[SUBMISSION DATE: JULY 22, 2025; EDITORIAL ACCEPTANCE DATE: JANUARY 16, 2026]

RESEARCH ARTICLE

Disrupted natal habitat imprinting triggers long-distance dispersal in captive-bred eagles

Asaf Mayrose,[1,2]* Ohad Hatzofe,[2] Yigal Miller,[2] David Troupin,[1] and Nir Sapir[1]*

[1] Department of Evolutionary and Environmental Biology, Faculty of Natural Sciences and Institute of Evolution, University of Haifa, Haifa, Israel
[2] Science Division, Israel Nature and Parks Authority (INPA). Jerusalem, Israel
* Corresponding author: Asaf Mayrose, asafmayrose96@gmail.com; Nir Sapir, nirs@sci.haifa.ac.il

ABSTRACT

Dispersal behavior and survival are critical properties of animal populations and are known to determine the success of reintroduction and reinforcement programs. We tracked 53 juvenile *Aquila fasciata* (Bonelli's Eagle), including wild-hatched and captive-bred individuals released via two different protocols, to test how early-life experiences shape dispersal and fitness outcomes. Captive-bred eagles were released either on their rearing site near their natal enclosure and foster parents or at a distant site without the parents. Dispersal patterns diverged strongly by group: distant-released individuals dispersed farther, and in markedly more directional, migration-like patterns, reaching as far as East Africa and the Arabian Peninsula. In contrast, on-site and wild-hatched eagles remained closer to their natal areas, showing variable and shorter dispersal trajectories on average. Despite comparable ages at dispersal onset, habitat use differed significantly, with distant-released individuals consistently occupying drier desert habitats. These patterns suggest that post-fledging experience promotes philopatry and shapes movement decisions, likely via natal habitat preference induction. Wild-hatched eagles exhibited significantly higher survival rates and recruitment success than both captive-bred groups, which suffered elevated mortality primarily due to electrocution and other anthropogenic threats. Surprisingly, shorter-range dispersal by on-site releases did not improve survival, likely reflecting high risk from local infrastructure (notably high incidents of electrocution). The high mortality of captive-bred birds raises concerns about the long-term effectiveness of current release strategies and highlights the paramount importance of conserving existing wild breeding pairs and their territories. Our findings demonstrate that both dispersal and fitness outcomes are influenced by the timing and spatial context of the release to the wild, with strong implications for raptor conservation and reintroduction programs. In particular, we highlight the importance of acquiring natal habitat preference during the post-fledging dependence period and recommend that release protocols preserve continuity with natal habitat when possible. Ultimately, this study underscores that fine-scale management of early-life experience can have enduring consequences for the spatial ecology and viability of reintroduced populations.

Keywords: captive breeding, dispersal movement, natal habitat preference, post-fledging period,

reintroduction, survival

How to Cite
Mayrose, A., O. Hatzofe, Y. Miller, D. Troupin, and N. Sapir (2026). Disrupted natal habitat imprinting triggers long-distance dispersal in captive-bred eagles. Ornithological Applications 128:duag000.

LAY SUMMARY

- Captive breeding helps save endangered species, but we need to understand how release methods affect survival and behavior of captive-bred animals.
- We tracked 53 *Aquila fasciata* (Bonelli's Eagle)—both wild-hatched and captive-bred birds—released using two different methods to study their movements and survival.
- Captive-bred eagles released far from their parents and rearing sites traveled much longer distances than wild-hatched eagles or eagles released near their rearing site, often reaching East Africa and Southern Arabia.
- However, all captive-bred eagles had lower survival than wild birds, with most deaths caused by electrocution from powerlines. The high number of powerlines near the release sites likely obscured survival differences between the long-range and short-range dispersers.
- These findings show that early life conditions and release strategies can shape the behavior and success of animals in the wild. This can help improve conservation efforts by guiding more effective release practices for threatened species.

La alteración de la impronta del hábitat natal desencadena dispersión a larga distancia en águilas criadas en cautiverio

RESUMEN

El comportamiento de dispersión y la supervivencia son propiedades críticas de las poblaciones animales y se sabe que determinan el éxito de los programas de reintroducción y refuerzo poblacional. Seguimos a 53 juveniles de *Aquila fasciata*, incluyendo individuos nacidos en estado silvestre y criados en cautiverio, éstos últimos liberados mediante dos protocolos diferentes, para evaluar cómo las experiencias tempranas moldean la dispersión y los resultados en términos de aptitud biológica. Las águilas criadas en cautiverio fueron liberadas ya sea en su sitio de crianza, cerca de su recinto natal y de sus padres adoptivos, o en un sitio distante y sin los padres. Los patrones de dispersión divergieron marcadamente entre grupos: los individuos liberados en un sitio distante se dispersaron más lejos y en trayectorias mucho más direccionales, similares a migraciones, llegando hasta África oriental y la península Arábiga. En contraste, las águilas liberadas en el sitio de crianza y las nacidas en estado silvestre permanecieron más cerca de sus áreas natales, mostrando trayectorias de dispersión más cortas y variables en promedio. A pesar de presentar edades comparables al inicio de la dispersión, el uso del hábitat difirió significativamente, ya que los individuos liberados en un sitio distante ocuparon de manera consistente hábitats desérticos más secos. Estos patrones sugieren que la experiencia posterior al emplumamiento promueve la filopatría y moldea las decisiones de movimiento, probablemente mediante la inducción de una preferencia por el hábitat natal. Las águilas nacidas en estado silvestre presentaron tasas de supervivencia y éxito de reclutamiento significativamente mayores que ambos grupos criados en cautiverio, los cuales sufrieron mortalidad elevada principalmente por electrocución y otras amenazas antropogénicas. Sorprendentemente, la dispersión a menor

distancia de los individuos liberados en el sitio de crianza no mejoró la supervivencia, lo que probablemente refleja el alto riesgo asociado a la infraestructura local (en particular, una alta incidencia de electrocuciones). La alta mortalidad de las aves criadas en cautiverio genera preocupación sobre la eficacia a largo plazo de las estrategias actuales de liberación y resalta la importancia primordial de conservar las parejas reproductoras silvestres existentes y sus territorios. Nuestros resultados demuestran que tanto la dispersión como los resultados en términos de aptitud biológica están influidos por el momento y el contexto espacial de la liberación al medio natural, con importantes implicancias para la conservación de rapaces y los programas de reintroducción. En particular, destacamos la importancia de adquirir una preferencia por el hábitat natal durante el período posterior al emplumamiento y recomendamos que los protocolos de liberación preserven, cuando sea posible, la continuidad con el hábitat natal. En última instancia, este estudio subraya que el manejo a escala fina de las experiencias tempranas puede tener consecuencias duraderas para la ecología espacial y la viabilidad de las poblaciones reintroducidas.

Palabras clave: cría en cautiverio, movimiento de dispersión, período posterior al emplumamiento, preferencia por el hábitat natal, reintroducción, supervivencia

INTRODUCTION

Translocating animals to restore populations and reduce extinction risks is a widely used conservation strategy that has successfully improved the viability of numerous populations and species (Seddon et al. 2014, Berger-Tal et al. 2020). However, despite its potential, reintroduction remains complex and prone to high failure rates (Fischer and Lindenmayer 2000, Taylor et al. 2017). Improving success rates requires a better understanding of the behavioral mechanisms driving the movement patterns of released individuals, as these directly influence survival and recruitment (Efrat et al. 2022, Egea-Casas et al. 2023).

For large raptors, the post-fledging dependence period is especially critical. During this time, juveniles develop flight and hunting skills under the guidance of their parents (Newton 2010). In captive breeding and reintroduction programs, where the young are raised by their biological parents, early nestling development can closely mimic natural conditions with minimal human intervention. However, this continuity is often disrupted at later stages when juveniles are translocated for release, either for reinforcing existing wild populations or for establishing new ones. To compensate for the absence of parental care, translocated juveniles are typically provisioned with food until they become self-sufficient (Sherrod 1987, Seddon et al. 2014, Egea-Casas et al. 2023).

Various release strategies have been developed to address this challenge, differing mainly in the timing of translocation and release. The classic “hacking” method involves moving nestlings prior to fledging to simulate natural departure from the nest (Sherrod et al. 1987), while a different approach involves delaying the release to skip the migratory season of the year and thereby reduce the risks associated with migration (Oppel et al. 2021, Efrat et al. 2022).

Another key developmental process potentially affected by translocation is natal habitat preference induction, which proposes that early-life experience shapes habitat preferences, leading individuals to favor environments resembling their natal sites later in life (Davis and Stamps 2004, Stamps et al. 2009). However, evidence for natal habitat preference induction in raptors remains limited and somewhat contradictory: although some studies report weak or no natal habitat fidelity (Delgado et al. 2010, Brown and Collopy 2013, Serrano 2018), others

demonstrate strong natal influences (Faccio et al. 2013, Fletcher et al. 2015, Orgeret et al. 2024, Penttinen et al. 2025), including recent findings on *Aquila fasciata* (Bonelli's Eagle) in the Southern Levant region (Mayrose et al. 2025). Notably, the potential impacts of natal habitat preference induction on dispersal behavior, particularly in translocated individuals, remain largely unexplored (Stamps and Swaisgood 2007). Disrupting the connection between juveniles and their natal habitat or parents and their influence on the young individuals could alter dispersal trajectories, with significant consequences for survival, recruitment, and settlement success. Understanding these dynamics is therefore crucial for improving the effectiveness of reintroduction programs.

In this study, we investigate how different release strategies influence the dispersal behavior and survival outcomes of captive-bred *A. fasciata*. Specifically, we compare 2 release approaches: (1) On-site release: Eaglets are released at the captive breeding facility, maintaining contacts with their natal habitat and biological or foster parents. (2) Distant translocation: Eaglets are relocated to a remote site, effectively severing parental ties and exposing them to an unfamiliar landscape.

