TIMING OF INDEPENDENCE IS EXPLAINED BY MOVEMENT ABILITY, BUT DEPENDS ON HOW INDEPENDENCE IS DEFINED FOR A LONG-LIVED RAPTOR

Hester Brønnvik[1,2], Martina Scacco[1,3], Michael Chimento[7,2,1] Enrico Bassi [4], Julia S. Hatzl [5], Petra Sumasgutner [6], Matthias Tschumi [5], Martin Wikelski [1,2], Svea Zimmermann [5], Kamran Safi*[1,2], Elham Nourani*[7,2,1]

[1] Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany.
[2] Department of Biology, University of Konstanz, 78464 Konstanz, Germany.
[3] Swiss Federal Institute for Forest, Snow and Landscape Research, ETH Zurich, 8903 Birmensdorf, Switzerland.
[4] ERSAF-Direzione Parco Nazionale dello Stelvio, 23100 Bormio (SO), Italy.
[5] Swiss Ornithological Institute, CH-6204 Sempach, Switzerland.
[6] Konrad Lorenz Research Center (KLF), Core Facility for Behavior and Cognition, Department of Behavioral and Cognitive Biology, University of Vienna, 4645 Grünau/Almtal, Austria.
[7] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78464 Konstanz, Germany.
* These authors contributed equally to this work.
Corresponding author: hbronnvik@ab.mpg.de. Am Obstberg 1, 78315 Radolfzell, Germany.

Number of words in the abstract: 220
Number of words in the main text: 3,545
Number of cited references: 63
Number of tables: 1
Number of figures: 1

ABSTRACT

Achieving independence from parental care requires animals to learn about their environment while acquiring vital skills. The timing and type of the transition to independence vary across species, with some achieving independence early, while others rely on prolonged parental care presumably to mature and develop vital skills. When independence is delayed until juveniles reach a certain level of skill, we can expect that skill acquisition rate and proficiency will predict the timing of independence. Here, we investigated whether the acquisition of soaring flight skills can predict the latency to engage in extra-territorial excursions and ultimately emigration from the natal territory marking the onset of independence in golden eagles (*Aquila chrysaetos*). While fine-scale soaring flight did not predict the propensity to go on excursions or the timing of emigration, movement at a daily scale did affect latency to excursions and emigration. Together, this indicates that soaring flight is learned quickly and early in life and that movement at the daily scale likely encompasses more than just flight capacity. Adult-like skill levels appear to be a necessary but not the determining factor for emigration, but may determine the timing of excursions. The difference we discovered between when individuals were capable of independence and when they committed to it may obscure the more general link between skill acquisition and the end of parental care in other systems as well.

Keywords: emigration, excursion, dispersal, flight, dependence period, *Aquila chrysaetos*

INTRODUCTION

Independence from parental care is necessary for all animals. Several key abilities are prerequisite to independence. Particularly, to be independent individuals must have sufficient foraging skill to locate, access, and perhaps process enough nutritious food [1–4]. Individuals must be able to do this in spite of the risks of predation and/or competition from which they will eventually not receive parental protection [5–7], meaning that they must be able to locate safety and compete for opportunities.

Because independence requires a certain level of maturity of skills and abilities, determining when individuals acquire these skills can allow us to predict the transition to independence. First, individuals must develop the physiological abilities to function—for example, gain the lung capacity to dive for prey [8], grow feathers that support flight, or build the musculoskeletal structures to accelerate and escape predators [9]. Second, animals must reach behavioral maturity through foraging, fighting, and refined movement skills. For many animals, such movement may be highly specialized—for example, cryptic prey approaching [10] or manipulation of tools [11]. Finally, individuals require environments that support their bids for independence including parental tolerance while their skills develop [12–16], available food [17, 18], suitable environments [19, 20], and potentially either social partners or sufficiently low competition [21–23]. These physical, behavioral, and habitat-specific criteria having been met, individuals can depart parental care.

The rate of skill acquisition has often been a reliable predictor for the timing of independence, as reflected in the initiation of dispersal from the natal area in many systems [15, 24, 25]. Yet in some systems, the time at which juveniles acquire adult levels of skill can fail to predict the time at which parental care ends [26–34]. This happens most often in long-lived species with broad behavioral repertoires and specialized behaviors. Thus, acquiring complex behaviors may require longer developmental periods and slower life histories (the "maturational constraints hypothesis" [35]) to allow time for a step-wise development of simpler behaviors adding to more complex ones.

The golden eagle (*Aquila chrysaetos*), is one such long-lived species and has an extended period of parental care. The duration of the golden eagle dependence period varies greatly in its Holarctic distribution, from roughly 39 to 250 days in Scotland [36], 44 to 395 days in France [37], 63 to 176 days in Norway [38], 84 to 269 days in Greece [39], and 143-283 days in Spain [40, pp. 200, 237]. During their dependence period, golden eagles rely on their parents for food and safety [16, 37, 39, 41–43].

Soaring flight is an important component of golden eagles' behavioral repertoire as they rely on soaring to scavenge and hunt, as well as for exploratory movement and migration. Eagles may also soar to avoid intraspecific territorial conflicts by riding updrafts high enough to escape detection or prevent physical attacks. By soaring, heavy birds like the golden eagle can cover large distances at high speeds and low energetic costs [44, 45]. Soaring flight is riding rising air currents, or updrafts, to gain height (potential energy) before gliding down to gain distance and control direction. Using updrafts efficiently means finding and staying inside of the strongest part of the updraft [46]. Updrafts form in several ways, among them are orographic updrafts that are formed by winds forced upwards by physical barriers like mountains [44, 47], gravity waves that form where a stable atmospheric layer is disturbed by rising air [48, 49], and thermal updrafts that form where sun-warmed ground heats the air above it [44, 50, 51]. Because updrafts are invisible, turbulent, and ephemeral, soaring is considered to be a particularly skillful form of movement requiring practice and learning [52].

Because eagles are so reliant on soaring, we can expect that their soaring skill is the largest component of their ability to move efficiently in terms of both time and energy. Consequently, learning to soar should predict when they are capable of independence. Thus, a growing body of work has focused on understanding what drivers affect the duration of the eagle dependence period [17, 39] and whether the timing of emigration (i.e., the initiation of dispersal) can be explained by variation in flight skills [16, 37, 43]. However, it seems that improvements in flight performance cease well before emigration [16, 37]. Two alternative explanations for this are: (i) movement proxies have been too coarse to capture the actual development of soaring skill [37], or (ii) emigration timing is not a reliable indicator of independence.

Previously used movement proxies might have been too coarse if they captured other behaviors in addition to soaring skill. For example, the proxy of observed distance traveled between days is likely influenced not only by soaring skills, but also by an individual's need to move, whether it has the energy to move, and whether it is safe while moving. However, fine-scale flight performance inside of updrafts can only occur in the context of an animal motivated to fly and provided supportive conditions. Thus, fine scale soaring performance may reveal patterns of skill acquisition that coarse scale daily movement metrics do not.

Emigration timing may not be a reliable indicator of independence if it is influenced by multiple factors, of which flight skill is only one. Whether parents are motivated to continue providing support, or to begin a new breeding effort instead, determines whether juveniles are tolerated within the natal territory. If the juveniles are allowed to stay, they may choose whether or not to stay based on food availability inside and outside the territory, competitive ability to locate and monopolize resources[53], and movement skill. In contrast, excursions from the territory—after which juveniles return to parental care—explicitly require parental tolerance, may occur even when parents still provide food, and do not require that juveniles be successful competitors. To have accomplished an excursion indicates at least the ability to perform long-distance movement without parental care. Thus excursions can be a better indicator of sufficient movement capacity for independence than is the decision to emigrate.

