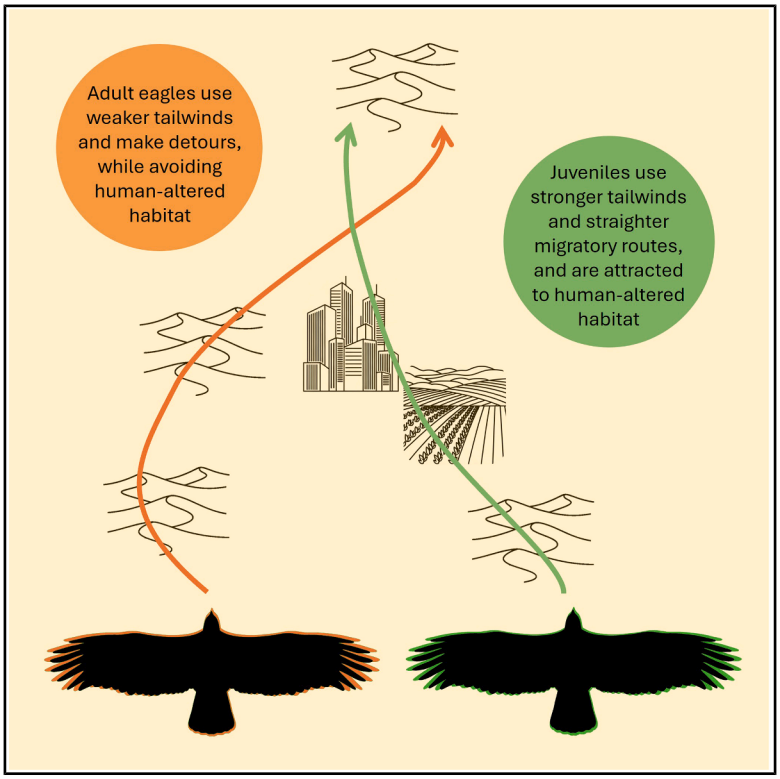
Report

Current Biology

Age-dependent response to anthropogenic habitat during migration of an endangered raptor

Graphical abstract



Authors

Ron Efrat, Yael Lehnardt, Alexandr Bragin, Evgeny Bragin, Tal Avgar, Todd Katzner, Nir Sapir

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In brief

Efrat et al. use complementary data sources and statistical methods to show how experience, weather, and landscape affect endangered eagles' migratory behavior. Most prominently, they present an experience-mediated effect of anthropogenic-altered habitats on route selection, with juvenile eagles being attracted to these habitats while adults avoid them.

Highlights

- Age, wind conditions, and anthropogenic habitat affect migratory decision-making
- Wind conditions affect endangered eagles' decision to migrate or stopover
- Juvenile eagles use stronger tailwinds and straighter migration routes
- The eagles shift from attraction to avoidance of human habitats as they age

Efrat et al., 2025, Current Biology *35*, 4301–4308
September 8, 2025
Published by Elsevier Inc.
https://doi.org/10.1016/j.cub.2025.07.061

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Report

Age-dependent response to anthropogenic habitat during migration of an endangered raptor

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https://doi.org/10.1016/j.cub.2025.07.061

SUMMARY

Decisions made by migrating animals can impact individual fitness and population dynamics.[1,2] For avian migrants, these decisions can be affected by environmental[3–7] and anthropogenic[8–12] factors and by internal[13–18] states. However, recent reviews have pointed to multiple gaps in our understanding of these decisions.[19–22] We studied the decisions made by migrating endangered Steppe Eagles *Aquila nipalensis* by tracking individuals for up to 7 years with GPS transmitters. We used weather reanalysis models and high-resolution remote sensing to obtain environmental and anthropogenic information.[23,24] Using complementary statistical methods, we differentiated between two behavioral states, migratory flights and stopovers, and studied how different factors shape the birds' movements and the transition between these states.[25,26] Most prominently, we detected effects of experience on the birds' response to anthropogenic habitats, with juvenile eagles drawn to them, adults avoiding them, and sub-adults showing no preference. Experience also affected the choice of tailwind and flight direction during migration, with juvenile individuals choosing stronger winds and more direct routes than more experienced eagles. During stopover, experienced eagles flew greater distances than less experienced eagles, and during both stopover and migratory periods, stronger tailwinds increased the distance birds moved. Finally, winds blowing toward the migratory direction increased the probability that a bird would initiate migration after a stopover, while opposite winds had the opposite effect. Our results advance our understanding of the ontogeny of bird migration and the effects of environmental and anthropogenic factors on migratory decision-making, with implications for the conservation of migratory species.