These groups of captive-bred individuals were compared with wild-hatched eagles across multiple dispersal-related metrics, including timing, distance, direction, and the environmental characteristics of their dispersal routes and temporary settlement areas. We also examined survival rates, causes of mortality and recruitment success, to evaluate the long-term implications of different early-life conditions.

Our research questions were as follows: (1) Do the dispersal patterns (timing, distance, direction, and habitat preferences) of juvenile *A. fasciata* differ between the 2 release approaches, and how do these properties differ from those observed in the wild population? (2) Do survival rates, mortality causes and recruitment outcomes differ between the 2 release approaches, and how do these metrices differ from those of the naturally hatched individuals?

We hypothesize that if post-fledging parental care and natal habitat preference induction have little influence on dispersal and survival, no major differences would emerge between the two release methods or between captive-bred and wild-hatched juveniles. Given the proximity of all natal and release sites, we would expect all groups to use similar dispersal areas and exhibit comparable fitness-related properties. Conversely, if parental association and natal habitat familiarity play a significant role, we anticipate observing marked differences in dispersal and fitness-related properties among the study groups. Because sex often shapes dispersal strategies, with females generally dispersing farther in many raptors (Newton 2010), including *A. fasciata* (Cadahía et al. 2010, Hernández-Matías et al. 2010), we also included it in our analysis.

Due to their broad and highly variably dispersal, from local movements to regional and even inter-continental long-distance journeys (Mayrose et al. 2025), *A. fasciata* offer a highly suitably system to explore how early-life experience shapes dispersal behavior and fitness. Specifically, to enhance the success of *A. fasciata* conservation outcomes, exploring the consequences of different release protocols and comparison to natural dispersal are critically required.

MATERIALS AND METHODS

Study Area

This study was conducted in the Mediterranean biogeographical area of the Levant region and more specifically in the Carmel and Galilee Mountains and the Golan Heights (Figure 1), over an

area of ~7,500 km² (Bitan and Rubin 1991, Sorek and Shapira 2018). The region features diverse and rugged topography, including mountains, plateaus, and deeply incised valleys, with elevations ranging from ~2,300 m above sea level in the northern Golan Heights to ~200 m below sea level near the Sea of Galilee. The landscape is shaped in part by the Great Rift Valley, which transects the region in a north-south direction. The climate is Mediterranean, with annual precipitation exceeding 1,000 mm in the north and decreasing to around 450 mm in the southern and eastern areas (Bitan and Rubin 1991, Sorek and Shapira 2018). Historically dominated by Mediterranean woodland and scrubland, roughly half of the natural vegetation has been replaced by agriculture in recent decades (Ben-moshe and Renan 2023). The area is densely populated, with an average population density of ~250 people per square km (Sorek and Shapira 2018).

Study Species

Aquila fasciata is a medium-sized raptor with a broad distribution range across Southeast Asia, the Middle East, and the Western Mediterranean (Orta et al. 2020). Although globally classified as Least Concern, many populations are declining due to habitat degradation, pesticides use, loss of prey, electrocution and collision with powerlines, and direct persecution (Westrip et al. 2022).

In the study area, the population experienced a steep decline, from several dozen breeding pairs in the 1950s to near extirpation by the 1970s (mainly due to secondary poisoning from agricultural pesticides), persisting at low levels into the early 2000s (Leshem 1976, Shirihai et al. 1996, Mayrose et al. 2019). To halt this decline, a national conservation program was launched in 1996, leading to several conservation actions under the “Spreading wings” project, which is a joint initiative of the Israel Nature and Parks Authority, the Society for the Protection of Nature in Israel (BirdLife Israel) and the Israel Electric Corporation, aimed at conserving breeding raptors. One of these actions was the establishment of a captive breeding and release program, designed to reinforce the wild *A. fasciata* population, particularly in the Mediterranean zone of northern Israel, from which the species was extirpated during the 1970s (Leshem 1976, Mayrose et al. 2017)

The life cycle of *A. fasciata* is composed of 2 major stages, which are characterized by markedly different behaviors. Territorial *A. fasciata* (mostly 3-yr old and older) are sedentary, with strong site fidelity and territoriality (Bosch et al. 2010, Martínez-Miranzo et al. 2016, Morollón et al. 2022). By contrast, juveniles are highly nomadic and show no territorial behavior (Real and Manosa 2001, Cadahía et al. 2010, Hernández-Matías et al. 2010). This stage, known as the dispersal period, begins at the age of 163 ± 17 days and lasts until the individuals become territorial, at least 2 years later (Real et al. 1998, Minguez et al. 2001). During this period, juveniles temporarily settle in Temporary Settlement Areas, rich in prey, before recruitment into breeding populations (Balbontíin and Ferrer 2009, Cadahía et al. 2009)

In the Iberian Peninsula, *A. fasciata* typically disperse 356 ± 156 km (Cadahía et al. 2010, Hernández-Matías et al. 2010). However, recent GPS telemetry data revealed exceptional long-range dispersal, including movements from Spain to Morocco and from the Aegean islands to Central Europe and East Africa (Life Bonelli EastMed 2024, Life Bonnelli Project 2024).

Captive Breeding and Release

In the study area, the captive breeding program for *A. fasciata* began in 2000, with the first captive-bred individuals released in 2003. Between 2003 and 2024, a total of 83 eagles were raised and released, averaging 3.8 ± 2.1 eagles per year (range: 1–7).

The program is based at the Hai-Bar Carmel Breeding Facility (hereafter HBC; 32.75°N,

35.01°E, Figure 1), which maintains 6 adult breeding pairs of *A. fasciata*. These individuals, originally from the wild in the study area, have been rendered non-releasable due to injuries, primarily from collisions or electrocution on powerlines. Most of these birds were collected from the wild as juveniles.

To maximize breeding success, eggs were removed from nests for artificial incubation, reducing the risk of damage by parents and often stimulating additional clutches. After hatching, chicks were either returned to their biological parents or placed with foster pairs. Nestlings were raised by adults in their enclosures and remained there for several weeks post-fledging, until they displayed independent behaviors, such as self-feeding and hunting. At this stage (100–170 days post-hatching; mean ± SD = 133.6 ± 26.2 days), eaglets were transferred to a large release aviary at 1 of 2 sites: (1) HBC facility, adjacent to their natal enclosure on Mount Carmel, a Mediterranean woodland region characterized by rocky slopes, pine and oak forests, and open scrubland. (2) Meshushim Nature Reserve, Golan Heights (hereafter GH; 32.56°N, 35.39°E), ~65 km northeast of HBC, situated on a basaltic plateau with open grasslands, scattered woodlands, and deep canyons.

Aviary size and structure were very similar at both sites (~6 × 4 × 3 m). The main difference between them lay in the continuity of connection to biological or foster parents and natal habitat: at HBC, eagles were released near their natal enclosures, preserving visual and vocal contact with their parents and maintaining familiarity with their native environment, whereas at GH, eagles were translocated to an unfamiliar landscape, severing both parental ties and connection to their natal habitat.

Eaglets spent an average of 27.3 days (range: 15–43 days) in the release aviary before being released. The release method was soft, as eagles were allowed to leave voluntarily through an open window. During this time, they were fed live prey, such as pigeons and quails, to stimulate their hunting skills. Post-release, supplementary feeding with dead prey continued until all released juveniles stopped returning to the site. When multiple eaglets reached the same developmental stage, they were moved to the aviary as a cohort (mean: 1.6 eaglets per cohort; range: 1–3).

This release method differs from classical hacking, where unfledged nestlings are translocated and raised in artificial nests at the release site (Sherrod et al. 1987, Negro et al. 2007, Egea-Casas et al. 2023). In contrast, our method allowed eaglets to spend extended time with their parents (biological or foster), promoting the development of essential hunting and other skills important to their survival, typical of the post-fledging dependency period (Sarasola et al. 2018). Consequently, juveniles were released closer to the end of this critical phase, potentially enhancing their proficiencies and survival in the wild.

Telemetry Data Collection

Between 2016 and 2023, a total of 53 *A. fasciata* were tagged for this study (Supplementary Material Table S1): 19 wild nestlings (7 females and 12 males), tagged across the study area between 2018 and 2023; 34 captive-bred juveniles from the HBC breeding facility, of which 21 eaglets (11 females and 10 males) were released at GH (2016–2019) and 13 eaglets (10 females and 3 males) were released at HBC (2020–2023).

Nestlings were fitted with 30-g solar-powered GPS-GSM transmitters (Ornitela OT-30). Tagging was carried out at 45–70 days of age using a pelvic harness made of Teflon and silicone (Anderson et al. 2020). This method has been shown to have no measurable negative effects on bird welfare or flight performance (Longarini et al. 2023, Viollat et al. 2024). Sex determination

was based on body mass, morphometric measurements and genetic analysis (Palma et al. 2001, Estellés-Domingo and López-López 2023, Viollat et al. 2024).

GPS and other sensors on the transmitters (tri-axial accelerometer and thermometer) were programmed to record at intervals of 15–60 min, depending on battery level. For standardization, all data were later subsampled to 60-min intervals across individuals and tracking days. The total mass of the transmitter and harness was below 3% of the individual's body mass, following recommended best practices (Kenward 2002). All handling procedures were conducted under permit from the Israeli Nature and Parks Authority (license #2495/2018). Movement data were archived in the Movebank repository (Study ID 108979007).

Habitat Type Along Dispersal Routes

Mean annual precipitation was used as a proxy for habitat type along the dispersal routes of the eagles. Precipitation values were extracted for each GPS location using the bioclimatic variable 12 (annual precipitation) from the WorldClim v2.1 dataset at 30 arc-second resolution (~1 km²), for the period 1970–2000 (Fick and Hijmans 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.

