Natal dispersal and process of recruitment in a long-lived, trans-continentally migrating bird

Paweł Mirski[1], Wouter Vansteelant[2,3], Patrik Byholm[4,5]

[1] Faculty of Biology, University of Białystok, Ciołkowskiego 1J, 15-245 Białystok, Poland

[2] BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Zaailand 110, 8911 BN Leeuwarden, The Netherlands

[3] Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, The Netherlands

[4] Organismal and Evolutionary Biology, University of Helsinki, PO Box 65, 00014 Helsinki, Finland

[5] Novia University of Applied Sciences, Raseborgsvägen 9, FI-10600 Ekenäs, Finland

ABSTRACT

Natal dispersal is a multi-step process. It commences when a juvenile departs from its natal site and concludes when it settles to breed for the first time. During this interim period, dispersing individuals of long-lived species undergo a wandering phase, which may span years. This phase remains one of the least studied aspects of species' life history. We utilized a unique GPS-telemetry dataset on a slow-life history migratory bird of prey – the European honey buzzard, tracked for multiple years after fledgling. Our aim was to assess how phenology, ranging behaviour and philopatry change as individuals gain experience. Individuals exhibited variability in the age at which they first returned to their breeding range, yet all survivors settled at sites proximate to their natal nests. In subsequent returns, immatures increased the time spent within the breeding range and narrowed their ranging to smaller areas situated even closer to their natal nests. Our study unveils the complexity and protraction inherent in natal dispersal, emphasizing the importance of individual experiences and migratory improvement for successful recruitment in long-lived species.

Keywords: floaters, homing, philopatry, immaturity, European honey buzzard, *Pernis apivorus*

INTRODUCTION

Most animals are forced to depart from their natal habitat upon attaining independence. The phenomenon of permanent displacement from the natal area to the site of initial reproduction has garnered significant attention among ecologists and is extensively deliberated under the term "natal dispersal" (Greenwood 1982). Natal dispersal strategy tend to vary greatly between and within species, and seem to emerge through a trade-off between establishing in familiar areas and habitats and conspecific attraction on the one hand, and avoiding intraspecies competition (Nilson 1989, Negro et al. 1997, Forero et al. 2002) and inbreeding (Alonso et al. 1998, Zedroesser et al. 2007, Ortego et al. 2008) on the other hand. The ultimate outcome of natal dispersal not only influences the life history and fitness of individual organisms (Forero et al. 2002, Nevoux et al. 2013, Luna et al. 2020) but also shapes the genetic and social structure of populations (Ekman et al. 2001, Ortego et al. 2008, 2011).

Dispersal constitutes a movement process, yet in many investigations, it is often distilled to a single metric: dispersal distance (Benton & Bowler 2005). Undoubtedly, it is a much more intricate phenomenon and challenging to track, especially among long-lived species that mature late. In such species, dispersal unfolds as a multistep process. Between the initial departure from the natal site and settling in a new breeding ground for the first time, dispersing individuals undergo a wandering phase (Benton & Bowler 2005, Penteriani & Delgado 2009). During this stage, long-lived species, even upon reaching maturity, frequently linger for a season, several seasons, or even their entire lives as floaters, seeking a mate or suitable breeding territory (Penteriani & Delgado 2009). Consequently, dispersal is more readily studied in short-lived and abundant species, while it is seldom examined in long-lived migratory species of low-density populations. Nevertheless, understanding the factors and mechanisms governing the survival and recruitment to breeding populations is not only of interest from a scientific perspective but is also crucial for conservation of rare species, e.g. to reveal bottlenecks of early-life survival (Cheng et al. 2019), temporary settlement areas (Nemček et al. 2016) and other aspects (Burger & Shaffer 2008).

In migratory species, wherein the period between leaving the natal site and initial breeding is preceded by one or more episodes of migration, dispersal is additionally complex. During this interim period, immature individuals may traverse thousands of kilometres to non-breeding grounds before returning to their breeding range. Inexperienced young migrants are susceptible to deviations during migration due to navigational errors or wind drifts, resulting in their positions often shifting further and in a more random manner than those of resident species (Vickers et al. 2023). Consequently, migration profoundly influences the dispersal process, resulting in relatively longer dispersal distances (Paradis 1998) and relatively lower levels of philopatry (Weatherhead & Forbes 1994) in species that

migrate longer distances. At the same time, high philopatry (i.e. dispersal distances in the order of tens of meters to kilometers) tends to be widespread even among migrants (Förschler & Bairlein 2010, Ceresa et al. 2016) and even in species that spend long periods outside the breeding range before their first breeding attempt (Coulson 2016). In doing so, migratory birds, demonstrate remarkably long-term spatial memory and homing abilities, as well as a strong bias towards natal environmental cues during recruitment (Keiser 2003, Healy & Hurly 2004). And so the precise mechanisms through which early-life movements outside the breeding range influence the natal dispersal process remain obscure.

An additional challenge for migrants, especially those undertaking long-distance journeys, is that they spend relatively little time in their breeding range prior to recruitment. While immature individuals of resident species may spend the entire autumn, winter, and early spring exploring resources and assessing competitors' distribution around potential breeding sites, migrants often have only a few weeks from arrival to recruit into the breeding population. In species with longer offspring development and parental care, floaters, despite being physiologically mature, may struggle to secure a territory and breed within the short window following their initial arrival from wintering sites. In such species, the dispersal process is protracted and typically encompasses the floater stage for at least one season. Importantly, individuals that do not improve their migration performance and arrival time might not even recruit into the breeding population (Sergio et al. 2017). All considered, this underscores the importance of better studying the link between migration timing and the natal dispersal and recruitment process in order to better understand avian demography.

The European honey buzzard (*Pernis apivorus*; therafter honey buzzard) serves as an example of a long-lived, long-distance migratory species with potentially intricate dispersal and recruitment strategies. Firstly, it is a specialist with a narrow diet, predominantly preying on wasp and hornet larvae (Gamauf 1999, van Manen et al. 2011, van Manen 2013) within tropical and temperate forests (van Manen et al. 2011, Howes et al. 2020a). This dietary specialization significantly influences its annual cycle and appears to constrain the suitable habitats where it can establish breeding populations. Secondly, migratory species of the honey buzzard genus undertake transcontinental migrations, covering several thousand kilometres between their temperate breeding and tropical non-breeding ranges (Higuchi et al. 2005, Strandberg et al. 2012), with juveniles and adults exhibiting a large ontogenetic shift in migratory behaviour (Kjellen et al 1992, Schmid 2000, Hake et al 2003, Vansteelant et al 2020). Thirdly, it is a secretive species, characterized by its brief residency in breeding areas, late spring arrival (during the full canopy season), and relatively low population density. Consequently, it has been inadequately studied in Europe, particularly in contrast to its relatively high conservation status (listed in Annex 1 of the Birds Directive).

