Developmental stage determines the realized energy landscape for a flight specialist

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Abstract

The heterogeneity of the physical environment determines the cost of transport for animals, shaping their energy landscape. Animals respond to this energy landscape by adjusting their distribution and movement to maximize gains and reduce movement costs. Much of our current knowledge about energy landscape dynamics focuses on factors external to the animal, particularly the spatio-temporal variations of the environment. However, an animal's internal state can significantly impact its ability to perceive and utilize the available energy, creating a distinction between the "fundamental" and the "realized" energy landscapes. Here we show that the realized energy landscape varies along the ontogenetic axis. Locomotor and cognitive capabilities of individuals change over time, especially during the early life stages. We investigate the development of the realized energy landscape in the Central European Alpine population of the golden eagle *Aquila chrysaetos*, a large predator that requires negotiating the atmospheric environment to achieve energy-efficient soaring flight. We quantified weekly energy landscapes using environmental features for 55 juvenile golden eagles, demonstrating that energetic costs of traversing the landscape decreased as the birds aged. In fact, the potentially flyable area within the Alpine region increased 2,170-fold during their first three years of independence. Our work contributes to achieving a predictive understanding of animal movement behaviors by presenting ontogeny as a mechanism shaping the realized energy landscape.

Keywords: Behavioral development, ontogeny, ecological niche, cost of transport, dispersal, soaring flight, bio-logging

Introduction

The physical characteristics of the environment determine the energetic cost of transport for animals, defining their "energy landscape" [1, 2]. Consequently, temporal dynamics in environmental conditions can affect the inherently spatially-explicit energy landscapes across time. For example, patterns of thawing and freezing of lakes and rivers shape the migratory routes of Caribou, as walking on ice is energetically preferable to swimming [3]. Variations of the energy landscape along the temporal axis are most notable for animals that move in moving media: water or air. Sharks adjust their core habitat use to make the most of temporary updrafts formed by tidal currents colliding with upward-facing slopes, which help them reduce the energetic costs of remaining buoyant [4]. Temporal variations in atmospheric conditions shape hourly [2] and seasonally [5] optimal flight routes for birds.

The spatio-temporal variation in the energy landscape is predictable to a great extent. Animals reduce and thus optimize the cost of transport by tracking these changes as they move through the energy landscapes. As such, the distribution and movement patterns of animals can be largely explained by the energy landscape [6], making energy landscapes useful for understanding ecological

and evolutionary processes. This knowledge is increasingly important for policy making to reduce human-wildlife conflicts, particularly for development of infrastructures [7, 8], and more generally in conservation planning [9]. Based on the timing and location of movement the energy landscape can be specific yet predictable for animals with similar morphology and movement modes, at the guild [2, 10], species [8], or sub-species [11] levels.

To date, our understanding of animals' interaction with the energy landscape has depended on factors extrinsic to the moving animal. Reconstructing the energy landscape solely based on the characteristics of the environment can be conceptualized similar to Hutchinson's concept of the fundamental ecological niche [12, 13]. Hutchinson defined the fundamental niche as the full range of environmental conditions in which a species can potentially exist and reproduce. Here we argue that the energy landscape too can, or possibly should, be conceptualized as the fundamental movement niche, defining the full range of physical environmental conditions within which a species can move while adhering to its movement-related energy budget, or sustainable cost of transport. However, just as animals do not occupy the entirety of their fundamental Hutchinsonian niche in reality [13], usually due to competition, various factors can contribute to an animal not having access to the entirety of its fundamental movement niche. Our current understanding of the energy landscape lacks a differentiation between a fundamental and a realized energy landscape.

An animal's realized energy landscape should depend on the motive to move and its internal state. For example, an animal's decision-making when moving might be the outcome of its strategy to maximize long-term fitness rather than short-term energy savings. Halsey et al. [14] introduced the concept of "individual energy landscapes", stating that the energy landscape fluctuates, for example, when an animal increases its speed to out-run a predator [14] or when infection or illness reduces an animal's movement capacity [15, 16]. As a consequence, the realized energy landscape varies in time from the perspective of the moving animal, sometimes irrespective of, but in interaction with and as a consequence of, the immediate environment.