RESULTS

Movement over consecutive migrations

The decision-making of migrating birds during migration can be affected by multiple factors.[3,8,13] We tested how experience and encountered natural and anthropogenic environments influence these decisions. To that end, we collected data on 80 individual autumn migrations from 20 Steppe Eagles between 2018 and 2024, tracking most individuals from hatching for up to 7 years. These included 18 migrations from 18 juvenile eagles (in their first migration), 22 from 12 sub-adults (second or third migration), and 40 from 11 adults (after third migration). To focus on the variables of interest, we limited our study area to the main part of the eagles' migration, excluding the crossing of major mountain ridges or water bodies that can affect the eagles' decision-making (Figure 1). Similarly, we only included data during autumn, from their arrival to the study area until December 31st of each tracking year, avoiding the effects of seasonally related changes in motivation. Our study area included desert landscapes dotted with human-altered habitats (Figure 1). Most tracked eagles left the study area by migrating further south. Yet, 24 individual tracking periods of 10 different individuals did not leave the study area before heading back north.

Tagged eagles arrived in the study area between September 20 and October 24. The mean arrival date at the study area of juvenile, sub-adult, and adult eagles was, respectively, September 29 ± 9.94 days, September 24 ± 18.3 days, and October 8 ± 20.2 days. Similarly, the mean last dates with tracking data in the study area were November 17 ± 33.5 days, November 16 ± 36.4 days, and November 23 ± 33.2 days. Thus, the different