Here, we used high-resolution GPS data along with daily-scale data to investigate movement patterns during the dependence period of juvenile golden eagles and determine their connection to timing of independence—proxied by excursions or emigration. Based on the assumption that the ability to go on excursions is a better indicator of independence than emigration, we test the specific predictions that (i) juvenile golden eagles will start to go on long-distance excursions when they attain adequate movement capacity, but (ii) delay emigration in spite of this capacity.

METHODS

Data collection

We used biologging data from a long-term study of juvenile golden eagles in the Alps (see [43] for details). We used data collected for a total of 97 juveniles over 2019-2024 (downloaded from the Movebank repository on January 25, 2025). Data included GPS and tri-axial acceleration (hereafter ACC). GPS data were recorded every 20 min. ACC data were collected in bursts, every five minutes for a duration of 7.9 s at 33.3 Hz. Additionally, the GPS loggers collected "super bursts" when the batteries were charged above a threshold, which mostly occurred during mid-day. These included 15 minute bursts of 1 Hz GPS and 20 Hz ACC. We used the super bursts for our analysis of soaring flight before dispersal.

Identification of emigration and excursions

Emigration is defined as leaving the natal territory and not returning at all or returning only briefly, marking the start of natal dispersal. Determining emigration dates can be challenging, especially for excursive species [36]. But for golden eagles, the area used by juveniles is a good indicator of the territory that their parents defend [54]. We manually drew polygons around the highest density of early locations for each individual (e.g. Figure S1) and defined this as the natal territory. For territories inside of Switzerland, we compared our polygons to those published in Bautista et al. [40, p. 368] and found they were in agreement, but we had no such comparisons for other countries. We defined emigration date as the day that an eagle in its first year of life left its natal territory and either did not return at all or returned for less than 24 hours.Young eagles that stopped transmitting within 10 days of leaving the territory (n = 4) were considered inconclusive and we did not count these as emigrations. We defined excursions as any movement outside of the natal territory before emigration, and focused our analysis on long-distance ($\geq$ 10 km) excursions (see supplemental code).

Classification of flight modes

We identified soaring and gliding flight using the GPS data. We isolated bursts of continuous 1 Hz GPS data and calculated turning angle and vertical speed between consecutive locations (using the *move* R package [55]). For the classification of the flight behavior, we applied a moving window of 25 s to calculate the absolute cumulative sum of the turning angles (hereafter cumulative turning angle) and a moving window of 5 s to calculate the average vertical speed. We then applied a k-means clustering algorithm with k = 2 on the average vertical speed to distinguish between soaring and gliding behavior. We sub-categorized soaring observations into circular soaring or linear soaring based on the cumulative turning angle, where a value $\geq$ 200 degrees indicated circular soaring. Observations with a ground speed $\leq$ 3.5 ms^{-1} were considered as non-classified ("other behavior").

Soaring performance metrics

We categorized each bout of circular soaring lasting at least 30 seconds and separated by not more than 60 seconds as a thermal. For each thermal, we calculated: (i) the vertical speed (height gained per time spent), (ii) the standard deviation in the turning angles per time spent, (iii) wind-corrected circling radius (using the *moveWindSpeed R* package [56, 57]), and (iv) the mean of the 1 Hz wind speeds [57].

Daily movement metrics

We extracted four metrics describing how young golden eagles moved on a daily basis. To consider overall mobility, we estimated ground speeds by down-sampling the data to consistent (15 minute) intervals and extracting the per day maximum. On the assumption that climbing in thermals requires skill, we extracted the maximum height above ellipsoid per day to reflect how high individuals flew [37]. We estimated the proportion of time spent in flight as observations per day with ground speeds $\geq$ 3.5 m/s given all observations on that day [37]. Finally, we down-sampled the data to one location in the hour of noon or 1:00 pm and calculated distances traveled between consecutive midday locations [16].

Time-to-event analysis

To understand the factors that contributed to timing of emigration and the first long-distance excursion, we built four separate time-to-event models (Table 1). The models used intervals of one day, thus we summarized our within-thermal performance data to per-day medians of circling radius, vertical speed, and wind speed. We coded each interval with a binary outcome (event = 1, no event = 0), with the interval right-censored (event = 0) if the event

(either first long-distance excursion or emigration) was not observed. The fine-scale data had gaps on days when the biologging devices did not transmit data classified as thermal soaring. If there were no data on the day of excursion/emigration, but there were data within ten days after this (excursions n = 3, emigration n = 6), we used the first of those thermals for the final skill level (i.e. last follow-up time). For the daily-scale metrics, the final skill level was measured on the day of first excursion/emigration.

Table 1. The four time-to-event models using movement metrics to predict latency to excursions or to emigration. We predicted each event (first long-distance excursion or emigration) at two scales: i) within soaring performance metrics summarized to per-day medians, and ii) the daily movements.

Model	**Formula**
Soaring performance	
A	time-to-excurse $\sim$ circling radius + vertical speed + wind speed
B	time-to-emigrate $\sim$ circling radius + vertical speed + wind speed
Daily movement	
C	time-to-excurse $\sim$ scaled daily distance + scaled daily maximum height
D	time-to-emigrate $\sim$ scaled daily distance + scaled daily maximum height

Daily distance traveled between midday locations was correlated with maximum daily ground speed (r = 0.50) and time spent in flight (r = 0.55), thus we only included daily distance and maximum flight height (which had a correlation of r = 0.17) in models C and D (Table 1). Because golden eagles can fly at up to 30 m/s [48], we z-scaled the daily movement metrics to use units of standard deviations rather than individual meters. We built separate models for the daily and thermal scales predicting time-to-event using Cox proportional hazards in the *survival* package in *R*. For all four models, we checked the proportional hazards assumption and the distribution of the Schoenfeld residuals [58].

RESULTS

Of the 97 juveniles, 65 emigrated before the spring of 2025 and 63 performed long-distance excursions. Only 14 individuals transmitted 1 Hz data containing classified thermal soaring flight before going on a long-distance ($\geq$ 10 km) excursion and 18 before emigration. These subsets of 14 and 18 individuals contributed data to our analysis of soaring performance metrics. For the daily movement metrics, 65 individuals contributed to the emigration models and 63 to the excursion models.

Eagles made their first long-distance excursions between 55 days and 246 days after tagging (median = 79, Figure S2 A). The maximum distances reached on these excursions varied between 10 km and 77 km (median = 16.7, Figure S2 B) and lasted between one hour and 13 days (median = 4.82 hours, Figure S2 C). Emigration occurred between 61 days and 283 days after tagging (median = 229, Figure S2 D).

None of the soaring performance metrics was significantly associated with excursion or emigration rates (Figure 1 A & B, Figure S3 A & B). However, the daily movement metrics had effects on both time-to-excursion and time-to-emigrate (Figure 1 C & D, Figure S3 C & D). For each standard deviation increase in daily distance (one sd = 6949 m) and in maximum daily height (one sd = 559 m), we found corresponding increases in the rate of excursions of 278% (hazard ratio = 3.775) and 71% (hazard ratio = 1.718) respectively, thus individuals traveling farther and flying higher were more likely to go on excursions. Each standard deviation

increase in daily distance was associated with a 27% (hazard ratio = 1.267) increase in rate of emigration and each standard deviation of height with a 55% (hazard ratio = 0.450) decrease in rate of emigration, thus individuals traveling farther and flying at lower heights were more likely to emigrate.

