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The consequences of food and flight efficiency for the timing of natal dispersal in golden eagles

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Permanent emigration from the natal range represents one of the most critical life history transitions in an animal's life and its timing can have long-lasting consequences. While early-life food conditions are known to affect emigration timing, their interplay with the development and expression of movement skills acting on emigration remains poorly understood. Here, we investigated the effects of postfledging flight and feeding behaviour on emigration timing in the Alpine population of the golden eagle, *Aquila chrysaetos*. We used ground-truthed accelerometer data from falconry golden eagles to train a random forest algorithm. Applying the algorithm to accelerometer bursts of wild birds allowed us to allocate each burst to a behaviour and derive time budgets. Then, we quantified individual-specific developmental rates and individual total frequency of both soaring and flapping flight (energy expenditure) and of feeding behaviour (energy intake) over the early postfledging dependency period and assessed their effect on emigration timing (days since fledging). We found that increased postfledging flight efficiency, characterized by the proportion of total time spent soaring versus flapping, was associated with early emigration but not the developmental rates of flight behaviours. These findings suggest that unmeasured environmental factors or innate activity differences rather than individual differences in flight skill development drive emigration timing. Neither frequent feeding nor nestling body condition was associated with characteristics of flight behaviours. Yet, frequent feeding resulted in early emigration. Despite the strong sexual dimorphism in golden eagles, we only found a difference in time spent flapping between sexes. Together, the results suggest that there might be two environmental factors, favourable food availability and suitable soaring conditions that allow for early emigration. Thus, in addition to food availability, the availability of uplifts in the parental territory facilitating soaring flight may represent a pivotal but underappreciated driver for emigration decisions in juvenile soaring birds.

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Permanent emigration from the parental territory, the onset of natal dispersal, is a key transition in the life of animals (Bowler & Benton, 2005; Clobert et al., 2012). The timing of emigration often affects settlement success with consequences for lifetime reproduction and survival (Mayer et al., 2017). By leaving their natal sites, juveniles lose benefits that accrue through site familiarity and parental care (Bonte et al., 2012) but gain opportunities to

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capitalize on new resources (Stillman et al., 2022), gather information about potential breeding sites (Reed et al., 1999) and conspecifics (Clobert et al., 2012), and avoid inbreeding (Bowler & Benton, 2005). Therefore, emigration should occur when the benefits of leaving outweigh the costs of staying (Bonte et al., 2012). This cost-benefit trade-off is known to be modulated by habitat conditions such as food availability (Baglione et al., 2006; Fattebert et al., 2019), particularly strongly shaped by conditions experienced during early life (Scherler et al., 2023) as well as by internal factors including sex (Edelman, 2011) and body condition (Rémy et al., 2011).

During the early life period, juveniles undergo significant locomotor developments and improve crucial movement skills such as predator escape (Hale, 1999), energy-efficient movement (Efrat et al., 2023) and foraging behaviour (Corbeau et al., 2020). Individual variation in early locomotor skill development can therefore not only affect immediate performance and body condition, but also behaviour and survival much later in life (Henry & Ulijaszek, 1996; Langley et al., 2020; Lindström, 1999). Many bird species use soaring and gliding flight to minimize energetic costs by making use of thermal and orographic energy in the form of uplifts (Williams et al., 2020). Since the energy expenditure of flapping flight increases proportionally with body mass (Hedenstrom, 1993), the use of low-cost soaring flight is particularly important for large and heavy birds. Thus, species with sexual size dimorphism might show sex differences in the use of low-cost flight and its developmental trajectories. Although the development of soaring skills is likely to shape future performance of soaring birds, there are few studies investigating the consequences of individual variation in early soaring behaviours (Rotics et al., 2021), particularly because variation in postfledging flight behaviours has been, up to now, difficult to quantify.

Differences in flight efficiency might drive the variation in the timing of emigration between individuals of the same population. Birds are endowed with a genetic blueprint for flight, but flight still requires extensive practice to mature (Harel, Duriez, et al., 2016; Ruaux et al., 2020). Appropriate environmental conditions that facilitate uplifts provide opportunities for practicing and honing the skills of extracting energy from atmospheric updrafts (Scacco et al., 2019). While young soaring birds can achieve ground speeds (Hemery et al., 2023) and cover daily distances comparable to adult birds (Weston et al., 2018), they often perform less well than experienced adults, particularly during marginal and challenging flight conditions (Harel, Horvitz, & Nathan, 2016; Sergio et al., 2022). Flying more efficiently may therefore facilitate early emigration, owing to the large effect that differential flight efficiency has on energy expenditure.

How much energy an individual has available depends largely on how much food it gets. Limited food and poor nutrition during growth are not only linked to poor physical state but also to reduced learning abilities (Brust et al., 2014). In birds, nestlings allocate most of their energy to growth (Flack et al., 2020). During the postfledging dependency period, the available energy in the form of food must be balanced to cover both the energetic costs of continued physical development (Bishop et al., 1996) and the costs of flight. Consequently, poor food availability can impair the development of movement skills during the postfledging dependency period (Scridel et al., 2023), resulting in a reduced ability to escape predators (O'Hagan et al., 2015) or a limited neurocognitive performance (De Rooij et al., 2010) and thus, in a prolonged postfledging dependency period. On the other hand, poor food availability also might cause early emigration due to food depletion in the parental territory (Rémy et al., 2011). Investigating how food availability acts on the ontogenetic pathway after fledging can thus deepen our understanding of potential energy trade-offs throughout developmental processes.

The golden eagle, *Aquila chrysaetos*, represents an ideal model species to investigate the effect of intrinsic and extrinsic factors experienced during the postfledging dependency period on emigration timing. Golden eagles are specialized in soaring flight, have an extended postfledging dependency period and show a highly variable emigration timing (Weston et al., 2013). Their size and weight allow for the fitting of tags that have the capacity to collect and transmit multiple high-resolution location and accelerometer data that enable identifying specific behaviours (Patterson et al., 2019). During the parental care period, juveniles are provided with food and protection from conspecific aggression (Jenny et al., 2024). They start to carry out independent forays into neighbouring territories prior to permanent emigration, in particular if they have a high-activity phenotype (Hatzl, 2024; Zimmermann et al., 2026). Thus, food-modulated differences in the development of energy-efficient flight behaviours can be an important driver of the ontogenetic trajectories to an independent life in golden eagles.

