

Assessing reintroduction outcome: comparison of the juvenile post-fledging dependence period between wild and reintroduced Bonelli's eagles in two Mediterranean islands

OLGA EGEA-CASAS

University of Valencia

PASCUAL LÓPEZ-LÓPEZ (✉ Pascual.Lopez@uv.es)

University of Valencia

ERNESTO ÁLVAREZ

Grupo de Rehabilitación de la Fauna Autóctona y su Hábitat (GREFA)

GIUSEPPE CORTONE

Ecologia Applicata Italia, Termini Imerese (PA)

MANUEL GALÁN

Grupo de Rehabilitación de la Fauna Autóctona y su Hábitat (GREFA)

JUAN JOSÉ IGLESIAS-LEBRIJA

Grupo de Rehabilitación de la Fauna Autóctona y su Hábitat (GREFA)

MARIO LO VALVO

University of Palermo

JUAN MARTÍNEZ

Grupo de Rehabilitación de la Fauna Autóctona y su Hábitat (GREFA)

STEFANIA MERLINO

Ecologia Applicata Italia, Termini Imerese (PA)

CARLOTA VIADA

LIFE Bonelli. Govern de les Illes Balears. Santa Eugènia. Mallorca. Balearic Islands

MASSIMILIANO DI VITTORIO

Ecologia Applicata Italia, Termini Imerese (PA)

Research Article

Keywords: island environment, movement ecology, post-fledging dependence period, raptors, reintroduction, telemetry

Posted Date: April 11th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1540050/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Islands are key areas for biodiversity; however, they are extremely sensitive to anthropic actions. This has led to local species extinctions, especially large predators such as raptors. Consequently, reintroduction and conservation projects aimed at reversing population decline of endangered species have recently gained popularity. Nevertheless, their relatively elevated cost and chance of failure make them controversial, hence assessing their effectiveness is essential. Within the early stages of raptors, the post-fledging dependency period (PFDP) is the one in which individuals must face dangers without having completely developed their skills. Thereby, comparing PFDP patterns concerning reintroduced and wild individuals is of major interest as it would help to plan and improve future conservation actions. We analyzed the behavior of 38 juvenile Bonelli's eagles (15 reintroduced and 23 wild) tracked through GPS telemetry, tagged as nestlings in two insular environments. The study period encompassed a total of nine-year movement data from reintroduced chicks in Mallorca (Spain) and wild chicks from Sicily (Italy). Movement parameters (i.e., age of first flight, age of dispersal, length of the PFDP, revisits to the natal or release area, and residence time in them) were analyzed together with their behavior during the PFDP for reintroduced and wild individuals. Similar movement patterns were obtained for both origins, although wild individuals revisited the natal site more often and dispersed earlier. Behavior was also similar, it varied throughout the PFDP, observing a more abrupt progress in wild individuals and an earlier development of travelling and hunting behaviors. Observed differences are probably related to food availability, which can improve body condition and thus delay onset of dispersal, together with parental presence, which can prompt an earlier ending of the PFDP by encouraging juvenile independence.

Introduction

Islands are key areas for biodiversity and for this reason many of them were included in the 25 Global Biodiversity Hotspots (Myers et al. 2000). The study of island environments has traditionally led to great advances within the field of ecology and conservation biology (MacArthur and Wilson, 1963; Diamond 1975) and this has led to consider islands as natural laboratories (Vitousek et al 2002). However, islands are not exempt from human activities, indeed they have been experiencing them since prehistory (Duncan et al. 2013) and more than 60% of recorded extinctions were insular endemic species (Gates and Donald 2000; Tershy et al. 2015). Due to their top position in food webs, large predators have experienced rapid population declines worldwide (Peltonen and Hanski 1991; Rosenzweig and Clark 1994). Consequently, different conservation plans including large predators like raptors have been developed to date (O'Rourke 2014; Dzialak et al 2007). These plans range from population monitoring and environmental management in order to improve local conditions for particular species or ecosystems, to reintroduction projects of endangered species, among others. In fact, overall extinction risk is greater for species that inhabit insular environments than continents (Hoffmann et al. 2010), and hence several conservation projects are being addressed to halt the decrease in population numbers of birds that have entered on the brink of extinction. One of the most popular actions of these projects is to reintroduce individuals in those areas where species went extinct in the past.

Reintroduction and relocation are specific methods widely used in conservation programs, and the study of their biological significance has been increasing dramatically since the 1990s (Seddon et al. 2007; Efrat et al. 2020). Among raptors, successful reintroductions in islands include species such as the Peregrine falcon (*Falco peregrinus*) (Tordoff and Redig 2001), the Mauritius kestrel (*Falco punctatus*) (Nicoll et al. 2004) and Seychelles' Kestrel (*Falco araea*) (Watson 1981; Ferrer et al. 2019). However, reintroduction projects are often controversial, mainly due to their potential high economic cost (Ferrer et al. 2017) and their possible lack of success (Fischer and Linder Mayer 2000), which is often perceived in detriment of conservation budget for wildlife in some areas (Seddon et al. 2007; Armstrong and Seddon 2008) instead of considering the sum of this and other conservation techniques a way of adding synergetic measures up.

One of the most crucial stages for birds of prey when colonizing new territories or settling in existing ones is the juvenile dispersal period or natal dispersal (Bowler and Benton 2005), which can be defined as the movements performed by juveniles of long-lived species, from their natal site to their first breeding site (Howard 1960, Greenwood 1980, Geenwod and Harvey 1982). In many cases, the departure from the natal site is preceded by exploratory movements during the phase known as the post-fledging juvenile dependence period (hereafter PFDP), which spans from the first flight from the nest to the onset of dispersal (Ferrer 1993; Balbontín and Ferrer 1993; Ramos et al. 2019). During this time, individuals usually perform exploratory flights of different lengths and eventually return to their natal area until the actual dispersal starts (Kenward et al. 1993; Walls and Kenward 1995; Cadahía et al. 2008; Weston et al. 2013). The PFDP is thus a critical stage of the early life of juveniles, where they must face natural and anthropic mortality risks in parallel to the development of flying, hunting and social skills (Weathers and Sullivan 1989; Ferrer 1992).

Global population decline of raptors (McClure et al. 2018; McClure and Rolek 2020) has led to the implementation of conservation programs worldwide. In Europe, European Union-funded projects addressed specifically to the conservation of endangered raptors throughout different European countries, including some of their islands, in Portugal, Spain, Italy, Cyprus, and Greece. Although the juvenile PFDP and onset of dispersal have been studied in raptors by means of radio-tracking and satellite telemetry (e.g., Cadahía et al. 2007b; Monti et al. 2012; López-López et al. 2014; Rahman et al. 2015) there is little knowledge on this stage of the life cycle of reintroduced individuals in comparison to wild individuals, especially in insular environments. This information is crucial for reintroduction projects in which much of the captive breeding efforts can be spoilt in the early stages of this process (Robert et al. 2015). To evaluate the effectiveness of these conservation measures, monitoring of different populations in which conservation actions are being performed is necessary (IUCN – SSC Species Conservation Planning Sub-Committee 2017). Nowadays, with the development of remote tracking technologies, the use of dataloggers allows not only accurate wildlife tracking for assessing conservation plans but also broadens the understanding of animal ecology in terms of movement ecology and animal behavior (Kays et al. 2015). Cutting-edge technologies, such as telemetry, provide researchers with massive amounts of precise locations, enabling the study of movement patterns and the interactions with other individuals or the environment. This technology can report crucial information of an

individual's location, accelerometry and physiological parameters (López-López 2016) throughout different stages of its life cycle. Dataloggers have been widely used to study raptors' dispersal (Cadahía et al. 2007b, Cadahía et al. 2010; Soutullo et al 2006) and, to a lesser extent, PFDP (López-López et al. 2014; Krüger and Amar 2017).