We would like to argue that the animals' ability to exploit the energy landscape is transformed across one of the most fundamental progressions in all animals' lives: the ontogenetic axis. As young animals progress through their developmental stages, their movement proficiency [17] and cognitive capabilities [18] improve and memory manifests [19]. Cognitive capabilities allow the animal to improve the perception of its environment and to make optimal decisions when choosing energy-efficient paths [20, 21]. Improved motor skills enable the animal to respond more appropriately to the perceived environment to utilize the maximum available energy and/or to avoid areas expensive to traverse [22–25]. And finally, memory allows the animal to recall past combinations of space and environmental conditions that affected its costs of movement [26]. Developmental changes and improvements in all these elements should be reflected in the animal's realized energy landscape, where hotspots of

energy gain within the landscape expand as young animals gain experience and master their specific movement behaviors.

We investigated the demographic shift in the realized energy landscape through gaining experience in a movement specialist, the golden eagle *Aquila chrysaetos*. As obligate soaring birds, golden eagles utilize ascending air currents, known as uplifts, to gain vertical altitude, which subsequently enables them to glide for horizontal displacement, without relying on energetically expensive wing flapping. Soaring flight is a learned and acquired behavior [24, 27], requiring advanced cognitive skills to locate uplifts as well as fine-tuned locomotor skills for optimal adjustment of the body and wings to extract the most energy from them. This flight mode enables soaring birds to cover long distances with minimal energy investments, almost as low as when resting [28]. We approach the energy landscape concept with a focus on energy availability. This is commonly done for soaring birds, as uplift and wind support can directly provide energy for flying birds [11, 29].

We used 46,000 hours of flight data collected using bio-logging devices during the transience phase of natal dispersal (hereafter post-emigration) of 55 wild-ranging golden eagles in the Central European Alps to test our hypothesis that the realized energy landscape of young birds gradually expands as they age. More specifically, we expected the habitat to become progressively cheaper to traverse as the birds aged, resulting in an expansion of flyable areas within the Alpine region as a consequence of gaining experience and flight proficiency.

Results

We explored the movement decisions of 55 juvenile golden eagles in the Central European Alps during their post-emigration commuting flights (i.e. non-stop flight bouts lasting at least 1 hour) from the first week until three years after emigration. Following a step-selection approach[30], at each movement step, we compared the observed step to 50 alternative steps that were available to each bird in space and time. These steps were compared in respect to the topography of the terrain, specifically Topographic Ruggedness Index (TRI) and distance to ridge lines, both useful proxies for occurrence of uplifts[29,31]. The resulting step-selection model distinguishing between the used and available conditions with a good predictive performance based on the normalized Root Mean Squared Error (RMSE = 0.14). Overall, the birds preferred to fly over areas with high potential for uplift formation, characterized by high values of TRI and lower distance to ridge lines (Fig. 1). The birds also preferred to fly with long step lengths, a trend that increased with age. As the birds grew older, they were less likely to avoid areas with lower TRI and higher distance to ridge lines (Fig. 2). We found individual variation in the coefficients for TRI and distance to ridge line (Fig. S1).

We used the step-selection model to predict the flyability of the Alpine region for each develop-

mental stage (week since emigration). This flyability index quantified the potential energy that a bird could obtain from its surroundings by considering topography and the bird's movement. This index serves as a measure of the suitability of a location for energy-efficient flight, reflecting the bird's ability to exploit favorable uplift conditions. We constructed energy landscapes for the juvenile golden eagles for each week since independence by predicting the flyability within the Alpine region. Based on these predictions, we determined the flyable area for the juvenile and immature golden eagles during the developmental phase at weekly increments. We defined flyable areas as the cells within a 100*100 m grid with a flyability value larger than 0.7. Our analysis show that hotspots of energy availability in the birds' landscape expanded over time (Fig. 3; Video S1). We found that the flyable area increased 2,170-fold from the first week until three years after emigration. From an initial 0.038 % in the first week after emigration, the flyable area followed a logistic growth curve to plateau at 81 % of the entire Alpine region becoming flyable in the third year (Fig. 4). The tracking data indicated that the golden eagles flew over an area of 92,000 km^2 by the third year after emigration.