Here, we investigated the effects of postfledging feeding, i.e. energy intake and postfledging energy investment into flight behaviours on the timing of permanent emigration from the parental territory in juvenile golden eagles. We first used simultaneous behavioural observations and tri-axial accelerometer data of captive golden eagles as well as machine learning methods to identify tri-axial accelerometer patterns associated with specific behaviours including flight and feeding behaviours. This initial step allowed us to identify and validate behavioural allocation and generate daily time budgets from the tri-axial accelerometer data of wild golden eagles. In a second step, we quantified the between-individual variation, body condition differences and sex differences in time investment into flight and feeding behaviours as well as their development throughout the early postfledging dependency period. This included the development and average extent of flight efficiency in terms of the time invested into soaring versus flapping flight. We expected (1) that individuals would become more flight-efficient with age by increasing the share of soaring in the total flight time, (2) that time spent feeding would affect flight behaviour development and (3) that females would have to rely more on flapping flight than males due to their higher weight. Finally, we investigated whether individual variation in the development of flight behaviours and the time spent feeding are associated with emigration timing, expecting that individuals with a rapid flight development, a high share of soaring flight and much time spent feeding would emigrate early. Decomposing the effect of flight development and the effect of the total time invested into flight behaviours on emigration timing allowed for the differentiation between two mechanistic interpretations: the effect of differences in flight skill development and the effect of nonmeasured factors facilitating flight behaviours. By using the new technologies of tri-axial accelerometer measures and machine learning algorithms to identify juvenile behaviour, our approach enabled us to study the effects of avian behaviour after fledging on later life history transitions, a key gap in the behavioural ecology of birds.

METHODS

Study Species

The golden eagle is a large apex raptor, highly adapted to make use of environmental energy for soaring flight. In central Europe, golden eagles are mostly restricted to the Alpine and Jura

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Mountain ranges (Haller, 1996). Territories include a mosaic of different habitats in which nests are built in rock cavities and less frequently in trees (Jenny et al., 2024). After a nestling period of ca. 11 weeks, juveniles remain within the natal territory for about 7 months (Jenny et al., 2024; Weston et al., 2013; Zimmermann et al., 2026). Throughout this extended natal dependency period, juveniles are provided with freshly hunted prey and sometimes carrion. The main prey species include Alpine marmots, *Marmota marmota*, grouse species (*Lyrurus tetrix, Lagopus muta*), as well as juvenile chamois, *Rupicapra rupicapra*, and ibex, *Capra ibex* (Haller, 1996; Jenny et al., 2024).

Data Collection

During 2018–2021, we equipped 36 golden eagle nestlings (Switzerland: $N = 27$; Italy: $N = 8$; Germany: $N = 1$; Fig. 1) at the age of 50 ± 3 days (Supplementary Table S1) with solar-powered biologging tags (e-obs GmbH, Munich, Germany). During the tagging event, body weight (g) and wing length (cm) were measured. The tags recorded both location (GPS) and tri-axial accelerometer data. Combined tag, ring and Teflon leg-loop harness (Hegglin et al., 2004) weight did not exceed 103 g, staying below 3% of an individual's body weight. The tags and harnesses were designed without a breakaway mechanism and remained attached throughout the study period; the tags continued to transmit data beyond the end of this study. Tri-axial accelerometer data were collected in bursts with a duration of 7.92 s at 5 min intervals between 0400 and 1700 hours GPS time.

Bursts were collected with a byte count of 1188 and a sample rate of 33.3 Hz on all three axes within a detection range of ± 4 g (gravitational force). The data were transmitted via a Global System for Mobile Communications (GSM) network once a day and stored in the study 'LifeTrack Golden Eagle Alps' on movebank.org (Wikelski et al., 2022). We determined fledging dates (permanent departure from the nest) and emigration dates (permanent departure from the parental territory) following spatiotemporal threshold approaches based on GPS locations described in detail in Hatzl (2024). Timing of fledging was defined as the date of a clear trajectory leading away from the nest location. To determine emigration timing, we adapted 'Method 7' described in Weston et al. (2013). We drew an 8 km radius around the centroid of juvenile home ranges and defined emigration time as the first GPS location outside this radius without any overnight return for more than 14 days. Golden eagles fledged on average on the 31 July ± 9 days and emigrated on average on the 12 February ± 40 days of the following year (Supplementary Fig. S1–S2). Sex was determined using DNA extracted from feather samples, which were collected at tagging. To analyse the samples, we used the DNeasy Blood and Tissue Extraction Kit (Qiagen Inc., Valencia, CA, U.S.A.). The primers used were 2550F and 2718R according to the method given in Fridolfsson and Ellegren (1999).

Behavioural Identification

We used direct behavioural observations of tagged individuals to detect patterns in tri-axial accelerometer data and link them to behavioural classes (Nathan et al., 2012). We obtained simultaneous behavioural and tri-axial accelerometer data (i.e. a ground-truthed data set) by recording tri-axial accelerometer data and behavioural information from captive individuals (Rast et al., 2020). We thus tagged and observed free-flying falconry golden eagles ($N = 6$) at the Adler-Arena Burg Landskron using the same tag type ($N = 8$) and leg-loop attachment system as in wild golden eagles. We collected data from both male ($N = 4$) and female ($N = 2$) falconry golden eagles, of which one individual was 1 year old, and all others were 3 years old or older. We exchanged tags between individuals to mitigate the impact of variation in tag positions between birds. With the exception of one bird that showed strong discomfort after fitting the harness, each bird flew with at least three different tags. The one individual showing discomfort behaviour was used only during one flight, after which we removed the harness again. This resulted in a total of 62 independent flights and 6610 tri-axial accelerometer bursts. Tri-axial accelerometer data were recorded with the same settings as in wild individuals, but with an interval of 1 s between bursts to maximize data collection. We recorded golden eagle behaviour using video footage with audio comments (Canon Inc. EOS R5 camera and a Canon Inc. EF 100–400 mm f/4.5–5.6L IS II USM lens). We annotated behavioural classes to video sequences following a predefined behavioural ethogram using Solomon Coder (version: beta 19.08.02) and matched behaviours to the corresponding tri-axial accelerometer burst according to time