Here we analyzed the juvenile PFDP in a threatened raptor, the Bonelli's eagle (*Aquila fasciata*), in two different islands of the Mediterranean Basin in relation to the origin of the individuals: reintroduced birds in Mallorca (Balearic Islands, Spain) in comparison to wild birds in Sicily (Italy). Our study is thus aimed at evaluating whether the individual's origin or sex has an effect on the natural behavior during the PFDP and onset of dispersal of the species, all of it from an island environment perspective by means of GPS/GSM telemetry. We examined this period by establishing different parameters at which individuals performed essential movements in addition to the different behaviors and their variation throughout the whole PFDP. If pre-release and post-release actions were successful, we would expect wild and reintroduced individuals to accomplish the different parameters at a similar age, except for the onset of dispersal, which presumably might take place later in captive-reared individuals as they are fed ad-libitum and, ultimately, do not account for parental presence to modify their behavior.

Materials And Methods

Study species

The Bonelli's eagle is a medium-sized long-lived raptor, unevenly distributed in the Palearctic, Afrotropical and Indomalayan regions. This eagle has experienced a considerable decline during the last decades, especially in Europe (BirdLife International 2015) where it shows a circum-Mediterranean distribution. These circumstances led to the Bonelli's eagle being considered by the IUCN as "nearly threatened" in Europe (BirdLife International 2015). Bonelli's eagles usually breed between January and June nesting in cliffs and trees. On average (\pm standard deviation), juveniles perform their first flight at the age of 63 ± 6 days and begin dispersal at an age of 163 ± 17 days, with a PFDP spanning 98 ± 18 days (Real et al. 1998).

Study area

This study took place in two Mediterranean islands: Sicily (Italy) and Mallorca (Spain), where European-funded Bonelli's eagle conservation actions are being performed. Through the second half of the last century, Bonelli's eagle populations in these islands decreased principally because of habitat degradation, direct persecution by poachers, poisoning, and electrocution on power lines (Real and Mañosa 1997; Real et al. 2001; BirdLife International 2015; Hernández-Matías et al. 2015; Iglesias et al. 2018). It even became locally extinct in Mallorca during the late 60s (Viada et al. 2015) and the Italian population diminished in such a way that they currently only breed in Sicily, becoming extinct from Sardinia (López-López et al. 2012; Di Vittorio et al. 2012). To counteract this situation, the European Union funded two projects: the "LIFE Bonelli" (LIFE12 NAT/ES/000701) for the conservation of Bonelli's eagle in Mallorca and the Iberian Peninsula, and the "LIFE ConRaSi" (LIFE14 NAT/IT/001017) for the conservation of Bonelli's eagle, along

with Egyptian Vulture (*Neophron percnopterus*) and Lanner Falcon (*Falco biarmicus*) in Sicily. Both islands are relatively large and close to mainland. Mallorca has an area of 3640 km² and it is 220 km apart from the Iberian Peninsula, whereas Sicily has a total extent of 25711 km² and is isolated from the Italic peninsula by the Strait of Messina which is 3 km wide at its narrowest point. These two islands have areas with an abrupt orography that provides cliffs and forests, which constitute a suitable environment for the establishment of new breeding territories (Cramp and Simmons 1980). They also contain scrubland areas and non-irrigated agricultural areas, which favor the presence of potential prey, including rabbits, pigeons and lizards (Di Vittorio et al. 2012; Viada et al 2015).

Tracking

Overall, 44 individuals were tagged from 2011 to 2019; 27 wild chicks were tagged in Sicily from 2017 to 2019, whereas 17 reintroduced juveniles were tagged in Mallorca from 2011 to 2016. Wild chicks were marked at the nest at the age of 45–50 days approximately following standard procedures (e.g., Cadahía et al. 2007a). Reintroduced individuals were either bred in captivity in different centers in Spain and France (GREFA, Vendée and Ardèche dependents of UFCS/LPO) (n = 11) or extracted from natural nests from different localities in Andalusia (Spain) (n = 9). When aged 45–55 days, reintroduced individuals were tagged and relocated to Mallorca. They were released through hacking cage and fed *ad libitum* avoiding contact with humans once the juveniles were inside the hacking. The hacking cage consisted of a big cage with an artificial nest in the inside together with perches. Juveniles spend the first days enclosed inside this artificial nest to protect them from predators. After 7–10 days the nest is opened, and juveniles can move around the cage. Inside this hacking cage juveniles were fed *ad libitum* with dead prey, when juveniles were around 75 days live prey was provided. Once all the juveniles were able to hunt and were in an adequate physical condition, hacking cage was opened for their release (Viada and Iglesias 2017). Hacking cages were located along the Serra de Tramuntana, in the northwest of Mallorca Island. Around the hacking area, juveniles were provided with platforms for external feeding, which was supplied until none of the released birds further visited the hacking area. Wild individuals were raised by their parents and were all tagged with solar-powered E-OBS dataloggers. Diet studies conducted in Sicily during the breeding season by collecting pellets from the nest showed that Bonelli's eagles fed mainly on pigeon and wild rabbit (Di Vittorio et al. 2018).

Juveniles were tagged with GPS/GSM transmitters. Reintroduced individuals were tagged with solar-powered dataloggers manufactured by Ecotone 30 g (n = 3), E-OBS 48 g (n = 6), NorthStar 45 g Geotrack s/n GC106 (n = 1) and Microwave PTT-100 45 g GPS/Argos solar (n = 7). Wild individuals were raised by their parents and were all tagged with solar-powered E-OBS dataloggers. Transmitters were mounted in a backpack configuration designed to ensure that the harness would fall off at the end of the tag's life (Garcelon 1985), which is approximately 3 years, as it varies depending on the sampling rate and battery size (Rempel and Rogers 1997). Although it has been proven that satellite backpack tagging of raptors has no effect on their ecology and behaviour (Sergio et al. 2015), Gracelon's harnessing method was selected because of its demonstrated lack of effect on soaring raptors (Garcia et al. 2021). The mass of the equipment, including the harness, metal ring and tag, was below 3% of the bird's body mass, which is

within recommended limits (Kenward 2000). Juveniles' sex was determined by morphometrics and genetic determination following Palma et al. (2001).

Given that transmitters were initially programmed to record locations at different time intervals depending on battery levels, we subsampled locations at five minutes intervals to homogenize the overall dataset. Data were retrieved, stored and downloaded from the online data repository Movebank ("<http://www.movebank.org>"). Only birds that completed the entire PFDP were considered for this study.

PFDP parameters and spatial analysis

To characterize the major events of the PFDP we calculated the following parameters: i) age of first flight; ii) age of dispersal; iii) length of the PFDP; iv) residence time; and v) number of revisits to the nest or hacking site. The age of first flight was calculated by means of the "recurse" R package (Bracis et al. 2018). This package allows establishing a central point and a circular area around it for which it counts the number of visits and time spent inside and outside the area. Thereby, we set the central point as the coordinates of the nest or hacking location. The radius was set to 50 m, which accounts for twice the nominal error of the GPS. As a result, we obtained the number of revisits and residence time around their nest or release site (i.e., nest or hacking). First flight day was set as the first time that juveniles registered a revisit, being recorded more than 50 m away for more than 30 minutes apart from the nest or hacking site, as long as it was followed by regular revisits through the following days, together with visual inspection of telemetry information.

