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Research Article

Dispersal and survival of *Aquila fasciata* (Bonelli's Eagle) differ across arid, semi-arid, and Mediterranean natal habitats

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ABSTRACT

Dispersal is an important ecological process influencing population viability, demography, and gene flow. For non-migratory raptors like the *Aquila fasciata* (Bonelli's Eagle), natal dispersal—the movement between the birthplace and the first breeding site—is a critical life stage. However, the role of natal habitat on the dispersal process and its implications for population viability and conservation remains poorly understood. This study examined how natal habitat across three distinct biogeographic regions influences dispersal movement, habitat use and survival of juvenile *A. fasciata* in the Levant (within areas administered by Israel and the Palestinian authority). Using global positioning system (GPS) telemetry, 55 juvenile eagles originating from Mediterranean, semi-desert, and desert habitats were tracked over their dispersal journeys. Key aspects such as dispersal direction, distance, temporary settlement areas (TSAs), territorial recruitment and mortality were analyzed in relation to the natal climatic conditions. Results revealed clear habitat-based differences in dispersal patterns. Desert-hatched eagles dispersed the farthest, with some crossing the Sahara and Arabian deserts to reach sub-Saharan Africa or southern Arabia, while Mediterranean and semi-desert eagles remained more localized. Water bodies acted as barriers, shaping dispersal routes and TSA distribution. Throughout dispersal, eagles occupied areas with precipitation levels similar to their natal sites, supporting natal habitat preference induction (NHPI) hypothesis. Recruitment data further indicated strong fidelity to natal climatic zones, with only 1 out of 11 eagles settling outside its natal zone. Mortality patterns varied by habitat types, with desert-hatched eagles experiencing the highest proportion of deaths outside the study area. These findings underscore the influence of natal habitat on dispersal, highlighting how local environmental conditions shape movement patterns, species distributions, and population trajectories. Understanding these patterns is crucial for raptor conservation, particularly in managing habitat-specific risks and transboundary movements.

Keywords: dispersal movement, habitat use, natal habitat preference, raptor conservation

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LAY SUMMARY

- We studied how young *Aquila fasciata* (Bonelli's Eagle) move from their hatch places until they mature and settle to breed, over a period of 2–4 years.
- Using global positioning system (GPS) tracking, we followed 55 eagles from 3 habitat types—Mediterranean, semi-desert, and desert—to examine their movement and settlement patterns.
- Eagles hatched in desert areas traveled much farther and more directly south, often crossing vast deserts like the Sahara and Arabian.
- Eagles typically settled in habitats resembling their hatch place, suggesting early-life habitat imprinting that influences their long-term behavior.
- These movement strategies affected survival and breeding recruitment, with notable differences in where and how eagles from different habitats died.
- This research provides valuable insights for more effective conservation of endangered *A. fasciata* in harsh and fragmented landscapes, suggesting that conservation efforts need to additionally focus on conserving key movement corridors and settlement areas.

La dispersión y la supervivencia de aquila fasciata difieren entre hábitats natales áridos, semiáridos y mediterráneos

RESUMEN

La dispersión es un proceso ecológico importante que influye en la viabilidad poblacional, la demografía y el flujo génico. Para rapaces no migratorias como ***Aquila fasciata***, la dispersión natal—el movimiento entre el lugar de nacimiento y el primer sitio de reproducción—es una etapa crítica de la vida. Sin embargo, el rol del hábitat natal en el proceso de dispersión y sus implicaciones para la viabilidad poblacional y la conservación sigue siendo poco comprendido. Este estudio examinó cómo el hábitat natal en tres regiones biogeográficas distintas influye en el movimiento de dispersión, el uso de hábitat y la supervivencia de juveniles de ***A. fasciata*** en el Levante (dentro de las áreas administradas por Israel y la Autoridad Palestina). Mediante telemetría GPS, se rastrearon 55 águilas juveniles originarias de hábitats mediterráneos, semidesérticos y desérticos a lo largo de sus trayectorias de dispersión. Aspectos clave como la dirección y distancia de dispersión, las áreas de asentamiento temporal (AAT), el reclutamiento territorial y la mortalidad fueron analizados en relación con las condiciones climáticas natales. Los resultados revelaron

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claras diferencias en los patrones de dispersión según el hábitat. Las águilas nacidas en el desierto se dispersaron más lejos, con algunas cruzando los desiertos del Sahara y de Arabia para llegar al África subsahariana o al sur de Arabia, mientras que las águilas mediterráneas y semidesérticas permanecieron más localizadas. Los cuerpos de agua actuaron como barreras, moldeando las rutas de dispersión y la distribución de las AAT. Durante la dispersión, las águilas ocuparon áreas con niveles de precipitación similares a sus sitios natales, lo que respalda la hipótesis de inducción de preferencia por el hábitat natal. Los datos de reclutamiento indicaron además una fuerte fidelidad a las zonas climáticas natales, con solo 1 de 11 águilas asentándose fuera de su zona natal. Los patrones de mortalidad variaron según el tipo de hábitat, con las águilas nacidas en el desierto experimentando la mayor proporción de muertes fuera del área de estudio. Estos hallazgos subrayan la influencia del hábitat natal en la dispersión, destacando cómo las condiciones ambientales locales moldean los patrones de movimiento, las distribuciones de las especies y las trayectorias poblacionales. Comprender estos patrones es crucial para la conservación de las rapaces, particularmente en la gestión de riesgos específicos del hábitat y de los movimientos transfronterizos.

Palabras clave: conservación de rapaces, movimiento de dispersión, preferencia por el hábitat natal, uso de hábitat

INTRODUCTION

Dispersal is a fundamental ecological process that shapes population viability, demography, distribution and gene flow (Bullock et al. 2002, Clobert et al. 2012). In non-migratory species, natal dispersal, the movement from the hatching site to the first breeding site, usually constitutes the longest displacement an individual undertakes during its lifetime (Greenwood and Harvey 1982, Paradis et al. 1998, Serrano et al. 2021). For large raptors like the *Aquila fasciata* (Bonelli's Eagle), a regionally endangered species, dispersal is prolonged and complex, often lasting several years. Adult *A. fasciata* are highly territorial and sedentary (Morollón et al. 2022), making juvenile dispersal critical for maintaining population dynamics, enabling gene flow and reducing inbreeding.

As the mobile, nonbreeding component of the population, dispersing individuals (commonly referred to as floaters) play an essential role in regulating spatial structure, ensuring demographic connectivity, and replacing lost breeders (Clobert et al. 2012, Dobson 2013, Serrano 2018). These floaters may remain in temporary settlement areas (TSAs) for extended periods, often waiting years for a suitable breeding opportunity to arise (Zuberogoitia et al. 2009). In some raptor species, floaters can comprise >50% of the population (Kenward 2006), and their presence is often indirectly observed through rapid mate replacement following mortality events (Newton 2010, Serrano 2018).

Because dispersing individuals are inexperienced and navigating unfamiliar environments, mortality rates at this stage are exceptionally high, accounting for nearly 90% of species mortality (Real and Mañosa 1997, Real et al. 2001). Understanding dispersal patterns and drivers is therefore crucial for conservation planning. Since many conservation programs focus primarily on breeding areas, they may overlook critical threats during dispersal, such as collisions with anthropogenic structures, habitat degradation, and human persecution (Ferrer and Harte 1997, Serrano 2018). Studying the dispersing individuals can reveal key areas that are important for population persistence, facilitating targeted conservation actions.

Among the key factors influencing dispersal are natal habitat characteristics, which can affect long-term movement patterns, survival, and recruitment (Grande et al. 2009, Penteriani and Delgado 2011, Azpillaga et al. 2018). These factors may affect both ecological mechanisms, such as natal territory quality influencing nestling body condition (Azpillaga et al. 2018), and behavioral mechanisms, such as early-life habitat imprinting (Davis and Stamps 2004). Given that population viability depends on the successful exchange of individuals among subpopulations, natal effects may scale up to influence population and metapopulation dynamics (Hernández-Matías et al. 2013, 2015).

One behavioral mechanism receiving increasing attention is natal habitat preference induction (NHPI), which describes how early experience in the natal environment increases the likelihood of selecting a similar habitat later in life (Davis and Stamps 2004, Stamps et al. 2009). Support for NHPI has been documented in mammals, reptiles, fishes, and birds (Orgeret et al. 2024); but in raptors, evidence remains sparse and inconsistent. Some studies report natal-habitat matching (Faccio et al. 2013, Fletcher et al. 2015, Orgeret et al. 2024) while others do not (Delgado et al. 2010, Brown and Collopy 2013, Serrano 2018). The picture may be further complicated by the possibility that NHPI responses in raptors change over the course of the dispersal process, and that individual variation in NHPI depends on the natal habitat type (Orgeret et al. 2024).

