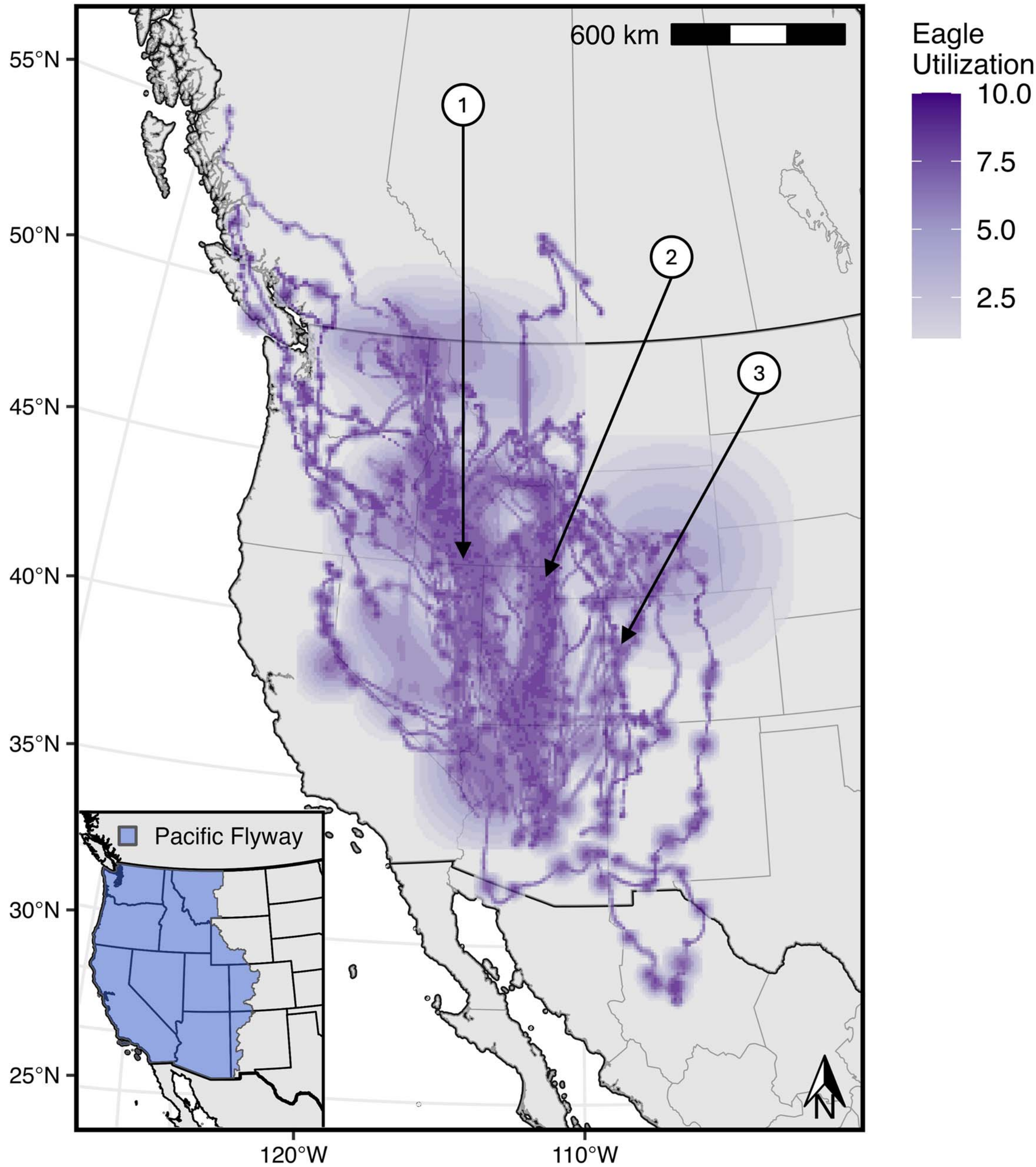

Figure 3. Utilization distribution map of Bald Eagles originating in Arizona, USA, during their migration and nonbreeding seasons. High eagle utilization values indicate areas with the highest probability of use, and lower values indicate a lower probability of use. The numbered arrows point to prominent migration routes through (1) western Utah, eastern Nevada, and western Idaho; (2) central Utah and eastern Idaho; (3) western Colorado and Wyoming. The inset shows the US Fish and Wildlife Service administrative boundaries of the Pacific Flyway.