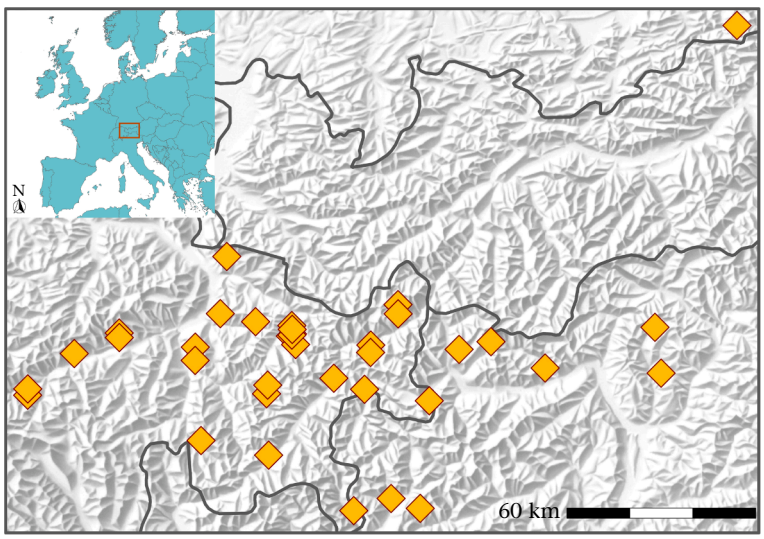


Figure 1. Tagging locations of juvenile golden eagles (orange diamonds; $N = 36$ individuals). Overlapping symbols represent tagging locations in the same or neighbouring territories ($N = 26$ territories). Basemap: Hillshade map derived from the swissALTI3D digital elevation model © Federal Office of Topography swisstopo.

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stamps. Tags recorded data in GPS time that had to be corrected by 18 leap seconds (year 2020) to match UTC time of video recordings. We determined seven behavioural classes (food intake, soaring flight, flapping flight, undulating flight, roosting, preening (i.e. body care) and walking). If multiple behaviours were present in a burst, the burst was assigned to the longest cumulative behaviour (Sur et al., 2017). We excluded bursts where the cumulative extent of a behavioural category did not contribute to more than half of the duration ($N = 121$ bursts) and bursts that contained more than two unique behaviours ($N = 379$ bursts) from subsequent analyses (Sur et al., 2017). To reduce the effect of unequal sample size between behavioural classes, we randomly subsampled over-represented classes to a maximum of 200 bursts per class. This resulted in 1012 bursts and seven behavioural classes in the ground-truthed falconry data set ('Falconry') used for training and testing the machine learning classification algorithm (see below).

In addition to the Falconry data set, we collected a 'Wild' data set consisting of 181 ground-truthed tri-axial accelerometer bursts of 12 tagged wild golden eagles (Supplementary Table S2). This data set allowed us to verify that the machine learning procedure we used to train the classification with falconry golden eagle data performed well in identifying behaviours of wild golden eagles. Additionally, it enabled us to assess how generalizable the algorithm was to data from new individuals (individual-selected testing data) and to reduce overestimation of classification accuracy (Dickinson et al., 2021). We located tagged individuals in the field using their most recent available GPS data and VHF signal and used the same behavioural classification protocol as for falconry golden eagles during observations in the field.

Behavioural Classification and Validation

All analyses were performed using the software R version 4.0.0 (R Core Team, 2020). We downloaded tri-axial accelerometer data from movebank.org using the package 'move' version 4.1.12 (Kranstauber et al., 2017) and applied a random forest algorithm to identify behavioural classes in tri-axial accelerometer data (Tatler et al., 2018) within the package 'randomForest' version 4.6–14 (Liaw & Wiener, 2002). We extracted 58 descriptive tri-axial accelerometer features from each tri-axial accelerometer burst (Supplementary Table S3) using an adapted function within the package 'moveACC' version 0.1 (Scharf, 2021). We split the Falconry data set into a training subset (80% of the data per class) and a testing subset (remaining 20%) and trained the algorithm using the training subset. We grew 2500 trees and used nine variables at each split using the package 'caret' version 6.0–88 (Kuhn, 2008). To improve model performance, we used repeated cross-validation with 10 repeats and upsampled rare classes to help reduce the effect of the remaining class imbalances. Using this model, we predicted behavioural classes in the testing subset of the Falconry data set, as well as in the Wild data set. We then compared predicted versus observed classes using a confusion matrix to evaluate accuracy, class-specific balanced accuracy, sensitivity and specificity.

Time Budget Analysis

We modelled the daily frequencies of behaviourally classified tri-axial accelerometer data in free-ranging wild eagles over 45 days following fledging to quantify the time spent in different behaviours during the early postfledging dependency period. This time period was chosen as it is the period in which activity has been shown to develop linearly (Weston et al., 2018), but before the time when individuals start making regular and long excursions. To analyse the effect of sex and time since fledging on time allocation to behavioural classes, we fitted a Bayesian multilevel multinomial model using the package 'brms' version 2.16.10 (Bürkner, 2021) to the 209 487 classified bursts. The model allowed us to capture the multinomial nature of time budget data while accounting for both fixed and random effects (Koster & McElreath, 2017). We modelled the proportion of bursts of each behaviour in relation to the time since fledging (in days, 0–44 days after fledging), the quadratic term of time since fledging (orthogonal to day) and sex (females $N = 19$; males $N = 17$) as fixed effects and applied a logit link function. Explanatory variables were checked for collinearity using pair plots and Spearman's rank correlation coefficient, r_S. As no correlation was present ($r_S \leq 0.6$), all variables were retained in the model. Date (day within a year, and year; 220 levels) and individual identity (ID) (36 levels) were included as random intercepts to account for nonindependence of data collected on the same date and from the same individual. Furthermore, we allowed for individual-specific variation in the linear effect of day (random slope). We extracted and standardized the individual-specific random intercepts and slopes to use them for further analyses of behaviours.

We ran four chains of 7000 iterations, of which we discarded 3500 as burn-in and used the remaining iterations to derive the posterior distribution of the model parameters. As recommended by Gelman (2006), we used weakly informative, normally distributed priors $N(0, 5)$ for population level effects and adapted the maximum tree depth to 15 to improve effective sample size for high dimensional models. We calculated posterior predictions from which we derived means and 95% credible intervals (95% CrIs) for fixed effects in different behavioural classes, while holding all other coefficients constant (Koster & McElreath, 2017). To ascertain chain convergence, we used $\widehat{R}$ values, effective sample sizes and posterior predictive checks (Brooks & Gelman, 1998). Effects of all statistical models with a posterior probability (PP) > 0.95 were considered as having a strong effect, and those with a PP > 90 and < 95 were considered as having a weak effect.