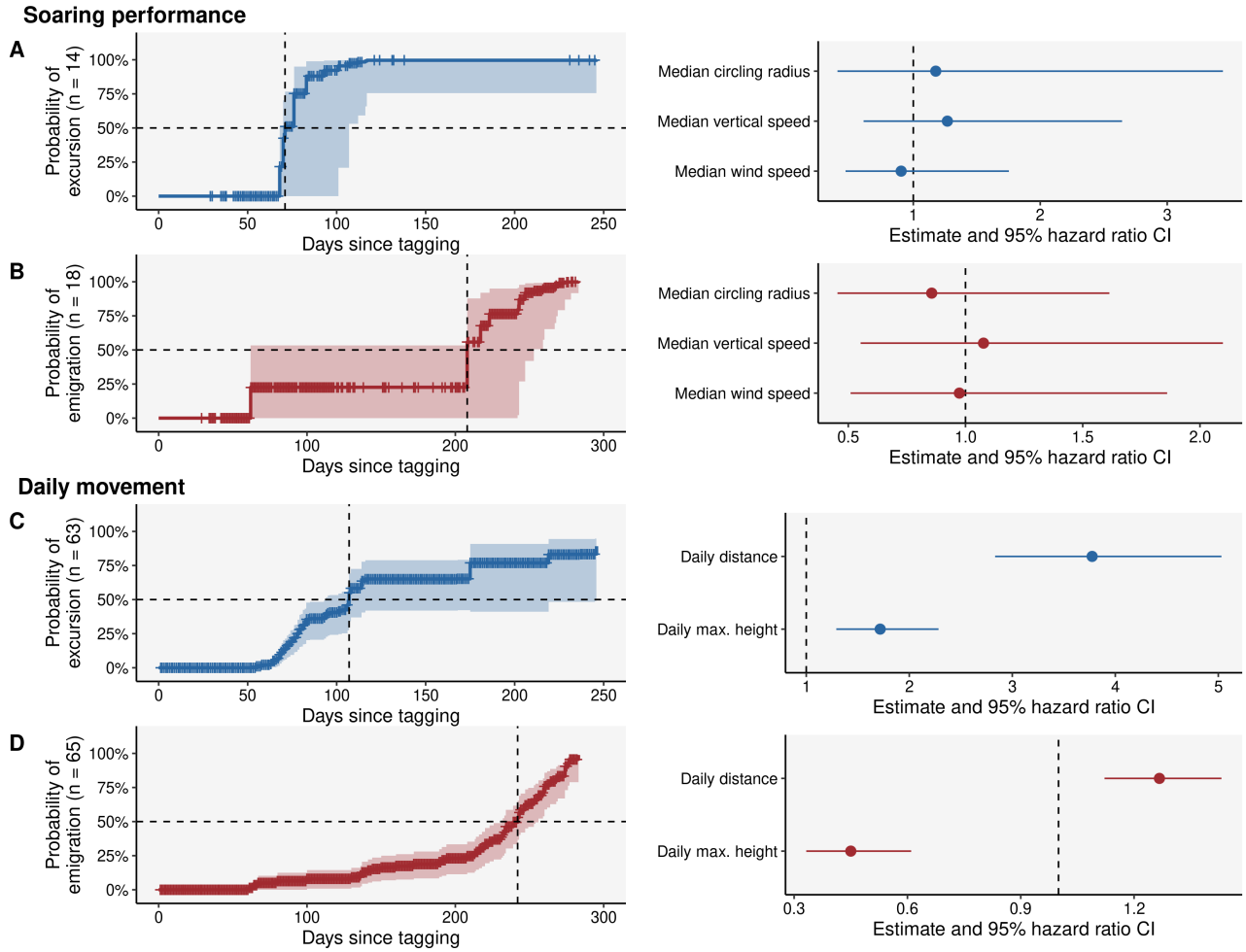

Figure 1. The association of soaring performance and daily movement metrics with time-to-excursion and time-to-emigrate. A) No per-thermal metric had a detectable effect on excursion timing. B) No per-thermal metric had a detectable effect on emigration timing. C) Both daily distance and daily maximum flight height had positive effects on time-to-excursion. D) Daily distance had a positive effect and maximum flight height had a negative effect on time-to-emigrate.

DISCUSSION

Independence from parental care should rely on movement capacity, but determining whether movement actually predicts independence is complicated by how movement is measured and how independence is defined. We used high-resolution GPS tracking of juvenile golden eagles to investigate the connection between two measures of movement capacity and two measures of time-to-independence. We found that metrics of thermal soaring flight could not predict the rate of excursions or emigration. Daily movement predicted both rate of excursions and rate of emigration, but weakly so and with inconsistent signals. We suggest that the missing signal in soaring flight may be caused by a rapid learning curve, whereas the inconsistency in daily metrics may be driven more by environment than by ability. Regardless, before permanent emigration from the natal territory most juvenile eagles are clearly capable of remaining outside of the parental territory for several days at a time and traversing large distances quickly, as demonstrated by their excursions.

We did not find any association between soaring flight performance and time-to-event, which could be because (i) eagles quickly reach their maximum soaring proficiency, and/or (ii) there was a pattern that our data did not capture. It is possible that the way eagles soar in thermals does not change with age as much as thermal structure itself changes with hour and season. Observations of juvenile eagles flying with their parents suggest that adult-like vertical speeds can be obtained within 60 days of leaving the nest [59, p. 227]. It may be that after approximately two months juveniles are exploiting the thermals they can find at peak proficiency. But we might also not have found a signature of learning because the early learning period of up to 60 days post-fledging accounts for only around 5% of our 1 Hz data. The poor coverage of the very early periods of post-fledging is because nestlings and fledglings tend to sit in the shade, thus the GPS devices rarely had full battery before eagles were spending time soaring with their backs exposed to sunlight. In addition, fledglings simply spend less time soaring (which is evident from behavioral classifications in the acceleration data [60]) and have shorter flight intervals, meaning that we were less likely to capture their flight in our burst data structure. Even if young eagles continue to improve after this early phase, our data were skewed to include more transmissions in the afternoon, which yield records of soaring performance predominantly during good soaring conditions. Thus juveniles could have performed relatively well during the data transmission even if they were not yet proficient in less supportive thermal conditions [52]. Our segmentation approach relied on identifying occasions of circling flight, and thus if juveniles were failing to circle consistently due to their inexperience or lack of skills, we might simply have removed those times and instances when juveniles struggled even if they were included in data transmission. Finally, we only accounted for circular, thermal soaring, but young eagles may rely more on orographic soaring [61] and how they perform in orographic uplifts may prove more important for them than thermals.

Coarser movement metrics, here at a daily scale, account also for the other soaring modes that eagles use and, in our data set, were measured both in poor weather and good weather. We did find effects of daily-scale movement on time-to-event. For excursions, moving further and climbing higher seemed to increase the rate of excursion. This increasing distance between midday locations suggests that eagles were moving across more of the natal territory shortly before leaving it. Climbing as high as possible allows young eagles to travel large distances quickly, and may also keep them safe while they cross the territories of neighboring adults. But, attaining maximum height is not simply skill-based, it is an interaction of how well eagles use uplifts and how strong those uplifts are. For emigration, the effect of flight height was reversed and additional height gained was associated with reduced rate of

departure. Maximum height has a clear seasonal trend with lower heights attained through the winter when boundary layer heights are lower (Figure S4), thus gaining less height may predict emigration not because of skill but because eagles tended to emigrate in spring but began excursions in fall.

This role of weather in movement underlines the fact that daily movement is influenced not only by movement capacity, but also by motivation (e.g. the availability of a carcass nearby) and weather conditions (e.g. avoiding flying in fog or rain). Thus, it is possible that in analyzing these daily movements, we were not directly addressing movement capacity itself. Rather, eagles may be most motivated to go on excursions when they are searching for feeding opportunities and also experiencing supportive weather conditions [16, 59]. Essentially, even while skills remain the same, motivations may change. For example, an eagle may move greater distances when foraging than when satiated but this will not be matched by a change in its fine-scale soaring performance. Foraging opportunities may also play a role in motivating both excursions and emigration, as individuals from less productive territories may need to escape these. We cannot directly account for prey densities or scavenging opportunities inside of the natal territories [62], but forests, water, and towns are not productive for golden eagles; we found that eagles in territories containing these less productive structures were less likely to survive (and/or transmit) to emigrate (Figure S5). Future studies will likely find that hunger motivates the movement decisions of juveniles.