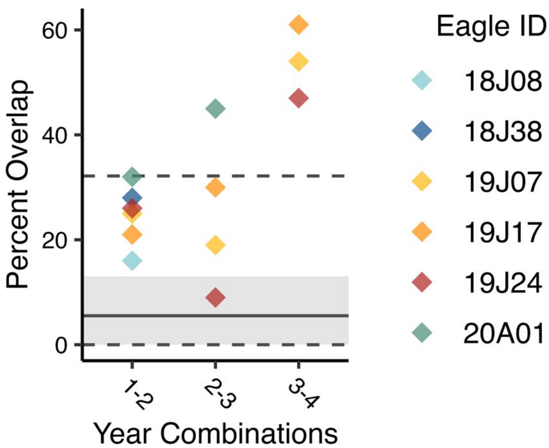

Figure 4. Percent overlap of consecutive migrations made by six Bald Eagles from Arizona, USA. Year combinations indicate overlap between the first and second, second and third, and third and fourth migration years (i.e., eagle years) that the eagle was tracked. The solid horizontal line shows the median percent overlap when eagle-year pairs involved distinct eagles (null model), the gray ribbon shows the middle 50% of overlap values in the null model, and the dashed horizontal line shows the middle 95% of overlap values in the null model.

fidelity than younger individuals in each of the consecutive-year combinations during which it was tracked (i.e., between tracking yr 1 and 2 and between tracking yr 2 and 3).

Stopovers. Stopover durations ranged from 1–122 d. On average, eagles spent 79.1 ± 4.5% of their days during migration at stopover locations ($n = 29$ migrations, 16 individuals). The percent of migration days that eagles spent at stopover locations increased with age ($\beta = 0.022$, 95% CI: 0.007, 0.037, $n = 29$ complete migrations) and age class (i.e., first year versus AFY; $\beta = 0.076$, 95% CI: 0.039, 0.115, $n = 29$ complete migrations).

We identified 109 "prominent" stopover locations where individual eagles remained for ≥10 d (Fig. 5). Two prominent stopover locations were in Mexico, three were in Canada, and 104 were in the USA. Overlap of individuals at specific stopover locations was generally low, but several bodies of water did serve as stopover locations for multiple birds. Such locations included Island Park Reservoir, ID ($n = 2$ eagles), Sheridan Reservoir, ID ($n = 2$ eagles), Blackfoot Reservoir, ID ($n = 3$ eagles), Lake Cascade, ID ($n = 2$ eagles), Johnson Valley Reservoir, UT ($n = 2$ eagles), and Crawford Thompson Canal, UT ($n = 2$ eagles). Within the USA, stopover locations were most frequent in areas with large amounts of surrounding shrub and forest land covers (Fig. 6). In addition, most eagles used stopover locations within 1.2 km of water or wetlands, although 4 (4%) and 2 (2%) buffered stopover locations had no open water or wetlands within 1.2 km, respectively.

DISCUSSION

We found that juvenile, subadult, and adult Bald Eagles tracked from Arizona consistently migrated north in boreal spring and summer and returned south in the boreal autumn before the breeding season. Eagles migrated along a broad front through Utah, Nevada, Colorado, Wyoming, Montana, Idaho, California, Oregon, Washington, and British Columbia, largely moved along mountain ranges, and made stopovers near rivers, lakes, and other water sources. While most eagles undertook seasonal migrations, one fledgling did not appear to migrate and remained within 225 km of its natal territory for the 443 d that it was tracked. Another individual roamed widely throughout the west-central United States and Canada before appearing to settle in northern California. Eagle migrations appeared to become more direct and efficient with age, with older individuals traveling shorter cumulative distances, spending more time in stopover locations, and possibly exhibiting higher route fidelity than recent fledglings.

The migration paths of individuals in our study align with the migration paths of 10 Arizona fledglings tracked between 1987–1989 using VHF telemetry (Hunt et al. 2009). Both studies demonstrated use of several common stopover locations (e.g., Lima Reservoir, MT, Blackfoot Reservoir, ID, and Yellowstone Lake, WY). By evaluating the movements of 25 additional eagles using GPS telemetry, more than 30 yr later and representing a broader range of ages, our study enhances understanding of the movement ecology of Bald Eagles in Arizona and further confirms that individuals within southern-latitude populations of Bald Eagles in North America commonly undertake northward, rather than southward, migrations.

As expected, most prominent stopover locations (98%) were near open water or wetland areas, which likely provide Bald Eagles with opportunities for hunting and scavenging. Stopover locations were most frequently in areas with large amounts of surrounding shrub and forest land covers (Fig. 5), but we note that these two land cover classes were also the most widely available across areas used by the eagles in our study. The high use of shrub and forest land cover classes may therefore simply reflect their greater availability to Bald Eagles in western North America.