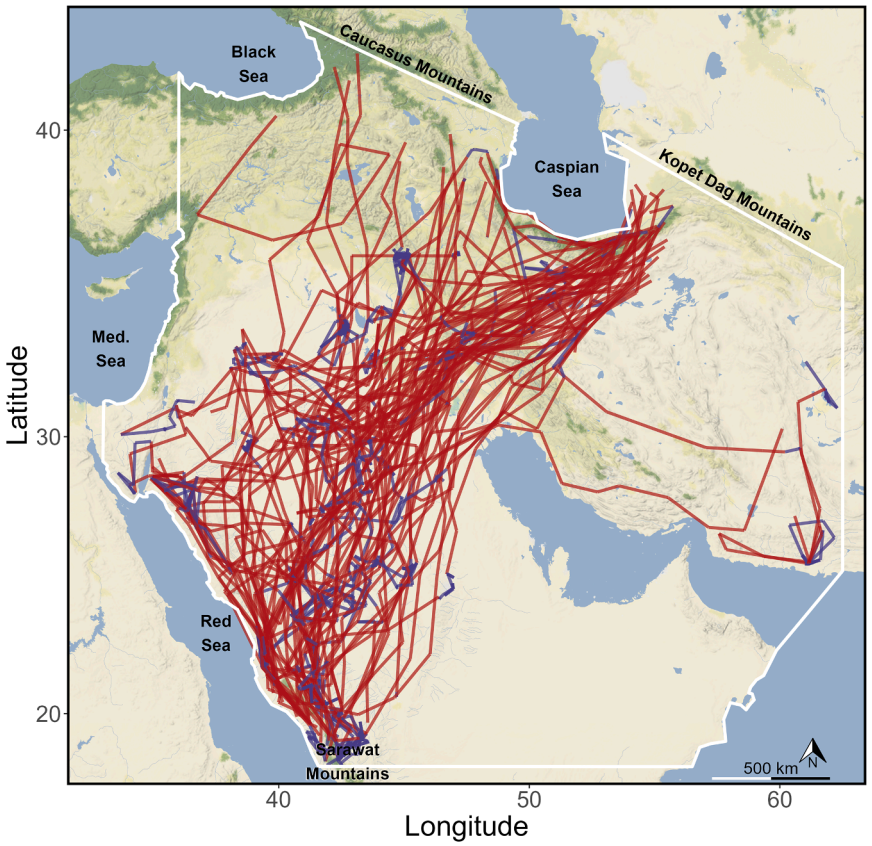

Figure 1. Study area and tracking data

Movement of tracked Steppe Eagles during autumn (migrating southward) in the study area colored according to behavioral state classified by a HMM: stopover (blue) and migratory (red). The white line denotes the borders of the study area, in which the eagles experienced similar geographical features and did not cross any major mountain ridges or water bodies (see STAR Methods for details). Green denotes densely vegetated areas. Map tiles by Stamen Design, under CC BY 4.0. Data by OpenStreetMap, under ODbL.
See also Table S1.

age groups overlapped during most of their time within the boundaries of the study area. This means that the age effects we detected were not likely due to within-season differences in the environment the birds experienced during migration.

Stopover and migratory states

We classified the behavior of the eagles into migratory and stopover states to understand their decision-making in each state and their decision to transition between the states. Using the hidden Markov model (HMM), we classified 2,186 days as stopover behavior and 1,126 as migratory behavior (Figure 1). Eagles traveled shorter distances on stopover days than during migratory flights (20.8 ± 33 and 178 ± 89.1 km; mean ± SD, respectively), and turn angles appeared more variable on stopover days (0.021° ± 1.99° and −0.021° ± 0.919° radians). During stopover, the step lengths of juvenile and sub-adult eagles were shorter than those of adults, but we did not detect age-related differences in step lengths during migration. A stronger daily tailwind increased step length for both states, with a greater effect on migratory steps (Table S1).

The model estimate for the mean probability that an eagle would change from a stopover behavioral state on a given day to a migratory behavioral state the next day was 0.064. The mean of the opposite transition probability, from migration to stopover, was 0.16. These probabilities were influenced by wind during the first 5 h of the day, the period in which the eagles are assumed to make the decision whether to migrate that day. Model estimates suggest that when the winds encountered by an eagle at a stopover state during the first 5 h of the day changed from blowing toward the migratory direction to blowing against it, the probability of transition to migratory flights was reduced. Specifically, this probability was reduced by 11.27% from 0.071 to 0.063 following a change in the wind V vector from −2.93 to 5.19 m/s, equivalent to the 10% and 90% quantiles of the distribution. Encountering the same quantiles of the wind distribution when in a migratory state increased the probability of transitioning to a stopover state by 76.92% from 0.13 to 0.23.

We found only weak evidence that the experience of the eagles affected the transition probabilities between states, either directly or as part of an interaction with wind. Similarly, we did not find evidence that these transition probabilities were affected by the proportion of human-altered habitat encountered at the end of each step, nor by the interaction of this proportion and the experience of the eagles (Table S1).

Migratory route decision-making

We used integrated step selection analysis (iSSA) to compare the conditions encountered by the eagles at every migratory step to the available conditions they could have encountered if they had used a different route that day. We found that the three age groups had contrasting responses to human-altered habitats, illustrating an experience-related difference. We compared the proportion of human-altered habitats at the end of the migratory steps (i.e., at the eagles daily roosting site) to the distribution of this proportion at the end of a random sample of available steps. We found that juvenile eagles were significantly drawn to human-altered habitats, choosing routes that end daily in a higher proportion of these habitats than would be expected from their distribution. By contrast, adult eagles significantly avoided these habitats, choosing less human-altered habitats than expected given their availability. Finally, sub-adults showed no significant selection for or avoidance of human-altered habitats (Figure 2; Table S2).