This study investigates how natal habitat influences dispersal behavior, habitat use, and survival in juvenile *A. fasciata* across 3 biogeographic zones that differ markedly in aridity. Using global positioning system (GPS) telemetry, we tracked 55 juvenile eagles from 3 distinct natal habitats (Mediterranean, Semi-desert, and Desert) to assess differences in dispersal onset, direction, distance, use of TSAs, as well as recruitment and mortality. Our findings provide new insights into the role of natal habitat in shaping dispersal strategies, with implications for population management and conservation.

The specific research questions were: (1) How does natal habitat influence dispersal timing, distance and direction? (2) Do *A. fasciata* exhibit NHPI in their choice of TSAs and breeding territories? And (3) are survival rates and mortality events influenced by natal habitats?

If NHPI has no significant impact on eagles' dispersal, no differences are expected between natal habitat groups. Contrastingly, if NHPI does play a role, we expect distinct differences in dispersal routes, TSA selection, survival rates, and recruitment sites among birds originating from different natal habitats. Because bird sex may influence dispersal, with females typically dispersing farther in many raptors (Newton 2010), including *A. fasciata* (Cadahía et al. 2010, Hernández-Matías et al. 2010), we also considered how bird sex might affect dispersal patterns.

MATERIALS AND METHODS

Study Area

This study was conducted in the Southern Levant, within areas administered by Israel and the Palestinian authority. The region exhibits a steep north–south aridity gradient, with annual precipitation ranging from over 1,000 mm in the north to <20 mm in the south, creating 3 major biogeographic zones: (1) Mediterranean woodland and scrubland (34% of the area, largely converted to agriculture); (2) Irano-Turanian semi-arid steppe (~13% of the area); and (3) Saharo-Arabian desert (53% of the area, driest zone) (Yom-Tov and Tchernov 1988, Sorek and Shapira 2018).

These zones align with the Koppen-Geiger climate classification (Peel et al. 2007): Mediterranean (Csa): hot-summer

Mediterranean climate; Semi-arid zone (BSh): hot semi-arid climate; and Desert (BWh): hot desert climate. The area is highly populated, particularly in its central and northern regions (~400 people km^{-2}; Sorek and Shapira 2018). Despite its small population (~25 breeding pairs), *A. fasciata* inhabit the entire aridity gradient (Figure 1), making this an ideal "natural laboratory" for studying NHPI effects on dispersal.

Study Species

Aquila fasciata is a medium-sized raptor with a distribution spanning Southeast Asia, the Middle East and the Western Mediterranean (Orta et al. 2020). Although globally listed as Least Concern, its populations are declining due to habitat degradation, prey depletion, electrocution and persecution (BirdLife International 2024).

In the study area, the population has declined from ~60 breeding pairs (1950s) to 15–25 pairs in the last decade (Leshem 1976, Shirihai et al. 1996, Mayrose et al. 2019) and the species is listed as regionally Critically Endangered (Mayrose et al. 2017).

Aside from early work on basic life history (Leshem 1976, Shirihai et al. 1996), *A. fasciata* in this region have received little scientific attention. To the best of our knowledge, their movement patterns in arid and desert environments, which

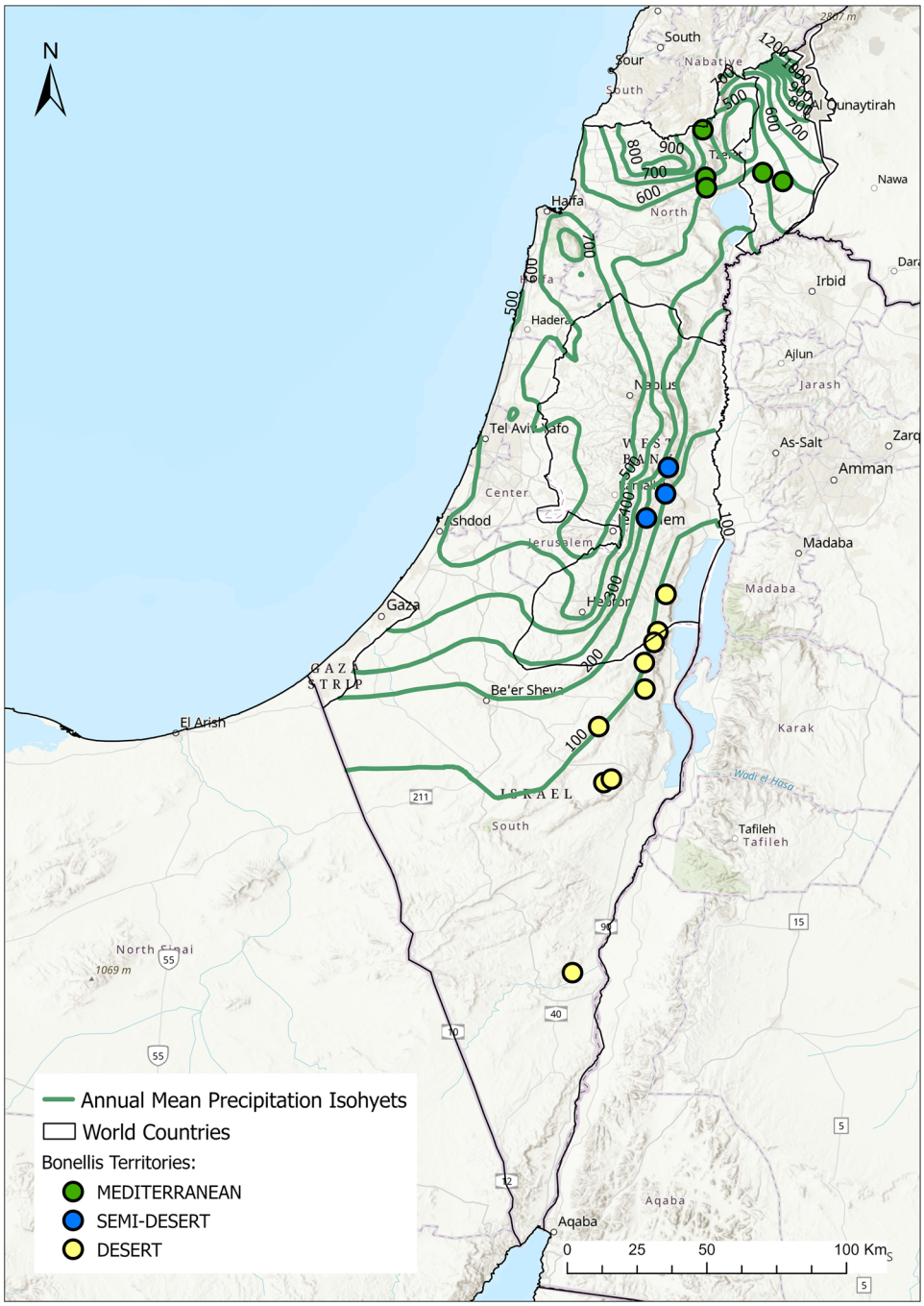

FIGURE 1. Map of the study area. Natal sites of the tagged *A. fasciata* are indicated by colored circles. Green lines delineate mean annual precipitation Isohyets, 100-mm resolution (Israel Meteorological Service 2024).

constitute a substantial portion of the species' range, remain largely undocumented.

The life cycle of *A. fasciata* is composed of 2 major stages, each characterized by distinct behavior. Adults (typically ≥3-year-old) are sedentary, with strong site fidelity and territoriality (Bosch et al. 2010, Martínez-Miranzo et al. 2016, Morollón et al. 2022), while juveniles are highly nomadic and show no territorial behavior (Real and Mañosa 2001, Cadahía et al. 2010, Hernández-Matías et al. 2010). The dispersal period begins at the age of 163 ± 17 days and lasts until the birds become territorial, at least 2 years later (Real et al. 1998, Minguez et al. 2001). During this period, juveniles temporarily settle in TSAs, before recruitment into breeding populations (Cadahía et al. 2009, Balbontín and Ferrer 2009). TSAs are typically lowland agricultural regions outside of core breeding areas and thus dispersing juveniles are segregated from territorial adults. These areas are characterized by high prey availability and low levels of competition, offering relatively safe foraging grounds for inexperienced individuals (Azpillaga et al. 2018, Real and Mañosa 2001, Serrano 2018).

In the Iberian Peninsula, *A. fasciata* disperse an average of 356 ± 156 km from their natal sites (Hernández-Matías et al. 2010, Cadahía et al. 2010). However, recent GPS telemetry data have revealed exceptional long-range dispersal, including movements from Spain to Morocco (Life Bonnelli Project 2024; https://www.lifebonelli.org/index.php/en/) and from the Aegean islands to Central Europe and East Africa (Life Bonelli EastMed 2024; https://www.lifebonelli.eu/en/). This wide variability in dispersal behavior, from localized settlement to transcontinental movements, makes *A. fasciata* a valuable model for investigating the ecological and behavioral drivers of dispersal, including NHPI.