Mortality Detection and Investigation

Eagle mortality events were detected through continuous monitoring of telemetry data. Mortality was suspected when the following criteria were met: repeated GPS fixes at a single location for more than 24 hr, stable body position indicated by at least three consecutive accelerometer readings, and abnormal tag temperature values. Upon detecting potential mortality, field teams attempted to locate the carcass and investigate the cause of death. However, as many incidents occurred in distant and inaccessible areas, remote investigation methods were also employed. These included analysis of orthophotos and ground-level imagery from platforms such as Google Earth and Google Maps. Investigations focused on identifying likely mortality causes, including electrocution, collisions, drowning, and roadkill.

Identification of Recruitment Events

Recruitment into the breeding population was determined using a combination of telemetry data analysis and field observations. GPS location data from eagles in their second calendar year and older were routinely examined to identify potential recruitment events, indicated by clustered GPS fixes near suitable breeding sites. To confirm recruitment, field visits were conducted to observe territorial and breeding behaviors. An eagle was considered recruited if it was observed multiple times within the same year at a certain location, exhibiting one or more of the following behaviors: courtship displays, mating, nest construction or direct involvement in breeding activities, such as incubation or feeding young (Hernández-Matías et al. 2010).

Data Processing

[THIRD LEVEL HEADING] **Mean daily distance from 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 2011) R packages. Data interpolation and smoothing for visualization were performed using the *Zoo* package (Zeileis and Grothendieck 2005) in R version 4.4.1 (R Core Team 2024). For each individual, the mean daily distance from

its natal site was calculated as the average of all GPS fixes recorded on that day. These daily means were then used to determine the average daily direction and distance for each eagle group.

To facilitate comparison of movement patterns across individuals hatched in different calendar years, tracking data were aligned relative to January 1 of the hatch year of each individual. Specifically, January 1 of the hatch year was designated as Day 1, January 1 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 (Figures 3 and 4). This approach was validated after confirming that the hatch year of an individual had no significant effect on dispersal direction and distance, when included as a random effect in the linear models.

[THIRD LEVEL HEADING] **Defining dispersal onset and periods for dispersal pattern comparison**

Dispersal onset was defined as the first day an individual was recorded outside its parental territory, arbitrarily determined as a 6-km radius from the nest, and did not return within 7 days (adopted with some changes from Real et al. 1998, Soutullo et al. 2006, Cadahía et al. 2008). Since the timing and length of the occupation of Temporary Settlement Areas varies between individuals, 3 fixed 10-day periods were selected for cross-group comparisons: 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 (peak of second winter, December 26 to January 4). These time windows ensured that comparisons occurred at the same seasonal period and at a similar age, with only minor variation due to hatch date differences.

Statistical Analyses

To address the first research objective (i.e., to test for differences in dispersal timing, direction, distance and habitat use among the 3 eagle groups: wild-hatched, HBC-released and GH released), we employed the following statistical approaches:

(1) Age of release, dispersal onset and distance: Testing the effects of eagle group and sex on the age of release, the age at dispersal onset and on mean dispersal distance was done using a linear mixed model (LMM), implemented via the *lmer()* function from the *lme4* package (Bates et al. 2015), with *p*-values for fixed effects obtained via the *lmerTest* package (Kuznetsova et al. 2017).

(2) Habitat use: Testing habitat use during dispersal, as reflected by mean annual precipitation values, was modeled using a GLMM with a Gamma distribution and a log link to accommodate the skewed response variable. These models were fitted with the *glmer()* function from the *lme4* package (Bates et al. 2015),

In both LMMs and GLMMs, eagle group (Wild, HBC, and GH), sex, and their interaction were included as fixed effects. Random intercepts were specified for natal year and natal site (for wild-hatched individuals) or parental pair (for captive-bred individuals), to account for grouping effects. Post-hoc comparisons among eagle groups were conducted using Tukey's adjusted pairwise contrasts via the *emmeans* package (Lenth 2023) providing corrected *p*-values for multiple comparisons. All models were repeated across the 3 predefined 10-day intervals, as described earlier.

(3) Correlation between dispersal onset and release age: To assess the relationship between age at release and age at dispersal onset, we used a Pearson correlation analysis in R version 4.4.1 (R Core Team 2024). Prior to analysis, both variables were checked for linearity and approximate normality through visual inspection of histograms and scatterplots.

(4) Directional analysis: To analyze directional data and to assess differences in dispersal direction between eagle groups over the 3 arbitrary 10-day periods, we used the Watson-Wheeler test for homogeneity of angles, separately applied for each of the 3 10-day periods. Angular data, treated as circular and ranging from 0° to 360°, were converted into circular objects using the *circular* R package (Agostinelli and Lund 2024). Statistical analyses were done using the *circular* (Agostinelli and Lund 2024) and *dplyr* (Wickham et al. 2023) packages.

To address the second research objective, to examine differences in survival, causes of mortality and recruitment rates among eagles from different groups, we employed the following approaches:

(1) Survival analysis: A Cox proportional-hazards model (Cox 1972) was used to estimate survival probabilities for the 3 eagle groups, while also accounting for sex. The proportional-hazards assumption for each variable was tested (Grambsch and Therneau 1994). Survival analysis and comparisons were conducted using the *survival* package (Therneau 2015) and visualized with the *survminer* package (Kassambara et al. 2016). Pairwise comparisons between eagle groups were carried out using Tukey-adjusted post-hoc tests via the *emmeans* package (Lenth 2023).

2. Mortality analysis: We investigated mortality causes across eagle groups to identify patterns and assess whether the distribution of mortality factors differed by natal group. All statistical analyses were performed using the base R *stats* package (R Core Team 2024).

For each individual, the distance from the release site (for captive-bred) or natal site (for wild-hatched) to the mortality location was calculated. Since the data did not meet normality assumptions (Shapiro–Wilk test), group differences in mortality distances were evaluated using the non-parametric Kruskal–Wallis test.

To evaluate the association between each of the 3 natal group and mortality cause, we consolidated mortality causes into 2 categories (electrocution vs. all other causes) due to small sample sizes.

Differences among natal groups were assessed using the Monte Carlo simulation version of Fisher's exact test with 10,000 replicates to accommodate low expected cell counts. Post-hoc pairwise comparisons were conducted using Fisher's exact test with Bonferroni correction to adjust for multiple comparisons. The analysis was performed in R using the *fisher.test()* function in the *stats* package (R Core Team 2024).

(3) Recruitment analysis: To assess differences in recruitment rates between wild-hatched and captive-bred eagles, we combined the 2 captive-bred groups (GH and HBC) due to low recruitment numbers and used Fisher's exact test, implemented using the *fisher.test()* function in the *stats* package (R Core Team 2024).

All statistical analyses were two-tailed with a significance level of $\alpha = 0.05$ and were conducted in R version 4.4.1 (R Core Team 2024). A summary of all statistical models, parameters, and results is provided in Supplementary Material Table S2.

RESULTS

This study included a total of 34 captive-bred *A. fasciata* that were compared to 19 wild-hatched eagles tagged in the Galilee and Golan highlands (Supplementary Material Table S1). Altogether, the study analyzed 1,302,772 GPS locations collected between 1 May 2016 and 1 July 2024.

Age at Release

The linear mixed-effects model showed that none of the fixed effects were statistically

significant, although males were released slightly earlier than females on average (estimate = –5.2 ± 12.3 days), and eagles released at GH were on average older at release (estimate = 11.8 ± 24.1 days). Thus, the analysis indicated that age at release did not differ significantly by sex, release site, or their interaction. All model assumptions were met, with residuals normally distributed (Shapiro-Wilk $p = 0.76$) and homogeneity of variance confirmed (Levene's $p = 0.58$). Most of the variation in release age was explained by the year of hatching.

Dispersal Onset Age

As expected, dispersal onset age was strongly correlated with the age at release among captive-bred individuals (Pearson's $r = 0.973$, $p < 0.0001$). On average, captive-bred individuals were released at 162.4 days of age and initiated dispersal at 172.4 days, spending ~10 days near the release site before departing. Dispersal onset age showed between-individual variation, but the linear mixed model revealed no statistically significant effects of either sex or release site on dispersal timing. Males tended to disperse slightly earlier than females (estimate = –10.3 days), but this trend was not significant ($p = 0.10$).

Despite the close link between the timing of release and dispersal onset in captive-bred individuals, no significant differences in dispersal onset age were detected across the three groups. Eagles released at GH tended to initiate dispersal somewhat later than wild-hatched birds (estimate = 10.99 days, $p = 0.44$), whereas those released at HBC dispersed at a similar age to wild-hatched juveniles (estimate = –1.03 days, $p = 0.93$).

In contrast, random effects for natal year and natal site/parental pair explained a considerable portion of the variance in dispersal onset (variance = 1310.8 and 169.0, respectively). Model assumptions were met, with normally distributed residuals (Shapiro-Wilk $p = 0.52$) and homogeneity of variance across groups (Levene's $p = 0.52$).

Dispersal Flight Direction and Distance

Clear differences were observed in the dispersal patterns of eagles released at GH compared to those released at HBC or wild-hatched individuals. GH-released individuals consistently traveled farther during their first two years of life, as shown by their raw trajectories (Figure 2) and average distance from the natal site (Figure 3). The results of the linear mixed-effects models across 3 standardized 10-day periods suggest a significant between-group effects ($p = 0.001$, 0.002 and 0.035 for the first, second and third periods, respectively). Sex had no significant effect on dispersal distance in any period.

In addition to traveling farther, GH eagles also dispersed in a more southerly direction (Figure 2). Seven of the 21 GH individuals overwintered near the southern edge of the Saharo-Arabian desert belt, reaching either East Africa or the southern Arabian Peninsula. By contrast, most HBC individuals remained within or near the study region, with only two individuals reaching the Balkans and the Caucasus Mountains, north of the study area.