Four young eagles departed their natal territories in 80 days or fewer. Although our sample is not yet large enough to test, these early departures suggest that movement and foraging skills may not be a constraint on emigration after 80 days. Eagle parents may stop actively provisioning juveniles at around 120 days [59, p. 228], which could also indicate that juveniles are capable of fending for themselves within four months of leaving the nest. This time-frame is close to the age at which most Alpine eagles started their long-distance excursions (Figure S2) and to the ages at which Alaskan (63 days[63]) and Norwegian (100 days [38]) golden eagles migrate. Taken together, this suggests that golden eagles achieve the ability to be independent with regard to maturity of movement skills in three to four months. Thus, in contrast to the hypothesis that acquisition of complex skills delays emigration (maturational constraints), it seems that soaring is unlikely to act as a constraint on eagle emigration after a very early age. In addition, this ability to be independent is better captured by excursion timing than by emigration timing.

Our findings suggest that the transition to independence in juvenile golden eagles is not a simple process following the smooth trajectory of a learning curve, but shaped by a combination of development, environment, and decisions. The variability in golden eagle emigration highlights that independence is often a choice. For golden eagles, soaring is a vital skill that allows them to hunt and scavenge, but they seem to acquire this skill—at least under optimal soaring conditions—long before they emigrate. Instead, they may engage in long-distance excursions after they acquire adult-like movement abilities, using excursions as an opportunity to practice moving and scavenging in unfamiliar environments and to prospect for available habitats from the safety of their natal territories [16, 38, 42, 64]. The golden eagle population in the Alps seems to be at its carrying capacity, with no territories unoccupied [40, p. 370]. Thus juveniles that are otherwise ready to disperse may simply have nowhere to go. Competitive ability, parental tolerance, conspecific densities, prey densities, hunting skills, and human disturbance are among many factors both internal and external to a young animal that are likely to interact in affecting the decision of whether or not to forgo parental care. Whereas movement capacity is certainly a necessary part of the ability to survive independently, it is just one factor contributing to the complex decision of whether and when

to become independent.

ETHICS.

The handling and ringing of golden eagle nestlings in Switzerland was carried out under the authorization of the Office for Food Safety and Animal Health (ALT) of the canton Grisons (licence No. GR 2017_06, GR 2018_05E, GR 2019_03E). In Italy, the permissions for handling, tagging and marking were obtained from autonomous region of South Tyrol (Dekret 12257/2018 and Dekret 8788/2020), as well as from the region of Lombardia for ringing and tagging through 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 scientifici(l.r. 26/93). In Austria, all procedures for handling, tagging and marking were approved by the Ethics committee of the University of Vienna (No. 2020-008) and permitted by the Federal Ministry for Education, Science and Research (No. 2020-0.547.571), Styria (BHLI-165942/2021-2) and Upper Austria (LFW-2021-263262/7-Sr). Finally, in Germany birds handled, tagged and ringed were done so under the permission issued by the government of Oberbayern (2532.Vet_02-16-88 and 2532.Vet_02-20-86). All procedures followed the ASAB/ABS guidelines for the ethical treatment of animals in behavioral research and teaching and all applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The handling of birds was performed with maximum care and minimal disturbance to nests and the landscape. Ethical approval for involving animals in this study was received through the application procedure for ringing permits and the scientific commission of the Swiss Ornithological Institute and the national authorities as well as the guidelines imposed through the European Commission on the basis of the guidelines of the FELASA (the Federation or the European Laboratory Animals Association).

DATA ACCESSIBILITY.

The raw tracking data used for this study will be made available via Movebank upon acceptance of the manuscript.

DECLARATION OF AI USE.

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

AUTHORS' CONTRIBUTIONS.

EN, KS, and HB conceived of the study. KS, EB, JSH, PS, MT, and MW facilitated the fieldwork and data collection. MC assisted with time-to-event analysis. SZ provided initial estimations of emigration timing. HB and MS processed the data. HB analyzed the data and wrote the first draft of the manuscript. All authors discussed the final results and commented on the manuscript.

CONFLICT OF INTEREST DECLARATION.

We declare we have no competing interests.

FUNDING.

EN was supported by the PRIME programme of the German Academic Exchange Service (DAAD) with funds from the German Federal Ministry of Education and Research (BMBF). HB was supported by the German Research Foundation (DFG, Emmy Noether Fellowship 463925853 to Andrea Flack). EN and MC were supported by the Centre for the Advanced

Study of Collective Behaviour, funded by the Deutsche Forschungsgemeinschaft (DFG) under Germany's Excellence Strategy (EXC 2117-422037984).

ACKNOWLEDGMENTS.

We thank Wolfgang Fiedler for indispensable support of the fieldwork. We are grateful to Emily Shepard for discussions on estimation of soaring skills metrics. We are sincerely grateful for the extensive efforts involved in tagging young eagles by all those listed in Nourani et al. 2024 [61]. We thank Andrea Flack for her patient support.