Location and Movement Data Collection

Between 2018 and 2023, 59 nestlings were tagged with 30-g solar-powered GPS-GSM transmitters (Ornitela OT-30). The total mass of the transmitter, including the Teflon-silicone harness, was <3% of body mass, adhering to recommended limits (Kenward 2002). Tagging occurred when nestlings were 45–60 days old, using a pelvic harness (Anderson et al. 2020). Bird sex was determined by body mass and morphometrics (Palma et al. 2001, Estellés-Domingo and López-López 2023). GPS and other sensors (tri-axial accelerometer, thermometer) sampling frequency was set to 15-60 min, depending on battery level. All data were standardized to 60-min intervals, and all eagle tracks were visually inspected to ensure there were no inaccurate locations, identified as points inconsistent with the eagle's flight path or movement speed.

Tagging was conducted under Israeli Nature and Parks Authority permit (2495/2018), and data were archived in Movebank (study 108979007).

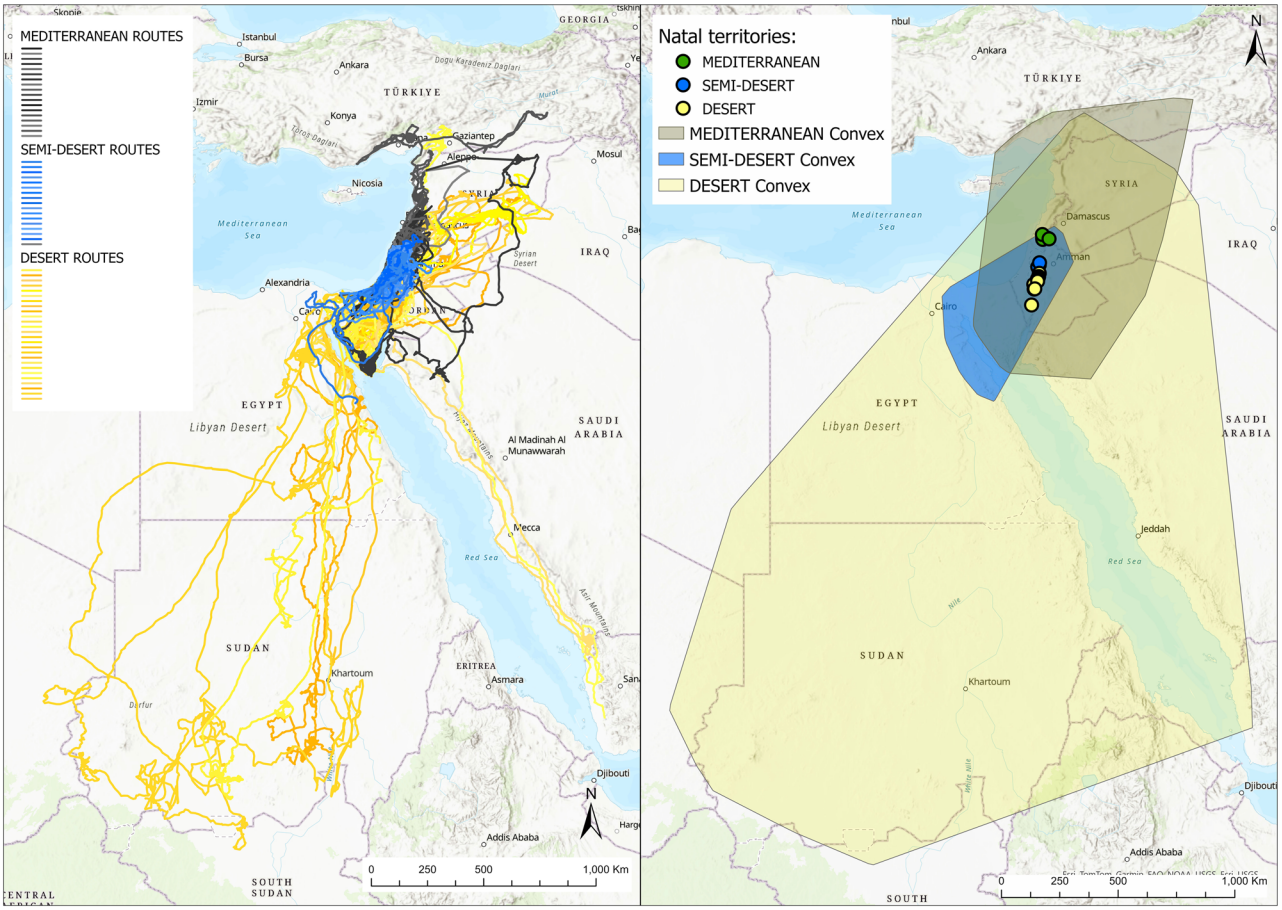

FIGURE 2. (left) Raw dispersal trajectories of 55 juvenile *A. fasciata* from the 3 natal habitat groups: Mediterranean (dark grey), Semi-desert (blue) and Desert (yellow and orange). (right) Natal territories (color circles): Mediterranean (dark green), Semi-desert (blue) and Desert (yellow) and 100% Minimum convex polygon encompassing all the dispersal locations of each eagle group.

Grouping Eagles by Biogeographic Zones and Characterizing Habitats Along Dispersal Routes

To assess if the natal habitat influenced the dispersal properties, tagged eagles were classified into 3 groups based on their natal site annual precipitation (Yom-Tov and Tchernov 1988, Huang et al. 2016): Mediterranean (>400 mm), Semi-desert (200–400 mm), and Desert (<200 mm). This classification follows a north-south aridity gradient and was determined using a spatial precipitation dataset (1991–2020, 1-km resolution) from the Israel Meteorological Service (2024). Noteworthy, this aridity gradient is rather steep, such that distances between Semi-desert and the nearest Mediterranean or Desert sites were relatively short (103.1 and 29.7 km, respectively).

To characterize eagles' habitat use during dispersal, mean annual precipitation was calculated for each GPS location using the CHELSA BioClim v2.1 dataset (1981–2010), 30 arc-s resolution, ~1 km at the equator (Karger et al. 2017). We selected mean annual precipitation as our sole habitat variable because it provides a continuous, spatially consistent, and temporally stable climatic measure suitable for comparisons across regions and seasons. This metric is ecologically relevant to prey availability and movement patterns and aligns with the aridity-based classification of natal sites, enabling consistent habitat characterization throughout the dispersal phase.

Mortality Detection and Investigation

Eagle mortality events were detected through continuous telemetry monitoring, based on static GPS locations (>24 hr at one point), stable body position (indicated by at least 3 consecutive accelerometer readings), and abnormal tag temperature readings. When possible, carcasses were located in the field and the cause of death was determined through external examination (e.g., singed feathers and burnt skin in the case of electrocution), or through x-rays and post-mortem necropsy when the cause of death was not clearly identified. Because many deaths occurred in inaccessible areas, remote investigation relied on