These differences in directional movement were statistically significant, as confirmed by Watson–Wheeler tests across the three periods ($W = 135.4$, 88.5, 57.6; all $p < 0.0001$), indicating a consistent difference in dispersal direction among the groups. Individuals released in GH showed a migration-like dispersal pattern, with peaks in their southward and northward movements aligning with the typical raptor migration timing along the Eastern Mediterranean flyway, that is, southward in September-October and northward in March-April (Figure 4).

Habitat Use Along Dispersal Routes

Analysis of mean annual precipitation along dispersal routes revealed distinct habitat-use patterns among the natal habitat groups. GH-released birds, which typically dispersed southward into the Saharo-Arabian desert, occupied significantly drier habitats compared to both wild-hatched and HBC-released individuals (Figure 4). These differences were confirmed by the GLMM and Tukey-adjusted post-hoc comparisons. They were highly significant during the first 2 predefined intervals: mid-winter (days 360–369) and mid-summer (days 543–552), with $p < 0.001$ for all comparisons. However, no significant difference was observed in the second winter period (days 725–734, $p = 0.26$). No significant differences in habitat use were detected between wild-hatched and HBC-released birds during any of the 3 periods.

Regarding sex differences, males tended to occupy areas with lower precipitation than females. This trend was not significant during the first interval ($p = 0.078$), but was highly significant during the second and third intervals ($p < 0.001$ for both).

Survival

Survival probabilities differed significantly among the 3 groups. The Cox proportional-hazards model revealed that both groups of captive-bred eagles experienced significantly higher mortality compared to the wild-hatched individuals. Eagles released at HBC had a hazard ratio of 3.89 ($p = 0.0017$), and those released at GH had a hazard ratio of 3.03 ($p = 0.0046$), indicating approximately threefold increases in mortality risk relative to the wild-hatched group. However, no significant difference was found between the 2 groups of the captive release sites ($p = 0.77$). Post-hoc pairwise comparisons confirmed these patterns, with wild-hatched eagles showing significantly better survival than individuals from both HBC ($p = 0.0047$) and GH ($p = 0.013$), while the difference between the 2 captive groups was not significant ($p = 0.77$).

Mortality Causes and Distribution

During the study period, 40 mortality events were recorded, including all the 34 captive-bred individuals and 6 of the wild-hatched eagles (three additional wild-hatched deaths occurred prior to dispersal and were thus excluded from analyses). Half of the mortality events occurred within the study area, while the other half were documented in adjacent regions, including southern Israel (6 events), Egypt (7 events), Saudi Arabia (3), and one event each in Azerbaijan, Turkey, Syria, and Sudan (Figure 2). On average, wild-hatched individuals died closer to their natal sites compared to captive-bred ones (Figure 5A), although this difference was not statistically significant (Kruskal-Wallis test: $H = 1.26$, $p = 0.53$).

Electrocution emerged as the primary cause of death (Figure 5B), responsible for 60% of all documented fatalities (24 of 40 individuals). Notably, 71% of electrocution events occurred within the study area and all 6 confirmed deaths among wild-hatched individuals were due to electrocution. Among captive-bred birds, electrocution accounted for 61.9% of deaths in the GH group and 38.5% in the HBC group. Fisher's exact test with Monte Carlo simulated p-value indicated that mortality patterns differed among the three groups ($p = 0.038$). However, post-hoc pairwise comparisons with Bonferroni correction ($\alpha = 0.017$) revealed no statistically significant differences among groups, though the comparison between the wild and HBC groups approached significance ($p = 0.018$; all other p-values > 0.1).

Drowning in water reservoirs was the second most frequent confirmed cause, accounting for 7.5% of deaths (3 events). Confirmed cases of direct persecution (e.g., trapping or shooting) were rare, with only two instances, both occurring far from the study area. About 25% of the mortality cases were labeled as “unknown”, many of them may actually reflect undetected

persecution (see Discussion).

Recruitment

Out of 53 tagged *A. fasciata*, 10 individuals (6 males and 4 females) survived to maturity and were documented recruiting into the breeding population. Eight of these 10 individuals were wild-hatched, representing 50% of the wild-hatched sample. In contrast, only 2 captive-bred individuals (6% of the captive birds) survived to breeding age. Both were females released at the GH site, and both settled in the same breeding territory in the northern Golan Heights, ~37 km from their release site. Unfortunately, this territory is intersected by hazardous powerlines and has experienced high turnover. Both GH-released females, as well as a wild-hatched female, were electrocuted at the site between 2019 and 2023, seemingly attracted by the same resident male. No recruitment was observed among eagles released from the HBC site, likely due to the combination of low survival rates and a limited sample size. Of the 13 juveniles released from HBC, most died before reaching adulthood; only one survived into its second calendar year but died in its fourth year before establishing a territory.

Fisher's exact test confirmed that recruitment rates differed significantly between wild-hatched and captive-bred eagles ($p = 0.0035$), indicating that wild individuals were ~7 times more likely to recruit (odds ratio = 7.03, 95% CI: 1.44–34.3).

DISCUSSION

This study compared the movement, survival and recruitment patterns of 3 groups of juvenile *A. fasciata*, 2 of them are captive-bred from the same breeding nucleus, released at different sites, and a third group of wild-hatched individuals, revealing significant differences among these groups in dispersal direction and distance, survival rates, causes of mortality, and recruitment probability.

The first captive-bred group was released at the HBC nature reserve and breeding facility, near their hatching sites and the enclosures where they were reared by either their biological or foster parents. The second captive-bred group was translocated after fledging to the Golan Heights, a site distant from their natal locations, where the birds were released into the wild. The third group consisted of wild-hatched eagles, naturally raised by their parents in nests within the study area.

Dispersal Onset

In the captive-bred eagles, dispersal onset was closely linked to the timing of release, emphasizing the influence of the reintroduction protocol. Unlike traditional hacking techniques where juveniles are released around fledging (Sherrod et al. 1987, Egea-Casas et al. 2023), our approach delayed release until near the end of the post-fledging dependence period. As a result, most captive-bred individuals initiated their dispersal within a short period after their release (mean = 10 days). Despite being released relatively late in the developmental process, no significant differences in dispersal onset were found between captive-bred and wild-hatched individuals. In contrast, random effects for natal year and natal site/parental pair explained a considerable portion of the variance in dispersal onset, suggesting that interannual environmental variation and site- or pair-specific factors (e.g., genetics or parental behavior) play a more substantial role in shaping dispersal timing.

Importantly, GH-released eagles were relocated to the release site ~ 27 days prior to release, yet their dispersal onset age was similar to the other groups. This suggests that GH

individuals spent less time in the vicinity of the release site prior to departure, potentially leading to weaker natal habitat preference induction, possibly contributing to their more extensive dispersal behavior. Notably, the wild-hatched individuals in our sample originated from the Golan Heights and adjacent Eastern Galilee highlands, which are geographically close and are characterized by a similar habitat type to that of the GH release site, yet they did not exhibit such extensive dispersal. This supports the interpretation that the differences in movement reflect a behavioral mechanism, rather than the selection of different habitat characteristics.

Dispersal Direction And Distance

The GH-released eagles displayed markedly different dispersal trajectories compared to both HBC-released and wild-hatched individuals. They consistently traveled farther during their first 2 years, as indicated by individual movement paths, group-level summaries, and statistical comparisons. These extended movements suggest reduced philopatry, likely driven by shorter parental association, limited environmental familiarity, and the absence of parental figures at the release site. Philopatry—the tendency to remain near or return to the natal area—is a key process influencing gene flow, population structure, and reintroduction success (Real and Mañosa 2001, Hernández-Matías et al. 2020). In *A. fasciata*, dispersal is sex-biased, with females typically recruiting farther from their natal sites than males (Hernández-Matías et al. 2010, Badia-Boher et al. 2024). Our findings align with these patterns but further indicate that early-life social and environmental experience can modulate philopatric behavior.

In addition to the longer dispersal distances, GH birds exhibited a pronounced southward dispersal bias. This pattern was particularly evident in winter, when approximately one-third of the GH birds reached the southern fringes of the Saharo-Arabian desert belt, including the East African Sahel and Arabian Peninsula.

In contrast, HBC-released eagles remained mostly within the study area and the Sinai Peninsula, rarely dispersing long-distances (one individual reached the Balkans, another the Caucasus Mountains). Wild-hatched eagles remained largely local. Dispersal directions differed significantly among groups, with HBC-released and wild-hatched individuals exhibiting shorter, more variable movements, consistent with patterns reported for wild *A. fasciata* in Spain (Minguez et al. 2001, Cadahía et al. 2010, Hernández-Matías et al. 2010). These patterns highlight the exceptional long-range directional dispersal of GH-released eagles.

In addition to traveling farther, GH birds exhibited a migration-like pattern, with marked southward movements peaking in September–October and northward returns in March–April. Similar behavior was observed in wild Bonelli's eagles from a desert origin (Mayrose et al. 2025) and to some extent in Bonelli's eagles from the northern Iberian Peninsula (Real and Mañosa 2001), though these individuals typically completed only one migratory cycle, whereas GH juveniles completed 2 cycles in their first 2 years. These seasonal movements resemble those of migratory raptor species in the study area (Shirihai et al. 2000) and may reflect an innate response to environmental cues in the absence of strong philopatry. Conversely, wild-hatched Mediterranean eagles and HBC-released birds, likely having developed stronger natal habitat preference induction, showed clear fidelity to landscapes resembling their natal areas and rarely ventured into desert regions. This pronounced habitat fidelity highlights the lasting influence of early-life experience and parental association on spatial behavior, supporting the view that natal habitat preference induction is a primary determinant of dispersal extent and direction in this species.

These findings suggest that release site and developmental context influence not only

dispersal distance and direction, but also seasonal movement patterns, with possible implications for survival and recruitment. The differences in dispersal behavior between the otherwise identical captive-bred groups support the idea that the post-fledging dependency period is critical for natal habitat preference induction development. Notably, our study design does not allow separation of the specific effects of parental interaction from habitat familiarity, as all GH individuals were both relocated and separated from their parents, limiting our ability to attribute the observed differences to either factor alone.

