Gaining proficiency in flight transforms energy landscapes during ontogeny

Elham Nourani [a,b] Louise Faure [a,b,c,1], Hester Brønnvik [a,b,1], Martina Scacco [a,b,1], Enrico Bassi [d], Wolfgang Fiedler [a,b], Martin U. Grüebler [e], Julia Hatzl [e,f], David Jenny [e], Andrea Roverselli [d], Petra Sumasgutner [g], Matthias Tschumi [e], Martin Wikelski [a,b], Kamran Safi [a,b]

[a] Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany.

[b] Department of Biology, University of Konstanz, 78464 Konstanz, Germany.

[c] Section Géographie, École normale supérieure de Lyon, BP 7000 69342 Lyon Cedex 07, France.

[d] ERSAF-Direzione Parco Nazionale dello Stelvio, 23100 Bormio (SO), Italy.

[e] Swiss Ornithological Institute, CH-6204 Sempach, Switzerland.

[f] Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, CH-8092 Zürich, Switzerland.

[g] Konrad Lorenz Research Center (KLF), Core Facility for Behavior and Cognition, Department of Behavioral and Cognitive Biology, University of Vienna, 4645 Grünau/Almtal, Austria.

[1] These authors contributed equally to this work.

Corresponding author: Elham Nourani. enourani@ab.mpg.de, mahle68@gmail.com; +491781750289
Am Obstberg 1, 78315 Radolfzell, Germany.

Classification: Biological Sciences - Ecology

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

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 within the landscape, giving rise to an "individual energy landscape". Here we show that an individual's 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 energy landscape during ontogeny in the Central European alpine population of the golden eagle *Aquila chrysaetos*, a large predator that requires negotiating the physical environment to achieve energy-efficient soaring flight. We constructed weekly energy landscapes using environmental features for 55 juvenile golden eagles and demonstrate 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 individual energy landscape.

Significance statement

Animals strategically negotiate their environment, making decisions about when and where to move to minimize costs. The energy landscape framework has provided the opportunity to predict the energetic costs of movement based on environmental conditions. However, we lack a comprehensive understanding of the dimensions along which the energy landscape changes. Using bio-logging data for 55 juvenile golden eagles tracked for up to three years after independence, we reveal that as young animals develop their movement skills, their landscape becomes cheaper to traverse. These findings suggest that the developmental stage impacts animals' ability to perceive and exploit the energy available in the landscape. This adds ontogeny as a new dimension to our predictive understanding of animal movement behaviors.

Introduction

The physical characteristics of the landscape determine the energetic costs 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 optimal flight routes for birds hourly [2] and seasonally [5].

The spatio-temporal variation in the energy landscape is predictable to a great extent. Animals reduce their energetic costs by tracking these changes as they move. The energy landscape can be predicted based on the timing and location of movement for animals that have similar morphology and movement modes, at the guild [2, 6], species [7], or sub-species [8] levels. As such, the distribution and movement patterns of animals can be explained by the energy landscape [9], making it crucial for understanding ecological and evolutionary processes. This knowledge is also increasingly important for decision making to reduce human-wildlife conflicts, particularly regarding the development of infrastructures [7, 10], and more generally in conservation planning [11].

To date, our understanding of the dynamics of the energy landscape has primarily highlighted the fluctuations in external conditions and how they affect moving animals. Although environmental conditions can predict energy availability in a given landscape, an animal's realized energy gain can depend on its internal state and the decisions made not only to minimize energy expenditure but to maximize fitness in general. The "individual energy landscape" fluctuates for example, when an animal increases its speed to out-run a predator [12] or when infection or illness reduces an animal's movement capacity [13, 14]. As such, the energy landscape is variable from the perspective of the moving animal, sometimes irrespective of the immediate environment.

Here we show that 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 [15] and cognitive capabilities [16] improve, and memory manifests [17]. Cognitive capabilities allow the animal to perceive its environment and to make optimal decisions in their quest of choosing energy-efficient paths. Movement skills enable the animal to respond appropriately to the perceived environment to utilize the maximum available energy and/or to avoid areas expensive to traverse. And finally, memory allows the animal to recall past combinations of space and environmental conditions that affected its costs of movement. Developmental changes and improvements in these elements should be reflected in the energy landscape, where hotspots of energy availability within the landscape are morphed along the ontogenetic trajectory of young animals, as they gain competence and master their specific movement behaviors.