The advantages of philopatry are already well explained in birds (Pärt 1994, Bensch et al. 1998), and this phenomenon is relatively common in birds of prey (Newton 1979). Therfore we expect to observe it also in honey buzzards, but the exsisting data on its natal dispersal primarily based on a small number of ringing recoveries (Roberts & Law 2014). Concomittantly, the age of first breeding remains understudied, with only a few cases recorded among British honey buzzards. Four males were observed breeding for the first time between the 4th and 7th calendar year, while two females bred in their 6th and 7th calendar year (Roberts & Law 2014). The relatively late age of first breeding in this species is associated with a tendency of the species to spend at least the 2nd calendar year in sub-Saharan Africa. Indeed, proven records of 2nd calendar year honey buzzards in Europe are extremely rare (Wright et al 2019 and refs therein), and early telemetry studies confirmed that immatures did not return to Europe before their third calendar year (Gamauf & Friedl 2011), or even later (Strandberg et al. 2012). However, these were limited to a small number of individuals, precluding comprehensive tracking of the entire dispersal and recruitment process in this enigmatic species. Here, we present longitudinal movement data of young honey buzzards tracked from their natal areas in Finland for up to seven years after fledging, thus revealing their process of natal dispersal and recruitment. We specifically aimed to understand the interplay between maturity, natal dispersal, recruitment, and migratory behavior in this complex and secretive species. It is well established from migration counts, ringing and tracking data (reviewed in Vansteelant & Agostini 2021) that juvenile honey buzzards migrate later and over a broader front than adults, with relatively few juveniles migrating through traditional overland flyways (Kjellen et al 1992, Vansteelant et al 2020), and juveniles taking more time to complete their first migration (Hake et al. 2003). Juvenile behaviour thus seems to be consistent with an innate vector-based orientation strategy, making them highly susceptible to wind drift (Thorup et al. 2003). Indeed, a previous study based on the same individuals that we study here showed that stochastic wind influences greatly influenced the route choice of juveniles on their first outbound migration, as well as the longitude at which they settled in tropical Africa (Vansteelant et al. 2017). The remainder of the natal dispersal process, in particular the first return migration and breeding range movements of young honey buzzards, have not been tracked until now. However, we do know that adult honey buzzards utilize distinct migration routes between seasons, engaging in so-called loop migration (Agostini et al. 2012). This suggests that young honey buzzards do not retrace their first outbound migration to home back to their breeding range, and that the longitude at which honey buzzards settle after their first outbound migration may influence return migration routes and natal dispersal distances. In general, however, we expect most honey buzzards to initiate their first return migration upon reaching sexual maturity in their 3rd calendar year, and to home back near to their natal areas to recruit as breeders.

METHODS

GPS-tracking dataset

As a part of ongoing work on honey buzzard migration and movement ecology (Vansteelant et al. 2017, Nourani et al. 2020, Howes et al. 2020, Brønnvik et al. 2022), young honey buzzards (n = 29) hatched in broods in southern Finland (latitude 61°14′–63°12′ N, longitude 21°16′–23°31′ E) were equipped with solar-powered Argos-GPS platform terminal transmitters (PTTs) (Microwave Telemetry Inc.) or Ecotone GSM-GPS-trackers (Ecotone) during 2011-2016 using body-loop harnesses made of Teflon ribbon. Adults (n = 9) were caught with dho-gazas nets at the nest. Tags' weight (22–27 g) corresponded to ca. 3% of the birds' body mass at deployment (908±83 g; avg ± s.d., *n* = 29). The amount of delivered GPS-fixes varied depending on tracker model and programming. The sex of birds was determined from DNA as extracted from blood samples using the salt extraction method. For more details on the field protocol see Vansteelant et al. (2017)

Ranging area

During consecutive wintering and breeding seasons, ranging areas were estimated to compare how the area of exploration changes with age and experience. The dataset comprised moderate-frequency GPS fixes, resulting in hundreds or occasionally dozens of fixes per season for some individuals. To compare ranging areas rather than estimate space use requirements, a geometric estimator – the 90% minimum convex polygon (mcp) – was employed. We considered alternative utilization distribution methods, but in case on non-territorial, wandering individuals of varying sample size and changing activity centres, utilization distribution methods overestimated the ranging area more than mcp.

Calculations were conducted using the *adehabitatHR* package (Calenge 2006) in R 4.1.1. Wintering ranging areas were calculated from the beginning of January until the end of March, when individuals had reached their wintering quaters and ceased moving long distances, until spring migration. Ranging areas upon returning to the breeding range were calculated from arrival until departure in the potential breeding range. By the latter we assumed southern Finland, where the tracked individuals originated and were expected to return, assuming the species is philopatric.

Phenological dates

To track how phenology of migration changed with age, departure from non-breeding range, arrival to and departure from the breeding range were noted in the Julian calendar. Because individuals differed in the latitude of their ranging in Africa and this affects the distance and migration duration, the date of departure from non-breeding range was recorded as the date of passing the 13th parallel (the approximate boundary of the desert zone). Arrival to the breeding range was determined as the first instance where an individual ceased moving northward by more than 50 km in the next 5 days. Departure from the breeding range was identified when an individual began moving southward by more than 50 km in the next 5 days.

Mortality

Confirmed and probable deaths of tracked individuals, especially during their first autumn migration, wintering, and returning migration, were recorded to compare mortality among naïve honey buzzards. Suspected mortality was investigated on-site when indicated by sensors showing low temperatures, absence of movement over several days, or suspicious movements in urbanized habitats. Mortality due to drowning during migration across the Mediterranean and Black Sea was inferred from signal loss at the sea shore. Tag failure was suspected in some cases, especially in the fourth-seventh year of tracking. Mortality ratios were estimated based on confirmed cases, excluding suspected tag failures.

Philopatry

To assess if immature honey buzzards tend to return and potentially settle close to their natal sites, we calculated the mean and minimum distance at which honey buzzards resided from their natal site in each consecutive breeding period. To do this we used the 'distance matrix' tool in QGIS 3.22 for each breeding season.

Analyses

Due to sample size limitations, statistical approaches were constrained. Wilcoxon tests were used to compare winter ranging areas between first and subsequent wintering episodes as well as to test sex differences in the year of first return to breeding range and date of arrival. Linear models in R were employed to test changes in dates of arrival and departure from breeding ranges, duration of

stay, wintering and summer ranging areas. Model residuals were assessed for normality with the Shapiro test and log-transformed in the case of ranging areas.

RESULTS

Extended Immaturity Period in Wintering Range

Out of the 29 tracked juveniles, 22 (76%) successfully reached wintering sites in Africa (Tab. 1). None of the juveniles returned to the breeding range in their second calendar year. During their first winter, honey buzzards ranged over extensive areas in Central-Western Africa, with some individuals traversing distances exceeding 2000 km along longitudinal or latitudinal axes (Fig. 1A). Subsequently, some individuals reduced their ranging areas considerably during the next winter, while others maintained extensive ranges. However, the decrease in wintering area between the first and next winter was statistically insignificant ($W = 57.5$, $p = 0.11$), and no significant changes were observed in later life stages, although breeding adults tended to range over smaller areas (Fig. S1).

In the 3rd calendar year, six out of eleven tracked individuals attempted to return to the breeding range, with only half of them succeeding. The individuals that skipped the returning journey all survived to the next calendar year, and most of those (four out of five) attempted to return to the breeding grounds in the following year, in their 4th calendar year. The last remaining individual, tried to return in his 5th calendar year, but did not succeed in crossing the Mediterranean Sea and contined to wander in non-breeding part of the range (Fig. 2). Finally, this male successfully returned to his natal area in his 6th calendar year. In total, only six individuals (21%) reached the breeding range between their 3rd and 6th calendar years. We did not confirm that establishing winter territories (represented by the size of winter ranging area) impacted the age of returning migration ($W = 47$, $p = 0.76$). Similarly, the change in winter ranging area between the first and second winters did not affect the decision to undertake the returning migration in the 3rd calendar year ($W = 10$, $p = 0.22$).

The First and Following Returns to the Breeding Range

All tracked individuals followed different paths during their first spring migration back to the breeding range when compared to their first autumn migration, with most paths not intersecting between autumn and spring (Fig. 2). Both clockwise and counterclockwise loop migrations occurred. Honey buzzards advanced their departure from non-breeding range with each following return episode. The trend was visible (Fig. 1C), but only close to significant (Tab. 2). The date of arrival to the

breeding range varied significantly between individuals especially during the first returning migration but tended to advance and narrow down slightly in subsequent returns (Fig. 1D, Tab. 2). The date of departure from the breeding range tended to delay across returns (Fig. 1E, Tab. 2). The mean departure date at first return was eight days earlier than the intial departure it their 1st calendar year and about 2 weeks earlier at their second and third return. Immature honey buzzards spent more time in the breeding range with each subsequent return (Fig. 1F, Tab. 2).