Experience-related differences were also apparent in the choice of flight direction and the choice of wind assistance. While all age groups tended to fly more directly toward their

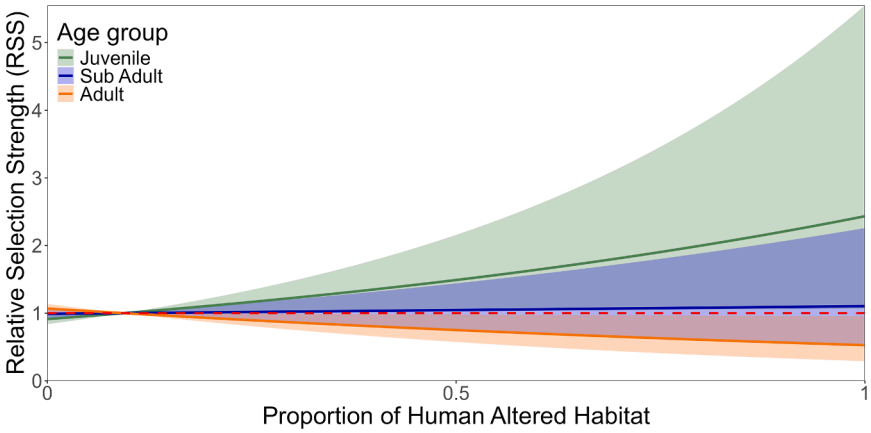

Figure 2. Experience-related selection of human-altered habitats

Selection by juvenile (green), sub-adult (blue), and adult (orange) Steppe Eagles for human-altered habitat, calculated as the proportions of human-altered habitat at a 0.25° × 0.25° square around the roosting site at the end of each migratory day. The *y* axis is the relative selection strength (RSS), compared with the mean of the variable plotted on the *x* axis. The dashed line represents an odds score of 1, i.e., no selection. Colored lines are the probability of use for each age group, and the shaded backgrounds are the 95% confidence intervals around these probabilities. Lines below the dashed line denote avoidance, and lines above the dashed line denote selection.

See also Table S2.

migratory destination (defined as the last location in the study area during the same year; see STAR Methods) compared with available trajectories, juvenile eagles chose more direct routes compared with the other age groups. Similarly, both sub-adult and adult eagles chose significantly stronger tailwinds than the available mean, and although this selection by juveniles was not significant, the trend of their selection was stronger than that of the other age groups (Figure 3; Table S2).

DISCUSSION

Animal migration can have major impacts on individual fitness and population dynamics through direct and carry-over effects.[2,27–29] Thus, understanding animal behavior during migration and the underlying factors that affect it is of great importance to animal ecology and conservation.[30,31] Here, we found internal-state, environmental, and anthropogenic effects on the decisions made by an endangered raptor during autumn migration, affecting both the species' stopover behavior and its migratory route. Although the impacts of each of these effects on animal movement have previously been considered independently, rarely have they been evaluated simultaneously. This approach allowed us to identify previously unreported effects on migrating birds' behavior. Most prominently, we show experience-related differences in the effects of human-altered habitats on the choice of migration routes.

The effect of anthropogenic habitat on migratory movements calls for special attention because of its potential implications in landscapes facing increasing human pressure.[32–34] Moreover, although there is abundant evidence for increased mortality of migrating birds due to anthropogenic factors, previous studies rarely addressed these effects on the behavior and movement of birds during migration.[35–37] The experience-mediated response of the Steppe Eagles to human-altered habitats, with young birds attracted to these sites but avoiding them as they age, provides important insights into how experience modulates wildlife response to human impacts on the landscape. In this case, these different responses can be explained by the contrasting implications of human-altered habitats for the fitness of birds. Steppe Eagles exhibit a diverse diet, shifting between active hunting and scavenging, often taking advantage of anthropogenic food sources such as dumpsites.[38–40] This allows the eagles to take advantage of the increased food availability landfills and agricultural areas supply compared with the surrounding environment.[11] However, these habitats also enhance human-induced risks such as persecution, poisoning, and electrocution.[2,41–43] All things considered, juvenile eagles appear willing to bear the cost of the added risk, perhaps because they require the added energetic input due to their lower foraging and flying efficiencies. By contrast, because they are more efficient foragers and fliers, for adults this trade-off has less value, and they appear more likely to avoid the risks these habitats induce.[11,44]