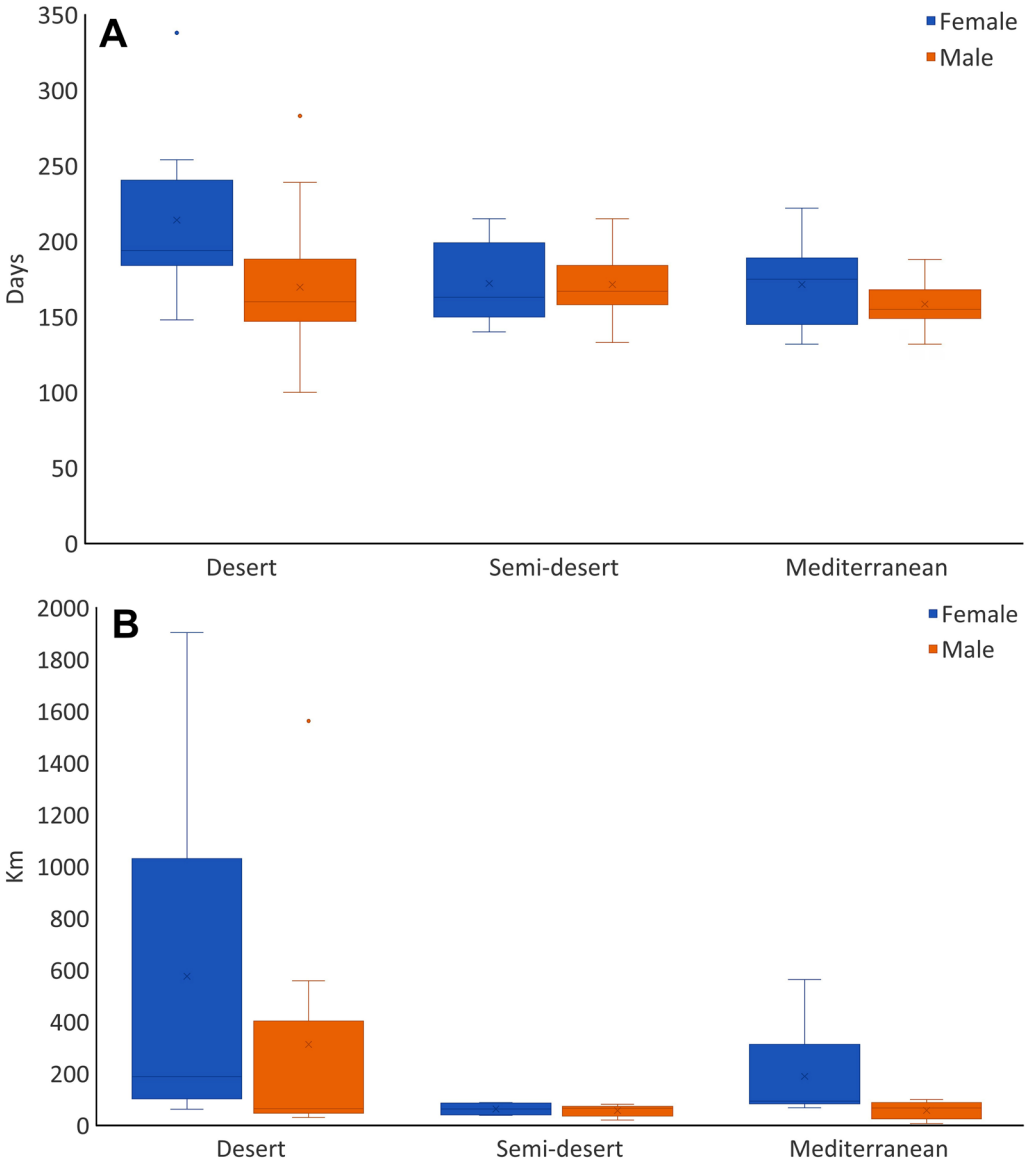

FIGURE 3. (**A**) Dispersal onset age (days) for each eagle natal habitat group. (**B**) Mean temporary settlement area (TSA) distance (km) for each eagle natal habitat group. Boxplots represent median (mid-box line), mean (X), 25% and 75% quartiles (box edges) and 5%, 95% of the data (whiskers).

orthophoto imagery and ground-level images (Google Earth, Google Maps) to assess likely mortality causes, such as electrocution, collision, drowning, or road-kill incidents.

The mortality analysis was restricted to the dispersal phase and therefore included only events that occurred after dispersal onset and before territorial recruitment.

Identification of Recruitment Events

Recruitment into the breeding population was determined using telemetry data and field observations. GPS data from 2nd year eagles and older were routinely examined to identify potential recruitment events, indicated by clustered fixes near suitable breeding sites. Recruitment was confirmed by field visits, where individuals exhibited territorial behaviors such as courtship displays, mating, nest construction or direct involvement in breeding activities such as incubation or feeding young.

Data Processing

Mean daily distance and direction relative to natal site

The direction and distance of each GPS fix relative to the natal site were calculated using the *Geosphere* (Karney 2013) and *adehabitatLT* (Calenge 2011a) R packages. To account for irregular sampling intervals, the *Zoo* package (Zeileis and Grothendieck, 2005) was used to interpolate missing daily locations and to generate continuous time series of distance data, which were used for visualization. The mean daily location of each individual relative to its natal site was calculated by averaging the latitude and longitude of all GPS fixes collected for that individual on a given day. This mean daily position was then used to compute the Euclidean distance and bearing from natal site. These daily values were then used to calculate group-level averages for each natal habitat group, enabling comparisons of dispersal distance and direction across time and groups.

To facilitate comparison of movement patterns across individuals hatched in different calendar years, tracking data were aligned relative to January 1st of each individual's hatch year. Specifically, January 1st of the hatch year was designated as day 1, January 1st of the second calendar year as day 366, and so on. This temporal alignment enabled the visualization and analysis of dispersal trajectories, regardless of hatch year (see Figures 4 and 5). This approach was validated after confirming that birds' hatch year had no significant effect on dispersal characteristics when included as a random effect in the linear models, as indicated by zero or negligible variance explained by this factor.

Defining dispersal onset age and temporary settlement areas (TSAs)

Dispersal onset was defined as the first day an eagle was recorded outside its parental territory, determined as a 6-km radius around the nest, and did not return to it within the following 7 days. This approach was adapted from method 3 of Cadahía et al. (2008), with slight modifications: the territory radius was expanded from 5.7 to 6 km, and the non-return criterion was changed from a number of transmitter fixes to a 7-day period.

TSAs were identified using 80% kernel estimation in *AdehabitatHR* (Calenge 2011b), excluding short-term stopovers (<14 days). TSA center was calculated as the harmonic mean of all GPS locations within that area. TSAs were visually inspected to ensure accuracy. Direction and distance were calculated from the eagle's natal site to the TSA center.

Since TSA occupation timing varies between individuals, 3 fixed 10-day periods were selected for cross-group comparisons. These periods were determined based on visual inspection of movement data (see Figures 4 and 5), identifying time windows during which the majority of tracked individuals showed minimal daily displacement. The selected periods were spaced 6 months apart: days 360–369 (mid-winter, end of the first calendar year, December 26 to January 4), days 543–552 (mid-summer, second calendar year, June 27 to July 6), and days 725–734 (end of second calendar year, December 26 to January 4). This ensured comparisons occurred at similar seasonal periods and ages, minimizing variation due to hatch date differences.

Statistical Analysis

Dispersal timing, distance, and direction

We used a series of statistical models to assess variation in dispersal timing, distance and direction among juvenile *A. fasciata* from different natal habitat types. All analyses were 2-tailed ($\alpha = 0.05$) and conducted in R version 4.4.1 (R Core Team 2024). For all models, we included natal habitat (Mediterranean, semi-desert, desert), sex, and their interaction as fixed effects. Natal year and natal site were tested as random intercepts and retained only when significant, based on variance estimates and model comparisons.

To analyze dispersal onset age, we fitted a linear model (LM), using the *lm()* function (R Core Team 2024). Pairwise comparisons among natal habitat groups were conducted using Tukey's-adjusted post-hoc tests via the *emmeans* package (Lenth 2023).

Mean dispersal distance was analyzed using a generalized linear mixed model (GLMM) with a gamma distribution and a log link, implemented via the *glmer()* function in the *lme4* package (Bates et al. 2015). This analysis was repeated separately to compare eagle distances from their natal sites during TSA periods and for each of the 3 fixed 10-day intervals.

To assess differences in mean TSA duration, which did not meet normality assumptions (based on Shapiro-Wilk test), we applied a Kruskal–Wallis test. Post-hoc comparisons among natal habitat groups were conducted using Wilcoxon rank sum tests with Bonferroni correction, implemented via the *pairwise.wilcox.test()* function (R Core Team 2024).

Differences in dispersal direction were analyzed separately for each of the 3 10-day intervals using the Watson-Wheeler test for homogeneity of angles. In this analysis, only natal habitat group was included as a predictor. Angular data (0°–360°) were processed and compared using the *circular* (Agostinelli and Lund 2024) and *dplyr* (Wickham et al. 2023) packages.

Habitat use during dispersal and recruitment

Habitat use during dispersal was evaluated using mean annual precipitation as a proxy for habitat type. To assess habitat use along dispersal routes, we compared the mean annual precipitation at all eagle locations recorded during each of the 3 predefined 10-day intervals, using a Kruskal–Wallis test followed by Wilcoxon post-hoc tests with Bonferroni correction between natal habitat groups, implemented via the *stats* package (R Core Team 2024). Analyses were conducted separately