Philopatry and First Establishment of Breeding Territories

The mean distance at which honey buzzards resided from their natal sites decreased significantly with each return (see Table 2, Figure 1G), averaging 296 km at the first return, 162 km at the second, and 135 km at the third (see Table S1). Similarly, the minimum distance to natal sites decreased with each return, ranging from 5 to 177 km at the first return (mean 53 km) to 0 to 174 km at the second return (mean 49 km). Five out of six returning individuals visited sites closer than 20 km from their natal sites, with four of them closer than 10 km. The area explored by individuals tracked, at least until the second return, showed a significant reduction (Fig. 1B, Fig. 3). During the first return, honey buzzards explored hundreds of square kilometres, whereas areas of only dozens of square kilometers were explored in the subsequent seasons. Some individuals confined their ranging to a portion of the area explored during the first return, while others moved to new, neighbouring areas that they had not explored before. Ranging areas showed significant overlap between the second and third return.

Two males were tracked long enough to locate their first nests and observe a central place foraging pattern around them. However, we haven't confirmed successful breeding. Lars built a nest in his 5th calendar year, during his third return to the breeding range, 16 km from the natal site. Mohammed built his nest in his 6th calendar year, during his first return to the breeding range, 189 km from the natal site. In his 7th calendar year, he refurbished the same nest, but in the 8th, he probably built another one. Mating and breeding, however, were not confirmed in either of these males.

Mortality Across the Long Dispersal Period

Mortality on the first autumn migration of honey buzzards reached 25% (7 out of 28). All, except for one, managed to cross the Mediterranean Sea. Once they reached their wintering sites in the tropics, 32% of juveniles perished at wintering sites during the first wintering season and one more individual (3.5%) in the second season. Finally, 39% of honey buzzards survived until their first

returning journey. Out of 11 individuals that survived long enough to undertake the returning journey, as much as five (45%) perished trying to reach Europe. One individual turned back, so only less than 50% of individuals that survived to this stage were able to reach the breeding range in the first try and 55% in total. Once the honey buzzards successfully completed their dispersal cycle, only two mortality cases were noted. Overall, only 21% of initially tracked individuals managed to return to their breeding range, while only 18% lived up to their second return to the breeding range, when potentially the first breeding attempt was possible.

DISCUSSION

Using GPS-GSM devices we were able to track the maturation and natal dispersal phase of honey buzzards from fledging to recruitment for the first time. Overall we reveal a remarkably protracted natal dispersal phase, which sheds new light on the importance of individual experience and migratory improvements for successful recruitment in this long-lived species.

The age of first return and first breeding

Our study showed that the age of first breeding might vary between individuals, and that the honey buzzard breeds at a later age as compared to similar-sized raptor species, including resident species, and short-distance as well as long-distance migrants. While we could confirm nest-building by two GPS-tracked Finnish males in the 5th and 6th calendar years, breeding attempts could not be confirmed for other birds of similar age, and most individuals showed continuous changes in breeding range movements for as long as they were tracked. These results agree with studies on British honey buzzards, which breed for the first time between the 4th and 7th calendar year (Roberts & Law 2014). The very late average age of first breeding is rather unexpected for a meso-predator like the honey buzzard. The similar-sized eurasian goshawk (*Accipiter gentilis*) can breed as early as the 2nd calendar year, with as much as 42% of females of this resident species starting to breed that early (Krüger 2005). Short-distance migrant eurasian buzzards (*Buteo buteo*) can also breed early, but the average age of first breeding is 3.5 years (Davis & Davis 1992), and also short-distance migrant red kites (*Milvus milvus*) breed for the first time between the 3rd and 8th calendar year, with an average of 3.6 years (Newton et al. 1989). Long-distance migrant black kites (*Milvus migrans*) start breeding between the 2nd and 8th calendar year (Sergio et al. 2017). Overall, variability in the age of first breeding is expected in territorial, long-lived species that inhabit relatively stable environments. Prior to breeding, they need to establish their territories over high-quality sites, while non-territorial species inhabiting temporal habitats show much more limited variation in recruitment age (Charlesworth 1994, Aubry et al. 2009, Acker et al. 2018).

Certainly, a number of factors affect the age of recruitment (discussed in the next subchapter), but in the case of the honey buzzard, the late age of first breeding seems to be associated with a long delay of first return migrations, and an unexpectedly large variation in the age of first returns. Individuals that return to the breeding range in their 3rd calendar year could likely attempt breeding in their 4th calendar year. By comparison, individuals like Mohammed (Tab. 1) that attempt a first return as late as the 5th calendar year (or do not succeed to return before the 6th calendar year) will necessarily recruit as breeders several years later. Such long delays of first return migraitons, far beyond the age of sexual maturation and the attainement of adult plumage, were wholly unexpected. The marked variation in the age of first return migrations, and the high survival rates of birds 'oversummering' in Africa at late age, suggests that honey buzzards face a trade-off between survival and attempting to return and recruit at early age. In this sense, it is striking that Mohamed, the bird to return at latest age, was one of the only birds for which attempted breeding could be confirmed in the field. Of course, it is possible that the age of first return is constrained by other factors like body condition or environmental factors, as has been posited for adult migrants that occasionally skip a northern summer by staying in sub-Saharan Africa (Sorensen et al 2017). However, the fact that at least half of all birds delay the first return at least two years, without engaging in failed or so-called 'reverse' migrations, suggest these between-individual differences reflect the viability of both 'fast' and 'slow' life-history strategies in this species. It is worth noting in this context that the longevity record in honey buzzards is 28 years, exceeding that of similarly sized raptors, and more similar to that of long-lived seabirds and vultures that also recruit at later age (Fransson et al 2023).

The process of recruitment to the breeding population

Tracking immature honey buzzards revealed that their recruitment to the breeding population greatly dependent on their migration performance. Suprisingly, first autumn migration was relatively safe for unexperienced juveniles, but the returning migration acted as a rigorous bottleneck, heavily affecting their survival. Only about 25% of tracked individuals managed to reach this stage, successfully passed the returning migration bottleneck and thus were able to start the recruitment process.

Recruitment in honey buzzards is fated to involve the floater stage. We found that on their first return to the breeding range, immatures arrive much later than the adults, usually in mid-June, but even as late as mid-July. This is weeks after the breeding adults and certainly too late to breed. The time of arrival visibly advanced with each subsequent return, due to a combination of advanced departures from Africa and reduced migration time, which in turn was mostly due to reduced stop-over time in experienced migrants. The overall time spent in the breeding grounds extended

analogously, while departure timing from Europe in autumn tended to remain stable from the 2nd autumn migration onwards. Already on the third return, honey buzzards spent on average 80 days in the breeding grounds, which is similar to adults (especially the ones that failed to breed). Therefore, the purpose of the first return in such long-lived migrant species seems to serve only for the exploration of the breeding grounds and possibly to initiate the annual routine and gain necessary experience in it.