To assess the onset of dispersal we calculated the Net Squared Displacement (NSD), which measures the squared distance between the origin and further locations to gauge movements patterns (Bunnefield et al. 2011; Cagnacci et al. 2016). Here, NSD was measured from the nest/hacking site location to all subsequent locations to obtain the day at which juveniles started dispersal. The onset of dispersal was distinguished by an abrupt departure in the NSD which was not followed by any return to the natal area in the following month (Supplementary Material S1: Fig. S1 – S2). The total length of the PFDP was thus calculated as the difference between the onset of dispersal and the date of the first flight. PFDP parameters were compared by means of Wilcoxon rank sum tests either regarding juveniles' origin or sex. Provided that we performed multiple comparisons, we adjusted the p-values using the Benjamini – Hochberg method implemented in the "p.adjust" function of the "Stats" R package (Benjamini and Hochberg 1995).

We analyzed temporal variations in behavior by classifying individual's behavior through an unsupervised approach to multivariate data clustering, the Expectation Maximization binary Clustering (EMbC) (Garriga et al. 2016). This algorithm allows annotation of behaviours through correlation as it considers the velocity and the turning angle of the individual between consecutive GPS locations recorded at regular intervals. Local estimates of velocity and turning angle establish segmentation limits, allowing categorization of behavior into four groups: high velocity-high turning angle (HH), high velocity-low turning angle (HL), low velocity-high turning angle (LH) and low velocity-low turning angle (LL). These four classes were classified into behaviors: HH as active hunting, HL as travelling/relocating, LH as

searching/foraging and LL as resting (for further details on this method see Garriga et al. 2016; review in Bennison et al. 2018).

We performed Linear Mixed Models (LMM) (Zuur et al. 2009) to assess differences in movement parameters in relation to sex, origin, and age. These parameters were the age of first flight, age of dispersal, length of the PFDP, residence time and number of revisits. In each LMM we settled as dependent variable each of the parameters, independent variables were “origin” and “sex”, and “year” was established as a random factor. EMbC results were also analyzed with LMM. In this case, the dependent variable was each of the movements obtained (i.e., hunting, travelling, foraging, and resting), “origin”, “sex” and “week” (i.e., week after fledging) were considered as independent variables, and “year” as random factor. We compared and ranked the different models using the Akaike’s Information Criterion (AIC) (Akaike 1973). The model with the lowest AIC value was selected as the best one. When two or more models were considered as valid (i.e., AIC values differed in less than two AICc units), modelling average was conducted to evaluate the contribution of each independent factor by means of the MuMin R package (Barton 2020). All analyses were performed in R Statistic software version 4.0.2 (R Core Team 2020). Statistical significance was set at $\alpha < 0.05$.

Results

From the 44 birds initially tagged, a total of 38 individuals were considered in this study: 15 from Mallorca and 23 from Sicily. Individuals which did not complete the dependence period or whose track was lost during this time span were not included. A total of 846 087 GPS locations were recorded and analyzed in this study.

Parameters

Overall, wild individuals tended to develop sooner than reintroduced ones (Fig. 1). The first flight (Fig. 1a) in wild individuals took place at an age of 64 ± 6 days (range 56 – 75 days), while reintroduced individuals flew at 68 ± 8 days (range 57 – 90 days), although no significant differences were found ($U = 221.50$, $P = 0.146$). The onset of dispersal (Fig. 1b) occurred at a significantly earlier age in wild birds (158 ± 18 days; range 125 – 211 days) than in reintroduced individuals (168 ± 22 days; range 137 – 223 days) ($U = 252.50$, $P = 0.018$). Thus, the whole dependence period (Fig. 1c), from first flight to dispersal, was shorter for wild birds (90 ± 20 days; range 54 – 151 days) than for reintroduced ones (100 ± 25 days; range 62 – 158 days) although no significant differences were found ($U = 22$, $P = 0.209$).

With regards to residence time (Fig. 1d), wild individuals spent less time in the nest area (7.43 ± 8.18 days; range 0.003 – 28.39 days) than reintroduced ones did in the hacking site (13.47 ± 12.04 days; range 0.03 – 34.34 days) although no significant differences were found ($U = 222$, $P = 0.144$). In contrast, the number of visits to the hacking site (Fig. 1e) for reintroduced individuals (17 ± 27 revisits; range 1 – 98 revisits) were significantly fewer than those of wild individuals to the nest (60 ± 50 revisits; range 1 – 187 revisits) ($U = 70$, $P = 0.002$).

Pooling wild and reintroduced birds, no differences between sexes were found for any of the analyzed parameters (all $P > 0.05$). Age of first flight was 66 ± 9 days (range 56 – 90 days) and 67 ± 5 days (range 57 – 75 days) for males and females, respectively ($U = 211, P = 0.346$). Males began dispersal at a slightly earlier age (157 ± 20 days; range 125 – 211 days) than females (163 ± 21 days; range 126-223 days) ($U = 220, P = 0.228$), resulting in a total dependence period of 91 ± 23 days for males (range 62 – 151) and 97 ± 21 days for females (range 54 – 158) ($U = 218, P = 0.25$). The residence time was 9.81 ± 10.94 days (range 0.003 – 34.34 days) and 9.82 ± 9.49 days (range 0.06 – 29.48 days) for males and females, respectively, with no significant differences observed ($U = 194, P = 0.663$). Similarly, no differences in the number of visits to the nest or hacking site were observed for males (49 ± 50 revisits; range 1 – 187 revisits) and females (43 ± 45 revisits; range 1 – 151 revisits) ($U = 192, P = 0.702$) (Fig. 1).

The best models differed for each parameter (Table 1). The age of first flight and the length of the PFDP were not affected neither by sex, origin, or their combination. The number of revisits were accounted for the origin, the additive effect of sex and origin, and their interaction. After model averaging of the best LMMs, origin influenced age of dispersal ($Z = 2.158; P = 0.003$) and number of revisits ($Z = 2.641; P = 0.008$). Finally, all factors were included as predictors of residence time in all models.

Behavior

When analyzing the movements from the different individuals, we observed that searching/foraging behavior decreased over time as travelling and active hunting increased (Fig. 2). LMM analyses showed that the differences in the share of time spent on each behavior varied as the PFDP progressed, mainly for hunting, traveling, and foraging (Table 2), although it did not have an effect on the resting behavior. Nevertheless, these transitions in the percentage of time invested in each behavior tend to be earlier and more abrupt in wild individuals than in reintroduced ones, especially for the travelling behavior (Fig. 2). In fact, at the end of the PFDP, at week 14, half of the individuals had already begun dispersal.

Regarding origin (Fig. 3), we observed that throughout the whole juvenile PFDP, most of the time was invested in searching/foraging and resting activities; searching/foraging accounted for 47.93% of the time for wild and a 49.62 % of the time for reintroduced birds. Wild individuals spent 11.57% of the time in active hunting activities while reintroduced ones invested 6.14%. Concerning movements of travelling and resting, they represented only 9.51% and 30.99% of the time, respectively, for wild individuals. In comparison, reintroduced individuals invested more time in resting, accounting for 37.90% of the time, and slightly less in travelling, which represented the 6.34% (Fig. 3).

Discussion

New advances in wildlife tracking have allowed obtaining a large number of records with great precision that would have never been recorded with traditional methods such as ringing or radio-tracking. However, one of the key challenges of studying wildlife with GPS/GSM telemetry is the lack of observational data that endows recorded locations with biological sense. To fill this gap, new tools that allow the categorization of movements in an automatized and objective way have arisen, enabling researchers to

analyze not only ecological parameters but also behaviors. Thanks to the development of devices that continuously track individuals and analytical tools that allow the study of movement data, here we have thoroughly analyzed the PFDP and given biological significance to individuals' movements.

Our results showed that the PFDP resulted in a similar time span for wild and reintroduced individuals, with both performing the first flight at a similar age. This first flight can only take place once juveniles are fully feathered, which occurs at an age of approximately 60 days (Gil-Sánchez 2000), and are in an appropriate physical condition. Our results agree with the ones obtained from the study conducted on Montagu's harrier (*Circus pygargus*), in which reintroduced and wild juveniles showed no differences during the PFDP and similar behavior (Amar et al. 2000).