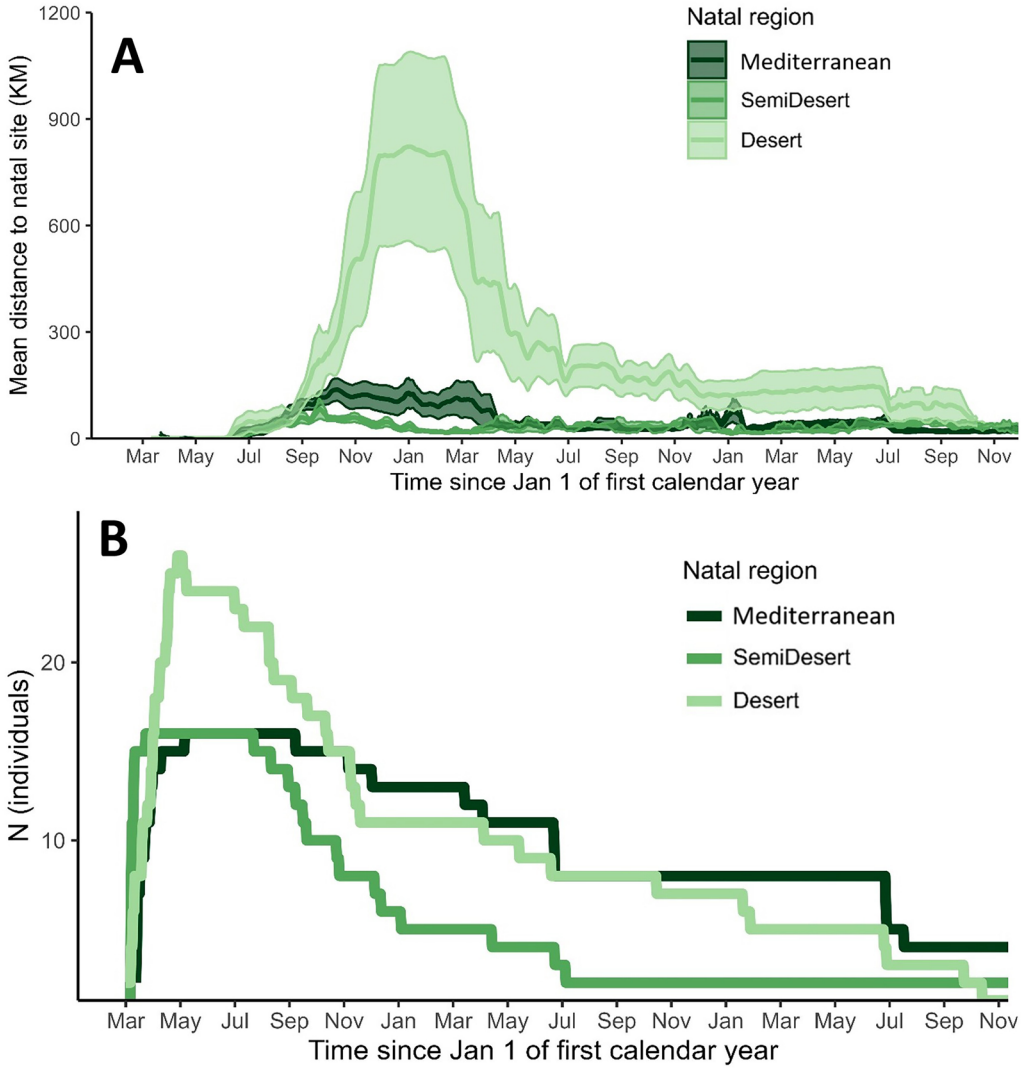

FIGURE 4. (**A**) Mean daily distances of the eagles from their natal sites. Mean and SD were calculated separately for each habitat group. (**B**) Sample sizes for each of the habitat groups, because it changes over time since tagging.

for each time interval and included all surviving eagles present during those periods.

For recruitment site selection, we compared recruitment distance and precipitation differences between natal and recruitment sites among males and females using Wilcoxon rank-sum tests, implemented via the *wilcox.test()* function (R Core Team 2024). Due to small sample size, statistical comparisons among natal habitat groups were not conducted, however, we report summary statistics and observed trends for context.

Survival and mortality analyses

We used 3 complementary approaches to evaluate survival and mortality patterns among natal habitat groups.

Survival analysis: The effect of natal habitat on survival was assessed using a Cox proportional-hazards model (Cox 1972), implemented via the *survival* package (Therneau 2015). The model accounted for censored observations, and assumptions were tested using the Grambsch and Therneau method (1994).

Qualitative mortality analysis: Cause-specific mortality rates were summarized descriptively for each habitat group to describe key risk factors such as electrocution or persecution, and to evaluate the relative contribution of local versus transboundary threats.

Statistical comparisons of mortality patterns: To evaluate differences in mortality distributions among natal habitat groups, we used categorical tests implemented via the base R *stats* package (R Core Team 2024). Chi-squared tests assessed associations between natal habitat group and mortality location (inside versus outside the study area) as well as the distribution of mortality causes. Fisher's exact tests were used for pairwise comparisons between groups, due to small expected cell counts in some categories. Mortality causes were classified into 3 categories for analysis: electrocution/collision, direct persecution/drowning, and unknown/disease.

RESULTS

Of the 59 tagged eagles, 55 were included in the statistical models after excluding 4 individuals that died shortly after fledging or that their sex could not be determined: 16 from the Mediterranean, 16 from the Semi-desert, and 23 from the Desert groups. All 59 individuals were included in the graphical

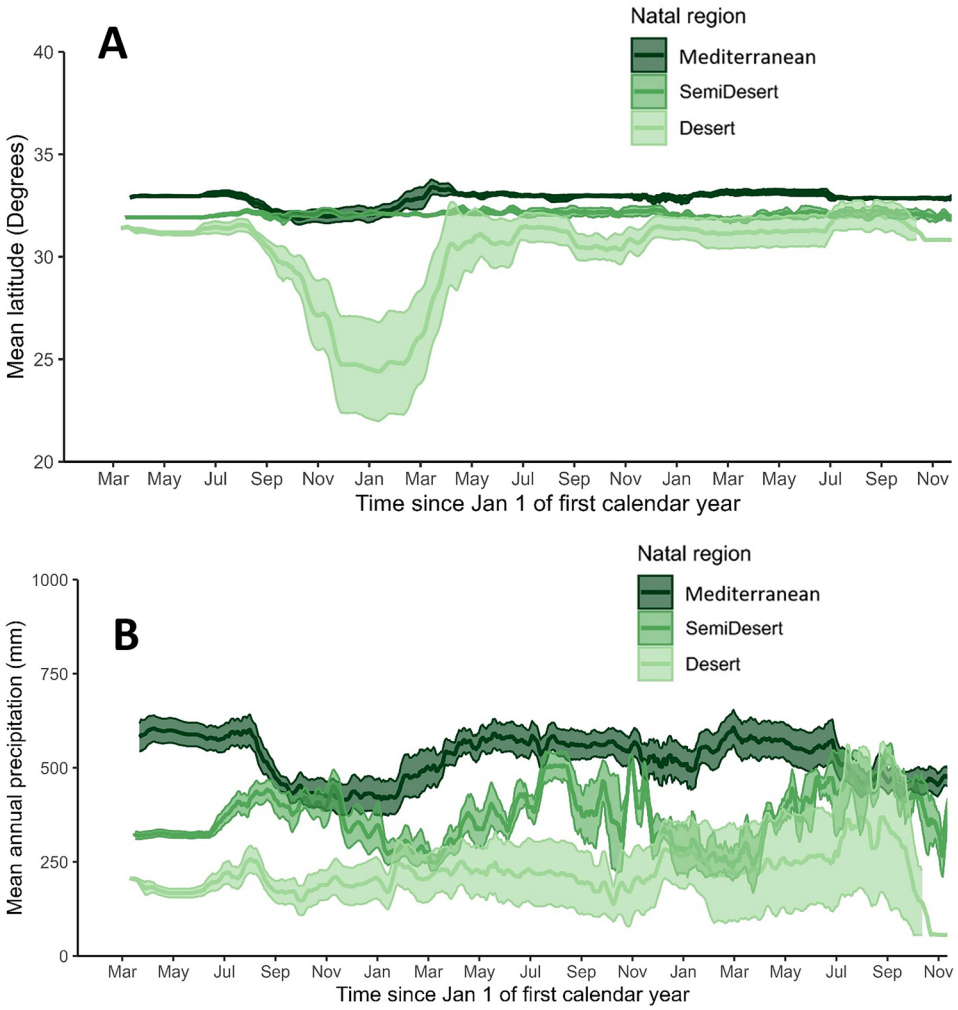

FIGURE 5. (**A**) *Aquila fasciata* movement across latitudes (daily mean and SD), calculated separately for each habitat group. (**B**) Mean and SD of mean annual precipitation along eagle dispersal routes, calculated separately for each habitat group.

representations and in the analysis of mortality causes (17 Mediterranean, 16 Semi-desert, and 26 Desert). The dataset comprised 954,642 GPS locations, collected between May 5, 2018 and July 1, 2024.

Dispersal Timing, Direction and Distance

The linear mixed-effects model explained 19.6% of the variation in dispersal onset age ($F = 2.83$, $p = 0.0475$). Males dispersed earlier than females (Figure 3A), with an average difference of 23.1 days ($p = 0.0335$). However, when analyzed separately within each group, this effect was significant only in the Desert group (males: 44.4 days earlier, $p = 0.0079$). Natal habitat did not significantly influence dispersal onset (Figure 3A), though Mediterranean eagles tended to disperse earlier than Desert eagles (24.0 days earlier, $p = 0.0578$) and earlier than Semi-desert eagles (13.4 days, $p = 0.2838$).

Of the 55 eagles studied, 50 engaged in TSA events lasting >14 days (range: 1–5 events per individual). The remaining 5 individuals died shortly after dispersal onset. The TSA events occurred predominantly during the first 2 calendar years of life, with some eagles continuing to occupy TSAs into their third and fourth years. A total of 129 TSA events were recorded, with duration ranging from 15 to 374 days (mean ± SD: 80.9 ± 69.0 days). TSA duration did not differ significantly by natal habitat ($p = 0.295$) and sex ($p = 0.221$), or their interaction ($p = 0.848$).