Especially during the first return, honey buzzards clearly ranged over much greater areas than in following seasons. Wide-ranging behaviour is typical for floaters in many bird species (Tanferna et al. 2013, Eeden et al. 2017, Mirski & Anderwald 2023). Floaters are presumed to make such movements to obtain information on nest and foraging site distribution and quality, which can be inferred from conspecific performance too (see review by Lenda et al. 2012). The sharp decrease in ranging area after the second return migration and prolonged stay in the breeding grounds suggests that already at that time, honey buzzards might recruit to the breeding population, or at least have chosen the area of settlement. Indeed, some of the birds tracked here were witnessed to build nests after the 2nd migration, in their 5th and 6th calendar year, respectively. Though nest-building does not yet equate to recruitment as an actual breeding individual, we think it is likely that most honey buzzards only engage in their first real breeding attempt after having experienced multiple migrations at 6-8 years of age. The exact age of first breeding in long-lived territorial species depends heavily on competitive skills (Becker & Bradley 2007) -which may include migratory performance (Sergio et al 2014, Flack et al 2024)- and habitat quality (van de Pol et al. 2007), with additional variation in our study species due to the variable age of first return.

Natal dispersal and philopatry

All the tracked individuals found their way back to Finland and located themselves relatively close (49 km, on average) from their natal sites, which agreed with our expectations on the existance of philopatry in this species. However, quite little is known on how philopatric birds actually find their way back home. Do they repeat the autumn migration backwards up to familiar landscapes? Do they home by learned gradients in environmental cues (Thorup & Holland 2009, Kishkinev et al 2021) to return to the place they imprinted during the post-fledgling period? Our study adds insight to these uncertainities by showing that most individuals performed a loop migration. First return routes crossed or got close to first outbound routes in only two out of six individuals that completed their first return migration. Yet all birds managed to home back to Finland, even if some first had to return southwards after bypassing the Gulf of Bothnia through Sweden. To achieve such accurate navigation, birds may

rely on a variety of mechanisms, such as bi-coordinate gradient maps, whereby they could infer their relative position by extrapolating from learned gradients in environmental cues (e.g. geomagnetic, olfactory). Imprinting on “home” areas takes place prior to abandoning natal sites (Sokolov 2000), as is evident from the fact that migratory birds that are displaced as eggs or chicks tend to return to the areas they were displaced to (Cade et al. 2000). Such imprinting takes time and might be one of the reasons why juveniles in many species, including honey buzzards, are migrating later than adults (Kjellen et al 1992, Hake et al. 2003, Vansteelant & Agostini 2021). Tracking data confirmed that juvenile Honey Buzzards were left by both adults at only 1 – 2.5 weeks after fledging (Zsiemer & Meyburg 2015). The extra time spent by juveniles around natal sites might therefore be used for further imprinting on the geographical location to which they will return via unknown routes, more than 18 months after they left.

Ethics

Measuring and ringing of birds, was done as inherent of the normal ringing permit (permit 2604) as issued by the Finnish Museum of Natural History. All fieldwork requiring special permits (taking blood samples for DNA sexing, sampling and storing DNA-samples, attachment of PTTs/trackers) confirmed to five separate licences as issued by Finnish authorities (EPOELY/135/07.01.2013, ESAVI/2195/04.10.07/2014, PIRELY/49/07.01/2013, VARELY/73/07.01/2013, VARELY/215/2015).

Data accessibility

Complete tracking dataset is stored in Movebank.

Declaration of AI use

We have not used AI-assisted technologies in creating this article.

Authors’ contributions

PM: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; WV: conceptualization, methodology, writing—original draft, writing—review and editing; PB: conceptualization, data curation, funding acquisition,

project administration, investigation, methodology, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest

We declare we have no competing interests.

Funding

This work was supported by Kone Foundation, Swedish Cultural Foundation in Finland, R.E. Serlachius Foundation, Svensk-Österbottniska Samfundet and Aktiastiftelserna (to PB).

Acknowledgements

We wish to thank Mikko Honkiniemi, Ari Rantamäki, Jari Valkama, Risto Vilén, Jouko Kivelä, Annika Rossi, Kari Palo, Hannu Vuoto, Daniel Burgas, Martti Peltola and Ismo Nousiainen for their help with tagging European honey buzzards in Finland.

REFERENCES

Acker P, Francesiaz C, Béchet A, Sadoul N, Lessells CM, Pijl AS, Besnard A (2018) Insights on dispersal and recruitment paradigms: sex- and age-dependent variations in a nomadic breeder. Oecologia 186:85–97. https://doi.org/10.1007/s00442-017-3972-7

Agostini N, Lucia G, Mellone U, Panuccio M, Von Hardenberg J, Evangelidis A, Kominos T. (2012) Loop migration of adult European Honey Buzzards (Pernis apivorus Linnaeus, 1758) through the Central-Eastern Mediterranean, Ital J Zool 79:280-286. https://doi.org/10.1080/11250003.2011.623245

Aikens E, Nourani E, Fiedler W, Wikelski M, Flack A (2024) Learning shapes the development of migratory behavior. PNAS 121:e2306389121. https://doi.org/10.1073/pnas.230638912

Alonso JC, Martín E, Alonso JA, Morales MB (1998) Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. Behav Ecol 9:243–252. https://doi.org/10.1093/beheco/9.3.243

Aubry LM, Cam E, Monnat J-Y (2009) Habitat selection, age-specific recruitment and reproductive success in a long-lived seabird. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, New York, pp 365–392

Becker PH, Bradley JS (2007) The role of intrinsic factors for the recruitment process in long-lived birds. J Ornithol 148:377–384

Bensch S, Hasselquist D, Nielsen B, Hansson B (1998). Higher fitness for philopatric than for immigrant males in a semi-isolated population of great reed warblers. Evolution 52: 877e883.

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev 80:205-225. https://doi.org/10.1017/S1464793104006645

Brønnvik H, Safi K, Vansteelant WM, Byholm P, Nourani E (2022). Experience does not change the importance of wind support for migratory route selection by a soaring bird. Roy Soc Open Sci 9: 220746.

Burger AE, Shaffer SA (2008) Perspectives in Ornithology Application of Tracking and Data-Logging Technology in Research and Conservation of Seabirds. Auk 125:253–264. https://doi.org/10.1525/auk.2008.1408

Cade TJ (2000) Progress in translocation of diurnal raptors. In: RD Chancellor and B-U Meyburg (EDS.), Raptors at risk. WWGBP/Hancock House, London, U.K, pp. 343-372.

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516-519.

Cheng Y, Fiedler W, Wikelski M, Flack A (2019) “Closer-to-home” strategy benefits juvenile survival in a long-distance migratory bird. Ecol Evol 9:8945–8952. https://doi.org/10.1002/ece3.5395

Charlesworth B (1994) Evolution in age-structured populations. Cambridge University Press, Cambridge

Ceresa F, Belda EJ, Monrós JS (2016) Similar dispersal patterns between two closely related birds with contrasting migration strategies. Popul Ecol 58: 421–427. https://doi.org/10.1007/s10144-016-0547-0

Coulson JC (2016) A Review of Philopatry in Seabirds and Comparisons with Other Waterbird Species. Waterbirds 39:229-240. https://doi.org/10.1675/063.039.0302

Davis PE, Davis JE (1992) Dispersal and age of first breeding of Buzzards in central Wales. British Birds 85:578-587.

van Eeden R, Whitfield DP, Botha A, Amar A (2017) Ranging behaviour and habitat preferences of the Martial Eagle: Implications for the conservation of a declining apex predator. PLOS ONE 12: e0173956. https://doi.org/10.1371/journal.pone.0173956

Ekman J, Eggers S, Griesser M, Tegelström H (2001) Queuing for preferred territories: delayed dispersal of Siberian jays. J Anim Ecol 70: 317-324.

Forero MG, Donázar JA, Hiraldo F (2002) Causes and fitness consequences of natal dispersal in a population of black kites. Ecology 83:858-872. https://doi.org/10.1890/0012-9658

Förschler MI, del Val E, Bairlein F (2010) Extraordinary high natal philopatry in a migratory passerine. J Ornithol 151:745–748. https://doi.org/10.1007/s10336-010-0495-y

Fransson T, Kolehmainen T, Moss D, Robinson R (2023) EURING list of longevity records for European birds.