Our results suggest that natal habitat preference induction and migratory tendencies may act as complementary or even opposing forces. Translocation during the post-fledging period may disrupt natal habitat preference induction development and facilitate stronger, less constrained migration-like behavior. Since this period involves exploratory behavior near the nest (Mañosa et al. 1998, Balbontín and Ferrer 2005, Delgado et al. 2010, Fletcher et al. 2015), it may represent a critical window for habitat learning and the establishment of philopatry (Davis and Stamps 2004). If so, and given that natal habitat preference induction is desirable in released individuals, traditional hacking—where translocation occurs before fledging (Sherrod et al. 1987)—may offer a better alternative. Supporting this, Egea-Casas et al. (2023) found no behavioral differences between wild-hatched and translocated *A. fasciata* released via hacking. However, their study focused on the post-fledging dependency period and was conducted on islands, where sea barriers constrain dispersal and may obscure patterns seen in open landscapes.

Survival and Recruitment

Wild-hatched eagles had significantly higher survival than both captive-bred groups, pointing to a strong survival advantage regardless of release method or site. Electrocution was the leading cause of death, followed by drowning in reservoirs. It is plausible that captive-reared birds, having grown up in artificial environments, are more prone to perch on powerlines or drink from manmade water sources, as reintroduced individuals often display behavioral differences from their wild conspecifics that can reduce their fitness (Champagnon et al. 2012). Additionally, direct persecution was observed only in captive-bred birds, possibly due to greater naivety and reduced fear of humans, coupled with the fact that they dispersed to regions where human persecution is more common. Notably, long-distance dispersal away from release sites has been identified as the most common behavioral challenge reported in animal translocation projects (Berger-Tal et al. 2020).

Despite their shorter dispersal distances, HBC-released eagles did not survive better than GH birds. This likely reflects high mortality risks in areas close to the release site and specifically the nearby Yizrael Valley, which, although attractive due to the existence of wide agricultural fields and water bodies, has dense powerline infrastructure (Mayrose et al. 2024). This highlights that longer dispersal may confer survival benefits when it leads the birds to forage in safer environments. Many GH birds survived long-distance movements but later died after returning to high-risk areas. In fact, despite their broader dispersal ranges, 67% of GH individuals died within the study area, compared to 54% of HBC juveniles.

Recruitment was extremely low among captive-bred individuals due to high mortality. Only two captive-bred eagles known to join the breeding population were GH-released females that settled relatively close (37 km) to their release site. This suggests some retention of site fidelity despite weaker natal habitat preference induction, but the very small sample limits further inference.

Recruitment rates in the study's reintroduction program were considerably lower than

those reported in other reintroduction efforts, such as Badia-Boher et al. (2024). However, that program operated on an island, where dispersing *A. fasciata* were geographically constrained by the surrounding sea, likely resulting in higher survival and recruitment. The low recruitment observed in our study raises questions about the long-term cost-effectiveness of captive breeding and release. Notably, Badia-Boher et al. (2024), found that releasing wild-reared, non-juvenile individuals—rather than captive-bred juveniles—enhanced early recruitment and reproduction, suggesting a more efficient and economically viable management strategy even in systems with higher baseline survival.

Our study underscores the trade-offs inherent in reintroduction strategies. Limiting long-range dispersal is often desirable to reinforce local populations and reduce mortality associated with long range movements in unfamiliar areas (Oppel et al. 2021, Efrat et al. 2022). From this perspective, releasing the eagles near the core breeding facility, as done at HBC, appears advantageous: these birds generally remained within the study area. However, the choice of release site must also consider local habitat quality and interactions with sympatric species. In fact, concerns about interspecific conflicts, particularly the risk of predation by *A. fasciata* on other reintroduced species, such as *Neophron percnopterus* (Egyptian Vulture) and *Falco biarmicus* (Lanner Falcon), were a key motivation for exploring an alternative release site at GH, in light of a confirmed predation of an *N. percnopterus* by a HBC-hatched *A. fasciata*.

Concluding Remarks

Our findings highlight the importance of natal habitat preference induction acquisition and timing, suggesting that it develops during the post-fledging dependency period, as evident by the distinct dispersal patterns of GH individuals. Given that the timing of natal habitat preference induction acquisition is rarely studied in birds (Davis and Stamps 2004, Stamps and Swaisgood 2007, Fletcher et al. 2015), our findings offer valuable insights for reintroduction biology and supports the view that habitat imprinting shapes long-term dispersal decisions (Stamps and Swaisgood 2007).

Finally, the high mortality of captive-bred birds raises concerns about the long-term effectiveness of current release strategies and highlights the paramount importance of conserving existing wild breeding pairs and their territories. Future reintroduction or reinforcement programs should aim to optimize survival and recruitment by carefully balancing dispersal management with habitat suitability, release timing, and mitigation of post-release threats.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

Acknowledgments

We extend our heartfelt thanks to Noam Leader, Uri Naveh, and Yehoshua Shkedi of the Israel Nature and Parks Authority's Science Division, who initiated this study, significantly contributed to its execution, and oversaw the application of its findings. We are also grateful to the dedicated team of climbers who accessed nests in some of the tallest and most remote areas and undertook the handling and tagging of nestlings: Walter Neser, Yotam Orchan, Elika Maatuf and Alon Malachi. Special thanks to the Hai-Bar Carmel breeding nucleus team, who care for the raptors with great dedication and are responsible for the rehabilitation and release of captive-bred individuals: Sapir Simchi, Avishai Bar-On and Lior Shaul. We also thank the Meshushim Nature Reserve team, led by Avishai Zukerman, for their role in the acclimatization and release of eagles

translocated from the HBC facility to the Golan Heights.

Funding statement
This study was conducted as part of the "Spreading Wings" project, a collaborative initiative of the Israel Nature and Parks Authority (INPA), the Society for the Protection of Nature in Israel (SPNI) and the Israel Electric Corporation (IEC), aimed at conserving Israel's breeding raptors. Additional support was provided by the Open Spaces Preservation Fund, Ministry of the Interior, Israel.

Ethics statement
Eagle handling and tagging were 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. YM oversaw the captive breeding program and coordinated the eagle releases. AM and OH collected the data; DT conducted the data analysis. AM and NS led the writing of the manuscript. All authors contributed critically to manuscript drafts and approved the final version 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; Movebank id: 108979007). All non-sensitive data and supporting materials have been archived in Figshare and are publicly available at https://doi.org/10.6084/m9.figshare.31342414.

LITERATURE CITED

Agostinelli, C., and U. Lund (2024). R package "circular": Circular Statistics (version 0.5-1). In *CRAN: Contributed Packages*. https://doi.org/10.32614/CRAN.package.circular

Anderson, D., V. Arkumarev, A. Botha, K. Bildstein, C. Bowden, M. Davies, O. Duriez, N. Forbes, A. Godino, R. Green, S. Krueger, S. Lambertucci, D. Orr-Ewing, C. Parish, J. Parry-Jones, and E. Weston (2020). A practical guide to methods for attaching research devices to vultures and condors. *Vulture News* 78:1–72.

Balbontín, J., and M. Ferrer (2009). Movements of juvenile Bonelli's Eagles *Aquila fasciata* during dispersal. *Bird Study* 56:86–95.

Balbontín, J., and M. Ferrer (2005). Factors affecting the length of the post-fledging period in the Bonelli's Eagle *Hieraaetus fasciatus*. *Ardea* 93:189–198.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, G. Grothendieck, P. Green and M. B. Bolker (2015). Package 'lme4.' *Convergence* 12:2.

Ben-moshe, N., and I. Renan (2023). *The National Program for Estimating the State of Israel's Nature*. The Steinhardt Museum of Natural History, Tel-Aviv, Israel.

Berger-Tal, O., D. T. Blumstein, and R. R. Swaisgood (2020). Conservation translocations: A review of common difficulties and promising directions. *Animal Conservation* 23:121–131.

Bitan, A., and S. Rubin (1991). *Climatic Atlas of Israel for Physical and Environmental Planning and Design*. Ministry of Transport, Jerusalem, Israel.

Bosch, R., J. Real, A. L. Tint E. Zozaya, and C. Castell (2010). Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*. *Ibis* 152:105–117.

Brown, J. L., and M. W. Collopy (2013). Immigration stabilizes a population of threatened cavity-nesting raptors despite possibility of nest box imprinting. *Journal of Avian Biology* 44:141–148.

Cadahía, L., P. López-López, V. Urios, and J. J. Negro (2008). Estimating the onset of dispersal in endangered Bonelli's Eagles *Hieraaetus fasciatus* tracked by satellite telemetry: A comparison between methods. *Ibis* 150:416–420.

Cadahía, L., P. López-López, V. Urios, and J. J. Negro (2010). Satellite telemetry reveals individual variation in juvenile Bonelli's Eagle dispersal areas. *European Journal of Wildlife Research* 56:923–930.

Cadahía, L., P. López-López, V. Urios, A. Soutullo, and J. J. Negro (2009). Natal dispersal and recruitment of two Bonelli's Eagles *Aquila fasciata*: A four-year satellite tracking study. *Acta Ornithologica* 44:193–198.

Calenge, C. (2011). Analysis of animal movements in R: The adehabitatLT package. *R Foundation for Statistical Computing, Vienna*, 22.

Champagnon, J., J. Elmberg, M. Guillemain, M. Gauthier-Clerc, and J. D. Lebreton (2012). Conspecifics can be aliens too: A review of effects of restocking practices in vertebrates. *Journal for Nature Conservation* 20:231–241.

Cox, D. R. (1972). Regression models and life-tables. *Journal of the Royal Statistical Society: Series B (Methodological)* 34:187–202.

Davis, J. M., and J. A. Stamps (2004). The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution* 19:411–416.