Discussion

We show that the flyable area for juvenile golden eagles increased during the developmental period. This increase, we argue, is most likely linked to the birds' improving ability to negotiate their atmospheric environment better as they aged, due to an increasing capacity to perceive and exploit the energy available in the landscape. Because we estimated flyability based on proxies of uplift formation, an important component shaping the energy availability landscape for soaring birds [11, 29], the gradual increase in flyable areas can be interpreted as a change in the realized energy landscape.

Our findings assert the concept of "individual energy landscapes". Initially described by Halsey[14], this concept suggests that the energy expenditure of an animal when moving is more complex than the cost of transport as determined solely by its morphology and the external environment. The locomotor decisions that an animal makes to maximize its fitness at any given point in time would also affect its energy expenditure. We present evidence that ontogeny also serves as a potential mechanism giving rise to individual energy landscapes, not only due to its impact on decision-making, but also due to the influence it exerts on the available options for the animal. During the early stages of their development, animals may not possess the full capacity to perceive their environment, as they will in later stages [20, 21]. Additionally, their motor skills are still being honed[24]. Consequently, younger individuals may respond less efficiently to the environmental conditions they must navigate, in contrast to older, more proficient individuals.

By relying on static topographic variables to build the energy landscapes, we ensured that the environment remained constant over time. Given that golden eagles' wing morphology remains unchanged during the post-emigration period from their natal territory[32,33], the changes in the energy

availability for the birds represented their mastering of soaring flight. Our findings reveal that as the eagles aged, they adopted longer step lengths, indicating an increasing ability to sustain longer uninterrupted flight bouts.

Furthermore, our results provide insight into the development of different flight modes. These birds can switch between orographic and thermal soaring[34]. Orographic soaring refers to utilization of upward air currents generated when wind encounters and flows over elevated topographic features such as hills, mountains, or cliffs. Locating orographic uplifts requires less experience, as they form predictably at mountain ridges[35,36], compared to locating and using more transient thermals which form less predictably over flat surfaces[29]. Our findings suggest that with increasing age, golden eagles place decreasing importance on ruggedness and proximity to ridge lines when deciding where to fly, indicating a learning progression from mastering orographic uplifts before tackling the more challenging thermal soaring.

The energy landscapes maps showed the amount of energy potentially available to juvenile golden eagles during progressing weeks since emigration (Video S1). These maps are based on a step-selection model built on the birds' empirical use of the landscape, the energy availability thus represents the energy that would be theoretically perceivable and exploitable by the birds in a specific developmental phase or age. The detailed perspective on an energy landscape which transforms over time with the accumulation of experience highlights the process of changes in the realized movement niche that would be available to the animals at a certain age. These changes in the ability to extract energy from the atmospheric column will induce age-specific consequences on movement capacity and the cost of transport.

We argue that the realized energy landscape does not represent the realized ecological niche nor the distribution range of animals, but rather the subset of the fundamental energy landscape that is available to the individual based on its ability to perceive and exploit the energy in the landscape. In our study, the realized movement patterns of the golden eagles within the Alpine region covered a small portion of the area predicted as flyable. This is because the birds' movement (and thus their realized individual and age-specific movement niches) will be defined not only by the energy landscape, but also by the interplay of philopatry, developmental requirements, the social landscape, and anthropogenic features. As golden eagles age, other crucial behaviors such as transitioning from predominantly scavenging to active hunting are also happening[37]. A transition that in itself also might depend on advanced flying skills. Thus, the choice of where to fly will not solely follow an energy-minimizing strategy while moving, but naturally also increasingly accommodate resource use opportunities. Additionally, older transient golden eagles are more susceptible to potentially deadly conflicts with territorial adult birds, influencing their movement decisions as they avoid established territories[38] affecting their landscape of fear and thus their decision landscape overall[39–41]. The distri-

bution of anthropogenic features could also impact the eagles' decision-making on where to fly[42]. The strong individual variation that we observed in the birds' response to distance to ridge lines (Fig. S1) could indicate variable landscape utilization strategies among the juvenile golden eagles in response to these factors and their interaction.