Gamauf A (1999) Is the European honey buzzard (*Pernis apivorus*) a feeding specialist? The influence of social hymenoptera on habitat selection and home range size. Egretta 42:57–85.

Gamauf A, Friedl C (2011) Zug- und Überwinterungsstrategien junger Wespenbussarde *Pernis apivorus*. Vogelwarte 49:290–291.

Greenwood PJ, Harvey PH (1982). The Natal and Breeding Dispersal of Birds. Annual Review of Ecology and Systematics 13:1–21. http://www.jstor.org/stable/2097060

Hake M, Kjellén N, Alerstam T (2003) Age-dependent migration strategy in honey buzzards *Pernis apiorus* tracked by satellite. Oikos 103:385–396.

Healy SD, Hurly TA (2004) Spatial Learning and Memory in Birds. Brain Behav Evol 63: 211–220. https://doi.org/10.1159/000076782

Higuchi H, Shiu HJ, Nakamura H, Uematsu A, Kuno K, Saeki M, Hotta M, Tokita KI, Moriya E, Morishita E, Tamura M (2005) Migration of Honey-buzzards *Pernis apivorus* based on satellite tracking. Ornithol Sci 4:109-115. 10.2326/osj.4.109.

Howes C, Byholm P, Symes CT (2020b) Forest availability and fragmentation drive movement behaviour of wintering European Honey-buzzard *Pernis apivorus* in Africa. Ardea 108: 115-128. https://doi.org/10.5253/arde.v108i2.a1

Howes C, Symes CT, Byholm P (2020a) Highly skewed sex and age ratios of European Honey Buzzard in southern Africa. J Ornithol 161: 539–548. https://doi.org/10.1007/s10336-019-01736-w

Keiser JT (2003) Homing Success of Migrants Versus Nonmigrants: Do Differences in Spatial Memory Generalize Across Spatial Scales?. Dissertations, Theses, and Masters Projects. William & Mary. Paper 1539626402.

Kishkinev D, Packmor F, Zechmeister T, Winkler HC, Chernetsov N, Mouritsen H, Holland RA (2021) Navigation by extrapolation of geomagnetic cues in a migratory songbird. Curr Biol 12;31(7):1563-1569.e4. https://doi.org/10.1016/j.cub.2021.01.051

Kjellén N (1992) Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. Ornis Scand 23:420-434.

Lenda M, Maciusik B, Skórka P (2012). The evolutionary, ecological and behavioural consequences of the presence of floaters in bird populations. North-West J Zool 8: 394-408.

Luna Á, Palma A, Sanz-Aguilar A, Tella JL, Carrete M (2020) Sex, personality and conspecific density influence natal dispersal with lifetime fitness consequences in urban and rural burrowing owls. PLoS ONE 15(2): e0226089. https://doi.org/10.1371/journal.pone.0226089

Mirski P, Anderwald D (2023) Ranging behavior of non-breeding and breeding adult white-tailed eagles. Diversity 15:1208.

Nilsson J-A (1989). Causes and Consequences of Natal Dispersal in the Marsh Tit, Parus palustris. J Anim Ecol 58(2):619–636. https://doi.org/10.2307/4852

Negro JJ, Hiraldo F, Donazar JA (1997). Causes of Natal Dispersal in the Lesser Kestrel: Inbreeding Avoidance or Resource Competition? J Anim Ecol 66:640–648. https://doi.org/10.2307/5917

Nemček V, Uhrin M, Chavko J, Deutschova L, Maderič B, Noga M (2016) Habitat Structure of Temporary Settlement Areas of Young Saker Falcon *Falco cherrug* Females during Movements in Europe. Acta Ornithol 51:93-103. https://doi.org/10.3161/00016454AO2016.51.1.008

Nevoux M, Arlt D, Nicoll M, Jones C, Norris K (2013) The short- and long-term fitness consequences of natal dispersal in a wild bird population. Ecol Lett 16:438–445.

Newton I (1979) Population ecology of raptors. T & AD Poyser, Berkhamsted

Newton I, Davis PE, Davis JE (1989) Age of first breeding, dispersal and survival of Red Kites *Milvus milvus* in Wales. Ibis 31:16-21.

Nourani E, Vansteelant WM, Byholm P, Safi K (2020) Dynamics of the energy seascape can explain intra-specific variations in sea-crossing behaviour of soaring birds. Biol Lett 16: 20190797. https://doi.org/10.1098/rsbl.2019.0797

Oppel S, Arkuma V, Bakari S et al (2021) Major threats to a migratory raptor vary geographically along the eastern Mediterranean flyway. Biol Conserv 262: 109277 https://doi.org/10.1016/j.biocon.2021.109277

Ortego J, Calabuig G, Aparicio JM, Cordero PJ (2008) Genetic consequences of natal dispersal in the colonial lesser kestrel. Mol Ecol 17:2051-2059. https://doi.org/10.1111/j.1365-294X.2008.03719.x

Ortego J, García-Navas V, Ferrer E, Sanz J (2011) Genetic structure reflects natal dispersal movements at different spatial scales in the Blue Tit, *Cyanistes caeruleus*. Animal Behav 82:131-137. https://doi.org/10.1016/j.anbehav.2011.04.007

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. J Anim Ecol 67:518-536. https://doi.org/10.1046/j.1365-2656.1998.00215.x

Pärt T (1994) Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. Anim Behav 48:401e409.

Roberts SJ, Law C (2014) Honey-buzzards in Britain. British Birds 107:668-691

Saurola P, Valkama J, Velmala W (2013) The Finnish Bird Ringing Atlas. Vol. I. Finnish Museum of Natural History and Ministry of Environment, Helsinki.

Schmid H (2000) Separate routes: autumn migration of juvenile and adult European Honey-Buzzards Pernis apivorus – a synthesis. Der Ornithologische Beobachter 97:191-222.

Sergio F, Tanferna A, Stephanis R, Lopez-Jimenez L, Blas J, Hiraldo F(2017). Migration by breeders and floaters of a long-lived raptor: implications for recruitment and territory quality. Anim Behav 131:59-72. https://doi.org/10.1016/j.anbehav.2017.07.011

Sokolov L (2000) Philopatry, dispersal and population structure of passerines on the Courish Spit of the Baltic Sea. Vogelwarte 40:302-314.

Sørensen IH, Schlaich AE, Klaassen RHG, Heldbjerg H, Koks BJ (2017) Rare case of an adult male Montagu's Harrier *Circus pygargus* over-summering in West Africa, as revealed by GPS tracking. J Ornithol 158: 753–760. https://doi.org/10.1007/s10336-017-1445-8

Tanferna A, López-Jiménez L, Blas J, Hiraldo F, Sergio F (2013) Habitat selection by Black kite breeders and floaters: Implications for conservation management of raptor floaters. Biol Conserv 160:1–9.

Thorup K, Alerstam T, Hake M, Kjellén N (2003) Can vector summation describe the orientation system of juvenile ospreys and honey buzzards? – An analysis of ring recoveries and satellite tracking. – Oikos 103: 350–359.