We investigated the ontogenetic transformation of energy landscapes in a movement specialist, an iconic master of its trade when it comes to flight: the golden eagle *Aquila chrysaetos*. As obligate soaring birds, golden eagles utilize ascending air currents, known as uplifts, to gain vertical elevation,

which subsequently enables them to glide for horizontal displacement, without relying on energetically expensive wing flapping. Soaring flight is a learned and acquired behavior [18, 19], requiring advanced cognitive skills to locate uplifts as well as fine tuned locomotor skills for optimal adjustment of the body and wings to gain 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 [20].

We used high-resolution bio-logging data collected during the transience phase of natal dispersal (hereafter post-emigration) of wild-ranging golden eagles in the Central European alps to test our hypothesis that improvement in soaring flight skills results in age-specific energy landscapes. 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 proficiency.

Results

We explored the movement decisions of 55 juvenile golden eagles in the 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 [21], 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 [22, 23]. The resulting step-selection model distinguishing between the used and available conditions had 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 (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 an energy availability index specific to the birds' developmental stage. The Perceived Energy Availability 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 Perceived Energy Availability index 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 Perceived Energy Availability index 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, might be linked to the birds' improving ability to negotiate their environment better as they aged, due to an increasing capacity to perceive and exploit the energy available in the landscape. Our findings assert the concept of "individual energy landscapes". Initially described by Halsey [12], 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 locomotory 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. Additionally, their motor skills are still in the process of improvement. 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 our 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 [24, 25], 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 flights.

Furthermore, our results also provide insight into the development of different flight modes. These birds can switch between orographic and thermal soaring [26]. 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 supposedly requires less experience, as they form predictably at mountain ridges [27, 28], compared to locating and using more transient thermals which form less predictably over flat surfaces [23]. Our findings suggest that with increasing age, golden eagles place decreasing importance on ruggedness and proximity to ridge lines when de-

ciding where to fly, indicating a learning progression from mastering orographic uplifts before tackling the more challenging thermal soaring.

Our energy landscapes show the amount of energy potentially available to juvenile golden eagles during progressing weeks since emigration. Because the maps are based on a step-selection model built on the birds' empirical use of the landscape, the energy availability represents the energy landscape 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 fundamental 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.

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 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 [29]. A transition that in itself also might depend on advanced flying skills. Thus, the choice of where to fly might not solely follow an energy-minimizing strategy while moving, but could also aim increasingly to 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 [30]. The distribution of anthropogenic features could also impact the eagles' decision-making on where to fly [31]. 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 [7] and individual energy landscapes [12], the realistic prediction of animals' energy landscapes appears a multifaceted challenge. By identifying the distinct dimensions along which individual energy landscapes can vary, 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 maturation of individual energy landscapes.

Materials and Methods

Bio-logging dataset. We used Global Positioning System tracking data from a long-term study of juvenile golden eagles in the 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 [32] 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 well below the recommended maximum 3% of the birds' body mass. We subset the data to correspond to the post-natal dispersal period up to three years after emigration. We identified emigration timing using recursions to the natal territory [33]. If an animal spent more than 14 consecutive days without recursions to a 7 km radius around its nest, we classified it as dispersed. 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) [34] 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. While 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 [35], the latter represents a proxy for orographic updrafts generated by deflection of the air current by a physical barrier [22, 27]. 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 [36]. As the landform categories depend on the size of the radius, several TPI classifications at different scales were obtained

using different radii [37, 38]. We selected a classification using a 10 m inner radius and 200 m outer radius on the basis of the thin 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 [39] 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 [21] 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 [21]. 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; [40]) in R [41], following the procedure suggested by Muff et al. [42].

To test the predictive performance of the model, we computed the normalized Root Mean Squared Error (RMSE) [43]. 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 [44].

We considered these predicted values as the Perceived Energy Availability index, a quantity representing the potential energy available in the landscape 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 Perceived Energy Availability index value 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" [45]. 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 when the manuscript is accepted.