Delgado, M. D. M., V. Penteriani, E. Revilla, and V. O. Nams (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology* 79:620–632.

Efrat, R., O. Hatzofe, Y. Miller, T. Mueller, N. Sapir, and O. Berger-Tal (2022). Postrelease survival of captive-bred Egyptian Vultures is similar to that of wild-hatched Egyptian Vultures and is not affected by release age or season. *Ornithological Applications* 124:duab065.

Egea-Casas, O., P. López-López, E. Álvarez, G. Cortone, M. Galán, J. J. Iglesias-Lebrija, M. Lo Valvo, J. Martínez, S. Merlino, C. Viada, and M. D. Vittorio (2023). Similar post-fledging behavior observed in wild and reintroduced juvenile Bonelli's Eagle in two Mediterranean islands. *Ornithological Applications* 125:duad037.

Estellés-Domingo, I., and P. López-López (2023). Non-invasive sex determination of nestlings and adult Bonelli's Eagles using morphometrics. *Animals* 13:1201.

Faccio, S. D., M, Amaral, C. J. Martin, J. D. Lloyd, T. W. French, and A. Tur (2013). Movement patterns, natal dispersal, and survival of Peregrine Falcons banded in New England. *Journal of Raptor Research* 47:246–261.

Fick, S. E., and R. J. Hijmans (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37:4302–4315.

Fischer, J., and D. B. Lindenmayer (2000). An assessment of the published results of animal relocations. *Biological Conservation* 96:1–11.
Fletcher, R. J., E. P. Robertson, R. C. Wilcox, B. E. Reichert, J. D. Austin W. M. Kitchens (2015). Affinity for natal environments by dispersers impacts reproduction and explains geographical structure of a highly mobile bird. *Proceedings of the Royal Society B: Biological Sciences* 282:2015.1545
Grambsch, P. M., and T. M. Therneau (1994). Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika* 81:515–526.
Hernández-Matías, A., J. Real, R. Pradel, A. Ravayrol, N. Vincent-Martin, F. Bosca, and G. Cheylan (2010). Determinants of territorial recruitment in Bonelli's Eagle (*Aquila fasciata*) populations. *The Auk* 127:173–184.
Karney, C. F. F. (2013). Algorithms for geodesics. *Journal of Geodesy* 87:43–55.
Kassambara, A., M. Kosinski, and P. Biecek (2016). survminer: Drawing Survival Curves using'ggplot2'.
Kenward, R. E. (2002). *A Manual for Wildlife Radio Tagging*. Academic Press, Cambridge, MA, USA.
Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software* 82:1–26.
Lenth, R. (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.5.
Leshem, Y. (1976). The biology of the Bonelli's Eagle (*Hieraaetus fasciatus*) in Israel. Research institute on Nature Preservation, Tel Aviv University, Israel (In Hebrew).
Life Bonelli EastMed (2024). Https://Www.Lifebonelli.Eu/En/.
Life Bonnelli Project (2024). Https://Www.Lifebonelli.Org/Index.Php/En/.
Longarini, A., O. Duriez, E. Shepard, K. Safi, M. Wikelski, and M. Scacco (2023). Effect of harness design for tag attachment on the flight performance of five soaring species. *Movement Ecology* 11:39.
Mañosa, S., J. Real, and J. Codina (1998). Selection of settlement areas by juvenile Bonelli's Eagle in Catalonia. *Journal of Raptor Research* 32:208–214.
Martínez-Miranzo, B., E. Banda, A. Gardiazábal, E. Ferreiro, and J. I. Aguirre (2016). Differential spatial use and spatial fidelity by breeders in Bonelli's Eagle (*Aquila fasciata*). *Journal of Ornithology* 157:971–979.
Mayrose, A., E. Haviv, O. Hatzofe, D. Troupin, M. Elroy, and N. Sapir (2024). Bonelli's Eagle electrocution risk in Israel can be reduced by 80% by insulating only 4% of the pylons. *Ornithological Applications* 126:duae004.
Mayrose, A., O. Hatzofe, D. Troupin, and N. Sapir (2025). Dispersal and survival of *Aquila fasciata* (Bonelli's Eagle) differ across arid, semi-arid, and Mediterranean natal habitats. *Ornithology* 143:ukaf051.
Mayrose, A., N. Leader, and O. Hatzofe (2019). Bonelli's and Golden Eagles populations in Israel, Data Summary and Recommendations. Report of the Israeli Nature and Parks Authority, Tel Aviv, Israel. (In Hebrew).
Mayrose, A., G. Vine, Z. Labinger, O. Steinitz, O. Hatzofe, E. Haviv, Y. Perlman, D. Alon, and N. Leader (2017). *The Israeli Red List of Threatened Breeding Birds*. The Society for the Protection of Nature in Israel and the Israel Nature and Parks Authority. Https://Aves.Redlist.Parks.Org.Il.

Minguez, E., E. Angulo, and V. Siebering (2001). Factors influencing length of the post-fledging period and timing of dispersal in Bonell's Eagle (*Hieraaetus fasciatus*) in southwestern Spain. *Journal of Raptor Research* 35:7.

Morollón, S., V. Urios, and P. López-López (2022). Home-range size and space use of territorial Bonelli's Eagles (*Aquila fasciata*) tracked by high-resolution GPS/GSM Telemetry. *Diversity* 14:1082.

Negro, J. J., J. H. Sarasola, and J. H. Barclay (2007). Augmenting wild populations and food resources. In *Raptor Conservation and Management Techniques* (D. M. Bird and K. S. Bildstein, Editors). Hancock House Publishers, Surrey, British Columbia, Canada. pp. 401–410.

Newton, I. (2010). *Population Ecology of Raptors*. A&C Black, London, UK.

Oppel, S., V. Saravia, V. Bounas, V. Arkumarev, E. Kret, V. Dobrev, D. Dobrev, P. Kordopatis, T. Skartsi, M. Velevski, N. Petrovski, T. Bino, M. Topi, I. Klisurov, S. Stoychev, and S. C. Nikolov (2021). Population reinforcement and demographic changes needed to stabilise the population of a migratory vulture. *Journal of Applied Ecology* 58:2711–2721.

Orgeret, F., U. G. Kormann, B. Catitti, S. Witczak, V. S. van Bergen, P. Scherler, and M. U. Grüebler (2024). Imprinted habitat selection varies across dispersal phases in a raptor species. *Scientific Reports* 14:26656.

Orta, J., G. M. Kirwan, D. A. Christie, P. F. D. Boesman, J. S. Marks, E. F. J. Garcia, J. del Hoyo, A. Elliott, J. Sargatal, and E. de Juana (2020). Bonelli's Eagle (*Aquila fasciata*), version 1.0. In *Birds of the World* (J. Del Hoyo, A. Elliott, J. Sargatal, DA Christie, and E. de Juana, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.boneag2.01

Palma, L., P. Beja, T. Guillemaud, M. L. Cancela, and L. D. Cancela (2001). Sexing Bonelli's Eagle nestlings: Morphometrics versus molecular techniques. *Journal of Raptor Research* 35:187–193.

Penttinen, I., C. Nebel, and T. Laaksonen (2025). Habitat imprinting in breeding territory selection of a long-lived bird of prey. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.70202

R Core Team (2024). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

Real, J., and S. Mañosa (2001). Dispersal of juvenile and immature Bonelli's Eagles in Northeastern Spain. *Journal of Raptor Research* 35:2.

Real, J., S. Mañosa, and J. Codina (1998). Post-nestling dependence period in the Bonelli's Eagle *Hieraaetus fasciatus*. *Ornis Fennica* 75:129–137.

Sarasola, J. H., J. M. Grande, and J. J. Negro (Editors) (2018). *Birds of Prey: Biology and Conservation in the XXI Century*. Springer, Cham, Switzerland.

Seddon, P. J., C. J. Griffiths, P. S. Soorae, and D. P. Armstrong (2014). Reversing defaunation: Restoring species in a changing world. *Science* 345:406–412.

Serrano, D. (2018). Dispersal in Raptors. In *Birds of Prey: Biology and Conservation in the XXI Century* (J. H. Sarasola, J. M. Grande, and J. J. Negro, Editors). Springer, Cham, Switzerland. pp. 95–121.

Sherrod, S. K., W. R. Heinrich, W. A. Burnham, J. H. Barclay, and T. J. Cade (1987). Hacking: A method for releasing peregrine falcons and other birds of prey. *Peregrine Fund.* *https://assets.peregrinefund.org/docs/research-library/manual-hacking-2017-02-28_163613.pdf*

Shirihai, H., E. Dovrat, D. Christie, and C. S. Roselaar (1996). *The Birds of Israel: A Complete Avifauna and Bird Atlas of Israel*. Academic Press, London, UK.
Shirihai, H., R. Yosef, D. Alon, G. Kirwan, and R. Spaar (2000). *Raptor Migration in Israel and the Middle East: A Summary of 30 Years of Field Research*. Technical Publishing International Birding and Research Center, Eilat, Israel.
Sorek, M., and A. Shapira (Editors) (2018). *The State of Israel's Nature. Hamaarag, Assessing the State of Israel's Nature Program*. The Steinhardt Museum of Natural History, Tel-Aviv, Israel.
Soutullo, A., V. Urios, M. Ferrer, and S. G. Peñarrubia (2006). Post-fledging behaviour in Golden Eagles *Aquila chrysaetos*: Onset of juvenile dispersal and progressive distancing from the nest. *Ibis* 148:307–312.
Stamps, J. A., V. V. Krishnan, and N. H. Willits (2009). How different types of natal experience affect habitat preference. *The American Naturalist* 174:623–630.
Stamps, J. A., and R. R. Swaisgood (2007). Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102:392–409.
Taylor, G., S. Canessa, R. H. Clarke, D. Ingwersen, D. P. Armstrong, P. J. Seddon, and J. G. Ewen (2017). Is reintroduction biology an effective applied science? *Trends in Ecology & Evolution* 32:873–880.
Therneau, T. (2015). A package for survival analysis in S. R Package Version 2(7), 2014.
Viollat, L., A. Millon, C. Ponchon, A. Ravayrol, T. Couturier, and A. Besnard, A. (2024). Both movements and breeding performance are affected by individual experience in the Bonelli's eagle *Aquila fasciata*. *Ecology and Evolution* 14:e70081.
Westrip, J. R. S., BirdLife International, A. Irizi, H. H. Benmammar, K. Rousselon, S. Buirzayqah, O. Haitham, G. Monchaux, and A. Riad (2022). *Aquila fasciata (Mediterranean assessment)*. *The IUCN Red List of Threatened Species* 2022: e.T22696076A210502275. https://dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T22696076A210502275.en.
Wickham, H., R. François, L. Henry, K. Müller, and D. Vaughan (2023). dplyr: A Grammar of Data Manipulation. CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.dplyr
Zeileis, A., and G. Grothendieck (2005). zoo: S3 infrastructure for regular and irregular time series. *Journal of Statistical Software* 14:1–27.