Thorup K, Holland RA (2009) The bird GPS - long-range navigation in migrants. J Exp Biol 212:3597-3604. https://doi.org/10.1242/jeb.021238

van de Pol M, Pen I, Heg D, Weissing FJ (2007) Variation in habitat choice and delayed reproduction: adaptive queuing strategies or individual quality differences? Am Nat 170:530–541

Van Manen W, van Diermen J, van Rijn S, van Geneijgen P (2011) Ecology of Honey Buzzard in the Veluwe Natura 2000 site (central NL) during 2008-2010, population level, breeding biology, habitat use and food (in Dutch). Natura 2000 report. Province of Gelderland, Arnhem NL/ Treetop foundation

van Manen W (2013) Biology of Honey Buzzards *Pernis apivorus* in the primaeval forest Białowieża, Poland. De Takkeling 21:101–126

Vansteelant WMG, Kekkonen J, Byholm P (2017) Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. Proc R Soc B 284: 20170387. http://dx.doi.org/10.1098/rspb.2017.0387

Vansteelant WMG, Agostoni N (2021) Honey Buzzard *Pernis apivorus*. Pp. 38-45 in: Panuccio M., Mellone U. and Agostini A. [eds.]. Migration Strategies of Birds of Prey in Western Palearctic. CRC Press, Boca Raton, Florida.

Vickers SH, Franco AMA, Gilroy JJ (2023) Non-reproductive dispersal: an important driver of migratory range dynamics and connectivity. Ecography: e06201. https://doi.org/10.1111/ecog.06201

Weatherhead PJ, Forbes M (1994) Natal philopatry in passerine birds: genetic or ecological influences? Behav Ecol 5:426–433. https://doi.org/10.1093/beheco/5.4.426

Wiltschko W, Wiltschko R (2017) Homing pigeons as a model for avian navigation? J Avian Biol 48: 66–74.

Wright J, Cavaillès S, Vansteelant WMG (2019) Photographic evidence of a 2nd calendar year female European Honey Buzzard *Pernis apivorus* on autumn migration in the Western Palearctic. Sandgrouse 41:101-104.

Zedrosser A, Støen O-G, Sæbø S, Swenson J (2007). Should I stay or should I go? Natal dispersal in brown bear. Anim Behavi 74:369-376. https://doi.org/10.1016/j.anbehav.2006.09.015

Ziesemer F, Meyburg B-U (2015) Home range, habitat use and diet of Honey-buzzards during the breeding season. British Birds 108:467– 481.

Table 1. Characteristics of GPS-tracking dataset of twenty nine Honey Buzzards from Finland, followed from fledging.

Name	Sex	Tracking start	Tracking end	Calendar year of return	Last data	Mortality	Mortality cause	Last signal site
Hans	M	03.08.2012	22.03.2014	-	1st wintering	Death	?	Cameroon
Ella	F	13.08.2013	16.12.2013	-	1st wintering	Death	?	Congo
Emma	F	06.08.2013	14.10.2013	-	1st autumn	Death	Shot	Sicily
Gilda	F	09.08.2012	08.11.2012	-	1st autumn	Death	Shot^	Niger
Ivar	M	07.08.2013	20.09.2013	-	1st autumn	Death	Predated	Estonia
Heidi	F	09.08.2013	28.11.2014	-	2nd wintering	Death	?	Gabon
Julia	F	17.08.2013	13.01.2014	-	1st wintering	Death	?	Congo
Kirsi	F	11.08.2012	13.11.2012	-	1st wintering	Death	Shot^	Nigeria
Lisa	F	03.08.2013	19.10.2013	-	1st autumn	Death	Predated	Deserts (Algeria)
Miikka	M	09.08.2013	04.04.2014	-	1st wintering	Tag failure	?	Nigeria
Per	M	02.09.2016	24.10.2016	-	1st autumn	Death	Exhaustion	Deserts (Algeria)
Piff	M	06.08.2011	17.02.2012	-	1st wintering	Death	?	Gabon
Roosa	F	29.08.2011	06.02.2012	-	1st wintering	Death	?	Congo
Rudolf	M	03.08.2012	02.02.2013	-	1st wintering	Death	?	Angola
Sven	M	07.08.2013	06.10.2013	-	1st autumn	Death	?	Algeria
Tor	M	29.07.2012	29.12.2012	-	1st wintering	Death	?	Angola
Ulla	F	06.08.2013	09.12.2013	-	1st wintering	Death	Collission	Congo
Viljo	M	03.08.2014	26.10.2014	-	1st autumn	Death	?	Deserts (Burkina Faso)
Venus	F	09.08.2012	11.05.2015	4*	1st return	Death	Exhaustion	Atlas mountains
Anni	F	06.08.2013	22.07.2016	4*	1st return	Unknown	?	Turkey
Edit	F	03.08.2013	18.06.2015	3*	1st return	Death	Drowned?	Medditeranean Sea
Matti	M	10.08.2013	29.05.2015	3*	1st return	Death	Predation?	Atlas mountains
Puff	F	07.08.2011	27.05.2013	3*	1st return	Death	Exhaustion?	Deserts (Mauritania)
Aida	F	03.08.2012	19.07.2014	3	breeding range	Death	Exhaustion^	Finland
Jaana	F	29.07.2011	20.05.2015	3	3rd return	Death	Exhaustion^	Deserts (Morocco)
Lars	M	10.08.2011	08.11.2015	3	5th wintering	Unknown	?	Cameroon
Mohammed	M	14.08.2013	25.09.2018	5* / 6	8th wintering	Tag failure?	?	Chad
Senta	F	09.08.2012	15.04.2018	4	3rd return	Unknown	?	Libya
Valentin	M	09.08.2012	09.10.2015	4	4th wintering	Tag failure	?	Nigeria

*- incomplete returning journey
^- confirmed mortality

Table 2. Results of linear models explaining change in migration strategy and ranging behaviour with experience in GPS-tracked Honey Buzzards from Finland, followed from fledging (*p*-values are rounded to two significant digits, significant values are bolded).

	Intercept	Beta coefficient	Standard error	*p*	Adjusted R^2
Departure from non-breeding range	143.05	-5.78	3.05	0.074	0.12
Arrival to breeding range	176.93	-7.4	6.76	0.30	0.02
Departure from breeding range	242.89	-1.3	2.12	0.55	-0.06
Duration of stay in the breeding range	32.18	16.51	6.83	**0.034**	0.29
Ranging area in breeding range (log)	13.15	-1.32	0.77	**0.0064**	0.46
Mean distance to natal site	376.23	-92.53	31.54	**0.014**	0.39