Acknowledgments

EN was supported by the PRIME program of the German Academic Exchange Service (DAAD) with funds from the German Federal Ministry of Education and Research (BMBF). LF was partially supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germanys Excellence Strategy EXC 2117 422037984 (grant M21-20 to EN). HB was partially supported by the DFG (Emmy Noether Fellowship 463925853 to Andrea Flack) and the International Max Planck Research School for Quantitative Behaviour, Ecology and Evolution (IMPRS-QBEE). We thank Michael Chimento for scientific and technical discussions. We are grateful for the crucial assistance of the mountain rescue teams of the Guardia di Finanza as well as the forestry and game wardens of South Tyrol/Alto Adige and the national park team in Gesäuse, as well as the Stelvio national park Italy. We also thank the accompanying veterinarians Drs. Michel Mottini and Gilberto Volcan for their time and expertise in the field. Following people assisted with field work in Slovenia: Teja

Curk, Toma Miheli, Bor Miheli, Gaber Miheli, Ruj Miheli and Miha nidari; in Italy: Adriano Greco, Klaus Bliem, Martin Trafoier, Claudio Angeli, Italo Armanasco, Anna Bonettini, Cristian Capitani, Paola Chiudinelli, Alessandro Mercogliano, Alberto Pastorino, Laura Tomasi, Antonella Cordedda and i carabinieri forestali, Jagdverband Südtirol; in Austria: Shane Sumasgutner; in Germany: Ulrich Brendel, Jochen Grab, Wolfgang Palzer; in Switzerland: Claudio Schorta, Claudia Gerber, Svea Zimmermann, Sam Cruickshank, Hannes Jenny, and Romano Salis.

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

Handling and ringing of golden eagle nestlings in Switzerland was carried out under the permit by the Amt für Lebensmittelsicherheit und Tiergesundheit (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).

References

[1] RP Wilson, F Quintana, VJ Hobson, Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. Royal Soc. B: Biol. Sci.* **279**, 975–980 (2012).

[2] EL Shepard, et al., Energy landscapes shape animal movement ecology. *The Am. Nat.* **182**, 298–312 (2013).

[3] M Leblond, MH St-Laurent, SD Côté, Caribou, water, and ice–fine-scale movements of a migratory arctic ungulate in the context of climate change. *Mov. Ecol.* **4**, 1–12 (2016).

[4] YP Papastamatiou, et al., Sharks surf the slope: Current updrafts reduce energy expenditure for aggregating marine predators. *J. Animal Ecol.* **90**, 2302–2314 (2021).

[5] E Nourani, NM Yamaguchi, A Manda, H Higuchi, Wind conditions facilitate the seasonal water-crossing behaviour of oriental honey-buzzards *Pernis ptilorhynchus* over the east china sea. *Ibis* **158**, 506–518 (2016).

[6] JF Masello, et al., How animals distribute themselves in space: Energy landscapes of Antarctic avian predators. *Mov. Ecol.* **9**, 1–25 (2021).

[7] M Scacco, et al., The species-specificity of energy landscapes for soaring birds, and its consequences for transferring suitability models across species. *Landsc. Ecol.* **38**, 239–252 (2023).

[8] E Nourani, WM Vansteelant, P Byholm, K Safi, Dynamics of the energy seascape can explain intra-specific variations in sea-crossing behaviour of soaring birds. *Biol. Lett.* **16**, 20190797 (2020).

[9] ELC Shepard, SA Lambertucci, From daily movements to population distributions: weather affects competitive ability in a guild of soaring birds. *J. The Royal Soc. Interface* **10**, 20130612 (2013).

[10] G Péron, et al., The energy landscape predicts flight height and wind turbine collision hazard in three species of large soaring raptor. *J. Appl. Ecol.* **54**, 1895–1906 (2017).

[11] E Berti, B Rosenbaum, U Brose, F Vollrath, Energy landscapes direct the movement preferences of elephants. *Authorea* (2023).

[12] LG Halsey, Terrestrial movement energetics: current knowledge and its application to the optimising animal. *J. Exp. Biol.* **219**, 1424–1431 (2016).

[13] SA Binning, AK Shaw, DG Roche, Parasites and host performance: incorporating infection into our understanding of animal movement. *Integr. Comp. Biol.* **57**, 267–280 (2017).

[14] A Risely, M Klaassen, BJ Hoye, Migratory animals feel the cost of getting sick: A meta-analysis across species. *J. Animal Ecol.* **87**, 301–314 (2018).

[15] A Corbeau, A Prudor, A Kato, H Weimerskirch, Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. *J. Animal Ecol.* **89**, 20–28 (2020).

[16] JM Fuster, Frontal lobe and cognitive development. *J. neurocytology* **31**, 373–385 (2002).

[17] AI Ramsaran, ML Schlichting, PW Frankland, The ontogeny of memory persistence and specificity. *Dev. Cogn. Neurosci.* **36**, 100591 (2019).

[18] R Harel, N Horvitz, R Nathan, Adult vultures outperform juveniles in challenging thermal soaring conditions. *Sci. reports* **6**, 27865 (2016).