Overall Dynamic Body Acceleration (ODBA), Flight Behaviour and Emigration Models

Separate flight behaviours might become energetically more efficient over the early postfledging dependency period. To investigate this potential efficiency improvement, we calculated overall dynamic body acceleration (ODBA), a measure often used as a proxy for energy expenditure (Wilson et al., 2008), for each burst of a flight behaviour. Then, we analysed effects of age after fledging, body condition and sex on ODBA of soaring and flapping flight separately by fitting generalized linear mixed-effects models (GLMMs). Body condition was assessed as the relative age-corrected weight residual from the mean weight (g) (measured at the time of tagging; higher than average >1; lower than average <1) divided by the relative age-corrected residual length (cm) of the right wing (measured at the time of tagging; higher than average >1; lower than average <1). We estimated body condition separately per sex to account for sexual dimorphism. We also included individual ID and date as random effects in both models and applied a log transformation of ODBA values to achieve a normal distribution of the residuals. We fitted the models in a Bayesian framework using the package 'brms' version 2.18.0 (Bürkner, 2021) running four Markov chains per model of 10 000 iterations each, of which we discarded 1000 as burn-in and retained every second iteration. We used weakly informative, normally distributed priors $N(0, 3)$ for population level effects.

To investigate the effect of the time spent feeding on the total time spent in soaring or flapping flight, as well as on the increase rate of both flight behaviours over the 45-day period, we used the

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standardized individual-specific random intercepts and slopes from the multinomial model (Hertel et al., 2020). The two individual measures allowed for the discrimination between (1) the individual variation in the total time engaged in a flight behaviour (standardized intercept, total frequency of behaviours) and (2) the individual increase of time investment into a flight behaviour (slope, developmental rate). We ran four linear models with (1) the individual-specific random intercept of soaring flight, (2) the individual-specific random slope of soaring flight, (3) the individual-specific random intercept of flapping flight and (4) the individual-specific random slope of flapping flight as response variables. We included the individual-specific intercept of feeding time as an explanatory variable to investigate the effect of energy intake on the characteristics of flight behaviours. We also accounted for potential effects of body condition and sex.

We further explored the relationships between behavioural variation and emigration timing by fitting a linear mixed-effects model. Emigration timing (i.e. the duration of the postfledging dependency period in days since fledging) was modelled with individual-specific intercepts and slopes of soaring and flapping flight, the individual-specific intercept of feeding and sex as fixed effects. We ran all five models (dependent variable: (1) the individual-specific random intercept of soaring flight; (2) the individual-specific random slope of soaring flight; (3) the individual-specific random intercept of flapping flight; (4) the individual-specific random slope of flapping flight; (5) emigration timing) 14 000 times, each time using a random draw of the individual random intercepts and slopes sampled from the posterior distribution of the Bayesian multinomial model. This approach allowed us to propagate uncertainty from the first model into the second by using one posterior draw per iteration (Korner-Nievergelt et al., 2017). To include the uncertainty of the subsequent models, for each of the 14 000 model runs (one for each draw), we again drew one sample from the joint posterior distribution. Hence, using a Bayesian approach allowed us to easily propagate error from one model into the final inference. Inferences were based on means, credible intervals and posterior probabilities across all draws. We centred and scaled all covariates (i.e. mean = 0, standard deviation = 1), which allows effect sizes to be directly comparable and increased model convergence. We excluded six individuals from the emigration model as data transmission ceased prior to emigration ($N = 4$) or emigration occurred earlier than 80 days postfledging ($N = 2$). In both cases in which juveniles emigrated before 80 days, we observed either the disappearance of one parent from the territory or active parental aggression directed towards the juvenile, also suggesting disappearance of a parental individual and change of territory owner. These observations indicate that parental mortality or replacement of a territory owner may result in such early emigration events (F. Thomas, local game warden, personal communication).

Ethical Note

Each tagging event was carried out by a licensed researcher, accompanied by experienced rangers and climbers to ensure animal welfare and safety. The birds were carefully immobilized by the ranger using a net within the nest. We used hoods on the birds and placed them into a falconry cloth that was wrapped around them to avoid them spreading their wings and injuring themselves. The eagles' feet and talons were not wrapped or otherwise restrained during tagging. The birds were subsequently handed to the tagging team stationed either above or beneath the nest. During the tagging, we removed the falconry cloth and left the birds free-standing but hooded and slightly held, as the birds were calmest like this.

Handling time was kept to a minimum and did not exceed 70 min for double broods and 40 min for single-chick nests, measured from initial immobilization to the bird's return to the nest. A prior assessment of the nest surroundings by long-distance observation and one-time direct on-site inspection of access points of particularly challenging terrain allowed us to ensure time-efficient tagging events. We repeatedly conducted long-distance observations of the plumage development using scopes to assess the age accordingly. We only tagged juveniles younger than 60 days as older birds increasingly express avoidance/flight behaviour, increasing the chance for triggering premature fledging. We observed the chicks one to several days after tagging and found no apparent signs of discomfort, such as excessive grooming or pecking at the logger or harness. The chicks continued to be cared for normally by their parents. The study as a whole was approved by the Scientific Advisory Board of the Swiss Ornithological Institute (Project approval number: 530300). Catching, ringing and tagging were conducted under the licences of the responsible institutions in the different countries and disturbance was kept to a minimum (Switzerland: Federal Food Safety and Veterinary Office Grisons, permit numbers GR 2017_06, GR 2018_05E, GR 2019_03E, GR/08/2021, and the Federal Office for the Environment, licence number TV201903E; Germany: birds were handled, tagged and ringed under the permission issued by the government of Oberbayern (2532.Vet_02-16-88 and 2532.Vet_02-20-86); Italy: the permissions for handling, tagging and marking were obtained from the autonomous region of South Tyrol (Dekret 12257/2018 and Dekret 8788/2020), as well as from the Regione Lombardia and Sondrio Province for ringing and tagging in Lombardia and South Tyrol by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale) with the Richiesta di autorizzazione alla cattura di fauna selvatica per scopi scientific (l.r. 26/93); Austria: permission for handling and tagging falconry golden eagles was issued by the Federal Ministry of Education, Science and Research of Austria, Nr.: GZ 2020−0.369.719).

RESULTS

Behavioural Classification

Validation of the classification algorithm using the two data sets showed that all behaviours except undulating flight could be reliably identified. The overall classification accuracy in the Falconry data set was marginally higher (92%) than in the Wild data set (87%). Class-specific balanced accuracy was relatively low for undulating flight (Falconry: 88%; Wild: 50%) but ranged from 72% to 98% for all other behaviours in both data sets (Supplementary Table S4−S5). The model identified the most important variables for distinguishing between behavioural classes to be the 'mean of the *Z* and *Y* axes' and 'pitch' (Supplementary Fig. S3).