Beyond the immediate energetic benefits and increased risk, our results also demonstrate how response to human-altered habitats changes route selection of migrating eagles. Our findings correspond with previous studies that have shown both avoidance and attraction of migrating birds to different anthropogenic changes of the natural habitat, such as noise pollution, light pollution, and infrastructure development.[8,45] Changes in the behavior of migratory species in response to anthropogenic food subsidies and specifically landfills have been shown for different species, mainly presenting changes during winter.[46–51] At the same time, there are fewer studies showing the effects of anthropogenic food subsidies on migratory phenology and route choice. A recent study showed that the routes of juvenile white storks (*Ciconia ciconia*) were affected by their use of landfills.[11] Additionally, it has been suggested that Steppe Eagles have dramatically changed their migration route following an increase in anthropogenic food subsidies, with many staying in Asia instead of wintering in Africa.[38,52,53] Our work demonstrates an important role for experience-dependent changes underpinning these behaviors, suggesting age-dependent attraction to and avoidance of human-altered habitats, possibly affecting important migratory properties.

Considering environmental, internal-state, and anthropogenic factors together allowed us to deepen our understanding of drivers of migratory behavior. Past studies often tested a single variable, producing important but limited understanding of complex migratory behaviors. For example, tailwind was shown to affect flight speed and migratory progress,[54,55] and birds were found to be less efficient during their first migration compared with later migrations.[56] Studies that tested the effects of more than one variable further improved our understanding of bird migration. For example, the strength of the effects of wind on

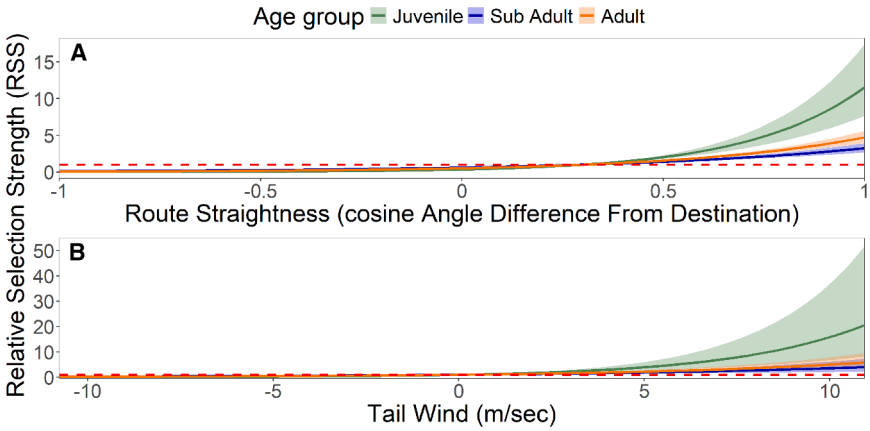

Figure 3. Experience-related choice of flight direction and tailwind

Differences between juvenile (green), sub-adult (blue), and adult (orange) Steppe Eagles in (A) their divergence from the direct route leading to their destination at the end of the study period, calculated as the cosine of the difference between the azimuth of flight and the azimuth required to fly directly to the destination. Larger values denote more direct flights. (B) Their choice of tailwind, negative tailwind being headwinds. The *y* axis is the relative selection strength (RSS), compared with the mean of the variable plotted on the *x* axis. The dashed line represents an odds score of 1, i.e., no selection. Colored lines are the probability of use for each age group, and the shaded backgrounds are the 95% confidence intervals around these probabilities. Lines below the dashed line denote avoidance, and lines above the dashed line denote selection. To ensure easy interpretation of the figure, the *x* axis in (B) presents common tailwind speeds and not the full scale of the variable in the data. See also Table S2.

migratory progress was shown to be age dependent.[14,16,57,58] By incorporating the effects of wind, age, and human-altered habitats in a framework that evaluates the decision-making of the birds, we were able to further understand the complexity of bird migration.