[19] G Ruaux, S Lumineau, E de Margerie, The development of flight behaviours in birds. *Proc. Royal Soc. B: Biol. Sci.* **287**, 20200668 (2020).

[20] O Duriez, et al., How cheap is soaring flight in raptors? a preliminary investigation in freely-flying vultures. *PLOS ONE* **9**, e84887 (2014).

[21] T Avgar, JR Potts, MA Lewis, MS Boyce, Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods Ecol. Evol.* **7**, 619–630 (2016).

[22] M Murgatroyd, T Photopoulou, LG Underhill, W Bouten, A Amar, Where eagles soar: Fine-resolution tracking reveals the spatiotemporal use of differential soaring modes in a large raptor. *Ecol. Evol.* **8**, 6788–6799 (2018).

[23] M Scacco, A Flack, O Duriez, M Wikelski, K Safi, Static landscape features predict uplift locations for soaring birds across europe. *Royal Soc. Open Sci.* **6**, 181440 (2019).

[24] GR Bortolotti, Age and sex size variation in golden eagles. *J. Field Ornithol.* **55**, 54–66 (1984).

[25] TE Katzner, et al., *Birds of the World* eds. PG Rodewald, BK Keeney. (Cornell Lab of Ornithology, Ithaca, NY, USA), (2020).

[26] TE Katzner, et al., Use of multiple modes of flight subsidy by a soaring terrestrial bird, the golden eagle *Aquila chrysaetos*, when on migration. *J. The Royal Soc. Interface* **12**, 20150530 (2015).

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

[28] AE Duerr, et al., Testing an emerging paradigm in migration ecology shows surprising differences in efficiency between flight modes. *PLOS ONE* **7**, 1–7 (2012).

[29] T Nygård, KO Jacobsen, TV Johnsen, GH Systad, Dispersal and survival of juvenile golden eagles (*Aquila chrysaetos*) from finnmark, northern norway. *J. Raptor Res.* **50**, 144–160 (2016).

[30] SA Poessel, PH Bloom, MA Braham, TE Katzner, Age-and season-specific variation in local and long-distance movement behavior of golden eagles. *Eur. J. Wildl. Res.* **62**, 377–393 (2016).

[31] JD Tack, BR Noon, ZH Bowen, BC Fedy, Ecosystem processes, land cover, climate, and human settlement shape dynamic distributions for golden eagle across the western US. *Animal Conserv.* **23**, 72–82 (2020).

[32] SS Zimmermann, "The early life of juvenile golden eagles (*Aquila chrysaetos*): sex and activity drive fledging time and pre-dispersal exploratory behaviour," M.Sc. thesis, Albert-Ludwig University Freiburg (2021).

[33] C Bracis, KL Bildstein, T Mueller, Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography* **41**, 1801–1811 (2018).

[34] J Garriga, JR Palmer, A Oltra, F Bartumeus, Expectation-maximization binary clustering for behavioural annotation. *PLOS ONE* **11**, e0151984 (2016).

[35] S Riley, S Degloria, S Elliot, A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain J. Sci.* **5**, 23–27 (1999).

[36] A Weiss, Topographic position and landforms analysis in *ESRI User Conference Vol 200, San Diego, CA.* (2001).

[37] A Das, H Nagendra, M Anand, M Bunyan, Topographic and bioclimatic determinants of the occurrence of forest and grassland in tropical montane forest-grassland mosaics of the Western Ghats, India. *PLOS ONE* **10**, e0130566 (2015).

[38] I Ilia, D Rozos, I Koumantakis, Landform classification using gis techniques. the case of Kimi municipality area, Euboea Island, Greece. *Bull. Geol. Soc. Greece* **47**, 264 (2016).

[39] O Conrad, et al., System for automated geoscientific analyses (saga) v. 2.1.4. *Geosci. Model. Dev.* **8**, 1991–2007 (2015).

[40] ME Brooks, et al., glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R J.* **9**, 378–400 (2017).

[41] R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria), (2022).

[42] S Muff, J Signer, J Fieberg, Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using bayesian or frequentist computation. *J. Animal Ecol.* **89**, 80–92 (2020).

[43] D Lüdecke, MS Ben-Shachar, I Patil, P Waggoner, D Makowski, performance: An R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* **6**, 3139 (2021).

[44] B Bolker, GR Warnes, T Lumley, Package gtools. *R Packag. "gtools" version 3.9.4* (2022).