SUPPLEMENTARY INFORMATION

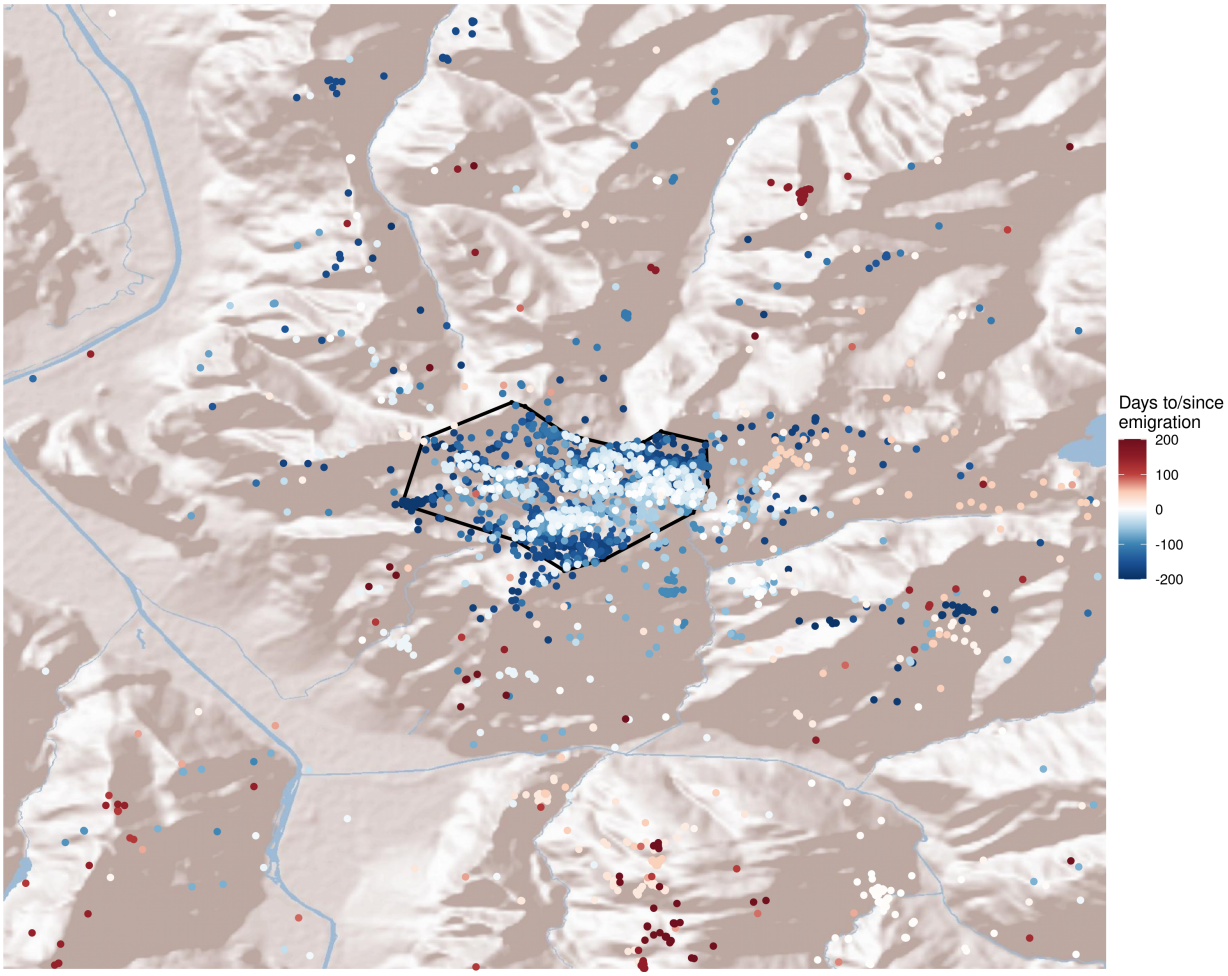

Figure S1. An example of a natal territory polygon in the context of terrain (OpenStreetMap data). Points in blue are pre-dispersal, white points are from the emigration date, and red points are during dispersal.

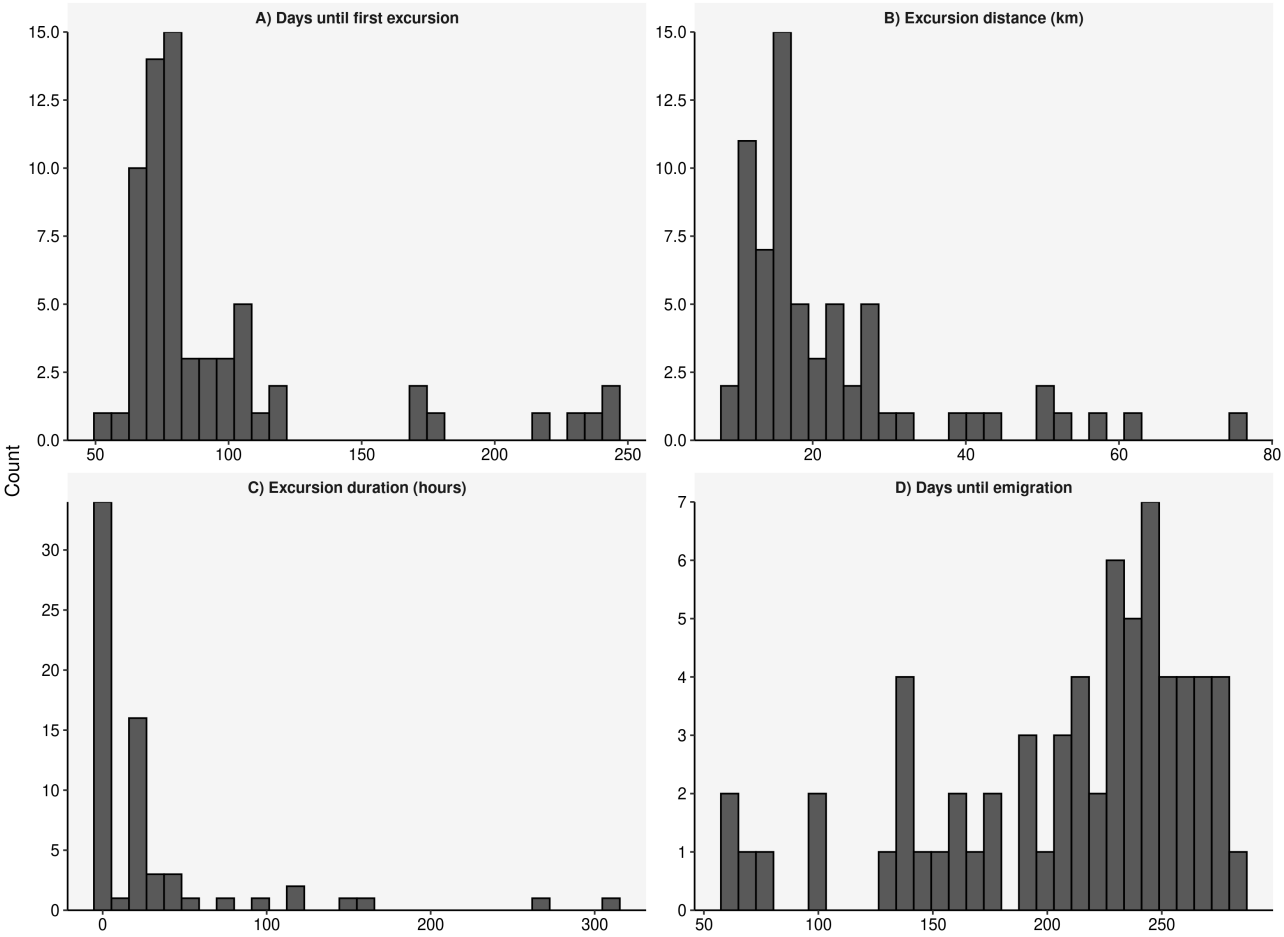

Figure S2. A) 75% of young golden eagles had made their first long-distance excursion within 100 days of tagging (roughly 145-155 days since hatching). B) These first excursions tended to be within 26 km of the natal territory border. C) These first excursions had a bimodal distribution of durations with one peak between 1 and 6 hours and another between 16 and 30 hours. D) Almost two thirds of the eagles emigrated after 200 days (n = 45) and only one third emigrated earlier (n = 21).