Wild individuals depend on their parents during the juvenile PFDP for food provisioning, however, towards the end of the PDFP, raptor parents tend to decrease investment in their offspring, reducing the amount of prey delivered to the juveniles (Ceballos and Donazar 1990; Arroyo et al. 2001). This reduction encourages juveniles to develop hunting and flying skills and promotes their departure from their natal area to avoid intraspecific competition (Trivers 1974). In fact, parental aggression towards the juveniles has been reported for the Spanish imperial eagle (*Aquila adalberti*) at the end of the PFDP (Alonso et al. 1986) and harpy eagle (*Harpia harpyja*) (Urios et al. 2017). Reintroduced individuals do not account for this parental presence, on the contrary, they are fed in order to keep them in the release site as long as possible to favor their return and settlement there. In this situation, juvenile Bonelli's eagles depart from the natal site presumably when they acquire an optimal body condition as seen in other raptors (Ferrer 1992; Walls et al. 1999; Delgado et al. 2010). However, raptor juveniles tend to expand their PFDP and remain in the parental territory to benefit from their hunting areas and protection from other conspecifics (Weston et al. 2018). The fact that reintroduced individuals disperse later supports the idea that the onset of dispersal is mostly driven by the individual, although parental presence can prompt it. Also, it is worth noting that food availability does not seem to prevent dispersal departure from their natal territory, as juveniles which were fed *ad libitum* eventually abandon their hacking site, although it could delay the onset of dispersal as seen in Vergara et al. (2010), where food supplemented kestrels tended to acquire independence later. Finally, Bonelli's eagle, as other raptors, is bounded to climate traits, which affect not only its distribution but also its breeding success (Ontivero and Pleguezuelos 2003; Carrascal and Seoane 2009; Di Vittorio and López-López 2014). Therefore, the warmer climate of Sicily could have favored an earlier development of wild eagles.

The age at which individuals performed their first flight, began dispersal and the total length of the PFDP were similar to those obtained by Real et al. (1998) who found that first flight occurred at an average age of 63 ± 6 days after hatching (range 52–66 days), dispersal began at an average age of 163 ± 17 days after hatching (range 143–177 days) and thus the whole PFDP lasted for 98 ± 18 days (range = 77–113 days, $n = 5$ in all cases). Although age of first flight showed similar results between both populations, in the case of reintroduced juveniles, they were not able to perform the first flight until the hacking cages were opened for them by the team, so probably there were some individuals that could have flown for the first time earlier. However, first flight is related to feather development, and it has been shown that *ad*

libitum feeding of captive juveniles favors feather growth (Lacombe et al. 1994). Also, food supplementation has been shown to allow juveniles to acquire a better physical condition and homogenizes their development, minimizing differences among them (Muriel et al. 2015), so probably body condition of hacked juveniles was similar when allowing them to leave the facility. In this way, reintroduced juveniles' age of first flight was similar not only to the one obtained for the wild population but also to that obtained in previous studies. The duration of the PFDP recorded here was longer than that reported in Balbontín and Ferrer (2005) which lasted for 77 ± 19 days (range = 50–114 days, $n = 28$). These differences were probably because they radio-tracked the chicks once a week and considered dispersal started when chicks were 3.5 km apart from the nest during two consecutive observations. This distance and timespan could correspond to a one-time excursion performed by the juvenile and not necessary the emancipation itself as discussed by Cadahía et al. (2007a). In fact, Nygård et al. (2016) defined an excursion in Golden Eagle (*Aquila chrysaetos*), as movements performed further than 10 km apart from the nest with a return to the surroundings of the nest, less than 5 km apart. Different tracking techniques, radio-tracking versus GPS/GSM telemetry, as well as the use of unbiased methods such as recursive analyses, can explain differences in the results obtained, with much more precision and accuracy in the later (Thomas et al. 2011).

During the whole dependence period, all individuals remained in the vicinity of the nest or hacking site a similar amount of time, although the difference in the number of times individuals visited the nest area suggest that parental prey deliveries in wild individuals take place around this area (Bustamante 1995). Reintroduced individuals made little use of the hacking cage, thus using the platforms around the area for feeding.

When observing the movements performed by the eagles throughout the whole dependence period, we found that there were not substantial differences between wild and reintroduced birds. Overall, changes in the share of time spent on each behavior throughout the PFDP were more gradual and occurred later in reintroduced individuals than in wild ones. This progressiveness on the percentage of each movement observed in all individuals and its delay is consistent with the development of flight skills, in which flights that involve flapping (i.e., searching/foraging) are firstly acquired and perfected with practice, and more complex movements (i.e., active hunting and travelling/relocating) are later developed (Riaux et al. 2020). In the Golden eagle, at the beginning of the dependence period, flapping flights were found, and complex movements developed later (Walker 2008), indeed, Weston et al. (2018) showed that the PFDP could be divided into two phases: ontogenic phase and maintained phase. During the ontogenic phase, eagles first increase their mobility, during the first 10 weeks (68 days), and later, this mobility was maintained until week 14 (99 days). However, the ability to perform complex movements seems to be acquired sooner if there is parental presence (Riaux et al. 2020). Juveniles learning from parents has also been observed in the Osprey (*Pandion haliaetus*), where hand-raised chicks acquired hunting skills without the presence of other conspecifics (Schaadt and Rymon 1982).

According to Balbontín and Ferrer (2005), two different hypotheses could explain the onset of dispersal: Resource Competition Hypothesis (RCH) (Howard 1960; Murray 1967) and the Ontogenic Switch

Hypothesis (OSH) (Holekamp 1986). The first one explains emancipation as a response to competition with their conspecifics for food resources, so under abundance of food they will not leave the parental territory. The OSH states that when resources are abundant, juveniles achieve earlier the optimal body condition and therefore emancipate earlier. Here, as Balbontín and Ferrer (2005), we observed that behavior in Bonelli's eagle juveniles might support the RCH, as reintroduced juveniles, which were fed *ad libitum*, delayed the age of dispersal. Similar results were obtained in juvenile golden eagles, which despite acquiring enough physical capacity, remained in their parental territory (Weston et al. 2018).

Studies aimed at assessing the outcome of reintroductions such as this one are essential to provide new insights in conservation biology, offering crucial information on the efficacy of different techniques with applications for future reintroduction projects. Our research highlights the importance of reintroductions together with an exhaustive monitoring of reintroduced individuals. Overall, wild and reintroduced eagles behaved in a similar way and neither sex nor year had an effect on the PFDP. In this way, the techniques used during the whole process did not affect the development and behaviour of individuals, as they do not differ substantially from the wild ones. Our results also illustrate that although parents are not responsible for the onset of dispersal, they can prompt an earlier ending of the dependence period and in conditions of high food availability, juveniles delay their onset of dispersal.

Declarations

Data Availability Statement

All data used in this study are publicly available upon request to data managers in the online data repository Movebank (www.movebank.org), project "Bonelli's eagle Mallorca. Life Bonelli / AQUILA a-LIFE" (project ID = 1019304600) and project "LIFE ConRaSi - Bonelli's eagle" (project ID = 268207241).

Author contributions

OE-C and PL-L contributed equally to this paper. OE-C and PL-L conceived the ideas and designed methodology; GC, MDV, MG, JJI, MLV, JM, SM, and CV collected the data; OE-C and PL-L analyzed the data; OE-C and PL-L led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Funding declaration

Bonelli's eagles' raw data were provided by two projects co-funded by European Union: "LIFE Bonelli" (LIFE12 NAT/ES/000701) in Mallorca and "LIFE ConRaSi" (LIFE14 NAT/IT/001017) in Sicily. The authors declare that no grants or other support were received during the preparation of this manuscript.