Conclusion

Spatial maps serve as valuable tools in informing conservation and management strategies by showing the general distribution and movement patterns of animals. Within this context, energy landscapes play an important role in identifying potential areas of conflict between animals and anthropogenic infrastructures such as wind farms. The predictability of environmental factors that shape the energy landscape has facilitated the development of these conservation tools, which have been extrapolated to animals belonging to the same ecological guild traversing similar environments. However, with recent development of concepts of species-specific[8] and individual-specific energy landscapes[14], the realistic prediction of animals' energy landscapes appears a multifaceted challenge. By identifying the distinct dimensions along which individual energy landscapes can vary, particularly along the demographic axis, we enhance our capacity to understand and predict these landscapes. Our research contributes to this broader understanding by revealing the stark influence of ontogeny in defining the aging of the realized energy landscape. By taking inspiration from the ecological niche definitions to conceptualize the energy landscape, we hope to improve further development of this concept, aiding the interpretation of variations in the energy landscape across many axes, both external and internal to the moving animal.

Materials and Methods

Bio-logging dataset. We used Global Positioning System tracking data from a long-term study of juvenile golden eagles in the resident population of Central European Alps. We used data collected for a total of 55 juveniles tracked over 2017-2023 (Table S1) with a regular sampling schedule of one GPS fix every 20 minutes during daytime (see[43] for details on fieldwork procedure and data sampling schedules). Nestlings were fitted with solar powered loggers manufactured by e-obs GmbH (Munich, Germany) using a leg-loop harness. The weight of the harness and logger (in total maximum 60g) was below the recommended maximum 3% of the birds' body mass. We subset the data to correspond to the transient phase of natal dispersal up to three years after emigration. We identified emigration timing using recursions to the natal territory[44]. If an animal spent more than 14 consecutive days without recursions to a 7 km radius around its nest, we classified it as dispersed. These thresholds were chosen based on expert knowledge of golden eagle behavior in the region. For two animals that had exceptionally large natal territories to start with, we increased the radii to 30 km to compensate

for this potential bias.

Track segmentation. We focused on commuting flights for investigating the energy landscape for the golden eagles. To extract commuting flights, we segmented the tracking data based on ground speed and flight altitude using Expectation-Maximization binary Clustering (EMbC)[45] applied at the population level (i.e. to all individuals). To calculate flight altitude above ground for each tracking point, we first calculated altitude above mean sea level as the difference between altitude above ellipsoid recorded by the bio-logging devices and the Global Geoid Model EGM96 (WGS 84). We then subtracted the ground elevation (Copernicus Digital Elevation Model; 25 m resolution *https://land.copernicus.eu/*) from altitude above mean sea level as an estimate of flight altitude. We labeled segments with high flight altitude and high speed as commuting flights and used these for further analysis. We sub-sampled the tracking data to hourly intervals to focus on commuting flights that were longer than one hour.

Topographic variables. We used two topographic variables as proxies for uplift availability: Topographic Ruggedness Index (TRI) and distance to ridge lines. The former describes the topographic heterogeneity of the terrain by calculating the mean of the absolute elevation difference between a cell and its adjacent cells[46] and the latter represents a proxy for orographic updrafts generated by deflection of the air current by a physical barrier[31,35]. To extract the ridge lines and TRI values, we used the Copernicus Digital Elevation Model. We identified the ridge lines based on the Weisss landforms classification using Topographic Position Index (TPI), a scale-dependent index which compares the elevation of each cell to the neighboring cells within a given radius[47]. As the landform categories depend on the size of the radius, several TPI classifications at different scales were obtained using different radii[48,49]. We selected a classification using a 10 m inner radius and 200 m outer radius on the basis of the narrow size of the identified ridge lines. Then, we calculated the distance from each pixel to the ridge line pixel using the function proximity raster from SAGA[50] to obtain a distance map to the ridge line. For both TRI and distance to ridge lines, we averaged neighboring cell values to achieve a 100 m cell size.