Dispersal distances varied significantly by habitat type and sex (Figures 2, 3B, and 4A). Desert eagles dispersed farther (437.0 ± 535.8 km) than Mediterranean (115.6 ± 133.0 km) and Semi-desert eagles (58.9 ± 20.7 km). Post-hoc pairwise comparisons confirmed significant differences between Desert and both Mediterranean ($\beta = 1.46$, $p < 0.001$) and Semi-desert eagles ($\beta = 1.80$, $p < 0.001$), whereas the difference between Mediterranean and Semi-desert eagles was not significant ($\beta = 0.34$, $p = 0.57$). Across all habitat groups, males dispersed shorter distances than females ($\beta = -0.75$, $p = 0.005$). These patterns were consistent across three 10-day periods. Desert eagles consistently dispersed farther than both Mediterranean ($\beta = 1.92$, 1.90, and 1.26; all $p < 0.001$) and Semi-desert eagles ($\beta = 3.20$, 1.85, and 1.80; all $p < 0.001$), while dispersal distances between Mediterranean and Semi-desert eagles remained non-significant in all three periods ($\beta = 1.27$, –0.04, and 0.55; all $p > 0.1$).

The Watson-Wheeler test (Supplementary Material Figure S1) confirmed significant between-group differences in dispersal direction across all three 10-day periods: First period (days: 360–369): $W = 158.09$, $df = 4$, $p < 0.001$, Second period (days:

543–552): $W = 11.062$, $df = 4$, $p = 0.0259$, Third period (days: 725–734): $W = 14.282$, $df = 4$, $p = 0.0064$. These results indicate distinct movement patterns among habitat groups. Desert eagles displayed long southward movements (Figure 5A), Mediterranean eagles traveled shorter southward movements, and Semi-desert eagles exhibited minimal movement without a clear directional trend. This pattern was most pronounced during the first winter, when many Desert eagles reached the Sinai Peninsula, Africa, or the Arabian Peninsula. However, by their second winter, the differences between the groups diminished, with eagles returning closer to their natal sites.

Desert eagles exhibited a bi-modal dispersal pattern, with most individuals (17 out of 23) dispersing short distances (≤450 km), primarily within the Negev and Sinai deserts. In contrast, six eagles undertook long-distance journeys (1,700–2,600 km), traversing the Saharo-Arabian desert to reach East African Sahel or the southern Arabian Peninsula. The Sinai Peninsula emerged as a frequent passage and settlement area for Desert-origin eagles, visited by 15 out of 23 individuals, along with 1 eagle from each of the Semi-desert and Mediterranean groups. Despite the geographic proximity to Africa and Arabia, only 3 eagles crossed open water, flying 14–95 km across the Gulf of Suez or the Straits of Tiran. Two of these individuals used Tiran and Sanafir islands as "stepping stones," reducing their over-water travel distance. Notably, all 6 eagles that eventually reached Africa or the Arabian Peninsula (either by crossing the sea or circumventing the gulfs), continued moving south for over 1,200 km.

Habitat Type Use Along Dispersal Routes and Recruitment Sites

Mean annual precipitation during dispersal

Analysis of mean annual precipitation along dispersal routes revealed distinct selection patterns among natal habitat groups. Eagles generally occupied areas with precipitation levels similar to their natal habitats (Figure 5B). The Kruskal-Wallis test, performed separately for each time period, confirmed significant differences in mean precipitation between natal habitat groups in all three periods (χ^2 = 99.671, 93.38, and 55.855; $df = 2$, all $p < 0.001$). Post-hoc pairwise comparisons showed that Mediterranean eagles consistently occupied areas with higher precipitation than Desert and Semi-desert eagles ($p < 0.011$ across all time periods). Semi-desert eagles selected intermediate precipitation areas, significantly higher than Desert eagles during the first two periods (days: 360–369 and 543–552, $p < 0.001$), but not in the last period (days: 725–734, $p = 0.31$).

Habitat preferences at recruitment sites

Of the 59 tagged eagles, 11 individuals (5 males and 6 females) survived to maturity and recruited into the breeding population (Supplementary Material Table S2). Recruitment distance varied by sex, with males settling closer to their natal sites (mean = 19.3 km, range: 6.8–50.7 km) than females (mean = 102.5 km, range: 13.3–335.5 km). Although females tended to recruit farther, the difference was not statistically significant ($W = 5.5$, p-value = 0.0996), possibly due to small sample size.

Recruitment distances also varied by natal habitat group, though small sample sizes limited statistical testing. Eagles from Mediterranean habitats recruited at an average distance of 18.4 km ($n = 6$), Semi-desert eagles at 13.3 km ($n = 2$), and Desert-origin eagles at 191.4 km ($n = 3$). Excluding a desert-origin female that recruited into a different biogeographic zone has little effect on this mean (193.1 km), reinforcing the trend that Desert-hatched eagles tend to recruit at greater distances, consistent with patterns observed in their dispersal trajectories and temporary settlements.

In terms of habitat fidelity, most eagles (10 out of 11) recruited into breeding territories within the same biogeographic zone as their natal site. The single exception was a desert-origin female that settled in a Mediterranean territory. The mean difference in annual precipitation between natal and breeding sites was 43 mm for males (range: 5–145 mm) and 149.2 mm for all females (range: 5–675 mm). Excluding the desert-origin female that settled in a Mediterranean zone, the mean precipitation difference for females decreased to 44 mm (range: 5–175 mm), similar to the male values.

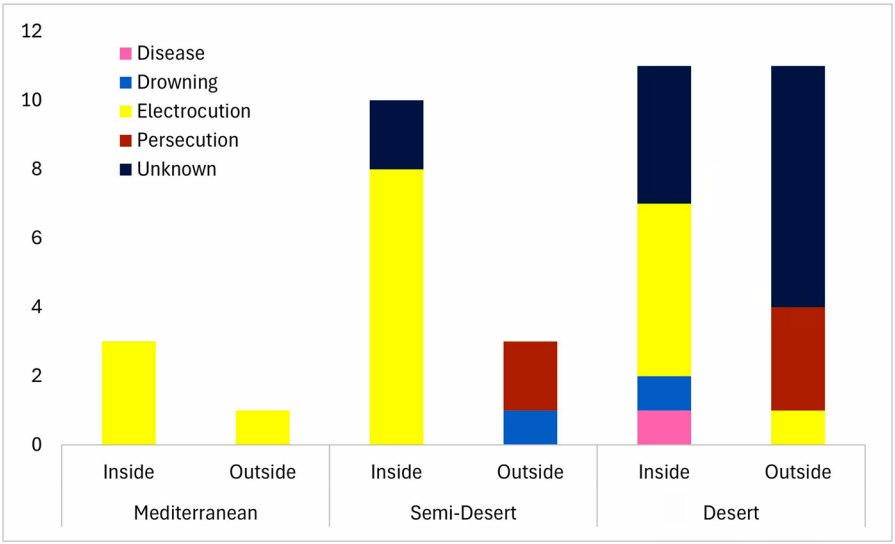

FIGURE 6. Summary of the recorded mortality events ($n = 39$) of eagles of the 3 habitat groups according to whether the event occurred inside or outside the study area.

Between-Group Differences in Mortality Causes and Survival

Mortality rates and causes

During the study period, 39 mortality events were recorded during the dispersal phase of the eagles, representing 66.1% of the tracked eagles (Figure 6). Of these, 61.5% occurred within the study area, while 38.5% took place in neighboring countries, including Egypt (8 events), Jordan, Lebanon, Turkey and Yemen (1–2 events each). The proportion of local mortality varied by natal habitat groups, with Mediterranean and Semi-desert eagles experiencing higher local mortality compared to Desert eagles (75.0% and 76.9% compared to 50.0%, respectively). However, these differences were not statistically significant ($\chi^2 = 2.84$, $df = 2$, $p = 0.24$).

Causes of mortality varied significantly across habitat groups ($\chi^2 = 10.9$, $df = 4$, $p = 0.028$). Pairwise comparisons showed a significant difference between Mediterranean and Desert eagles ($p = 0.023$), whereas differences between Semi-desert and Desert ($p = 0.06$) and between Mediterranean and Semi-desert ($p = 0.34$) were not significant.

Electrocution was the leading cause of mortality, accounting for 70.8% of deaths within the study area and 13.3% of deaths outside it, comprising 46.2% of total recorded deaths. Electrocution accounted for 100%, 61.5% and 27.3% of the mortality cases of the Mediterranean, Semi-desert and Desert groups, respectively. Direct persecution (trapping/shooting) accounted for 5 deaths, representing 33.3% of mortality events outside the study area. Given the high proportion of unknown mortality cases (46.7%) outside the study area, persecution-related deaths are likely underreported, as many human-related mortality causes cannot be confirmed solely through telemetry data.