Competing interests' statement

The authors have no relevant financial or non-financial interests to disclose.

References

- Alonso JC, González LM, Heredia, B, González JL (1987) Parental care and the transition to independence of Spanish Imperial Eagles *Aquila heliaca* in Doñana National Park, southwest Spain. *Ibis* 129: 212– 224.
- Akaike H (1974) A New Look at the Statistical Model Identification. *IEEE Trans Automat Contr* 19:716-723.
- Amar A, Arroyo B E, Bretagnolle V (2000) Post-fledging dependence and dispersal in hacked and wild Montagu's Harriers *Circus pygargus*. *Anim Behav* 63:235-244.
- Armstrong D P, Seddon, P J (2008) Directions in reintroduction biology. *Trends Ecol Evol*
<https://doi.org/10.1016/j.tree.2007.10.003>
- Arroyo B E, Cornulier T De, Bretagnolle, V (2002) Parental investment and parent–offspring conflicts during the postfledging period in Montagu's harriers. *Anim Behav* 63:235–244.
- Balbontín, J, Ferrer, M (2005) Factors affecting the length of the post-fledging period in the Bonelli's Eagle *Hieraaetus fasciatus*. *Ardea* 93:189–198.
- Balbontín, J, Ferrer, M (2009) Movements of juvenile Bonelli's Eagles *Aquila fasciata* during dispersal. *Bird Study* 56:86-95.
- Barton K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Benjamini Y, Hochberg Y (1995) Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *J R Stat Soc Ser B* 57:289-300.
- Bennison A, Bearhop S, Bodey T W, Votier S C, Grecian W J, Wakefield E D, Hamer K C, Jessopp M (2017) Search and foraging behaviors from movement data: A comparison of methods. *Ecol Evol* 8:13–24.
- BirdLife International (2015) *Aquila fasciata*. The IUCN Red List of Threatened Species 2015: e.T22696076A60132541. Downloaded on 16 September 2020.
- Bowler D E, Benton T G (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80:205-225.
- Bunnefeld N, Börger L, van Moorter B, Rolandsen C M, Dettki H, Solberg E J, Ericsson G (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *J Anim Ecol* 80:466-476.
- Bustamante, J (1995) The duration of the post-fledging dependence period of Ospreys *Pandion haliaetus* at Loch Garten, Scotland. *Bird study* 42:31–36.

- Bracis C Bildstein K Mueller T (2018) Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*. 10.1111/ecog.03618, <http://dx.doi.org/10.1111/ecog.03618>.
- Cadahía L, López-López P, Urios V, Negro J J (2007a) Estimating the onset of dispersal in endangered Bonelli's Eagles *Hieraaetus fasciatus* tracked by satellite telemetry: A comparison between methods. *Ibis*. <https://doi.org/10.1111/j.1474-919X.2007.00781.x>
- Cadahía L, Urios V, Negro J J (2007b) Bonelli's Eagle *Hieraaetus fasciatus* juvenile dispersal: hourly and daily movements tracked by GPS. *Bird Study*. <https://doi.org/10.1080/00063650709461484>
- Cadahía L, López-López P, Urios V, Negro J J (2010) Satellite telemetry reveals individual variation in juvenile Bonelli's eagle dispersal areas. *Eur J Wildl Res*. <https://doi.org/10.1007/s10344-010-0391-z>
- Cagnacci F, Focardi S, Ghisla A, Van Moorter B, Merrill E H, Gurarie E, Heurich M, Mysterud A, Linnell J, Panzacchi M, May R, Nygård C R, Rolandsen C Hebblewhite M (2016) How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. *J Anim Ecol* 85:54-68.
- Carrascal L M, Seoane J (2009) Factors affecting large-scale distribution of the Bonelli's eagle *Aquila fasciata* in Spain. *Ecol Res* <https://doi.org/10.1007/s11284-008-0527-8>
- Ceballos O, Donazar J A (1990) Parent-offspring Conflict during the Post-fledging Period in the Egyptian Vulture *Neophron percnopterus* (Aves, Accipitridae) *Ethology*. <https://doi.org/10.1111/j.1439-0310.1990.tb00402.x>
- Cramp S, Simmons K E L (1994) *The birds of the western Palearctic*. Oxford: Oxford University Press.
- Di Vittorio M, López-López P (2014) Spatial distribution and breeding performance of Golden Eagles *Aquila chrysaetos* in Sicily: implications for conservation. *Acta Ornithol* 49:33-45.
- Di Vittorio M, Lo Valvo M, Di Trapani E, Sanguinetti A, Ciaccio A, Greci S, Zafarana M, Giacalone G, Patti N, Cacopardi S, Rannisi P, Scuderi A, Luiselli L, La Grua G, Cortone G, Merlino S, Falci A, Spinella G, López-López P (2019) Long-term changes in the breeding period diet of Bonelli's eagle (*Aquila fasciata*) in Sicily, Italy. *Wild. Res.* doi.org/10.1071/WR18081
- Di Vittorio M, Sará M, López-López P (2012) Habitat preferences of Bonelli's Eagles *Aquila fasciata* in Sicily. *Bird Study*. <https://doi.org/10.1080/00063657.2012.656577>
- Diamond J M (1975) Assembly of species communities. In: J.M. Diamond M. L. Cody (eds.) *Ecology and Evolution of Communities*, Cambridge: Harvard University Press, pp 342-444
- Duncan R P, Boyer A G, Blackburn T M (2013) Magnitude and variation of prehistoric bird extinctions in the Pacific. *PNAS*. <https://doi.org/10.1073/pnas.1216511110>

- Dzialak M R, Lacki M J, Vorisek S (2007) Survival, mortality, and morbidity among peregrine falcons reintroduced in Kentucky. *J Raptor Res* [https://doi.org/10.3356/0892-1016\(2007\)41\[61:SMAMAP\]2.0.CO;2](https://doi.org/10.3356/0892-1016(2007)41[61:SMAMAP]2.0.CO;2)
- Efrat R, Hatzofe O, Miller Y, Berger-Tal O (2020) Determinants of survival in captive-bred Griffon Vultures *Gyps fulvus* after their release to the wild. *Conserv Sci Pract* 2:e308.
- Ferrer M (1992) Regulation of the period of postfledging dependence in the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* 134, 128-133. Ferrer, M. (1993) Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* 135: 132-138.
- Ferrer C, Ferrer J, Ferrer M (2019) Apparent Natural Recolonization of an Island by the Seychelles Kestrel (*Falco araea*) *J Raptor Res* 53: 355-357.
- Ferrer M, Morandini V, Baguena G, Newton I (2018) Reintroducing endangered raptors: A case study of supplementary feeding and removal of nestlings from wild populations. *J Appl Ecol* <https://doi.org/10.1111/1365-2664.13014>
- Fischer J, Lindenmayer D B (2000) An assessment of the published results of animal relocations. *Biol Conserv* [https://doi.org/10.1016/S0006-3207\(00\)00048-3](https://doi.org/10.1016/S0006-3207(00)00048-3)
- Garcelon D K (1985) Mounting backpack telemetry packages on bald eagles. Arcata: Institute for Wildlife Studies. García, V., Iglesias-Lebrija, J. J., Moreno-Opo, R. (2021) Null effects of the Garcelon harnessing method and transmitter type on soaring raptors. *Ibis* 163: 899-912.
- Garriga J, Palmer J R B, Oltra A, Bartumeus F (2016) Expectation-maximization binary clustering for behavioural annotation. *PLoS One*. R package version 2.0. 3.
- Gates S, Donald P F (2000) Local extinction of British farmland birds and the prediction of further loss. *J Appl Ecol* 37:806-820.
- Gil-Sánchez J M (2000) Efecto de la altitud y de la disponibilidad de presas en la fecha de puesta del águila-azor perdicera (*Hieraaetus fasciatus*) en la provincia de Granada (SE de España) *Ardeola*, 47, 1-8. Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162.
- Greenwood P J, Harvey P H (1982) The natal and breeding dispersal of birds. *Ann Rev Ecol Syst* 13: 1-21.
- Hernández-Matías A, Real J, Parés F, Pradel R (2015) Electrocutation threatens the viability of populations of the endangered Bonelli's eagle (*Aquila fasciata*) in Southern Europe. *Biol Conserv* 191:110-116.
- Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SH, Carpenter K E, Chanson J, Collen B, Cox N A, Darwall W R T, Dulvy N K, Harrison L R, Katariya V, Pollock C M, Quader S, Richman N I,