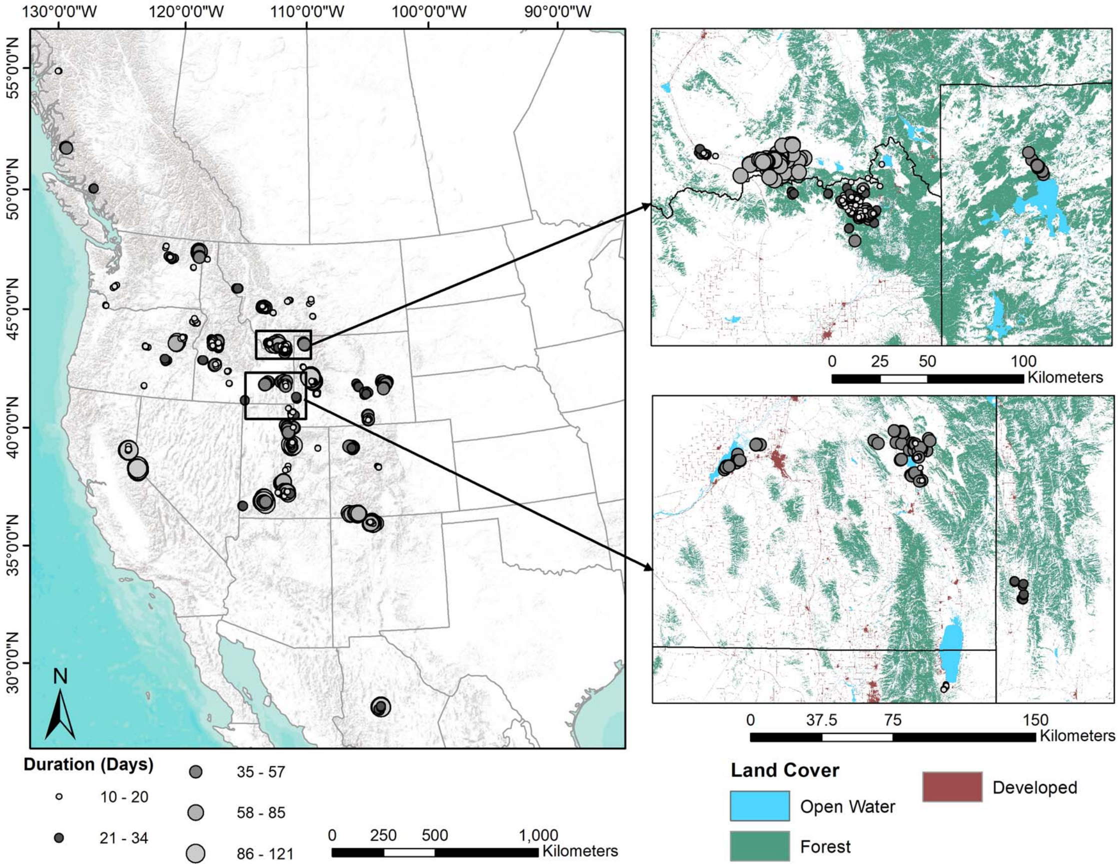

Figure 5. Prominent stopover locations of Bald Eagles migrating from Arizona, USA, between 2017 and 2023. Points denote areas where migrating eagles spent ≥10 d without moving greater than 20 km. Point size scales with stopover duration.

Although the sample of individuals for which we had multiple complete migration paths was small, our results provided preliminary evidence that Arizona Bald Eagles show fidelity to migration paths across years and that fidelity may increase with age. This pattern is consistent with the hypothesis that eagles become more familiar with potential migration routes over time and tend to settle into a relatively stable and regularly used route. Additional research is needed, however, to test this hypothesis. Fidelity to migration routes and nonbreeding sites is shown in other avian species (Newton 2008, Phillips et al. 2017, Koczur and Ballard 2022) and we encourage comprehensive studies on this subject for Bald Eagles to better understand the prevalence of this pattern and the extent to which migration route fidelity has positive fitness benefits (e.g., increased access to prey resources, reduced energy expenditure).