Postfledging Behaviours

During the first 45 days of their postfledging dependency period, juvenile golden eagles spent most of the time roosting (69.62%; 143 765 bursts) and preening (12.93%; 26 698), followed by feeding (9.43%; 19 462) and walking (2.24%; 4621). Flight behaviours contributed comparably little to the overall time budget, with soaring shown in 8301 (4.02%), flapping in 3383 (1.64%) and undulating in 257 bursts (0.12%). However, the behavioural composition not only changed considerably over time (Fig. 2, Supplementary Fig. S4−S5, Supplementary Table S6) but also

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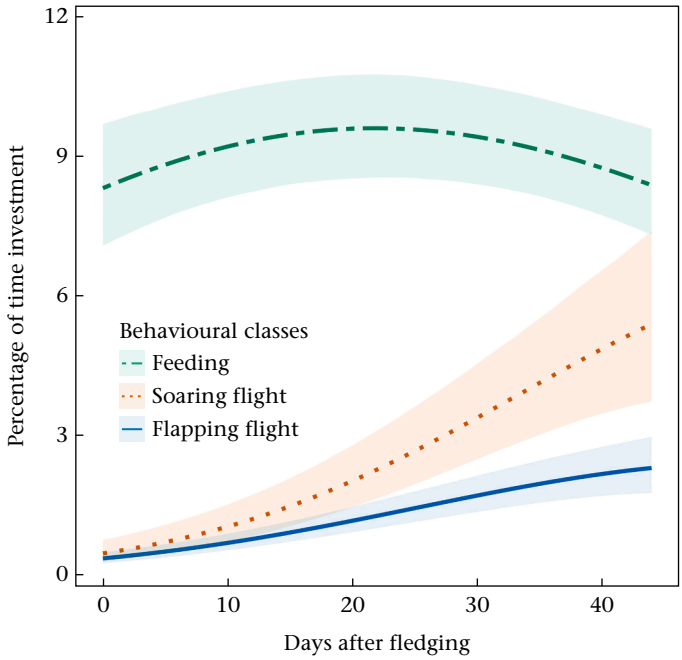


Figure 2. Change in the percentage of the time invested into feeding, soaring flight and flapping flight during the first 45 days after fledging. Lines represent means and shaded areas indicate 95% credible intervals (95% CrIs) from model predictions for females.

varied greatly between individuals (Supplementary Fig. 6). With time since fledging, birds spent decreasing amounts of time roosting, preening and walking, whereas flapping and soaring flights became more frequent (Fig. 2, Supplementary Fig. S4). In addition, time spent in soaring flight increased faster than time spent in flapping flight (Fig. 2, Supplementary Fig. S5). Time spent soaring increased by a factor of 12 and reached 5.4% (95% CrI = [3.70, 7.38]) in females and 5.8% (95% CrI = [4.04, 7.96]) in males at the end of the 45-day period. Time spent flapping only increased by a factor of seven and reached 2.3% (95% CrI = [1.75%, 2.96%]) in females and marginally more in males (mean = 2.7%, 95% CrI = [2.03, 3.55]). Time spent soaring was positively correlated with time spent flapping (Pearson correlation: $r = 0.67$). Time spent feeding increased from 8% of the day (95% CrI = [6.66, 9.37]), peaking at day 23 postfledging with 9.6% of the day (95% CrI = [8.53, 10.75]), then decreased again to 8% thereafter (Fig. 2, Supplementary Fig. S4–S5). Roosting remained the dominant behaviour throughout the 45 days. The proportion of time spent preening and walking clearly differed between sexes, with males investing more time in preening and walking (Supplementary Table S6).

During the first 45 days postfledging, undulating flight showed the highest overall dynamic body acceleration ODBA per burst (mean ± SD = 0.77 ± 0.26 *g*), followed by flapping flight (mean ± SD = 0.69 ± 0.28 *g*). Soaring flight had a considerably lower ODBA than the other two flight behaviours (mean ± SD = 0.23 ± 0.09 *g*) and was closer in ODBA to feeding (mean ± SD: 0.20 ± 0.10 *g*). With a mean (± SD) of 0.02 ± 0.04 *g*, roosting had by far the lowest ODBA (Supplementary Fig. S7). Over the 45 days postfledging, ODBA per burst decreased for flapping (males: from 0.79 g (95% CrI = [0.37, 1.65]) to 0.60 g (95% CrI = [0.28, 1.27]); females: from 0.75 g (95% CrI = [0.36, 1.59]) to 0.57 g (95% CrI = [0.27, 1.21])), but did not change considerably for soaring (Table 1, Supplementary Fig. S8), indicating an increase in energy efficiency of flapping flight during the early postfledging dependency period. We found a difference between males and females in the ODBA of flapping flight, with

Table 1
Model estimates for the analysis of factors associated with overall dynamic body acceleration (ODBA) of flight behaviours

		Estimate	95% CrI	PP (> or < 0)
ODBA soaring flight	**Fixed Effects**			
	Intercept	**-1.61**	**[-1.88, -1.34]**	**1**
	Days after fledging	**-0.01**	**[-0.02, -0.01]**	**0.99**
	Body condition	0.05	[-0.22, 0.33]	0.66
	Sex (male)	0.03	[-0.02, 0.08]	0.88
	Random Effects			
	Bird	0.07	[0.05, 0.10]	
	Date	0.09	[0.07, 0.11]	
ODBA flapping flight	**Fixed Effects**			
	Intercept	**-0.55**	**[-0.78, -0.32]**	**1**
	Days after fledging	**-0.07**	**[-0.08, -0.05]**	**1**
	Body condition	0.08	[-0.14, 0.31]	0.77
	Sex (male)	**0.05**	**[0.01, 0.09]**	**0.99**
	Random Effects			
	Bird	0.04	[0.02, 0.07]	
	Date	0.06	[0.04, 0.08]	

Estimates of linear models investigating factors associated with ODBA of flapping and soaring flight during the first 45 days postfledging. Parameter means (Estimate), 95% credible intervals (95% CrIs) and posterior probabilities (PPs) are given. Effects with a posterior probability ≥ 0.95 are considered to have a strong effect and are given in bold.

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males showing higher ODBA values compared to females. Yet, we found neither a sex effect on ODBA of soaring flight nor an effect of body condition on ODBA of either flight behaviour (Table 1).