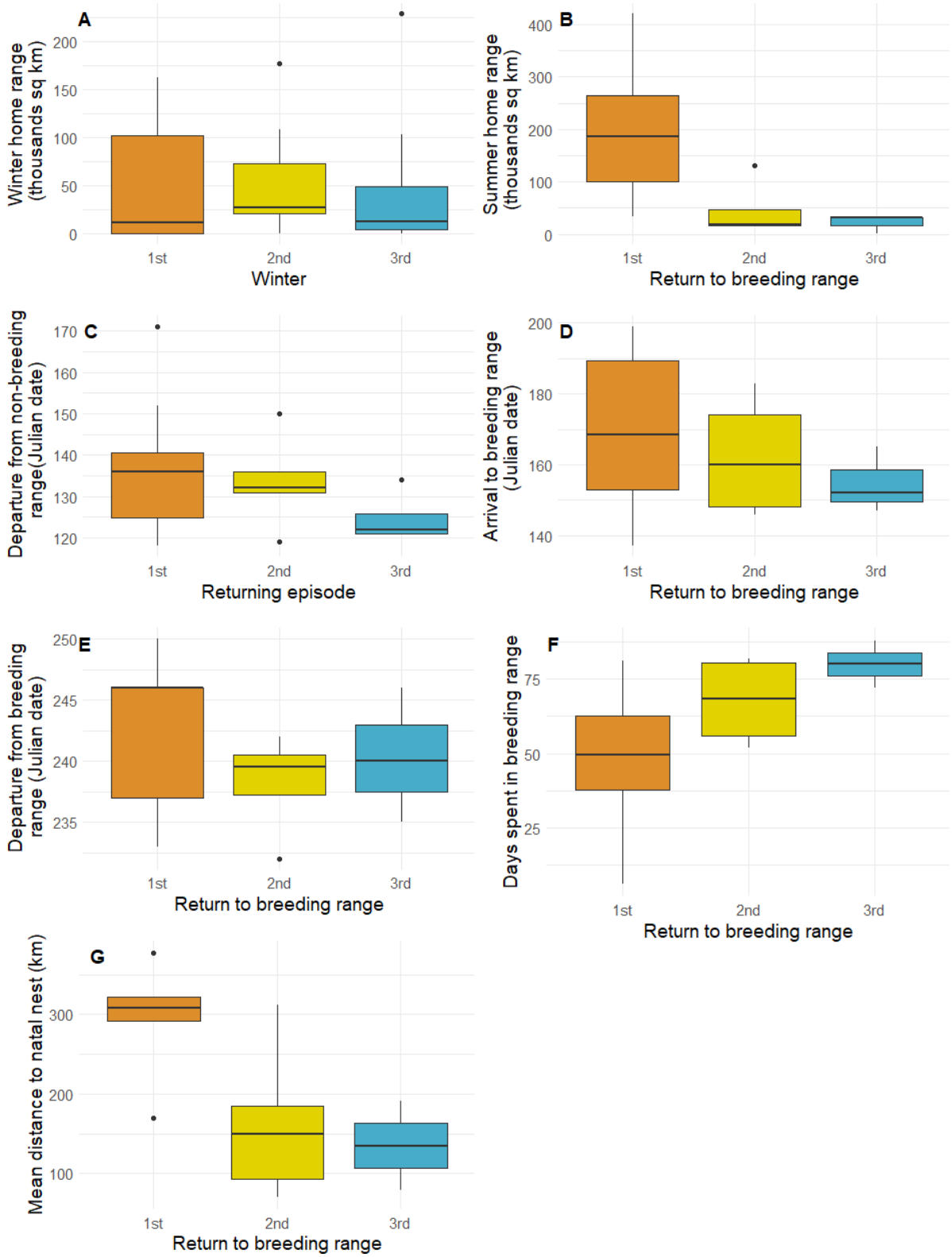

Figure 1. Differences in migration strategy and ranging behaviour with age (A) o or migratory experience (B-G) in GPS-tracked Honey Buzzards from Finland, followed from fledging. A - Size of winter ranging areas (January-March), B Size of summer ranging areas, C - Date of departure from non-breeding range, D - Date of arrival to breeding range, E - Date of departure from breeding range (start of autumn migration), F - Duration of stay in the breeding range, G - Mean distance to natal nest during breeding season.

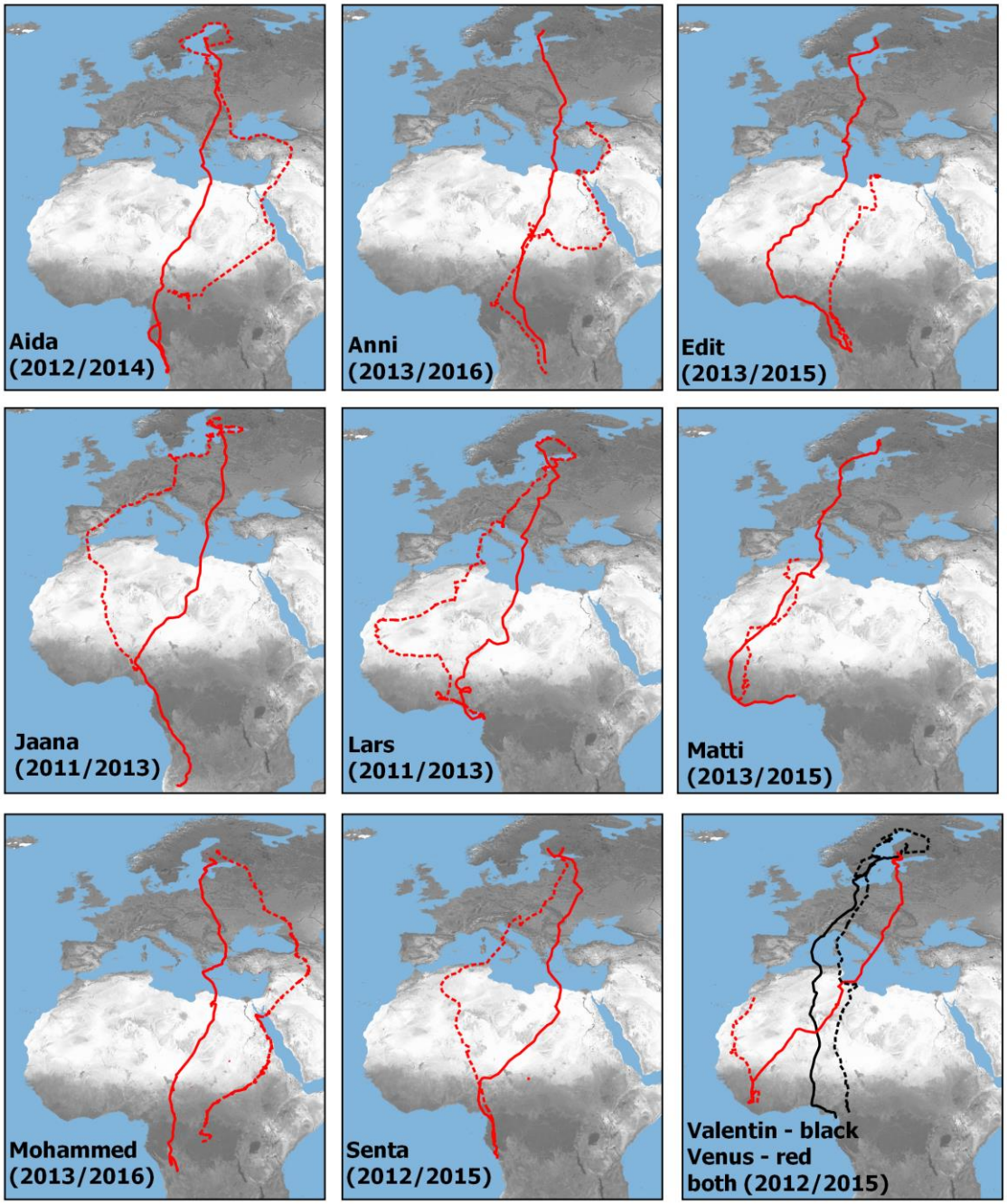

Figure 2. First autumn (continuous line) and first returning (dashed line) migrations of GPS-tracked Honey Buzzards from Finland. The names of individuals provided in each map correspond to the details given in Table 1. The year of the first autumn and returning migrations, respectively, are given in brackets.