Northward Migrations. Nonbreeding migration of Bald Eagles to the north instead of to the south was first described for eagles breeding in Florida, USA (Broley 1947, Mojica et al. 2008), and has since been documented in populations from other states including California (Hunt et al. 1992b), Texas (Mabie et al. 1994), Arizona (Hunt et al. 2009), Maryland (Mojica et al. 2016), and Kentucky (Slankard et al. 2022). This migration behavior, though relatively common among Bald Eagles, is generally uncommon among migratory birds (Newton 2008). Other flying species that have exhibited this behavior in the northern hemisphere include Red-tailed Hawks (*Buteo jamaicensis*) breeding in southern California (Bloom et al. 2015), Cooper's Hawks (*Accipiter cooperii*) in southern California (Bloom et al. 2017), Long-legged Buzzards (*Buteo rufinus*) breeding in Israel (Friedemann et al. 2020), and tricolored bats (*Perimyotis subflavus*) breeding in Florida (Smith et al. 2022). In each case, the population breeds near the southern extent of its species' distribution. Comparative studies of populations

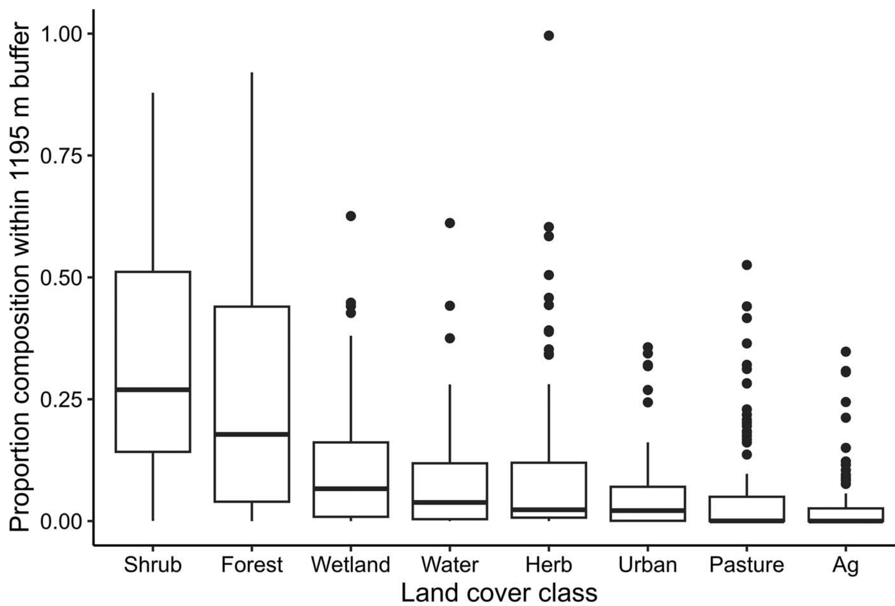

Figure 6. Proportion of land cover classes within a 1195-m-radius circular buffer around prominent migration stopover locations within the USA ($n = 104$), for juvenile and subadult Bald Eagles tracked from Arizona, USA. Land cover classes were derived from the 2021 National Land Cover Database: Herb = herbaceous land covers; Ag = agricultural land covers.

breeding at low latitudes relative to the rest of their species can provide insights into the development, costs, and benefits of this adaptation.

Bald Eagles are facultative, partial migrants that exhibit various annual movement strategies, including migratory, nomadic, and sedentary behavior (Wheat et al. 2017). Differences among populations are likely driven by climate and abundance of year-round resources, while differences among individuals within a population can reflect factors such as age, sex, breeding status, and competition with conspecifics (Fudickar et al. 2021). The Bald Eagle population in Arizona presumably migrates northward and spends the nonbreeding season in the northwestern United States and southwestern Canada to access food resources that are currently and/or were historically present during spring and summer, including spawning salmon, nesting waterfowl, and ungulate carcasses to scavenge (Hunt et al. 2009).

For breeding adults with nesting territories, it may be advantageous to move north during the nonbreeding season so as not to deplete resources in and around their nesting territories, particularly in years of low food availability (McCrary et al. 2019). Although none of the eagles we studied bred while being tracked, the adult male that previously bred did make regular migrations during each of the 3 yr it was tracked (at age 5, 6, and 7). This suggests that migratory movements may not halt once an eagle reaches breeding age or status. Future studies of nonbreeding-season movements of Arizona Bald Eagles with established nesting territories would help determine if breeders exhibit similar migration patterns to pre-breeders and floaters.