Modeling the energy landscape. We used a step-selection approach[30] to summarize the environmental conditions in which the birds chose to commute. Each pair of consecutive points in the tracking dataset was considered as one step. For each step, we generated 50 random steps that originated at the observed steps' start point, but had alternative end points to represent alternative movement decisions that the bird could have taken. The location of the alternative end points were selected by drawing from a gamma distribution fitted to the step lengths and a von Mises distribution fitted to the turning angles of all the empirical tracking data. The result was a stratified dataset with one used and 50 alternative points in each stratum.

All used and available points were associated with TRI and distance to ridge line values. We found no autocorrelation ($r < 0.5$) among our predictor variables TRI, distance to ridge line, step length, and week since emigration (as a continuous variable). The predictor variables were z-transformed prior to modeling to ensure comparability of the coefficient estimates. We used a conditional logistic regression to build a step-selection function to model and predict the energy landscape. We included step length as one of the predictors in our model, to take the movement characteristics of the growing juveniles into account[30]. To track the changes in the importance of the topographic variables over time, we included three-way interaction terms for the TRI and distance to ridge line, with step length and week since emigration. To account for individual variation, we included the random effect of individuals on the slopes of TRI and distance to ridge line. The model was fit using the Template Model Builder (TMB;[51]) in R[52], following the procedure suggested by Muff et al.[53].

To test the predictive performance of the model, we computed the normalized Root Mean Squared Error (RMSE)[54]. This metric can be interpreted as the standard deviation of the unexplained variance, with lower values indicating a smaller difference between observed data and the model's predicted values.

To better interpret the interaction terms between the topographic variables and week since emigration, we made predictions using the model for different combinations of TRI and week as well as distance to ridge line and week. In the new datasets that we generated to make these predictions, we set the variables that were not represented in the interaction term to their average values and set the grouping factor that represented the stratum as missing data. We made the predictions on the scale of the link function and converted them to values between 0 and 1 using the inverse logit function[55]. We considered these predicted values as the flyability index, representing the potential energy available in the landscape to support flight, based on the uplift proxies (TRI and distance to ridge line) and the movement capacity (step length) of the birds included in the model.

Energy landscape maps To investigate the changes in the energy landscape across the ontogenetic axis, we used our model to create prediction maps for weekly increments during the first three years after emigration. We made our prediction maps for the entire extent of the Alpine region ("Perimeter of the Alpine Convention" layer available via Permanent Secretariat of the Alpine Convention). For each week since emigration, we created a new dataset to make predictions for each 100 m x 100 m cell. We assigned the mean step length value for each given week in the new datasets.

To explore the changes in flyable areas over time, we defined landscape flyability as flyability values above 0.7. We then estimated the total flyable areas for each week since emigration. The Alpine region covers 190,544.7 km^2 (based on the Alpine perimeter layer mentioned above). As a final step, we compared the eagles' flyable area in weeks 1 and 156 with the total area of the Alpine region.

Data, Materials, and Software Availability

The tracking data used for this study will be made available via Movebank upon acceptance of the manuscript. All data needed to replicate the findings of this paper can be accessed via an Edmond repository "Energy landscape Ontogeny"[56]. The code needed for data analysis and plotting can be found at `https://github.com/kamransafi/GoldenEagles/tree/main/WP3_Soaring_Ontogeny/MS2_flight_landscape/public`. DOIs will be generated for these repositories and reported in the manuscript prior to publication.

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Author contribution

KS and EN conceived the study. KS, EB, WF, MUG, JH, DJ, AR, PS, MT, and MW supported, organized, and conducted the fieldwork and data collection. LF prepared the topography layers. HB and MS prepared the tracking data for analysis. EN analyzed the data and wrote the manuscript with input from KS, LF, HB, and MS. All authors discussed the final results and commented on the manuscript.

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).