The average daily sum of ODBA for soaring increased from 0.17 g (95% CrI = [0.11, 0.27]) at day 1 to 1.83 g (95% CrI = [1.26, 2.51]) at day 45 and for flapping from 0.41 *g* (95% CrI = [0.29, 0.57]) to 2.07 *g* (95% CrI = [1.58, 2.68]). Average ODBA per flight burst (including both soaring and flapping flight bursts) decreased from 0.47 *g* to 0.33 *g* during the 45 days postfledging, a reduction of 30%, suggesting that flight became less demanding due to both an increase in flight efficiency and a higher share of soaring.

Factors Associated with Individual Differences in Flight Behaviours

Individual flapping and soaring flight characteristics were not related to the time spent feeding by the same individual (Table 2). Thus, we found no effect of an individual's time spent feeding on its increase in the rate of soaring or flapping flight (individual-specific random slope), the measure for the speed of flight skill development, and no effect of the time spent feeding on the total time spent soaring or flapping (individual-specific random intercept), the measure for differences in the total frequency of flight behaviours. We also found no effect of body condition or sex on any of the individual flight characteristics, except that males showed a stronger increase in flapping flight over the postfledging dependency period than females.

Effects of Flight and Feeding Behaviours on Emigration

Individuals emigrated from the natal territory a mean (± SD) of 199 ± 40 days after fledging (range 103–254 days, $N = 30$). Consequently, as most juveniles fledged at the end of July, 70% of individuals emigrated between February and March (Supplementary Fig. S1–S2). Juveniles that spent more total time soaring emigrated earlier than juveniles soaring less (Table 3, Fig. 3a). Also, juveniles that spent much of their time feeding emigrated earlier than those that spent little time feeding (Table 3, Fig. 3b). After accounting for the effects of soaring and feeding behaviour, individuals that spent much of their time in flapping flight tended to emigrate later than individuals that spent little time in flapping flight (Fig. 3c). In contrast to time spent soaring or flapping, an increase in the rate of soaring or flapping over the 45 days postfledging did not affect emigration timing, suggesting that factors facilitating soaring flight rather than individual differences in the rate of flight skill development foster early emigration. Males and females did not differ in their timing of emigration (Table 3). The results including the two individuals emigrating substantially earlier than their peers showed qualitatively similar effects with reduced effect sizes and certainties (Supplementary Table S7).

Table 3
Model estimates for the analysis of factors associated with emigration timing

	Estimate	95% CrI	PP (> or < 0)
Intercept	**195.22**	**[169.04, 221.59]**	**1.00**
Time spent flapping	*17.70*	*[-5.62, 41.80]*	*0.93*
Increase of flapping	5.20	[-14.99, 25.79]	0.70
Time spent soaring	**-23.88**	**[-47.33, -0.51]**	**0.98**
Increase of soaring	-4.81	[-24.63, 14.42]	0.69
Time spent feeding	**-16.27**	**[-33.74, 1.49]**	**0.97**
Sex (male)	6.10	[-33.67, 45.80]	0.63

Estimates of linear models investigating the factors associated with characteristics of flight behaviours over the 45-day period postfledging (relative slope: increase; relative intercept: invested total time), with parameter means (Estimate), 95% credible interval (95% CrIs) and posterior probabilities (PPs) derived from random draws of 14 000 linear mixed-effects models. Effects with a posterior probability ≥ 0.95 are considered to have a strong effect and are shown in bold; effects with a PP ≥ 90 and ≤ 95 are considered to have a weak effect and are shown in italics.

DISCUSSION

The results of this study show that the behaviour expressed by juvenile animals during the parental dependency period is associated with the timing of gaining independence and the onset of natal dispersal, a key life history transition. This is particularly true for juvenile locomotor behaviour, suggesting that the development of movement skills during early life may play an important role in shaping subsequent life history stages. In addition, we provide a methodological framework for quantifying behavioural time budgets of wild animals from ground-truthed, high-resolution accelerometer data.

Using a random forest trained on a data set of behavioural observations and tri-axial accelerometer data from captive falconry golden eagles proved to be a highly effective approach for identifying both dynamic and static behaviours from tri-axial accelerometer data in free-ranging golden eagles. Classification performed well across data from both falconry and free-ranging individuals, even maintaining high predictive performance when applied to a

Table 2
Model estimates for the analysis of factors associated with flight behaviours

		Estimate	95% CrI	PP (> or < 0)
Increase of soaring	Intercept	13.92	[-35.02, 64.03]	0.71
	Time spent feeding	1.19	[-4.12, 6.40]	0.68
	Body condition	-8.33	[-57.47, 40.22]	0.63
	Sex (male)	0.97	[-8.71, 10.74]	0.58
Time spent soaring	Intercept	0.61	[-1.32, 2.52]	0.74
	Time spent feeding	0.10	[-0.10, 0.30]	0.84
	Body condition	-0.68	[-2.57, 1.20]	0.77
	Sex (male)	0.00	[-0.50, 0.50]	0.50
Increase of flapping	Intercept	-2.68	[-35.62, 29.97]	0.57
	Time spent feeding	1.67	[-1.81, 5.38]	0.83
	Body condition	1.88	[-30.27, 34.51]	0.54
	Sex (male)	**5.55**	**[-0.99, 12.46]**	**0.95**
Time spent flapping	Intercept	-0.30	[-1.86, 1.25]	0.65
	Time spent feeding	*0.10*	*[-0.06, 0.26]*	*0.90*
	Body condition	0.30	[-1.24, 1.84]	0.66
	Sex (male)	-0.03	[-0.45, 0.40]	0.55

Estimates of linear models investigating the factors associated with characteristics of flight behaviours over the 45-day period postfledging (relative slope: increase; relative intercept: invested total time), with parameter means (Estimate), 95% credible interval (95% CrIs) and posterior probabilities (PPs) derived from random draws of 14 000 linear mixed-effects models. Effects with a posterior probability ≥ 0.95 are considered to have a strong effect and are shown in bold; effects with a PP ≥ 0.90 and ≤ 0.95 are considered to have a weak effect and are shown in italics.

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fully independent data set of individuals not included in the training phase. The successful validation on independent wild individuals suggests that our model can be applied to golden eagle data sets of different age classes collected using similar tag configurations and might be applicable to other soaring bird species. This opens the door to more detailed, systematic and fine-scale behavioural analyses of soaring birds during various life history stages.

By applying the random forest to accelerometer data of wild golden eagles, we found that increased flight efficiency (increased soaring–flapping ratio) across the entire 45-day period after fledging was associated with early emigration from the natal territory. In addition, much time engaged in feeding (an indicator for postfledging food availability) advanced emigration, but the time spent feeding had no effect on flight behaviours. Our results thus suggest that postfledging food availability had only a limited effect on flight behaviour in golden eagles. Yet, both high food availability and factors associated with a high total frequency of soaring flight independently advanced the onset of natal dispersal.