Considering only wind and age, we show that juvenile eagles fly more directly toward their destination and choose routes with stronger tailwinds than experienced eagles. These findings seem at first counterintuitive,[15,16,44,58] as they suggest that inexperienced eagles might be more efficient than experienced eagles. However, by testing the effects of human-altered habitats and how they change with age, we were able to provide a possible explanation. A more direct route with stronger tailwinds possibly requires flying over areas with increased risk, as evident from the finding that these inexperienced eagles were more likely to use human-altered habitats. Thus, choosing more direct routes might be a result of less developed navigational skills and lack of previous knowledge about risky areas, resulting in the young eagles making fewer detours around dangerous anthropogenic sites.[59,60]

This explanation means that the avoidance of human-altered habitats does not stem from a learning process of the risk these habitats induce. Instead, we assume that young eagles perceive these habitats as risky, possibly due to anthropogenic disturbances encountered in these areas,[8] but still select them over less-risky habitats because of the benefits they offer, such as high food abundance. Thus, the difference in the selection of human-altered habitats between the different age groups may stem from a change in the selection of an optimum for the trade-off between food availability and anthropogenic risks. This change probably results from the improvement of different skills with gained experience and age,[14,15,44] allowing experienced birds to more easily forage at non-anthropogenic food sources. Additionally, while the eagles probably aimed to conserve energy during stopovers, as suggested by the finding that they moved more with stronger tailwinds, we also found that during these periods adult eagles moved more than the other age groups. This may present another cost of choosing natural over anthropogenic habitats, as natural food sources are less spatiotemporally predictable, and thus their use requires movement over larger areas. We suggest that the choice of less straight routes and weaker tailwinds made by more experienced eagles may result from a shift in migration optimization considerations, made possible by improvement of their migratory skills. Thus, first-time migrants prioritize time or energy minimization over risk avoidance, while more experienced migrants prioritize risk avoidance at the cost of energy or time.[13,61,62]

Notably, wind had a strong effect on the probability that the eagles would transition between behavioral states. We found that stronger wind blowing to the north, against the general direction of migration, during the first hours of the day increased the probability of initiating a stopover and decreased the probability of initiating a migratory flight. This implies that, as predicted, strong headwinds hinder migration.[4,6,22,63] Interestingly, this finding seems to contradict the findings reported by Thorup et al., which found no significant effect of headwinds on the decision to initiate a stopover in another soaring raptor, the osprey *Pandion haliaetus*.[64] However, they did not specifically address the decision to stop but instead compared the wind conditions between migratory and stopover days. Using HMM and focusing on wind in the early part of the day allowed us to more precisely test the migration-stopover transition and to gain further insights about the function of stopover for the eagles.[21,25]

To conclude, our findings present multifaceted insights regarding migratory behavior, stopover behavior, and the transition between the two, enabled by using a combination of data sources and statistical methods. Specifically, we highlight important insights regarding stopover ecology and function, enabled using HMM; those regarding route choice, achieved using iSSA; and the use of remote sensing and landscape features alongside tracking data in the study of bird migration.[12,21,22,65–68] Our study fills important knowledge gaps regarding the decision-making process of migrating birds.[2,19,29,33] Specifically, we focus on the joint effects of experience, anthropogenic threats, and environmental conditions on the route choice and migratory behavior of a large, soaring raptor. Importantly, experience-related differences in attraction to or avoidance of anthropogenic habitats have rarely been studied in the context of bird migration.

Further understanding of the use of human-altered habitats by Steppe Eagles and other species alongside studies of migration flyways over wide spatiotemporal scales can further improve our understanding of the evolutionary ecology of bird migration.[69,70] This improved understanding can substantially contribute to the conservation of migratory species and entire migration systems.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Ron Efrat (ronefrat3@gmail.com).

Materials availability

This study did not generate new, unique reagents.

Data and code availability

Data and original codes have been deposited at Zenodo and Movebank Data Repository and are publicly available.[71,72] Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

ACKNOWLEDGMENTS

We thank the Israeli Wildlife Hospital for their important work for wildlife and specifically for the rehabilitation of Steppe Eagles, including those tagged for this study. We also thank Yossi Leshem for his support of this project and Jon Morant, two anonymous reviewers, and the editors for comments that improved the manuscript. We dedicate this paper to the memory of our co-author Evgeny Bragin, who made a massive contribution to the study and conservation of raptors in Central Asia. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. Steppe Eagle tagging was funded by the University of Haifa and a private donor.

AUTHOR CONTRIBUTIONS

R.E.: writing – review & editing, writing – original draft, resources, formal analysis, data curation, and conceptualization; Y.L.: writing – review & editing, resources, and conceptualization; A.B.: writing – review & editing and resources; E.B.: resources; T.A.: writing – review & editing and conceptualization; T.K.: writing – review & editing, resources, funding acquisition, and conceptualization; N.S.: writing – review & editing, funding acquisition, and conceptualization.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS
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- QUANTIFICATION AND STATISTICAL ANALYSIS
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.07.061.