- Rodrigues S L, Tognelli M F, Vié J, *et al.* (2010) The impact of conservation on the status of the world's vertebrates. *Science* 330:1503–1509.
- Holekamp K E (1986) Proximal Causes of Natal Dispersal in Belding's Ground Squirrels (*Spermophilus Beldingi*) *Ecol Monogr* 56:365–391.
- Howard W E (1960) Innate and Environmental Dispersal of Individual Vertebrates. *Am. Midl Nat* 63:152–161.
- IUCN – SSC Species Conservation Planning Sub-Committee. (2017) Guidelines for Species Conservation Planning. Version 1.0. Gland, Switzerland: IUCN. xiv + 114 pp.
- Kays R, Crofoot M C, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. *Science* [10.1126/science.aaa2478](https://doi.org/10.1126/science.aaa2478)
- Kenward R E (2000) A manual for wildlife radio tagging. London: Academic press.
- Kenward R E, Marcström V, Karlbom M (1993) Post-nestling behaviour in goshawks, *Accipiter gentilis*: I. The causes of dispersal. *Anim Behav* 46:365-370.
- Krüger S, Amar A (2017) Insights into post-fledging dispersal of Bearded Vultures *Gypaetus barbatus* in southern Africa from GPS satellite telemetry. *Bird Study* 64: 125-131.
- Lacombe D, Bird D M, Hibbard K A (1994) Influence of reduced food availability on growth of captive American kestrels. *Can J Zool* 72: 2084-2089.
- López-López P (2016) Individual-based tracking systems in ornithology: welcome to the era of big data. *Ardeola* 63:103-136.
- López-López P, Sarà M, Di Vittorio M (2012) Living on the edge: assessing the extinction risk of critically endangered Bonelli's Eagle in Italy. *PLoS One* 7:e37862.
- López-López P, Gil J A, Alcántara M (2014) Post-fledging dependence period and onset of natal dispersal in bearded vultures (*Gypaetus barbatus*): New insights from gps satellite telemetry. *J Raptor Res.* <https://doi.org/10.3356/JRR-13-00072.1>
- MacArthur R H, Wilson E O (1967) *The Theory of Island Biogeography*. Princeton: Princeton University Press.
- McClure, C. J., Rolek, B. W. (2020) Relative conservation status of bird orders with special attention to raptors. *Front Ecol Evol* 8:593941.
- McClure C J, Westrip J R, Johnson J A, Schulwitz S E, Virani M Z, Davies R, Symes A, Wheatley H, Thorstorm R, Amar A, Buij R, Jones VR, Williams NP, Buechley ER, Butchart, S. H. (2018) State of the world's raptors: Distributions, threats, and conservation recommendations. *Biol Conserv.* <https://doi.org/10.1016/j.biocon.2018.08.012>.
- Monti F, Sforzi A, Marie Dominici J (2012) Post-

- fledging dependence period of ospreys *pandion haliaetus* released in central Italy: Home ranges, space use and aggregation. *Ardeola*. <https://doi.org/10.13157/arla.59.1.2012.17>
- Muriel R, Ferrer M, Balbontín J, Cabrera L, Calabuig C P (2015) Disentangling the effect of parental care, food supply, and offspring decisions on the duration of the postfledging period. *Behav Ecol* 26: 1587-1596.
- Murray Jr B G (1967) Dispersal in vertebrates. *Ecology*, 48:975-978.
- Myers N, Mittermeier R A, Mittermeier C G, Da Fonseca G A B, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Nicoll M A C, Jones C G, Norris K (2004) Comparison of survival rates of captive-reared and wild-bred Mauritius kestrels (*Falco punctatus*) in a re-introduced population. *Biol Conserv* 118:539-548.
- Nygård T, Jacobsen K-O, Johnsen T V, Systad G H (2016) Dispersal and Survival of Juvenile Golden Eagles (*Aquila chrysaetos*) from Finnmark, Northern Norway. *J Raptor Res* 50:144–160.
- Ontiveros D, Pleguezuelos J M (2003) Influence of climate on Bonelli's eagle's (*Hieraaetus fasciatus* V. 1822) breeding success through the Western Mediterranean. *J Biogeogr*. <https://doi.org/10.1046/j.1365-2699.2003.00860.x>
- O'Rourke E (2014) The reintroduction of the white-tailed sea eagle to Ireland: People and wildlife. *Land use policy*. <https://doi.org/10.1016/j.landusepol.2013.10.020>
- Palma L, Mira S, Cardia P, Beja P, Guillemaud T, Ferrand N, Cancela M L Da Fonseca LC (2001) Sexing Bonelli's eagle nestlings: morphometrics versus molecular techniques. *J Raptor Res* 35:187-193.
- Peltonen A, Hanski I (1991) Patterns of island occupancy explained by colonization and extinction rates in shrews. *Ecology* 72:1698-1708.
- Rahman M L, Batbayar N, Purev-Ochir G, Etheridge M, Dixon A (2015) Influence of nesting location on movements and survival of juvenile saker falcons *falco cherrug* during the post-fledging dependence period. *Ardeola*. <https://doi.org/10.13157/arla.62.1.2015.125>
- Ramos R F, Silva J P, Carrapato C, Rocha P, Marques P A, Palmeirim J M (2019) Spatial behaviour of Spanish Imperial Eagle *Aquila adalberti* juveniles during the dependence period revealed by high-resolution GPS tracking data. *J Ornithol* 160: 463-472.
- Real J, Grande J M, Mañosa S, Sánchez-Zapata J A (2001) Causes of death in different areas for Bonelli's Eagle *Hieraaetus fasciatus* in Spain. *Bird study*, 48:221-228.
- Real J, Mañosa S, Codina J (1998) Post-nestling dependence period in the Bonelli's Eagle. *Ornis Fennica*, 75:129-137.