The Sinai Peninsula emerged as a key mortality hotspot, with 6 recorded deaths, accounting for 15.4% of all mortality events. Of these, 4 were suspected cases of direct persecution, while the cause of the remaining 2 was unknown. This mortality rate is disproportionately high given that eagles spent only 6.7% of their total tracking time in Sinai, suggesting that this region poses a particularly high risk for dispersing eagles.

Survival analysis

The Cox proportional-hazards model revealed significant differences in apparent cumulative survival probabilities among eagles from different biogeographic origins (Figure 7). Eagles from the Mediterranean region exhibited the highest survival rates, while Semi-desert eagles had a 3.37 times higher mortality risk compared to Mediterranean eagles (hazard ratio = 3.37, 95% CI: 1.26–8.97, $p = 0.0151$). Desert eagles also showed increased mortality risk (hazard ratio = 2.26, 95% CI: 0.87–5.90), though this difference was not statistically significant ($p = 0.0953$).

Sex did not have a significant impact on survival probability. Male eagles exhibited a 1.38 times higher mortality risk than females (hazard ratio = 1.38, 95% CI: 0.66–2.89, $p = 0.3860$), but this trend was not statistically significant.

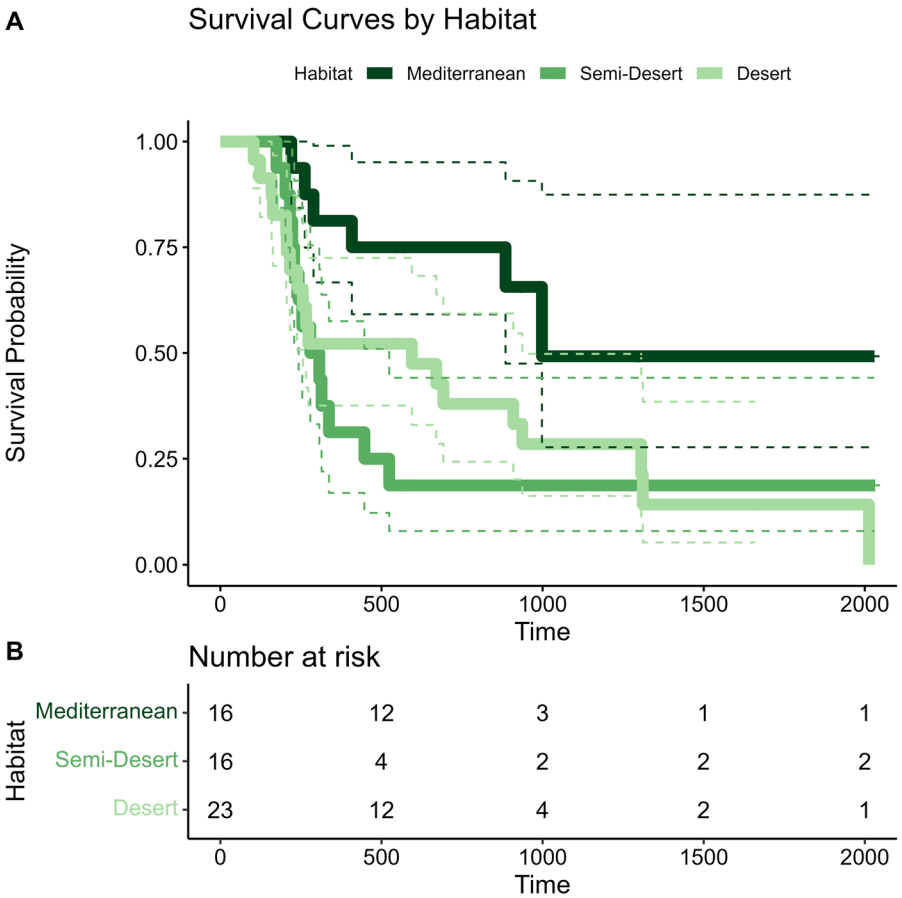

FIGURE 7. Survival probabilities of *A. fasciata* from different natal habitats based on Cox proportional-hazards model. (**A**) Comparison of apparent cumulative survival among Mediterranean (dark green), Semi-desert (green), and Desert (light green) groups. (**B**) Sample sizes in each habitat group over time (days).

DISCUSSION

This study examined the dispersal patterns of juvenile *A. fasciata* originating from 3 biogeographic regions, revealing significant differences in movement direction, dispersal distances, temporary settlements, survival, and recruitment patterns.

Dispersal Timing and Distance

Dispersal onset differences

Although not statistically significant, we observed a consistent trend in dispersal onset age: Mediterranean eagles tended to disperse earlier, while Desert eagles delayed dispersal. This pattern aligns with the ontogenic switch hypothesis (OSH), which suggests that juveniles in harsher environments benefit from extended parental care and resource familiarity, allowing more time to acquire the skills and physiological state required for independent survival (Balbontín and Ferrer 2005). In contrast, these results appear to contradict the resource competition hypothesis (RCH), which predicts earlier dispersal in resource-poor environments due to increased competition with conspecifics (Balbontín and Ferrer 2005, Egea-Casas et al. 2023). According to RCH, we would expect earlier dispersal in resource-poor desert territories, but we observed the opposite. However, RCH may operate through both offspring and parental dynamics. Parents may limit the dependence period to preserve their own future reproductive investment. Thus, the length of the post-fledging period may reflect a parent–offspring conflict, where offspring benefit from prolonged care while parents may favor early independence (Alonso et al. 1987, Ferrer 1992). Notably, a similar pattern of delayed dispersal has been also documented in *Aquila chrysaetos* (Golden Eagle) in the Negev Desert (part of our study area), compared to conspecifics in less arid regions (Soutullo et al. 2006), This suggests that delayed dispersal in desert environments may represent a broader phenomenon, occurring in species whose overall distribution is centered in more temperate regions.

Sex differences in dispersal timing and distance

Males dispersed significantly earlier than females, a pattern that contrasts with some previous findings (Balbontín and Ferrer 2009, Cadahía et al. 2010) but aligns with results from a recent multi-population study (Egea-Casas et al. 2023). Sex-biased dispersal is common in birds, with females typically dispersing farther (Greenwood 1980, Serrano 2018), while differences in timing are more variable and less frequently addressed. Because female raptors are usually larger than males (Palma et al. 2001, Orta et al. 2020), they may require more time to reach optimal body condition for dispersal. However, to our knowledge, there is currently no empirical evidence from raptor species that directly supports this hypothesis.

In terms of dispersal distance, our findings are consistent with previous studies on *A. fasciata* (Cadahía et al. 2010, Hernández-Matías et al. 2010), with females traveling farther than males. This difference was evident in Desert and Mediterranean groups but not in the Semi-desert group, likely due to limited sample size and early mortality among long-distance dispersers. Hernández-Matías et al. (2010) also reported a significant interaction between sex and population of origin in shaping natal dispersal and recruitment distances, which they attributed to territorial density and intraspecific competition. However, such factors may be more relevant during recruitment than during early dispersal stages. Juvenile *A. fasciata* are not territorial and tend to congregate in temporary settlement areas (Balbontín 2005, Balbontín and Ferrer 2009, Cadahía et al. 2010), suggesting that early movement patterns may be shaped more by individual properties and environmental conditions than by territorial competition.

Influence of Natal Habitat on Dispersal and Recruitment

We observed significant differences in dispersal patterns across natal habitat types. Mediterranean and Semi-desert eagles exhibited moderate dispersal distances, while Desert-origin eagles dispersed significantly farther and in a more southerly direction. To our knowledge, this pattern of natal habitat-driven variation in dispersal distance and orientation has not been previously documented in *A. fasciata* or other large raptor species.

Previous studies have shown that juvenile *A. fasciata* tend to inhabit open, low-laying agricultural habitats, likely due to higher prey availability and reduced competition with territorial adults (Balbontín and Ferrer 2009, Cadahía et al. 2010, Caro et al. 2011). Geographic variation in prey availability has also been proposed as a driver of population-level differences in dispersal distances (Moleón et al. 2009, Cadahía et al. 2010, Hernández-Matías et al. 2010).

In our study, the extended and more directional movements of Desert-hatched eagles may reflect a combination of ecological constraints and behavioral imprinting. Mediterranean and Semi-desert eagles typically encountered their preferred habitat—prey-rich agricultural valleys—early in their dispersal, which may have reduced their need to travel farther. Additionally, their movements were limited by geographic barriers, including the Mediterranean Sea to the west and surrounding deserts to the south and east. Encountering these inhospitable landscapes early in the dispersal process may inhibit further travel, reinforcing natal fidelity and facilitating local settlement. Conversely, Desert-hatched eagles, accustomed to arid conditions, face limited dispersal opportunities to the north, pushing them to continue southward through arid landscapes in search of prey-rich areas like the Sahel and southern Arabian Peninsula. This interpretation suggests that both environmental factors (prey availability and landscape features) and innate preferences (NHPI) may contribute to shaping the complex dispersal patterns observed in *A. fasciata* across different natal habitats.