Received: February 18, 2025
Revised: June 16, 2025
Accepted: July 24, 2025
Published: August 21, 2025

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Code to complete all statistical analyses	This study	https://doi.org/10.5281/zenodo.15973935
GPS data	This study	https://doi.org/10.5441/001/1.695
Experimental models: Organisms/strains		
Steppe Eagle (*Aquila nipalensis*, n = 21, 2018-2019)	Kazakhstan	N/A
Steppe Eagle (*Aquila nipalensis*, n = 3, 2020-2021)	Israel	N/A
Software and algorithms		
R Software version 4.4.3	R Software version 4.1.2	N/A

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We tagged Steppe Eagles with GPS-GSM solar-powered transmitters, 21 as nestlings in northwest Kazakhstan and three as free-flying birds before their release in winter or spring in southern Israel following rehabilitation at the Israeli Wildlife Hospital. Steppe Eagles in Kazakhstan were trapped and tagged as part of the work done by authorized governmental employees. Steppe Eagles were tagged in Israel under permits 2020/002495 and 2021/002495.

METHOD DETAILS

Movement data

We tagged eagles with Ornitrack-30 GPS transmitters (Ornitela, Lithuania) that weighed 30 g, less than 2% of the body mass of a full-grown eagle.[73] Transmitters were attached with Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA) using a backpack harness configuration for nestlings and a leg-loop harness configuration for rehabilitated birds.[74] GPS locations were obtained every 5-80 minutes, depending on battery voltage. We identified errors in GPS locations caused by jamming of GPS signals[75] by plotting the routes on a map and identifying locations strongly diverging from the routes of the eagles. We then removed from our data locations that we identified as jammed locations.[75] Overall, we used data from 20 eagles: 18 that were tagged as nestlings and two that were tagged as adults. The four birds not considered included one nestling that wintered north of the study area, and two nestlings and one rehabilitated bird stopped sending data before migrating south through the study area.

Study area and season

To minimize the effects of factors beyond the scope of our interest, we only used data obtained in an area of the Middle East characterized by similar geographical features, with no major mountain-ridges or large waterbodies. In the north, the border was defined by the Kopet Dag and Caucasus mountain-ridges and the Caspian and Black seas. Preliminary data exploration suggested that the passage of these mountain ranges led to frequent stopovers and behavioral changes which we did not observe in our study area. In the south, the border was defined by the Red Sea and the Sarawat Mountains in Saudi Arabia, at latitude 18° (Figure 1). The majority of this area is characterized by similar elevations, climate zones, biomes, and human population densities.[76]

Similarly, to control for variation beyond the scope of our research interest, such as motivation and weather differences, we only included data acquired during autumn migration,[77,78] prior to 31 December. Because all eagles spent the summer north of the study area, we defined autumn migration as any movement that started north of the study area and entered the study area. Importantly, while some eagles continued their autumn migration outside the area of interest, some stayed in that area throughout winter.

QUANTIFICATION AND STATISTICAL ANALYSIS

Used data

All data handling, including preparation for statistical analyses, running models and plotting figures was done using R software.[79,80] We describe model estimates as significant if their 95% confidence intervals do not overlap with zero.

To answer our study questions, we used GPS data on a daily scale, i.e., movement between consecutive roost locations. We identified roost locations by finding the locations in which the eagles spent the night, assuming that they did not move after dark. We defined night as the time after dusk and before dawn and identified the roost site as the location acquired closest to midnight, between dusk and dawn. We calculated daily displacement (step length, in km) as the beeline distance between consecutive roost sites and turning angle as the angle between consecutive daily steps (in radians).

To model the effects of experience, we divided the tracked eagles into three groups: juveniles migrating for the first time, subadults migrating for the second and third times, and adults migrating for the fourth time or later.[14,15,39] To ensure that the differences we found between the three age groups were caused by experience rather than by variation in the time each age group spent in the study area (which could influence food availability or climatic conditions), we compared the date range in which each age group was present in that area.