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Figures and figure legends

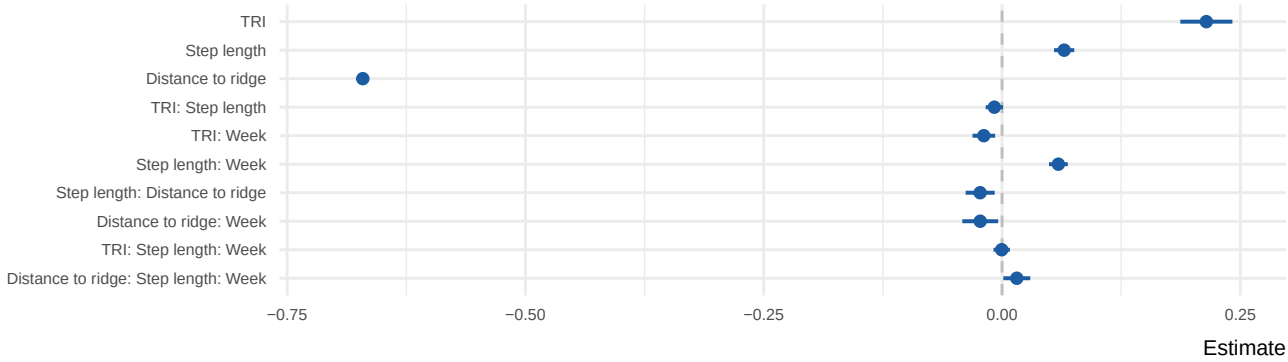

Figure 1: The coefficient estimates of the step selection function fitted using glmmTMB. All variables were z-transformed prior to modeling. The error bars show 95% confidence intervals.

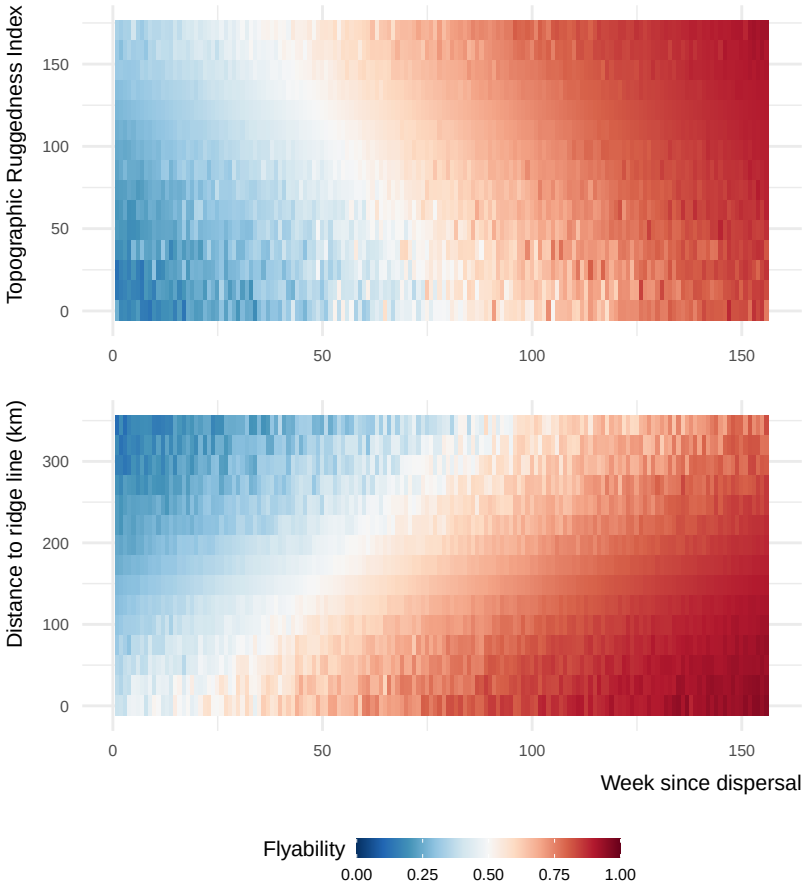

Figure 2: Flyability index predicted using the step-selection model for combinations of topography and week since emigration values. The interactions between Topographic Ruggedness Index (TRI) and distance to ridge lines with week are among the set of criteria that young eagles used for selecting where to fly during their commuting flights.