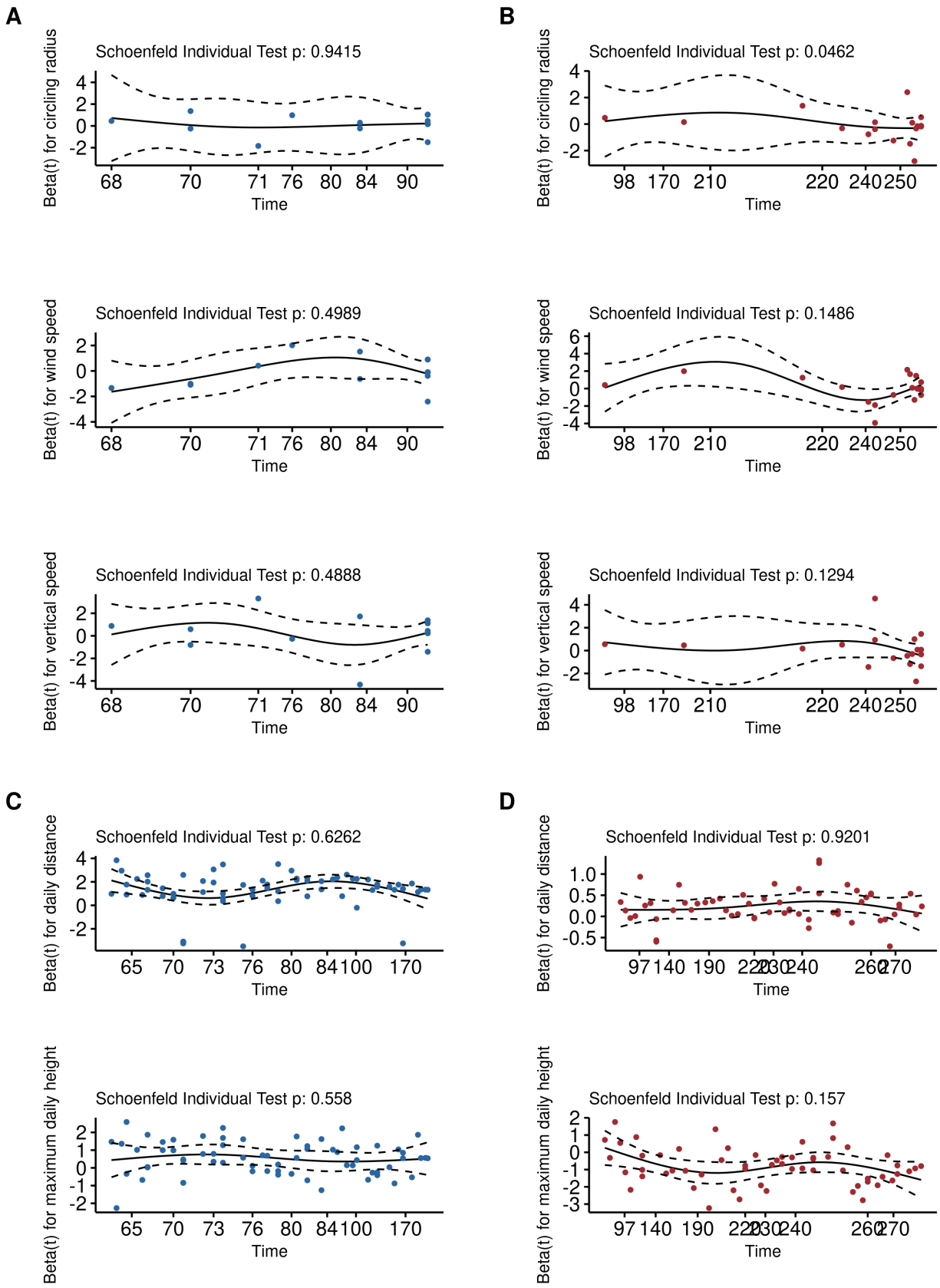

Figure S3. The Schoenfeld residuals show no significant time-dependent effects. A) The residuals for fine-scale data predicting time-to-excursion. B) The residuals for fine-scale data predicting time-to-emigration. C) The residuals for daily-scale data predicting time-to-excursion. D) The residuals for daily-scale data predicting time-to-emigration. These residuals correspond to panels A-D of Figure 1.

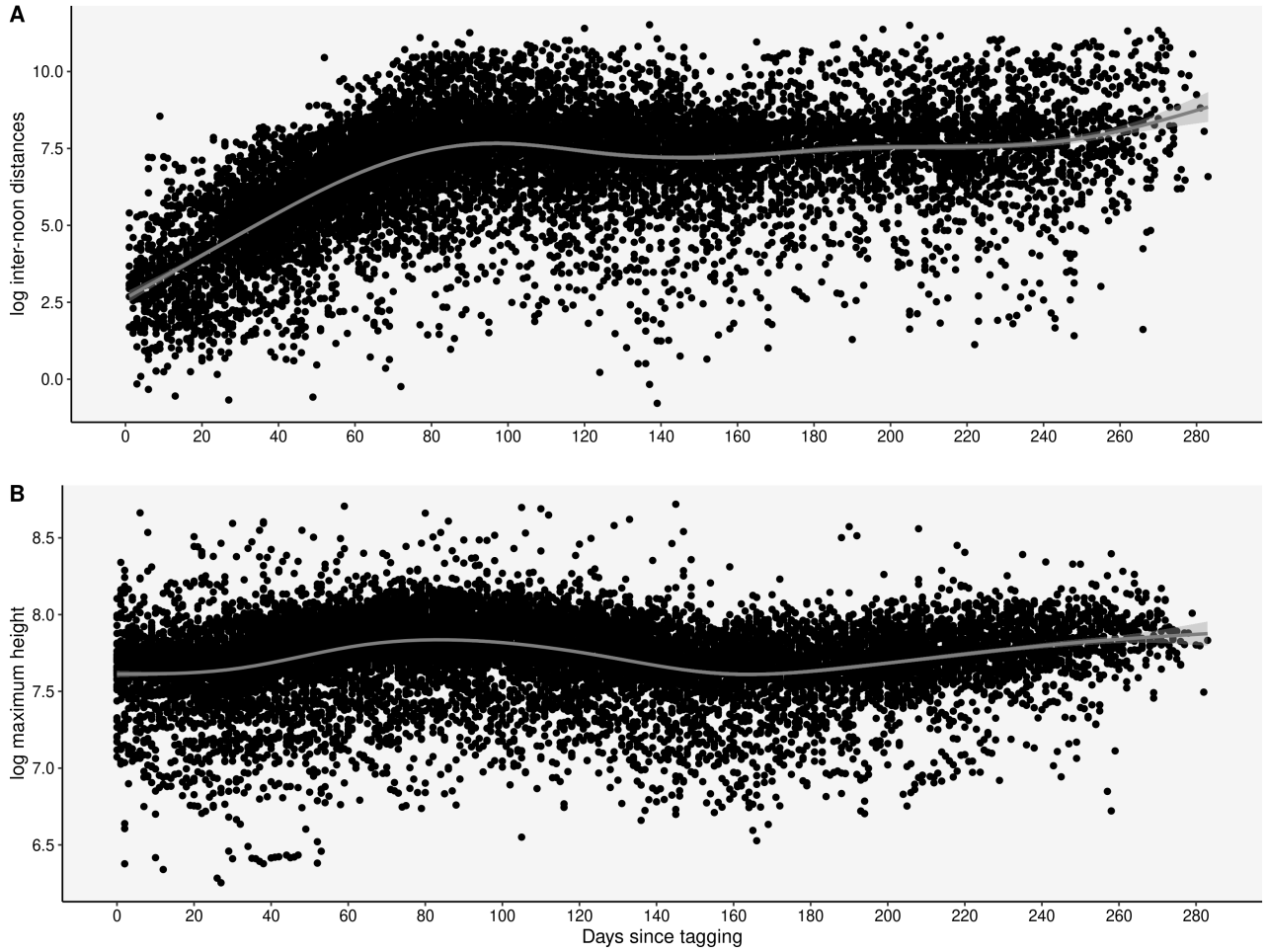

Figure S4. A) Distances between consecutive midday locations increases until around 80 days after tagging and then levels off. B) Maximum height reached per day also initially increases until around 80 days after tagging, but then decreases until 160 days before increasing again. The interval of 80 to 160 days corresponds roughly to October through December. The median days-to-excursion was 79.