Figure 1. Study area, including *A. fasciata* (Bonelli's Eagle) wild natal territories and captive-breeding facility and release sites. HBC = Hi-Bar Carmel captive breeding facility and release site, GH = Golan Heights release site. (Inset) Study area location within the Middle East.

Figure 2. Individual dispersal trajectories of *A. fasciata* (Bonelli's Eagle), color-coded by group: wild-hatched (green, $n = 16$), captive-bred released at distant site in the Golan Heights/GH (pink, $n = 21$), and captive-bred released on-site at Hi-Bar Carmel/HBC (blue, $n = 13$). Black crosses mark mortality locations.

Figure 3. (**A**) Mean daily distance (± SD) from natal/release site as a function of time since tagging. Captive-bred eagles released at distant site in the Golan Heights (GH, pink) exhibited significantly longer-range dispersal compared to captive-bred eagles released on-site at Hai Bar Carmel (HBC, purple) or wild-hatched eagles (green). (**B**) Temporal changes in sample sizes for each group as a function of time since tagging. *N* denotes the number of individual eagles in each group.

Figure 4. (**A**) Latitudinal movements of *A. fasciata* (daily mean ± SD), showing pronounced seasonal southward dispersal by captive-bred eagles released at distant site in the Golan Heights (GH, pink) compared to captive-bred eagles released on-site at Hai Bar Carmel (HBC, purple) or wild-hatched eagles (green). (**B**) Mean annual precipitation (± SD) along eagles' dispersal routes. Captive-bred eagles released at distant site in the Golan Heights (GH, pink) occupied much drier desert habitats compared to captive-bred eagles released on-site at Hai Bar Carmel (HBC, purple) or wild-hatched eagles (green), which remained primarily in Mediterranean habitats.

Figure 5. Mortality patterns among study groups ($n = 40$ events). (**A**) Proximity of death locations to natal/release sites. On average, wild-hatched eagles died closer to natal areas than captive-bred individuals. Boxplots display median, interquartile range (25th–75th percentiles), and 5th/95th percentile whiskers. (**B**) Causes of mortality by group. Electrocution dominated (60%), while drowning, direct persecution, and unidentified causes occurred only outside the study area and were restricted to captive-bred eagles.

Figure 6. Survival curves of the 3 eagle groups, showing a much higher survival rate for wild eagles (green) compared to the 2 captive bred groups: released in Hi-Bar Carmel (HBC, blue) and the Golan Heights (GH, pink).