Postfledging Development of Flight Skills and Efficiency

Juvenile golden eagles improved flight efficiency rapidly after leaving the nest. By increasing the use of soaring flight, juveniles reduced the flight costs by ca. 30% during the first 45 days after fledging. This was possible because flapping flight showed a threefold higher ODBA, a proxy for energy expenditure (Wilson et al., 2006), than soaring flight, corroborating previous findings (Duriez et al., 2014; Scacco et al., 2023). Being able to quickly reduce flight costs likely allows juveniles to reduce energetic requirements associated with movement, therefore freeing up energy for other aspects of ontogeny. This energy can be used for building up experience (Corbeau et al., 2020) and enhancing memory (Ramsaran et al., 2019) and cognitive performance (Thornton & Lukas, 2012). Our results therefore suggest that, at the population level, the early change to a predominant use of soaring flight might be important for further development of skills towards independence. Because of the crucial implications of energy-efficient movement on the energy budget, rapid development of flight efficiency can take ontogenetic priority over other physical or behavioural developments when resources are limited (Berghänel et al., 2015). Yet, soaring development, and thus flight efficiency, is not terminated at the point of emigration, but continues far beyond emigration (Nourani et al., 2024).

Neither our proxy for postfledging food intake (time spent feeding) nor nestling body condition, a proxy for early life food condition (Catitti et al., 2024) affected flight characteristics during the first 45 days postfledging. This was not the case for the increase in flight behaviours or for the total time flying, suggesting that food conditions in the parental territory are not strongly associated with early flight behaviours. Thus, these results also suggest that postfledging flight behaviour might not only be driven by the urge to find food but is likely a result of practicing and refining flight techniques.

Despite the pronounced sexual size dimorphism in golden eagles, with females being substantially larger and heavier than males, we found only small sex differences in early flight behaviours of juveniles. In adult soaring birds, sexual dimorphism often correlates with differences in flight performance (Alarcón et al., 2017), but the large sex differences in movement or energetics may be absent in young birds and might emerge only in later developmental stages (Donázar et al., 1999). Nevertheless, our results from the early postfledging dependency period showed sex-related differences in flapping flight: males flapped slightly more often than females, the increase in flapping flight was steeper in males than females, and ODBA per flapping burst was higher in males than in females. These findings may be due to the larger wing surface of females that improve uplift use, especially as first-year females are significantly lighter with a lower wing loading compared to adult females, a correlation not observed in males (Lish et al., 2016). Thus, females might be able to use uplifts more efficiently, which results in lower flapping frequencies during flapping flight and less frequent flapping flight compared to males.

Effects of Individual Flight Behaviours on Emigration Timing

Despite the rapid acquisition of soaring skills at the population level, juvenile golden eagles showed large individual variation in the total frequency of postfledging flight behaviours, and thus flight efficiency. The soaring–flapping ratio differed considerably between individuals, suggesting high variation in energy expenditure per unit of time in flight. Juveniles showing a high overall flight efficiency (i.e. a high frequency of soaring flight, but not a steep increase in soaring flight) emigrated earlier compared to their peers with lower flight efficiency, indicating that the expression of soaring flight might be an important driver for becoming independent. Soaring birds with a lower share of soaring flight generally show low climb rates (Harel, Duriez, et al., 2016) and disadvantages in foraging success (Navarro & González-Solís, 2007). Even though well-skilled and experienced soaring birds use flapping flight for take-off and landing (Duriez et al., 2014; Williams et al., 2020), as well as for changing from one uplift to another (Williams et al., 2020), we suggest that juvenile golden eagles with low frequency of soaring flight spend less time in uplifts. Short flight periods of soaring flight could result in reduced flight elevations and travelling distances, especially when wind conditions are challenging, as well as increased energetic costs due to more frequent shifts between uplifts (Harel, Horvitz, & Nathan, 2016). These benefits of postfledging flight efficiency are likely to exceed the immediate energy savings during the postfledging dependency period. The early emigration then represents a possible mechanism to translate these benefits into the post-emigration phase.

While we expected that a steep increase in soaring behaviour during the postfledging dependency period will result in early emigration, this was not the case. Rather, an increase in total time spent soaring (with similar flapping frequencies, i.e. increased flight efficiency) was associated with early emigration. Even though a more rapid skill development has been previously linked to better cognitive performance (Cadoret et al., 2018) and higher survival (Rotics et al., 2021), our results indicate that golden eagles were already equipped with a strong genetic blueprint for learning the basics of energy-efficient flight, as has been suggested for other soaring species (Corbeau et al., 2020). Our results therefore suggest that factors resulting in an increased frequency of soaring irrespective of the rate of increase in soaring flight are indicative of early emigration. We see two possible explanations for this pattern: individual differences in innate flight activity levels and differences in flight conditions in the vicinity of the nest facilitating soaring flight. Our data do not allow for disentangling these intrinsic and extrinsic factors responsible for an increased soaring expression during the period after fledging. However, our finding that the frequency of flapping flight tended to show the opposite effect of the frequency of soaring flight points more towards environmental differences facilitating soaring flight than innate differences in flight activity levels. As young soaring specialists heavily rely on orographic uplifts (Bohrer et al., 2012; Nourani et al., 2024), the local conditions affecting soaring flight include static characteristics like exposition, slope and ruggedness, as well as dynamic components including wind speed, direction and solar radiation (Duriez et al., 2014; Scacco et al., 2019). Therefore, the availability of easy-to-exploit uplifts in the parental territory could represent an