- Rempel R S, Rodgers A R (1997) Effects of differential correction on accuracy of a GPS animal location system. *J Wildl Manage* 61:525–530.
- Robert A, Colas B, Guigon I, Kerbiriou C, Mihoub J B, Saint-Jalme M, Sarrazin F (2015) Defining reintroduction success using IUCN criteria for threatened species: a demographic assessment. *Anim Conserv*, 18: 397-406.
- Rosenzweig M L, Clark C W (1994) Island extinction rates from regular censuses. *Conserv Biol* 8:491-494.
- Ruau G, Lumineau S, De Margerie E (2020) The development of flight behaviours in birds: Bird flight development. *Proc R Soc B Biol Sci*. <https://doi.org/10.1098/rspb.2020.0668>
- Schaadt CP, Rymon LM (1982) Innate fishing behavior by ospreys. *J Rapt Res*, 16:61–62
- Seddon PJ, Armstrong D P, Maloney R F (2007) Developing the science of reintroduction biology. *Conserv Biol*. <https://doi.org/10.1111/j.1523-1739.2006.00627.x>
- Sergio F, Tavecchia G, Tanferna A, López Jiménez L, Blas J, De Stephanis R, Marchant T A, Kumar N Hiraldo F (2015) No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *J Appl Ecol*, 52: 1665-1675.
- Soutullo A, Urios V, Ferrer M (2006) Post-fledging behaviour in Golden Eagles *Aquila chrysaetos*: onset of juvenile dispersal and progressive. *Ibis* 148:307–312.
- Tershy B R, Shen K W, Newton K M, Holmes N D, Croll D A (2015) The importance of islands for the protection of biological and linguistic diversity. *BioScience*. <https://doi.org/10.1093/biosci/biv031>
- Tordoff H B, Redig P T (2001) Role of genetic background in the success of reintroduced peregrine falcons. *Conserv Biol* 15:528-532.
- Thomas B, Holland J D, Minot E O (2011) Wildlife tracking technology options and cost considerations. *Wildl Res*. <https://doi.org/10.1071/WR10211>
- Trivers R L (1974) Parent-offspring conflict. *Integr Comp Biol* 14:249-264.
- Urios V, Muñoz-López R, Vidal-Mateo J (2017) Juvenile dispersal of harpy eagles (*Harpia harpyja*) in Ecuador. *J Raptor Res*, 51: 439-44.
- Viada C, Parpal L, Morro B, Mayol J (2015) El águila de Bonelli (*Aquila fasciata*) en Mallorca: Su extinción y su reintroducción. In: *Servei de Protecció d'Espècies (Eds.) Llibre Verd de Protecció d'Espècies a les Balears, Balearic Islands*, pp 283-294.
- Viada C, Iglesias JJ (2017) La jaula hacking: nuevo sistema para el LIFE Bonelli. In: *Life Bonelli (Eds.) Recuperación integral de las poblaciones de águila perdicera en España*. Navarra, pp 111-121.

Vergara P, Fargallo J A, Martínez-Padilla J (2010) Reaching independence: food supply, parent quality, and offspring phenotypic characters in kestrels. *Behav Ecol*, 21: 507-512.

Vitousek P M (2002) Oceanic islands as model systems for ecological studies. *J Biogeogr*.
<https://doi.org/10.1046/j.1365-2699.2002.00707.x>

Walker D G (1987) Observations on the post-fledging period of the Golden Eagle *Aquila chrysaetos* in England. *Ibis*. <https://doi.org/10.1111/j.1474-919X.1987.tb03163.x>

Walls S S, Kenward R E (1995) Movements of radio-tagged Common Buzzards *Buteo buteo* in their first year. *Ibis* 137:177-182.

Watson A J (1981) Population ecology, food and conservation of the Seychelles Kestrel (*Falco areaea*) on Mahè (Doctoral dissertation, University of Aberdeen)

Weathers W W, Sullivan, K. A. (1989) Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol Monogr* 59:223-246.

Weston E D, Whitfield D P, Travis J M, Lambin X (2013) When do young birds disperse? Tests from studies of golden eagles in Scotland. *BMC ecology* 13:42.

Weston E D, Whitfield D P, Travis J M, Lambin X (2018) The contribution of flight capability to the post-fledging dependence period of golden eagles. *J. Avian Biol.*, 49: e01265.

Zuur A, Ieno E N, Walker N, Saveliev A A, Smith, G. M. (2009) *Mixed effects models and extensions in ecology with R*. New York: Springer Science Business Media.

Tables

Table 1.- Model selection ranking for each parameter (i.e., age of dispersal, age of first flight, PFDP length, number of revisits and residence time) in relation to origin, age, sex, their additive effects and their interaction. Best models are highlighted in bold. (df = degrees of freedom, AIC = Akaike Information Criterion, AICw = model weight).

Parameter	Model	df	AIC	Δ AIC	AICw
First flight	Intercept	3	-53.459	0.000	0.859
	Origin	4	-49.302	4.157	0.107
	Sex	4	-46.735	6.725	0.030
	Origin + Sex	5	-42.622	10.837	0.004
	Origin + Sex + Origin*Sex	6	-37.134	16.325	0.000
Age dispersal	Intercept	3	-40.543	0.000	0.677
	Origin	4	-38.578	1.965	0.254
	Sex	4	-35.413	5.130	0.052
	Origin + Sex	5	-32.961	7.581	0.015
	Origin + Sex + Origin*Sex	6	-28.585	11.957	0.002
PFDP length	Intercept	3	5.507	0.000	0.772
	Origin	4	9.034	3.527	0.132
	Sex	4	10.049	4.542	0.080
	Origin + Sex	5	13.617	8.110	0.013
	Origin + Sex + Origin*Sex	6	16.914	11.407	0.003
Revisits	Origin	4	141.118	0.000	0.463
	Origin + Sex	5	142.490	1.372	0.233
	Origin + Sex + Origin*Sex	6	142.726	1.609	0.207
	Intercept	3	145.049	3.931	0.065
	Sex	4	146.430	5.312	0.032
Residence Time	Origin + Sex + Origin*Sex	6	182.204	0.000	0.356
	Origin	4	183.454	1.251	0.190
	Origin + Sex	5	183.623	1.419	0.175
	Intercept	3	183.999	1.795	0.145
	Sex	4	184.152	1.948	0.134

Table 2.- Model selection ranking for each behavior obtained by means of the Expectation Maximization Binary Clustering (EMbC) algorithm (i.e., resting, foraging, travelling and hunting) in relation to origin, age, sex, their additive effects and their interaction. Best models are highlighted in bold. (df = degrees of freedom, AIC = Akaike Information Criterion, AICw = model weight).

Movement	Model	df	AIC	Δ AICc	AICw
Resting	Intercept	3	-519.261	0.000	0.889
	Origin	4	-514.754	4.507	0.093
	Sex	4	-511.368	7.893	0.017
	Week	22	-405.127	114.135	0.000
	Sex + Origin + Week	24	-393.253	126.009	0.000
	Sex + Origin + Week + Origin*Sex*Week	76	-224.237	295.025	0.000
Foraging	Week	22	-208.067	0.000	0.969
	Sex + Origin + Week	24	-201.208	6.859	0.031
	Sex	4	-162.891	45.176	0.000
	Intercept	3	-162.688	45.379	0.000
	Origin	4	-156.887	51.179	0.000
	Sex + Origin + Week + Origin*Sex*Week	76	-35.3233	172.743	0.000
Travelling	Week	22	-729.816	0.000	0.998
	Sex + Origin + Week	24	-716.607	13.209	0.001
	Intercept	3	-713.564	16.252	0.000
	Sex	4	-708.759	21.057	0.000
	Origin	4	-707.531	22.285	0.000
	Sex + Origin + Week + Origin*Sex*Week	76	-465.041	264.775	0.000
Hunting	Week	22	-1172.54	0.000	0.943
	Sex + Origin + Week	24	-1166.94	5.604	0.057
	Origin	4	-1097.35	75.186	0.000
	Intercept	3	-1096.12	76.425	0.000
	Sex	4	-1091.92	80.622	0.000
	Sex + Origin + Week + Origin*Sex*Week	76	-861.499	311.042	0.000