In addition to these possible mechanisms, we observed seasonal south–north movements, particularly among desert-hatched eagles, suggesting a possible innate migratory tendency. These movements resemble known raptor migration patterns in the Eastern Mediterranean and are supported by field observations of *A. fasciata* flying alongside other actively migrating raptors (Shirihai et al. 1996, authors' personal observations). Such partial or facultative migration behavior has been documented in other species traditionally considered non-migratory (Van Doren et al. 2017, Helm and Gwinner 2006). Our findings regarding the different tendencies of eagles from different regions to migrate may suggest that migratory behavior and NHPI may interact to shape dispersal trajectories.

These behavioral tendencies may be further shaped by physical and geographical barriers, such as large water bodies, which are known to constrain the movements of large soaring birds due to the scarcity of thermals (Newton 2010). This

constraint may be amplified by NHPI, as Levantine *A. fasciata*, typically originating far from the coast, may perceive the sea as an unfamiliar and inhospitable environment, which they actively avoid.

This interaction between environmental familiarity and geographic barriers may help explain the bi-modal movement patterns observed among desert-origin eagles. Many individuals settled temporarily in the Sinai Peninsula, only a few continued beyond it into Africa and Arabia. The triangular shape of Sinai, bordered by the Gulfs of Suez and Aqaba, acts as a natural funnel directing eagles southward, where they become effectively "trapped" between large water bodies. Those that managed to cross or circumvent these barriers traveled over 1,200 km further south, highlighting the sea's role as a significant, though not absolute, barrier to dispersal.

The decision to cross appears to be influenced by the width of the water body and whether the eagle can see the far shore. This is supported by contrasting observations in *A. fasciata* tagged in Cyprus, which is surrounded by broader expanses of open sea and where individuals have never been documented crossing the waters of the Mediterranean Sea surrounding the island (Kassinis et al. 2022). The funneling effect at Sinai likely has important survival implications, as the region has emerged as a mortality hotspot, where dispersing eagles face elevated risks from persecution and electrocution.

Another recent study on NHPI in raptors (Orgeret et al. 2024) found that during early dispersal, individuals tended to use habitats resembling their natal environment. However, at the settlement stage, NHPI responses were more variable—some individuals exhibited positive NHPI (preference for similar habitats), while others displayed negative NHPI (avoidance of natal-like habitats). The strength and direction of these responses also varied by natal habitat type, highlighting the role of both individual and environmental context in shaping NHPI expression. Our recruitment data provides preliminary support for positive NHPI in *A. fasciata*, with 10 out of 11 eagles establishing breeding territories within the same biogeographic zone as their natal site, although the small sample size precluded statistical analysis of this process. The single exception—a desert origin female that recruited into a Mediterranean territory—occurred in a site with high turnover rate due to electrocution (3 females electrocuted there between 2019 and 2023, INPA, unpublished data). While this case may represent a broader phenomenon by which individuals from less disturbed desert areas are drawn to breeding territories in more resource-rich but hazardous environments, it should be interpreted with caution, as only one individual deviated from the otherwise consistent pattern of natal habitat fidelity.

Differences in Mortality Causes and Survival

Mortality patterns reflected dispersal behaviors, with Desert eagles experiencing higher mortality outside the study region due to their long-range movements. Electrocution was the dominant cause of death, particularly within the study area. The decline in the proportion of electrocution-related mortality from Mediterranean to Desert eagles may be explained by both infrastructure distribution and dispersal patterns. Mediterranean and Semi-desert eagles mostly remained within the study area, where electrical infrastructure is dense and direct persecution pressures are low. Conversely, Desert eagles frequently dispersed into neighboring countries where powerline density is lower, but human persecution is more prevalent (Brochet et al. 2016). These patterns highlight how the interaction between movement behavior and regional threat profiles can differentially affect mortality across natal habitat groups.

As previously observed in Western Europe (Hernández-Matías et al. 2015), electrocution remains the leading cause of mortality for dispersing juvenile *A. fasciata*. Although mitigation through powerline insulation is costly and slow, it has been shown to be highly effective and to significantly enhance long-term population viability (Chevallier et al. 2015). In light of these findings, a mitigation program to insulate powerlines has been initiated in the study region (Mayrose et al. 2024).

The Sinai Peninsula emerged as a major mortality hotspot, accounting for twice the expected deaths relative to the time eagles spent there. Many of these deaths were suspected direct persecution, aligning with broader trends of raptor hunting in the Eastern Mediterranean, particularly in Egypt (Brochet et al. 2016). The high proportion of unknown mortality cases (46.7%) outside the study area suggests that persecution-related deaths are likely underreported due to the difficulty of confirming human-related mortality from telemetry data alone.

Overall, these findings underscore the complex, transboundary nature of the threats faced by *A. fasciata*. Effective conservation strategies must address both infrastructure-related risks within the study area and wildlife persecution in the broader region.

Survival analysis revealed a lower trend of apparent cumulative survival probabilities for Semi-desert and Desert eagles compared to Mediterranean eagles, with a statistically significant difference only between Semi-desert and Mediterranean groups. These differences may be attributed to differential dispersal patterns or habitat quality. Desert eagles, which exhibited longer dispersal ranges, had lower survival rates, suggesting a potential survival cost associated with long-distance movements. While this pattern is intuitive, empirical studies quantifying mortality as a function of dispersal distance in raptors are still limited (Real and Mañosa 2001, Serrano 2018), though similar costs have been associated with migration (Oppel et al. 2015, Sergio et al. 2019).

Notably, the Desert group also had the highest proportion of mortality outside the study area (50%), consistent with their broader spatial movements. Semi-desert eagles, despite showing moderate average dispersal distances, had the lowest survival rate among the groups. This unexpected result may reflect a chance outcome within the Semi-desert group, where all three individuals that initiated long-distance movements died shortly after dispersal onset. Had these individuals survived longer, it is likely they would have increased the average dispersal distance for the Semi-desert group, potentially affecting the relationship between dispersal patterns, mortality and survival. Physical condition prior to dispersal may also influence survival. Although not statistically significant, dispersal timing trend among the groups, following the difference in annual precipitation among the three regions, may reflect variations in body condition, as proposed by the ontogenic switch hypothesis. Habitat quality differences could influence both dispersal timing and eaglet survival during the early independence period.

Concluding Remarks

This study provides new insights into the dispersal, survival, and recruitment dynamics of *A. fasciata*, with direct implications for conservation planning. Our findings emphasize the need to protect not only breeding territories but also key

dispersal corridors and settlement areas that support juvenile development across the full dispersal process.

A striking result of our study is that *A. fasciata* subpopulations in the Levant, despite being geographically adjacent, exhibit markedly different dispersal behaviors, shaped by the distinct ecological conditions of their natal habitats. This underscores the critical importance of preserving the full spectrum of habitat diversity across the landscape, as each subpopulation may play a unique role in maintaining the species' adaptive capacity and regional viability. The southern Levant populations also represent some of the most arid environments within the species' global range, and to our knowledge, desert-origin *A. fasciata* have never been systematically studied. This makes the region not only a conservation priority but also an important case study for understanding how arid-land raptor populations function under increasing environmental pressures.

Tackling electrocution, the leading cause of mortality, remains a top priority. A national powerline insulation program has been launched (Mayrose et al. 2024), and our data support prioritizing areas of high juvenile movement and recruitment. However, other threats, especially direct persecution, continue to take a heavy toll across the region.

Finally, our findings on natal habitat preference induction (NHPI) provide a deeper understanding of how early-life experience shapes dispersal strategies. These insights can inform future reinforcement programs, population connectivity modeling, and targeted conservation interventions that account for behavioral and ecological diversity within the species. In sum, safeguarding the ecological heterogeneity and connectivity of *A. fasciata* populations across this complex and fragmented landscape is essential for their long-term persistence.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

Eagle handling and tagging weres conducted under Israeli Nature and Parks Authority permit (2495/2018).

Conflict of interest statement

There were no conflicts of interest related to this study.

Author contributions

AM, DT, OH and NS conceived the ideas and designed methodology; OH and AM collected the data; DT and AM analyzed the data; AM and NS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Due to the sensitive nature of telemetry data on an endangered species, the full dataset is not publicly available. However, the dataset used in this study can be accessed upon request through Movebank (Study: Bonelli's Eagle Israel; https://www.movebank.org/cms/webapp?gwt_fragment = page = studies,path = study108979007). All non-sensitive data and supporting materials have been archived in Figshare and are publicly available at https://doi.org/10.6084/m9.figshare.30047593.

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