[45] E Nourani, Energy landscape Ontogeny. Edmond repository: https://doi.org/10.17617/3.FM4EJC (2023).

Figures and figure legends

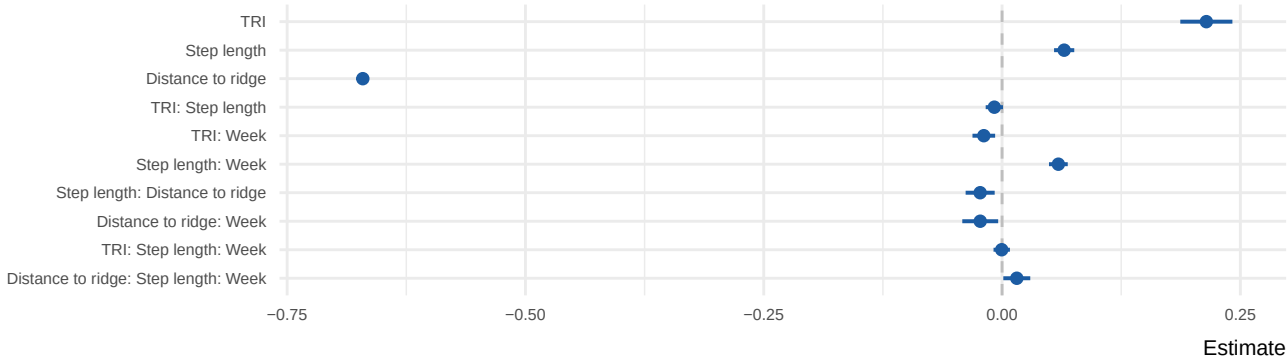

Figure 1: The coefficient estimates of the step selection function fitted using glmmTMB. All variables were z-transformed prior to modeling. The error bars show 95% confidence intervals.

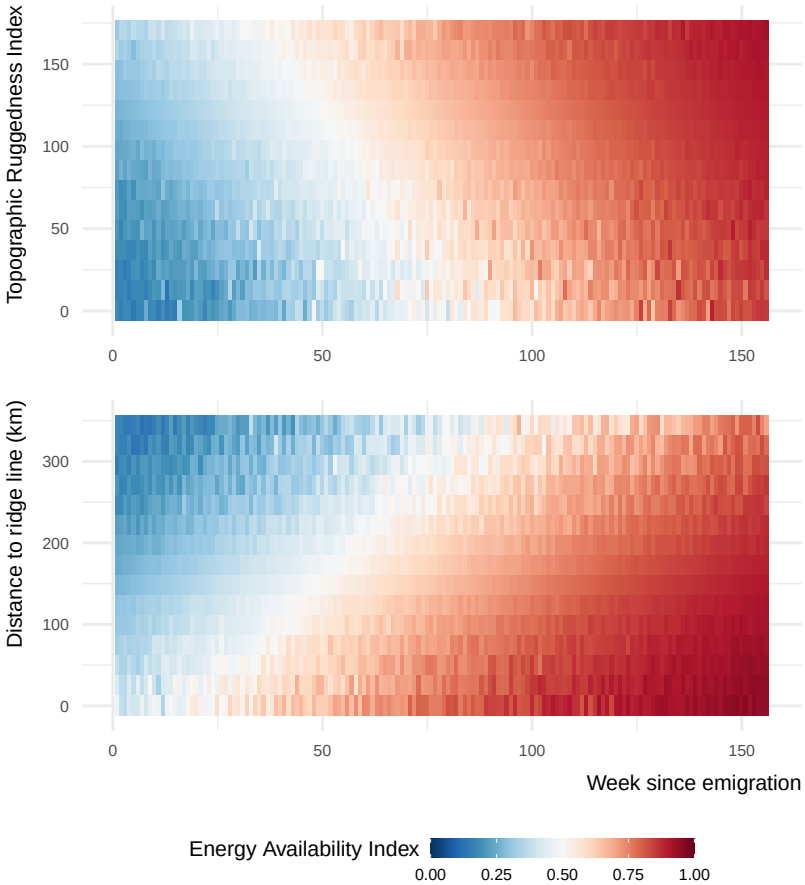

Figure 2: Perceived Energy Availability index predicted using the step-selection model for combinations of topography and week since emigration values. The interactions between Topographic Ruggedness Index (TRI) and distance to ridge lines with week are among the set of criteria that young eagles use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