Figures

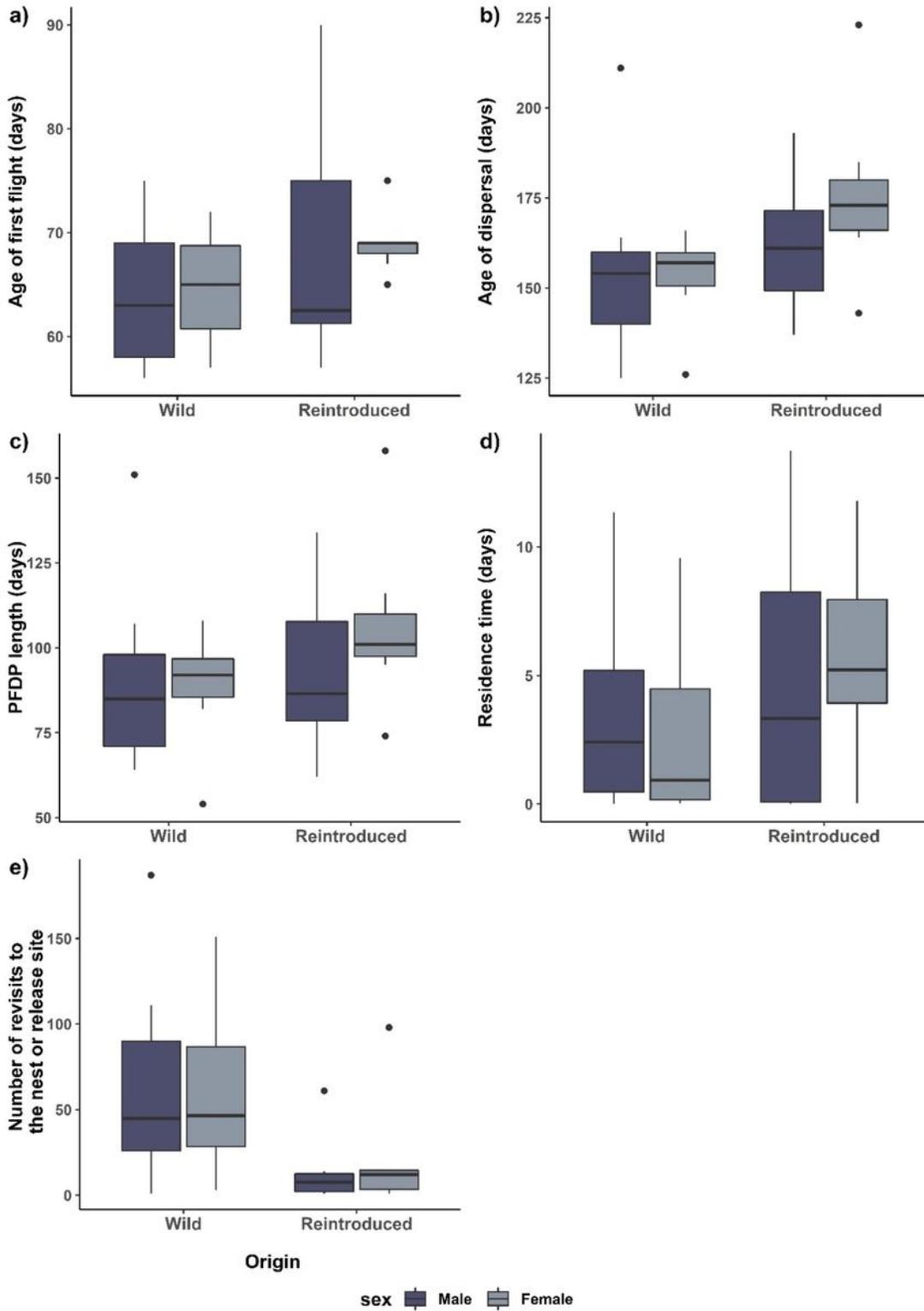


Figure 1

Comparison of five parameters used to characterize the post-fledging dependence period of wild and reintroduced juvenile Bonelli's eagles in two Mediterranean islands, Sicily and Mallorca, respectively. Boxplots represent median as well as 25% and 75% quartiles. Outliers are shown as dots.



Figure 2

Percentage of time spent by juvenile Bonelli's eagles on the four categories of behavior computed using the unsupervised Expectation Maximization binary Clustering (EMbC) method throughout the juvenile post-fledging dependence period by origin and sex. Grey areas represent standard error.

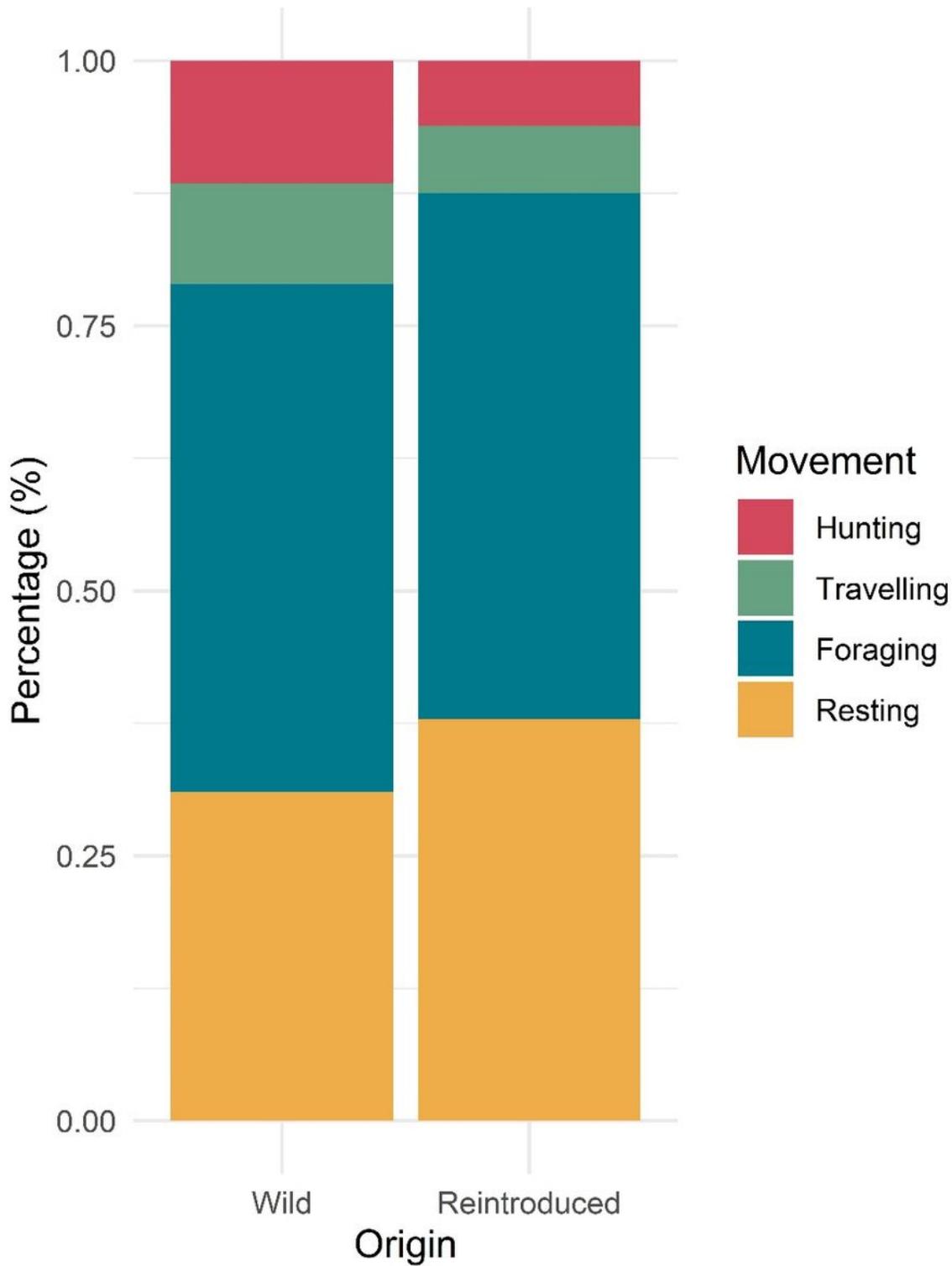


Figure 3

General share of time of juvenile Bonelli's eagles spent on the four categories of behavior obtained by means of the Expectation Maximization Binary Clustering (EMbC) algorithm by origin (i.e., wild or reintroduced) during the PFDP.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplMatBiodCons.docx](#)