Figure 1

Figure 2

Click here to access/download;Figure;ORNITH-APP-25-134_Figure 2.jpg

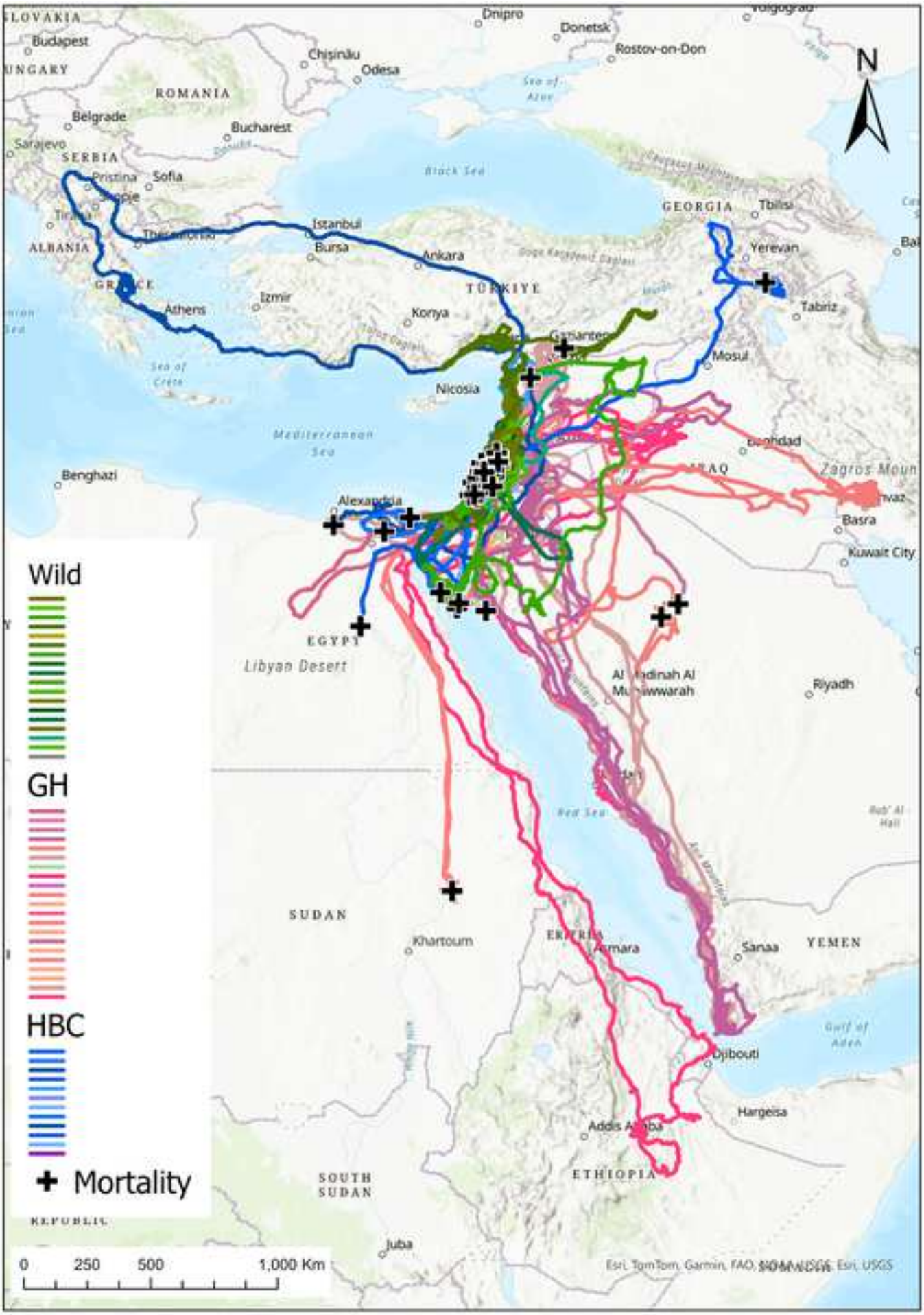


Figure 3

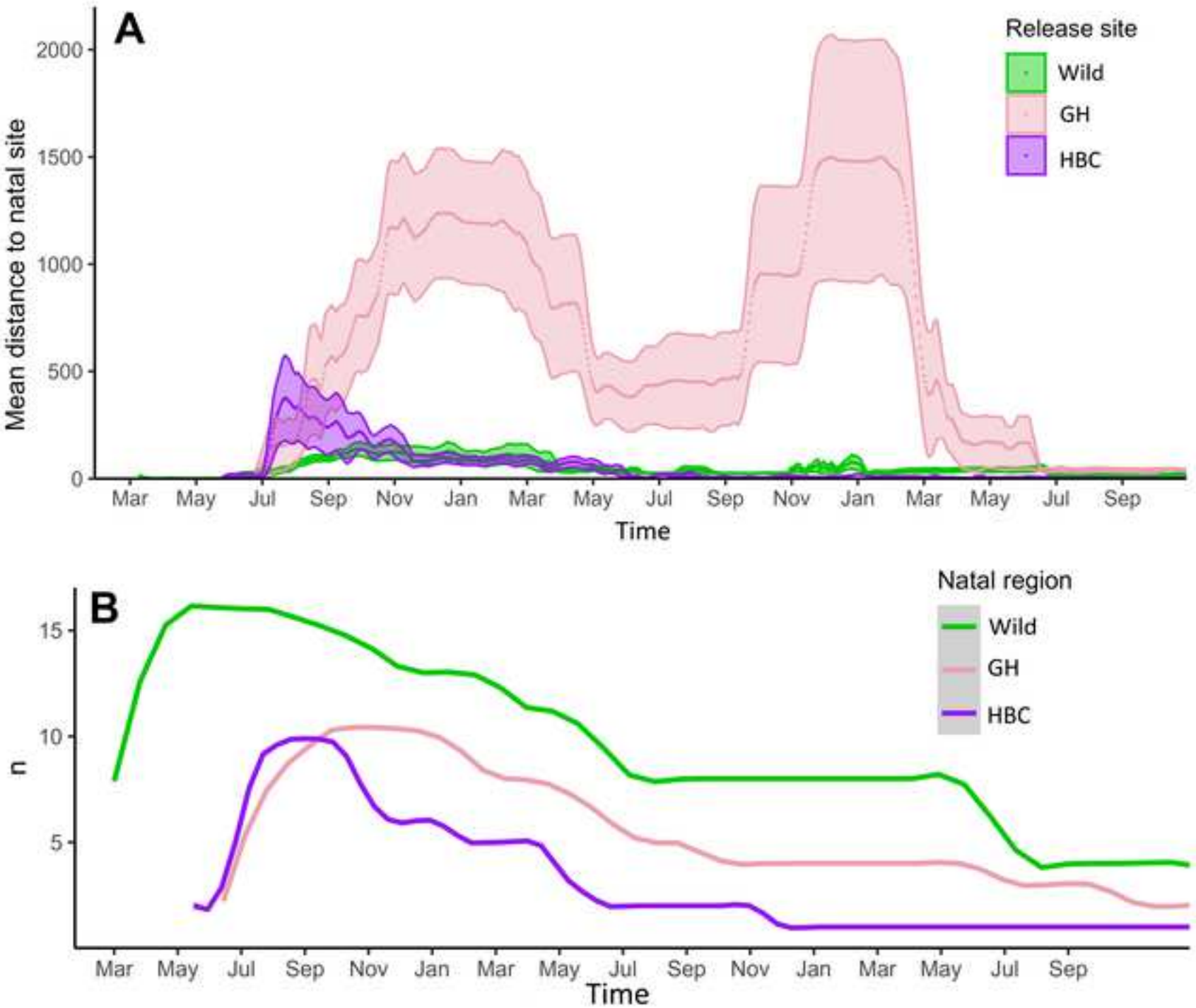


Figure 4

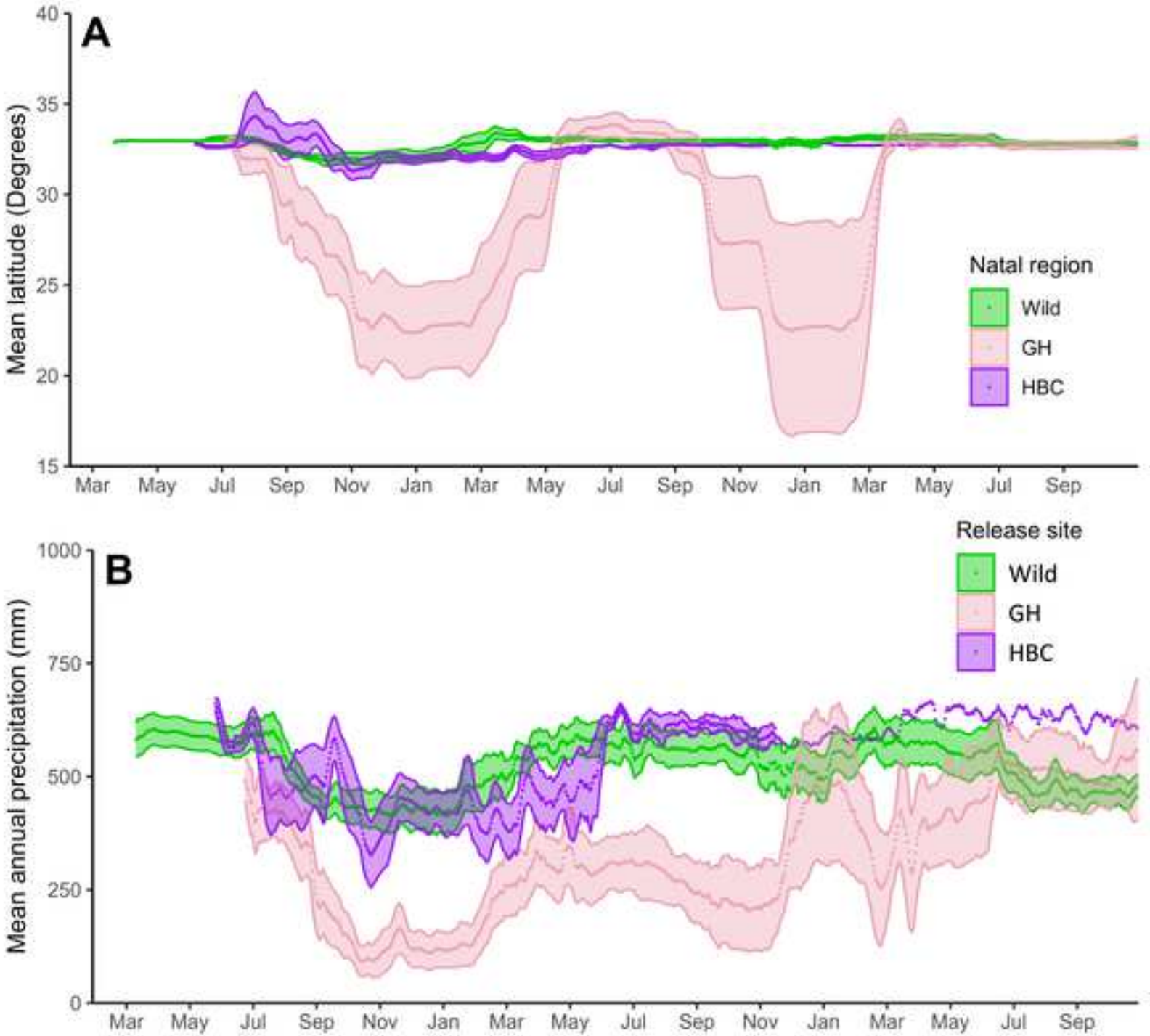
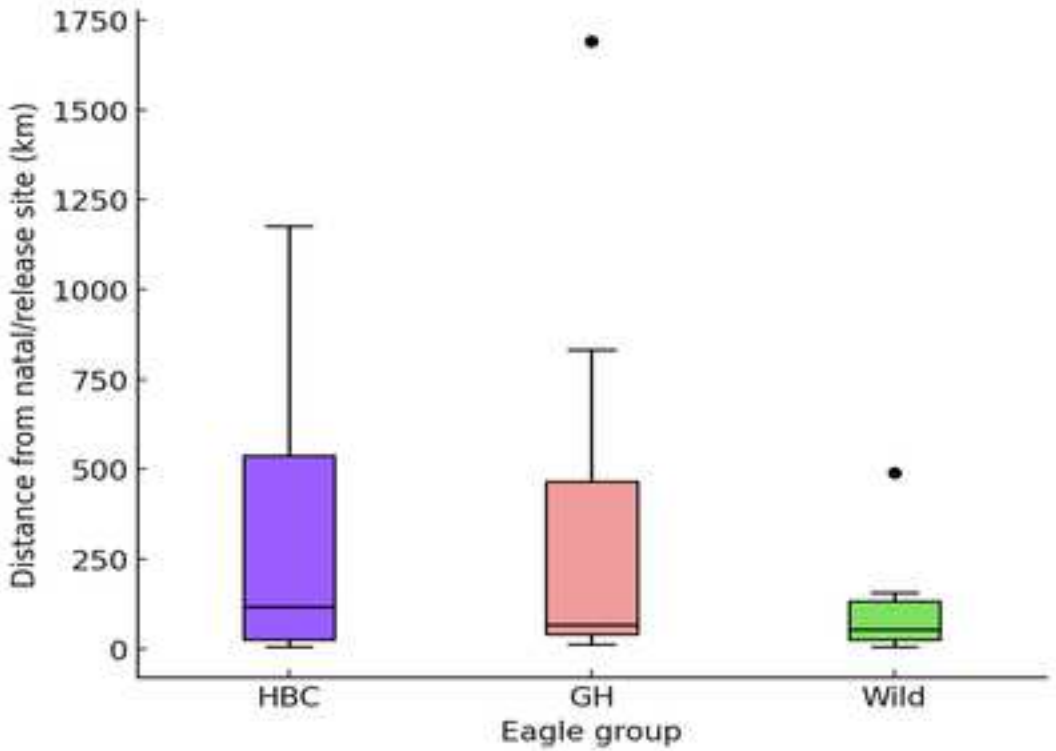


Figure 5



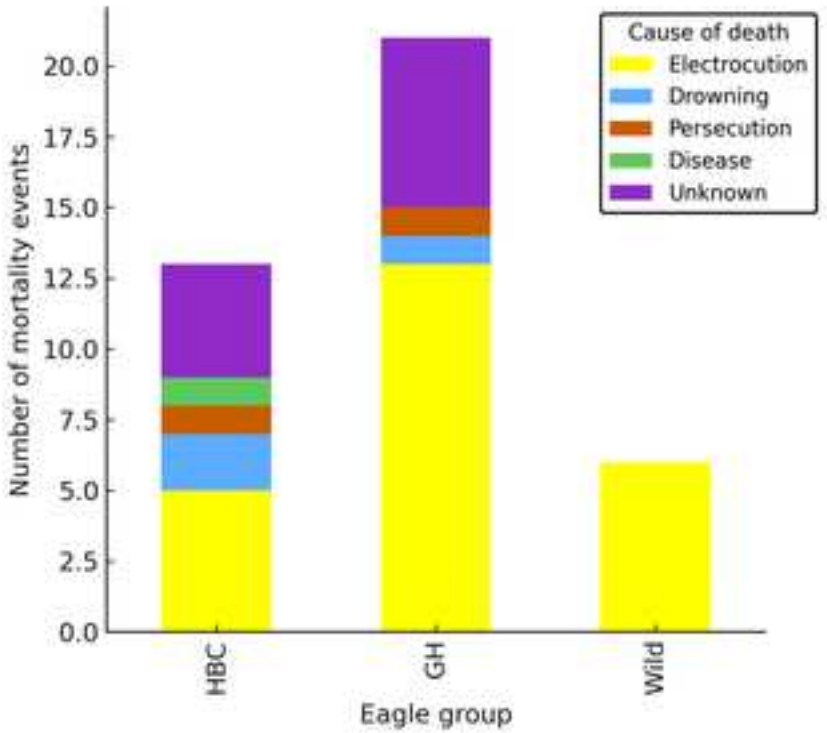


Figure 6