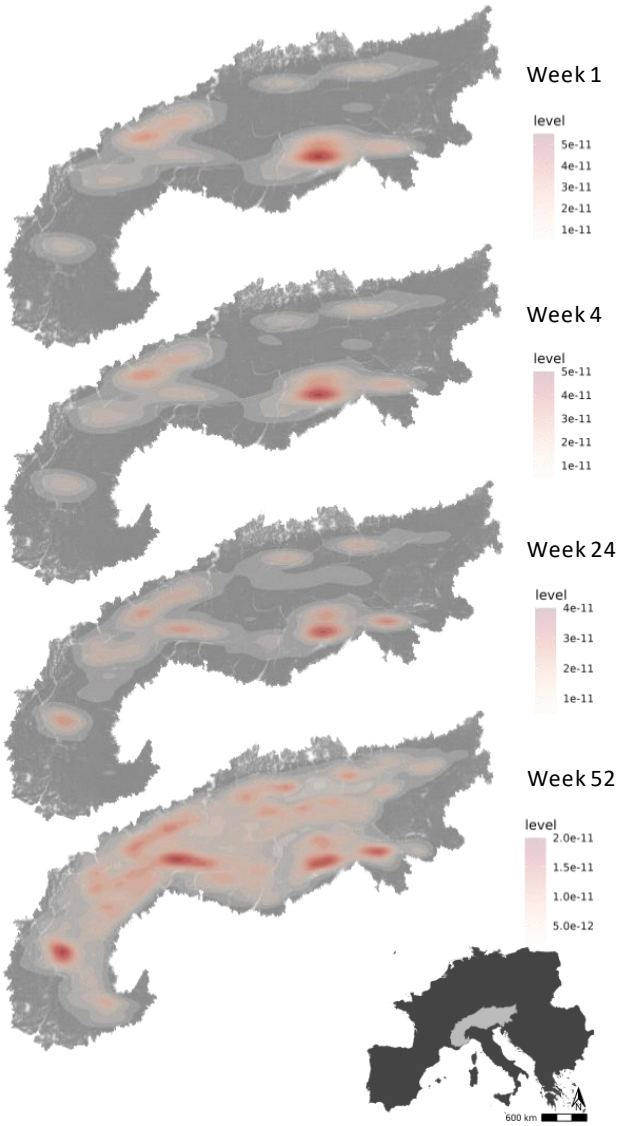

Figure 3: Hotspots of energy availability for golden eagles' flight in the Alps. Flyable areas were defined as cells within a 100*100 m grid with the Perceived Energy Availability index above 0.7 based on our step-selection model. The maps show the 2D kernel density estimation of flyable areas for golden 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 Supplementary video S1.

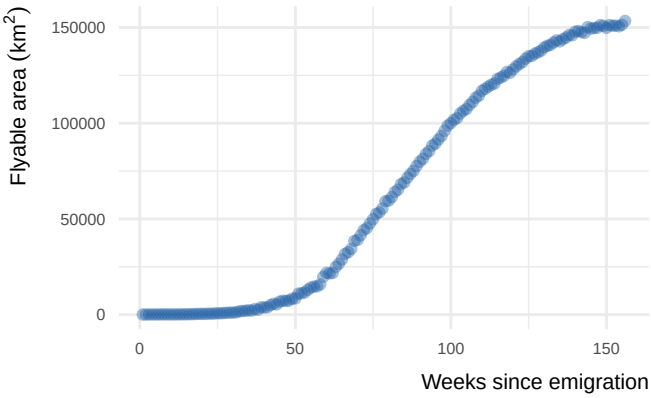

Figure 4: The flyable area for juvenile golden eagles in the Alpine region from the first week until three years after emigration. Flyable area was defined as the total number of cells within a 100*100 m grid with a Perceived Energy Availability index larger than 0.7 based on the step-selection model.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

Supporting Information for

Gaining proficiency in flight transforms energy landscapes during ontogeny

Elham Nourani, Louise Faure, Hester Brønnvik, Martina Scacco, Enrico Bassi, Wolfgang Fiedler, Martin U. Grüebler, Julia Hatzl, David Jenny, Andrea Roverselli, Petra Sumasgutner, Matthias Tschumi, Martin Wikelski, Kamran Safi.