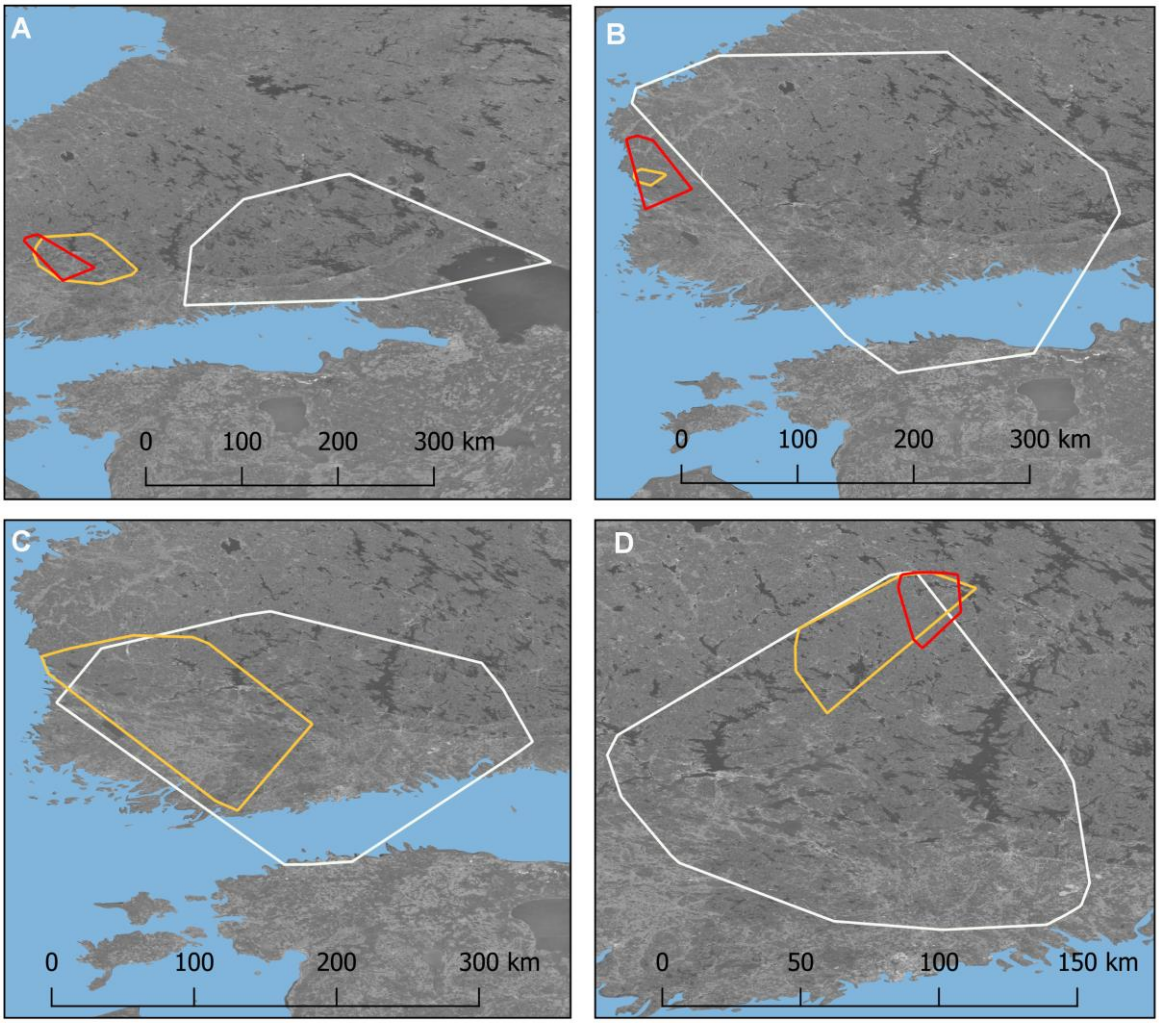

Figure 3. Change in summer ranging areas estimated with 90% minimum convex polygons of immature Honey Buzzards from Finland after first (white line), second (yellow line) and third return (red line). Plots A, B, C and D show ranging areas of Senta, Lars, Janna and Mohammed, respectively (see Tab. 1 for characteristics of individuals).

Supplemental Material

Table S1. Distance of immature Honey Buzzards from their natal sites, once returned to breeding range.

Id	Sex	# return	Calendar year	Min (km)	Mean (km)	Comment
Aida	f	1	3	177.4	295.3	
Jaana	f	1	3	27.3	291.0	
Jaana	f	2	4	7.0	149.3	
Lars	m	1	3	43.6	321.0	
Lars	m	2	4	12.5	92.8	
Lars	m	3	5	0.4	79.3	
Senta	f	1	4	47.2	321.6	
Senta	f	2	5	2.9	70.7	
Valentin	m	1	4	18.3	376.9	
Valentin	m	2	5	299.9	311.2	Only 2 fixes
Mohammed	m	1	6	5.0	169.2	
Mohammed	m	2	7	174.6	184.9	
Mohammed	m	3	8	174.9	190.8	
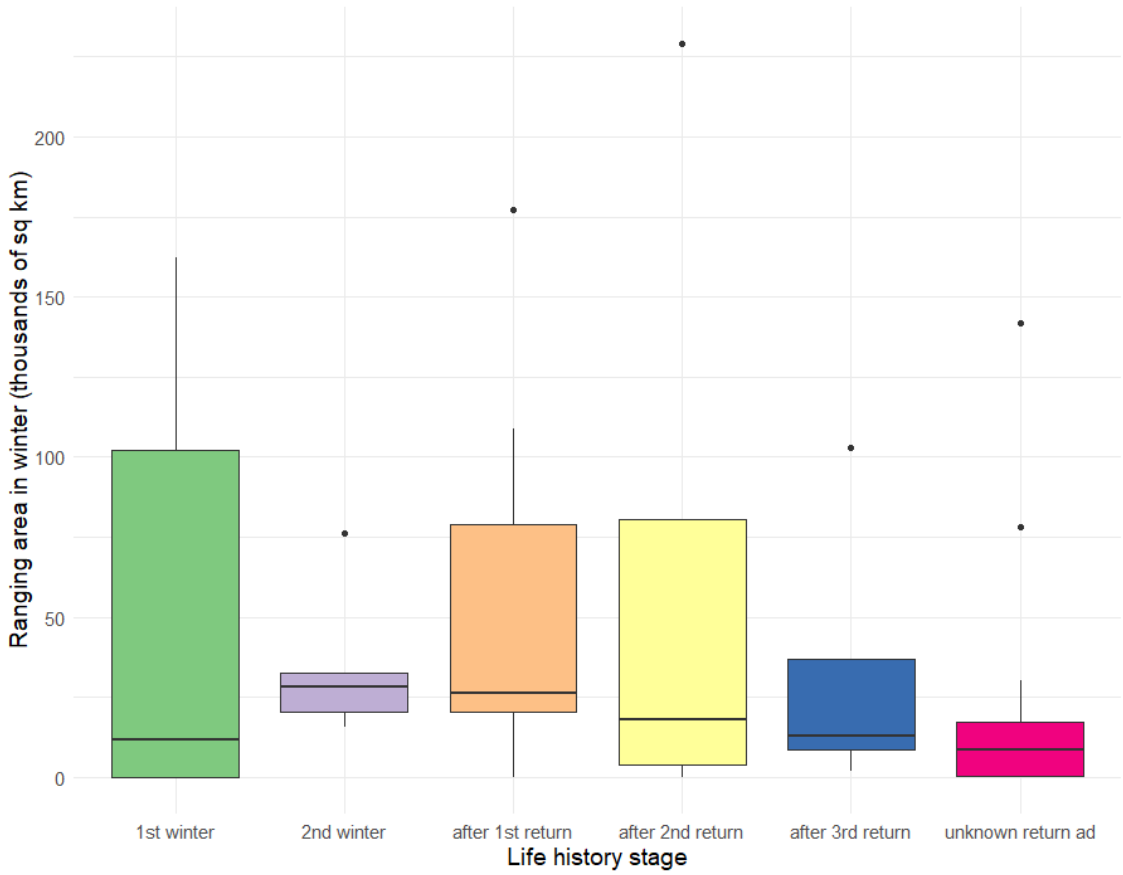
Figure S1. Winter ranging areas of Finnish Honey Buzzards in Africa across their life history. Ranging areas were estimated with 90% minimum convex polygon for the period of January-March. Note that some individuals spent more than two winters in Africa without returning to breeding range, while other overwintered only twice and started the migration cycle in their third calendar year. Therefore after first two winters, their grouped to categories of their migratory experience. The last bar shows adults of unknown age, but caught already as breeders.