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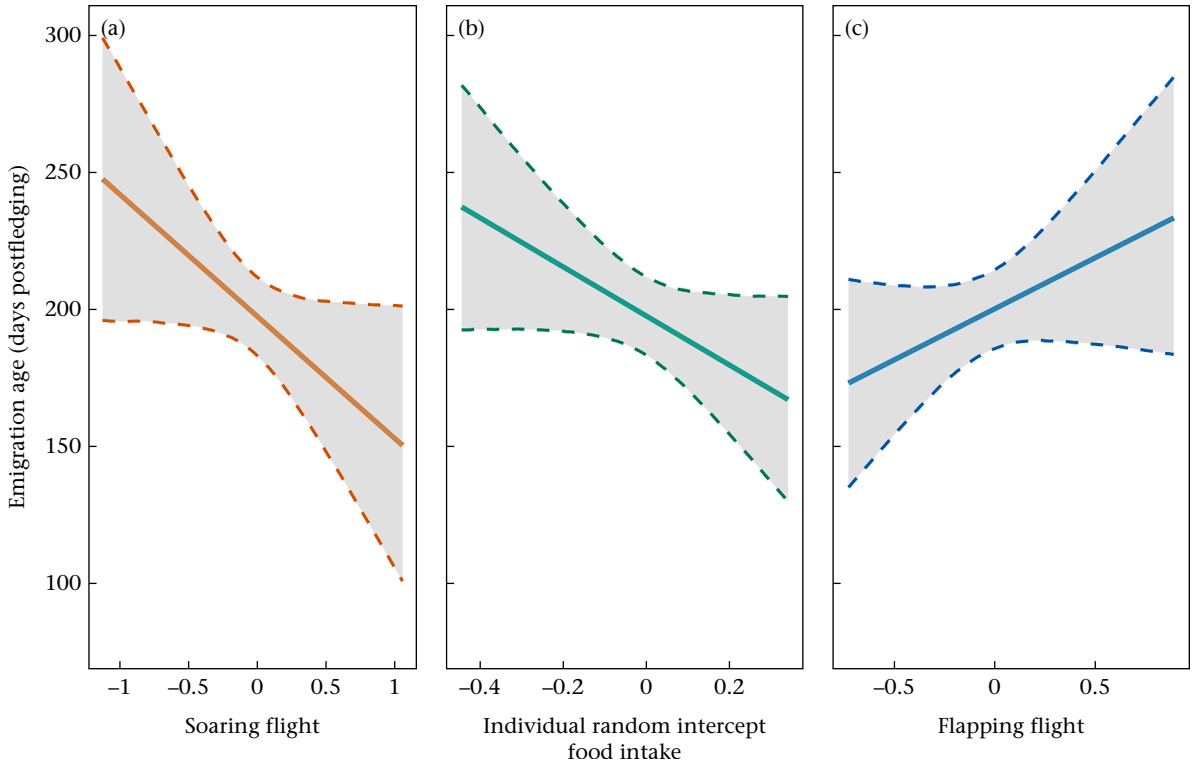


Figure 3. Effects of time investment into (a) soaring, (b) feeding and (c) flapping on emigration age. The solid line shows the mean and the dashed lines show the 95% credible intervals (95% CrIs) from model predictions for females.

underappreciated driver for emigration decisions. This might be particularly relevant for golden eagles in the Alps, as emigration occurs in winter when uplift conditions are highly challenging (Nathan et al., 2012).

Effects of Individual Feeding Behaviour on Emigration Timing

Although we found no effect of differences in time spent feeding on flight behaviours, individuals spending much time feeding emigrated earlier than their peers. Favourable feeding conditions thus seem to provide advantages in addition to those derived from efficient flight behaviours. As juvenile golden eagles are provided with food by their parents, much time spent feeding likely reflects high food availability and/or high parental care. Favourable food conditions during the nestling period are already known to affect later life stages, including shifts in the timing of natal dispersal (Scherler et al., 2023) and increased survival rates (Perrig et al., 2017). Improved nestling food conditions can also induce physiological changes such as improved immune defence or reduced stress levels (Catitti et al., 2022). Therefore, we suggest that favourable feeding conditions during the postfledging dependency period likely provide long-lasting benefits that might be translated through differences in the timing of emigration (Hatzl, 2024).

Conclusions and Future Directions

The results of this study indicate that juveniles experiencing favourable postfledging conditions during the early postfledging dependency period can maximize energy intake and minimize energy expenditure. These conditions promote an early emigration from the parental territory. Thus, favourable food resources (energy intake) and probably also favourable energy resources in terms of environmental uplifts (energy expenditure) seem to show independent advancing effects on the timing of natal dispersal. In addition to the higher expected similarity in emigration timing of individuals in the same territory due to local variation in prey abundance (Fattebert et al., 2019) and topographical features fostering uplift (Scacco et al., 2019). Annual variation in emigration timing is expected to be further related to food provisioning and finer-scale weather conditions affecting soaring conditions (Vansteelant et al., 2015) in the parental territory. However, the correlative nature of our results and their diverse interpretations call for future validation, especially in terms of understanding the underlying mechanisms leading to the behavioural differences in the early postfledging dependency period as well as the mechanisms underlying how these behavioural differences translate from the early to the late postfledging dependency period.

Optimal timing of emigration could have subsequent benefits such as improved information gathering or competitive advantages as shown in other systems (Clobert et al., 2012; Rotics et al., 2021). We therefore suggest that both food availability and uplift availability in the parental territory translate into long-term positive fitness consequences in juvenile golden eagles. To test these expectations, we need to follow tagged individuals throughout the entire life cycle to obtain information about their survival, settlement timing and lifetime reproductive success.

Late emigration might also affect the next reproductive cycle of the parents due to a potential trade-off between a prolonged investment into the current offspring and the next brood (Grüebler & Naef-Daenzer, 2008; Jenny et al., 2024). Many breeding pairs in our study population do not reproduce yearly (Jenny, 1992; Jenny et al., 2024) and emigration of juveniles often occurs close to the new breeding season of the subsequent year, potentially

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restricting the next breeding attempt of the parents. It is thus likely that the decision to emigrate is affected by the parent–offspring conflict over the optimal timing of emigration (Trivers, 1974). However, the role of parental care strategies and trade-offs as drivers of emigration timing is beyond the scope of this study but deserves attention in future studies. Nevertheless, our study points towards an important role of parental breeding habitat selection and settlement decisions for juvenile postfledging behaviours and emigration decisions. By occupying territories with high-quality food resources and high-quality energy landscapes, parents may provide their young with important prerequisites for a successful start into independence.

Author contributions

Julia S. Hatzl: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Matthias Tschumi:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Conceptualization. **Enrico Bassi:** Writing – review & editing, Resources, Project administration, Funding acquisition, Data curation. **Sam S. Cruickshank:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **David Jenny:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Loïc Pellissier:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Kamran Safi:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Anne K. Scharf:** Writing – review & editing, Supervision, Software, Resources, Methodology, Formal analysis. **Petra Sumasgutner:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Martin U. Grüebler:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Data Availability

The raw data and R code for this study are available at https://doi.org/10.5281/zenodo.19002502.

Declaration of Interest

We declare we have no competing interests.

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Supplementary Material

Supplementary material associated with this article is available at: https://doi.org/10.1016/j.anbehav.2026.123712.

The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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