Corresponding author: Elham Nourani
Email: enourani@ab.mpg.de

This PDF file includes:

Figure S1
Legend for Video S1
Table S1

Other supporting materials for this manuscript include the following:

Video S1

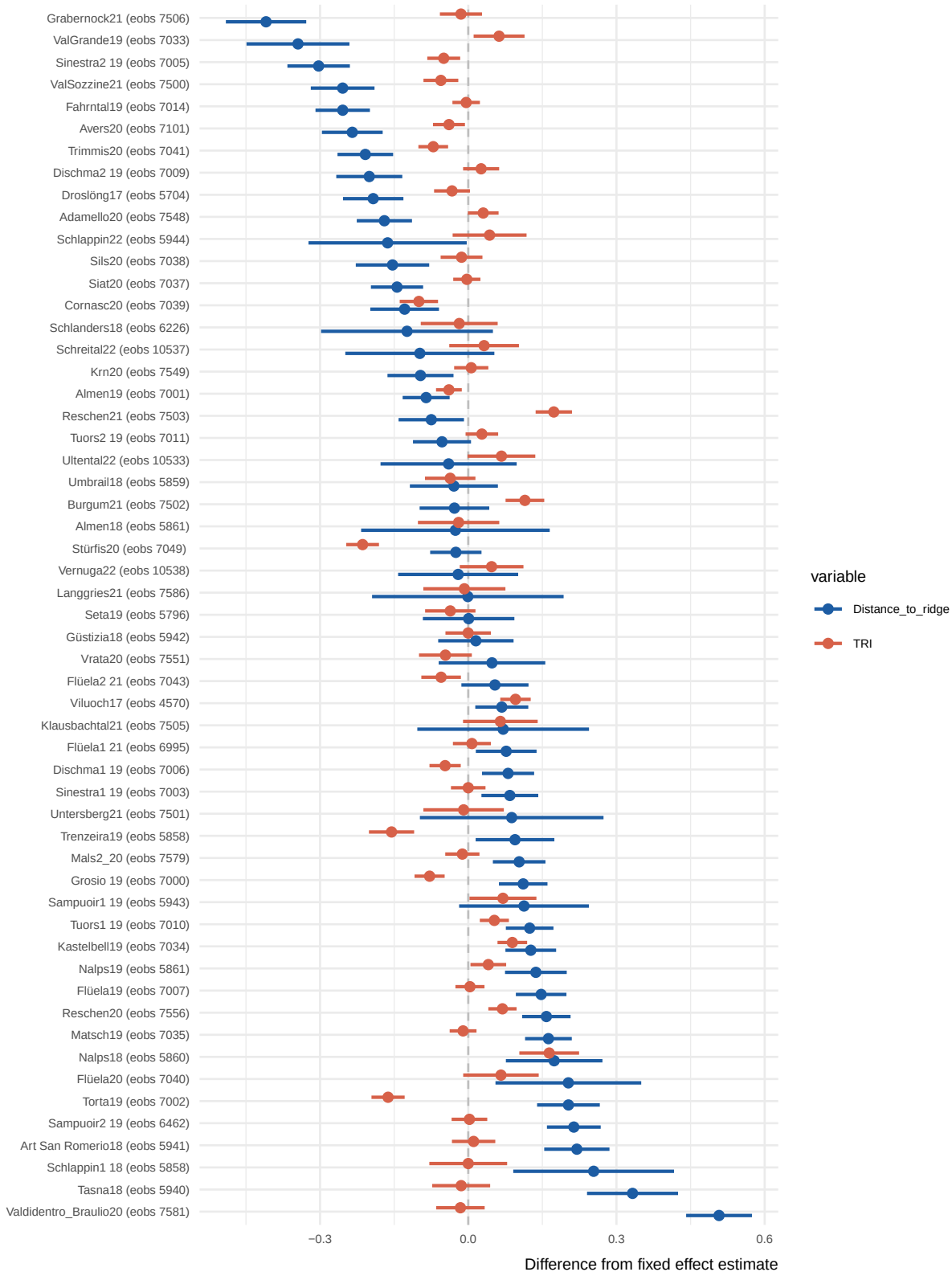

Figure S1: Individual-specific slopes for Topographic Ruggedness Index (TRI) and distance to ridge line. The difference between each individual's estimate from the fixed effect estimate (Fig. 1) is shown. Individuals are ordered based on their distance to ridge line estimates.