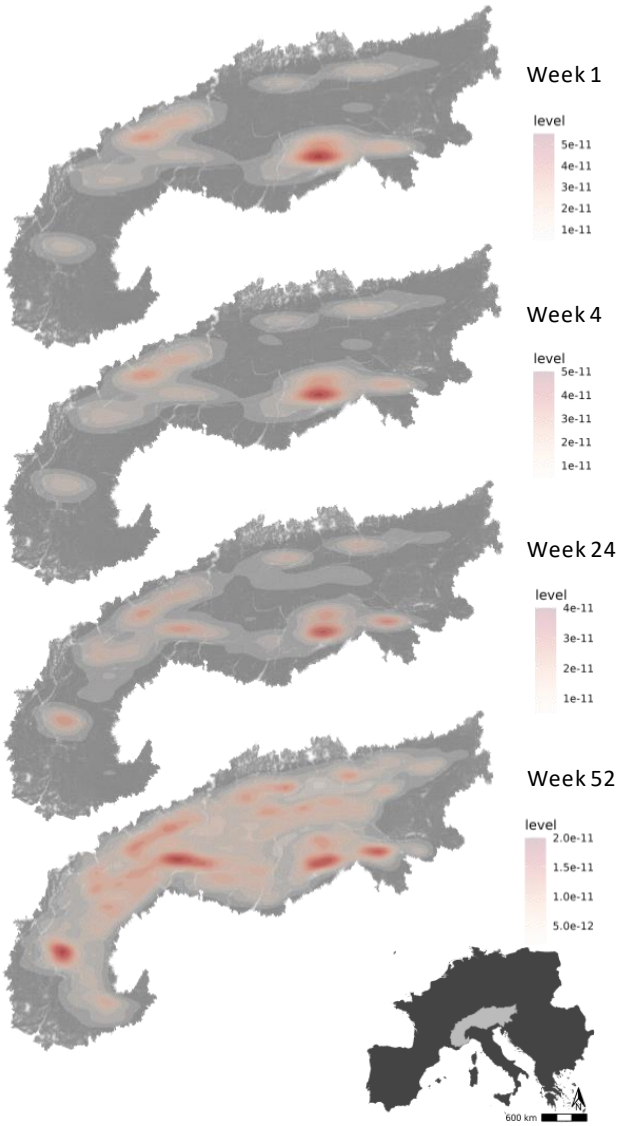

Figure 3: Hotspots of energy availability for golden eagles' flight in the Alps. Flyable areas were defined as cells within a 100*100 m grid with predicted flyability above 0.7 based on our step-selection model. The maps show the 2D kernel density estimation of flyable areas for golden eagles at different timestamps since dispersal: week 1, week 4 (one month), week 24 (six months) and week 52 (one year). The raw prediction maps for every week since dispersal are shown in the video S1.

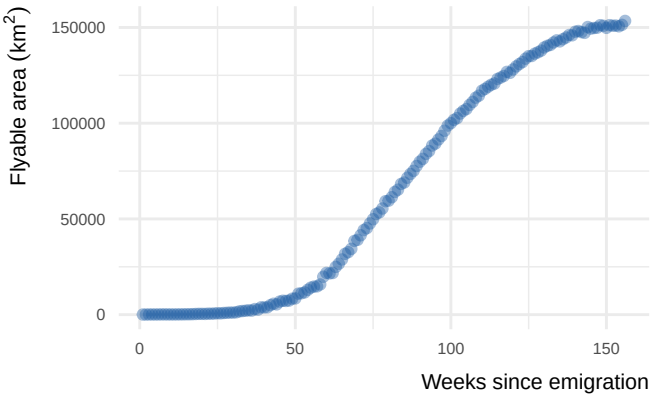

Figure 4: The flyable area for juvenile golden eagles in the Alpine region from the first week until three years after emigration. Flyable area was defined as the total number of cells within a 100*100 m grid with predicted flyability larger than 0.7 based on the step-selection model. The positive trend shows that juvenile golden eagles can fly over a larger portion of the Alpine region as they age.