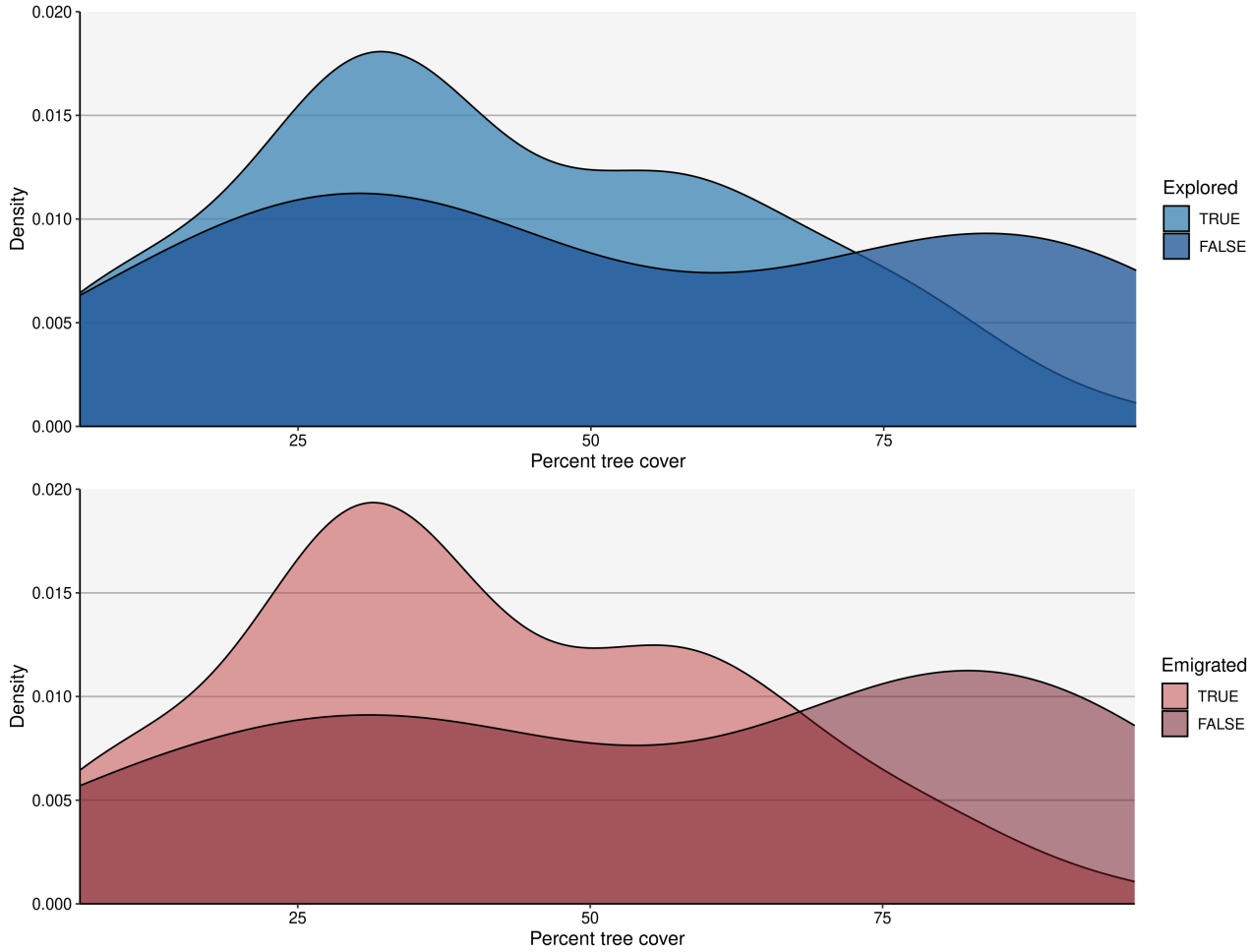

Figure S5. Individuals from territories with forest, lakes, and towns were less likely to survive/transmit to emigration. We estimated how much of the natal territory was covered in unproductive forest, lakes, and towns by taking the percentage of the hand-drawn polygon with the given land use types in ESA WorldCover data (https://esa-worldcover.org/en) at 30 arc second resolution using the *geodata* package in *R*.

REFERENCES

1. Meinertzhagen, R. The education of young ospreys. *Ibis* **96,** 153–155 (1954).
2. Davies, N. & Green, R. The development and ecological significance of feeding techniques in the Reed Warbler (Acrocephalus scirpaceus). *Animal Behaviour* **24,** 213–229 (1976).
3. Kitowski, I. Play behaviour and active training of Montagu's harrier (Circus pygargus) offspring in the post-fledging period. *Journal of Ethology* **23,** 3–8 (2005).
4. Catlin, D. H., Felio, J. H. & Fraser, J. D. Effects of water discharge on fledging time, growth, and survival of piping plovers on the Missouri River. *The Journal of wildlife management* **77,** 525–533 (2013).
5. Gersick, A. S., Snyder-Mackler, N. & White, D. J. Ontogeny of social skills: social complexity improves mating and competitive strategies in male brown-headed cowbirds. *Animal Behaviour* **83,** 1171–1177 (2012).
6. Putman, B. J., Coss, R. G. & Clark, R. W. The ontogeny of antipredator behavior: age differences in California ground squirrels (Otospermophilus beecheyi) at multiple stages of rattlesnake encounters. *Behavioral Ecology and Sociobiology* **69,** 1447–1457 (2015).
7. York, C. A. & Bartol, I. K. Anti-predator behavior of squid throughout ontogeny. *Journal of Experimental Marine Biology and Ecology* **480,** 26–35 (2016).
8. Grecian, W. J. *et al.* Environmental drivers of population-level variation in the migratory and diving ontogeny of an Arctic top predator. *Royal Society Open Science* **9,** 211042 (2022).
9. Herrel, A. & Gibb, A. C. Ontogeny of performance in vertebrates. *Physiological and biochemical Zoology* **79,** 1–6 (2006).
10. Schiel, N., Souto, A., Huber, L. & Bezerra, B. M. Hunting strategies in wild common marmosets are prey and age dependent. *American journal of primatology* **72,** 1039–1046 (2010).
11. Rutz, C. *et al.* The ecological significance of tool use in New Caledonian crows. *Science* **329,** 1523–1526 (2010).
12. Heinsohn, R. G. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *The American Naturalist* **137,** 864–881 (1991).
13. Castillo-Guerrero, J. A. & Mellink, E. Maximum diving depth in fledging blue-footed boobies: Skill development and transition to independence. *The Wilson Journal of Ornithology* **118,** 527–531 (2006).
14. Ridley, A. R. & Raihani, N. J. Variable postfledging care in a cooperative bird: causes and consequences. *Behavioral Ecology* **18,** 994–1000 (2007).
15. Davies, N. Parental care and the transition to independent feeding in the young spotted flycatcher (Muscicapa striata). *Behaviour,* 280–295 (1976).
16. Weston, E. D., Whitfield, D. P., Travis, J. M. & Lambin, X. The contribution of flight capability to the post-fledging dependence period of golden eagles. *Journal of Avian Biology* **49** (2018).
17. Engler, M. & Krone, O. Movement patterns of the White-tailed Sea Eagle (Haliaeetus albicilla): Post-fledging behaviour, natal dispersal onset and the role of the natal environment. *Ibis* **164,** 188–201 (2022).

18. Scherler, P. *et al.* Determinants of departure to natal dispersal across an elevational gradient in a long-lived raptor species. *Ecology and Evolution* **13,** e9603 (2023).

19. Molteno, A. & Bennett, N. Rainfall, dispersal and reproductive inhibition in eusocial Damaraland mole-rats (Cryptomys damarensis). *Journal of Zoology* **256,** 445–448 (2002).

20. Walls, S. S., Kenward, R. E. & Holloway, G. J. Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal. *Journal of Animal Ecology,* 190–197 (2005).

21. Nicolaus, M. *et al.* Social environment affects juvenile dispersal in great tits (Parus major). *Journal of Animal Ecology* **81,** 827–837 (2012).

22. Perry, S., Godoy, I., Lammers, W. & Lin, A. Impact of personality traits and early life experience on timing of emigration and rise to alpha male status for wild male white-faced capuchin monkeys (Cebus capucinus) at Lomas Barbudal Biological Reserve, Costa Rica. *Behaviour* **154,** 195–226 (2017).

23. Sen, S. *et al.* Social correlates of androgen levels and dispersal age in juvenile male geladas. *Hormones and Behavior* **146,** 105264 (2022).

24. Bustamante, J. Post-fledging dependence period and development of flight and hunting behaviour in the red kite Milvus milvus. *Bird Study* **40,** 181–188 (1993).