Despite the unusual northward, nonbreeding behavior exhibited by Bald Eagles banded in Arizona, the pathways that the eagles used during migration were spatially similar to the pathways followed by other migrating raptors in western North America. The Pacific Flyway is an administrative delineation used by the US Fish and Wildlife Service that encompasses the migration routes of several taxa of western birds. Hoffman et al. (2002) used discriminant functions to further delineate the Pacific Flyway based on the migratory movement of five raptor species (Sharp-shinned Hawk [*Accipiter striatus*], Cooper's Hawk, American Goshawk [*Accipiter atricapillus*], Red-tailed Hawk, American Kestrel [*Falco sparverius*]). The majority of Bald Eagle movements we observed aligned well with the flyway described by Hoffman et al. (2002) as the Intermountain Flyway, which ranges from Alaska to Mexico east of the Sierra Nevada and west of the Rocky Mountains and Sierra Madre Occidental.

Five birds moved outside of this range: two farther east along the Rocky Mountains within the Rocky Mountain Flyway and three farther west along the coasts of Washington and British Columbia within the Pacific Coast Flyway (Hoffman et al. 2022).

Return to Arizona and Emigration Dynamics. The population of Bald Eagles in Arizona has been considered demographically closed in previous studies, with rates of immigration or emigration to other states assumed to be negligible (Allison et al. 2008, Cappello et al. 2024). Since intensive studies and banding of the Arizona population began in the 1980s, there has been only one known instance of a Bald Eagle that hatched in another state (Texas) and recruited to the Arizona breeding population, and only three instances where Arizona-hatched eagles have been observed breeding in another state (two in California at similar latitudes to nesting territories in Arizona, and one in Utah).

The isolation of the Arizona population is likely due to the limited surface water in the southwestern USA and northern Mexico, resulting in low availability of suitable habitat in much of the region and a concentration of eagles in central Arizona near the confluence of the Salt and Verde Rivers. However, as the Arizona Bald Eagle population continues to grow, competition for nesting territories may increase, leading to greater numbers of nesting territories outside of central Arizona (e.g., areas along the Colorado River; McCarty et al. 2022). Under this scenario, the assumption of demographic closure may become increasingly tenuous. In this study, we saw evidence that 1 of the 24 (4%) Bald Eagles tagged as nestlings was likely to recruit as a breeder in northern California, but this eagle's premature mortality from electrocution prevented verification. We also note that several 1-yr-old eagles spent substantial time during the breeding season in northern Mexico. Of those eagles, one survived until the following year (age 2) and spent the breeding season in Arizona where there is a small breeding population of Bald Eagles. For the individuals that did not survive until the following year, we cannot rule out that they may have emigrated to sites in Mexico. Although our study overall indicates that most nestlings return to Arizona as subadults, it also suggests a low level of emigration. Sparse banding and monitoring in surrounding states currently limits obtaining a more complete understanding of emigration and immigration rates within Arizona's Bald Eagle population. Monitoring eagles through continued telemetry studies could help quantify these rates and may be more feasible than substantially increasing banding and resighting efforts in Arizona and its surrounding states.

Conclusions and Management Implications. We show that Bald Eagles from Arizona generally follow migratory pathways used by other North American raptors. Our findings also highlight the importance of reservoirs, lakes, and riparian habitat along the Pacific (Intermountain) Flyway. Bald Eagles and other raptors face various mortality risks during migration, including collision with wind turbines (Pagel et al. 2013)) and collisions with and electrocution by electrical infrastructure (Mojica et al. 2020). Identifying high-use stopover locations, migratory pathways, and the landscape features influencing eagle use of those locations are important first steps to evaluating risk posed to migrating eagles by existing or planned energy infrastructure.

SUPPLEMENTAL MATERIAL (available online). Figure S1: Hourly locations of Bald Eagles banded in Arizona, USA between 2017 and 2023. Figure S2: Hourly locations of Bald Eagles banded in Arizona, USA between 2017 and 2023. Figure S3: Hourly locations of Bald Eagles banded in Arizona, USA between 2017 and 2023. Figure S4: Hourly locations of Bald Eagles banded in Arizona, USA between 2017 and 2023. Figure S5: Hourly locations of Bald Eagles banded in Arizona, USA between 2017 and 2023. Figure S6: Hourly locations of Bald Eagles banded in Arizona, USA between 2017 and 2023. Figure S7: Hourly locations of Bald Eagles banded in Arizona, USA between 2017 and 2023. Figure S8: Hourly locations of Bald Eagles banded in Arizona, USA and carrying GPS tags between January and April 2017–2023. Figure S9: Hourly locations of Bald Eagles banded in Arizona, USA and carrying GPS tags between May and August 2017–2023. Figure S10: Hourly locations of Bald Eagles banded in Arizona, USA and carrying GPS tags between September and December 2017–2023.

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