Legend for Video S1

The energy landscape from the perspective of the aging golden eagles. We used a step-selection approach to determine how juvenile golden eagles responded to topographic conditions during their commuting flights. Topography is a predictor of uplift potential and can be used as a proxy for energy availability for a soaring birds like the golden eagle. We used a step-selection model to predict a Perceived Energy Availability index across the Alpine region from one week to three years after emigration. The actual amount of energy available in the landscape is constant, but the distribution of Perceived Energy Availability index changes. This is because the birds' ability to perceive and exploit the energy within the landscape improves as they age, making the landscape cheaper to traverse from the birds' perspective. The Perceived Energy Availability index quantifies the suitability of a location for efficient flight, with higher values indicating areas where the bird is more likely to benefit from favorable uplifts. It represents the perceived energy landscape that the bird can exploit based on the given topographic conditions and its own movement abilities.

Table S1. Details of bio-logging data included in the study. The country and year of tagging for each individual, and the tracking duration (in terms of weeks since dispersal) that each individual contributed to the analysis, are reported. All individuals carried Bird Solar Tags manufactured by e-obs GmbH, Germany (either 45 gr or 25 gr.)

Individual local identifier	Country	Tagging year	Weeks post-dispersal
Adamello20 (eobs 7548)	Italy	2020	106
Almen18 (eobs 5861)	Switzerland	2018	1
Almen19 (eobs 7001)	Switzerland	2019	156
Art San Romerio18 (eobs 5941)	Switzerland	2018	60
Avers20 (eobs 7101)	Switzerland	2020	105
Burgum21 (eobs 7502)	Italy	2021	42
Cornasc20 (eobs 7039)	Switzerland	2020	59
Dischma1 19 (eobs 7006)	Switzerland	2019	156
Dischma2 19 (eobs 7009)	Switzerland	2019	83
Droslöng17 (eobs 5704)	Switzerland	2017	102
Fahrntal19 (eobs 7014)	Italy	2019	156
Flüela1 21 (eobs 6995)	Switzerland	2021	61
Flüela19 (eobs 7007)	Switzerland	2019	156
Flüela2 21 (eobs 7043)	Switzerland	2021	49
Flüela20 (eobs 7040)	Switzerland	2020	8
Grabernock21 (eobs 7506)	Italy	2021	61
Grosio 19 (eobs 7000)	Italy	2019	156
Güstizia18 (eobs 5942)	Switzerland	2018	83
Kastelbell19 (eobs 7034)	Italy	2019	141
Klausbachtal21 (eobs 7505)	Germany	2021	2
Krn20 (eobs 7549)	Slovenia	2020	80
Langgries21 (eobs 7586)	Austria	2021	46
Mals2_20 (eobs 7579)	Italy	2020	65
Matsch19 (eobs 7035)	Italy	2019	156
Nalps18 (eobs 5860)	Switzerland	2018	42
Nalps19 (eobs 5861)	Switzerland	2019	60
Reschen20 (eobs 7556)	Italy	2020	130
Reschen21 (eobs 7503)	Italy	2021	60
Sampuoir1 19 (eobs 5943)	Switzerland	2019	9
Sampuoir2 19 (eobs 6462)	Switzerland	2019	72
Schlanders18 (eobs 6226)	Italy	2018	4
Schlappin1 18 (eobs 5858)	Italy	2018	3
Schlappin22 (eobs 5944)	Switzerland	2022	7
Schreital22 (eobs 10537)	Germany	2022	19
Seta19 (eobs 5796)	Switzerland	2019	19
Siat20 (eobs 7037)	Switzerland	2020	107
Sils20 (eobs 7038)	Switzerland	2020	62
Sinestra1 19 (eobs 7003)	Switzerland	2019	156
Sinestra2 19 (eobs 7005)	Switzerland	2019	156
Stürfis20 (eobs 7049)	Switzerland	2020	100
Tasna18 (eobs 5940)	Switzerland	2018	17
Torta19 (eobs 7002)	Switzerland	2019	69
Trenzeira19 (eobs 5858)	Italy	2019	29
Trimmis20 (eobs 7041)	Switzerland	2020	119
Tuors1 19 (eobs 7010)	Switzerland	2019	156
Tuors2 19 (eobs 7011)	Switzerland	2019	156
Ultental22 (eobs 10533)	Italy	2022	6
Umbrail18 (eobs 5859)	Switzerland	2018	37
Untersberg21 (eobs 7501)	Germany	2021	2
Valdidentro_Braulio20 (eobs 7581)	Italy	2020	24
ValGrande19 (eobs 7033)	Italy	2019	46
ValSozzine21 (eobs 7500)	Italy	2021	60
Vernuga22 (eobs 10538)	Italy	2022	12
Viluoch17 (eobs 4570)	Switzerland	2017	137
Vrata20 (eobs 7551)	Slovenia	2020	16