25. Jenkins, J. M., Thompson III, F. R. & Faaborg, J. Behavioral development and habitat structure affect postfledging movements of songbirds. *The Journal of Wildlife Management* **81,** 144–153 (2017).

26. Johnson, S. J. Development of hunting and self-sufficiency in juvenile red-tailed hawks (Buteo jamaicensis). *Journal of Raptor Research* **20,** 4 (1986).

27. Donazari, J. A. & Ceballos, O. Post-fledging dependence period and development of flight and foraging behavior in the Egyptian vulture Neophron percnopterus. *Ardea* **78,** 387–394 (1990).

28. Langen, T. A. Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, Calocitta formosa. *Animal Behaviour* **51,** 575–588 (1996).

29. Wheelwright, N. T. & Templeton, J. J. Development of foraging skills and the transition to independence in juvenile Savannah Sparrows. *The Condor* **105,** 279–287 (2003).

30. Stone, A. I. Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (Saimiri sciureus). *Ethology* **112,** 105–115 (2006).

31. Holzhaider, J. C., Hunt, G. R. & Gray, R. D. Social learning in New Caledonian crows. *Learning & Behavior* **38,** 206–219 (2010).

32. Schuppli, C., Graber, S. M., Isler, K. & van Schaik, C. P. Life history, cognition and the evolution of complex foraging niches. *Journal of Human Evolution* **92,** 91–100 (2016).

33. Collet, J., Prudor, A., Corbeau, A., Mendez, L. & Weimerskirch, H. First explorations: ontogeny of central place foraging directions in two tropical seabirds. *Behavioral Ecology* **31,** 815–825 (2020).

34. Corbeau, A., Prudor, A., Kato, A. & Weimerskirch, H. Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. *Journal of Animal Ecology* **89,** 20–28 (2020).

35. Deaner, R., Barton, R., Van Schaik, C., Kappeler, P. & Pereira, M. Primate life histories and socioecology (2003).

36. Weston, E. D., Whitfield, D. P., Travis, J. M. & Lambin, X. When do young birds disperse? Tests from studies of golden eagles in Scotland. *BMC ecology* **13,** 1–13 (2013).

37. Hemery, A., Mugnier-Lavorel, L., Itty, C., Duriez, O. & Besnard, A. Timing of departure from natal areas by golden eagles is not constrained by acquisition of flight skills. *Journal of Avian Biology* **2023,** e03111 (2023).

38. Nygård, T., Jacobsen, K.-O., Johnsen, T. V. & Systad, G. H. Dispersal and survival of juvenile Golden Eagles (Aquila chrysaetos) from Finnmark, northern Norway. *Journal of Raptor Research* **50,** 144–160 (2016).

39. Sidiropoulos, L. *et al.* Dispersal Ecology of Golden Eagles (Aquila chrysaetos) in Northern Greece: Onset, Ranging, Temporary and Territorial Settlement. *Diversity* **16,** 580 (2024).

40. Bautista-Rodríguez, J. & Ellis, D. *The Golden Eagle Around the World* ISBN: 978-0-88839-775-1 [Hardback] (Hancock House Publishers, Nov. 2024).

41. Walker, D. Observations on the post-fledging period of the Golden Eagle Aquila chrysaetos in England. *Ibis* **129,** 92–96 (1987).

42. Murphy, R. K. *et al.* First-year dispersal of Golden Eagles from natal areas in the southwestern United States and implications for second-year settling. *Journal of Raptor Research* **51,** 216–233 (2017).

43. Zimmermann, S.-S. *The early life of juvenile golden eagles (Aquila chrysaetos): sex and activity drive fledging time and pre-dispersal exploratory behaviour* MA thesis (Albert-Ludwig University Freiburg, 2021).

44. Bohrer, G. *et al.* Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters* **15,** 96–103 (2012).

45. Duerr, A. E. *et al.* Flight response of slope-soaring birds to seasonal variation in thermal generation. *Functional Ecology* **29,** 779–790 (2015).

46. Reddy, G., Celani, A., Sejnowski, T. J. & Vergassola, M. Learning to soar in turbulent environments. *Proceedings of the National Academy of Sciences* **113,** E4877–E4884 (2016).

47. Zaremba, T. J. *et al.* Vertical motions in orographic cloud systems over the Payette River basin. Part II: Fixed and transient updrafts and their relationship to forcing. *Journal of Applied Meteorology and Climatology* **61,** 1733–1751 (2022).

48. Garstang, M., Greco, S., Emmitt, G. D., Miller, T. A. & Lanzone, M. An instrumented golden eagle's (aquila chrysaetos) long-distance flight behavior. *Animals* **12,** 1470 (2022).

49. Carrard, T. *et al.* Golden eagles regularly use gravity waves to soar in the Alps: new insights from high-resolution weather data. *bioRxiv,* 2024–10 (2024).

50. Scorer, R. & Ludlam, F. Bubble theory of penetrative convection. *Quarterly Journal of the Royal Meteorological Society* **79,** 94–103 (1953).

51. Greenhut, G. K. & Singh Khalsa, S. J. Updraft and downdraft events in the atmospheric boundary layer over the equatorial Pacific Ocean. *Journal of Atmospheric Sciences* **39,** 1803–1818 (1982).

52. Harel, R., Horvitz, N. & Nathan, R. Adult vultures outperform juveniles in challenging thermal soaring conditions. *Scientific reports* **6,** 27865 (2016).

53. Gjershaug, J. O., Halley, D. & Stokke, B. G. Predefinitive plumage in the golden eagle (Aquila chrysaetos): a signal of aggression or submission? *Journal of Raptor Research* **53,** 431–435 (2019).

54. Hemery, A., Duriez, O., Itty, C., Henry, P.-Y. & Besnard, A. Using juvenile movements as a proxy for adult habitat and space use in long-lived territorial species: a case study on the golden eagle. *Journal of Avian Biology,* e03212 (2024).

55. Kranstauber, B., Smolla, M. & Scharf, A. K. *move: Visualizing and Analyzing Animal Track Data* R package version 4.2.4 (2023). `https://CRAN.R-project.org/package=move`.

56. Weinzierl, R. *et al.* Wind estimation based on thermal soaring of birds. *Ecology and Evolution* **6,** 8706–8718 (2016).

57. Kranstauber, B. & Weinzierl, R. *moveWindSpeed: Estimate Wind Speeds from Bird Trajectories* R package version 0.2.4 (2023). `https://CRAN.R-project.org/package=moveWindSpeed`.

58. Schoenfeld, D. Partial residuals for the proportional hazards regression model. *Biometrika* **69,** 239–241 (1982).

59. Watson, J. *The golden eagle* 227–228 (Bloomsbury Publishing, 2010).

60. Hatzl, J. S. *Tracking behavioural trajectories: early-life effects on natal dispersal patterns in golden eagles (Aquila chrysaetos)* PhD thesis (ETH Zurich, 2024).

61. Nourani, E. *et al.* Developmental stage shapes the realized energy landscape for a flight specialist. *eLife* **13,** RP98818 (2024).

62. Steenhof, K., Kochert, M. N. & Mcdonald, T. L. Interactive effects of prey and weather on golden eagle reproduction. *Journal of Animal Ecology,* 350–362 (1997).

63. McIntyre, C. L. & Collopy, M. W. Postfledging dependence period of migratory golden eagles (Aquila chrysaetos) in Denali National Park and Preserve, Alaska. *The Auk* **123,** 877–884 (2006).

64. Soutullo, A., López-López, P., Cortés, G. D., Urios, V. & Ferrer, M. Exploring juvenile golden eagles' dispersal movements at two different temporal scales. *Ethology Ecology & Evolution* **25,** 117–128 (2013).