We downloaded the U and V wind vectors at 900 hPa and a 0.25° spatial resolution from the ERA5 hourly database[23] hosted at Copernicus Data Climate Store using the R package ecmwfr.[81] We then annotated each GPS location acquired between dawn and dusk with the wind data closest to the location and the time at which it was acquired. Finally, we calculated tailwind speed by finding the speed of the wind vector parallel to the direction of flight between consecutive locations.

We downloaded land cover data from the European Space Agency (ESA) WorldCover 10 m 2020 product, which provides land-cover information at 10 m resolution, derived from satellite imaging.[24] This landscape dataset consists of 11 land cover classifications, nine of which are natural habitats that include different types and levels of vegetation cover and water sources and the other two are anthropogenic, specifically built-up areas and croplands. We calculated the proportion of the 10 m cells that included these two human-altered habitats for every 0.25° by 0.25° square, thus matching the spatial resolution of these land cover data with that of the wind data (Figure S2).

Analytical approach

We aimed to understand the decisions made by the eagles throughout all the stages of their migration through the study area. Specifically, we were interested in the decisions made during stopovers and migratory flights and the shift between these two behavioral states. We assumed that these were affected differently by environmental, internal-state and anthropogenic factors. To that end, we employed two statistical models, Hidden Markov Models (HMM)[25] and integrated Step Selection Analysis (iSSA),[26] using the same metrics: the distributions of daily step lengths and turning angles. First, using HMM we differentiated between local (stopover) and migratory behavioral states and tested what factors shape the daily movement patterns in each of these states. Second, using the same model, we tested the probability of transition between the two behavioral states, and the factors that affected it. Finally, using iSSA we tested the choice of route during the migratory behavioral state. Importantly, considering daily steps as those that occurred between roost sites allowed us to maintain the assumptions of these models because the lack of movement at night meant we could treat the steps as equally spaced in time, with 24 hours between the start and end of each step.

We ran HMM using the hmmTMB package in R[82] to estimate the probability that each day was in either a migratory or a stopover behavioral state. We expected that the two behavioral states would differ in step length and turn angle, assuming a longer step length and smaller turn angle for the migratory behavioral state compared to the stopover behavioral state. We also expected that there would be a non-random probability that the eagle would stay in the same state on consecutive days (i.e., that state transitions are Markovian). We set the initial model parameters (i.e., step length and turn angle) using the suggest_initial function in the hmmTMB R package. We then estimated the mean step lengths and turning angles in each behavioral state and the probability of transition between the states (see Figure S1 for step length and turn angle distributions).

We predicted that the step lengths during both states would increase in favorable wind conditions and with experience of the eagles.[15] We evaluated these effects by including daily tailwind and the age of the eagles as predictors for step length. For the probability of transition between the two states we made the following predictions. First, we predicted that the probability of transition from stopover to migratory behavioral states will increase with favorable winds encountered early during the day, when the eagles make the decision to initiate a migratory flight (Figure S3), and that the probability of transition from a migratory state to a stopover state will increase with unfavorable winds during the same time. Second, we predicted that more experienced eagles would tend to switch less often between behavioral states, as inexperienced birds are expected to interrupt their migration more than experienced birds.[21] Third, we predicted that the effects of wind would differ according to the experience of the eagles. To evaluate these predictions, we included the following covariates for explaining the different transition probabilities: the mean wind V vector (positive values being wind blowing south to north, opposite the general migratory direction) during the first five hours after dawn (Figure S3), the age of the eagles, and the interaction of age and the wind V vector. We also predicted that unfavorable habitats encountered at the end of the step would increase the probability of transition between migratory flights and stopovers, and that the effects of the encountered habitat would differ according to the experience of the eagles. To evaluate these effects, we included the following covariates explaining the probability of transition between migratory flights and stopovers: the proportion of human altered habitat encountered at the end of the step and the interaction between this proportion and the age of the eagles. Finally, for both the estimation of step length and that of the probabilities of transitions between the two states, we included a random intercept for individuals, to account for between-individual differences. All continuous covariates in the HMM were scaled by dividing the values by the root mean square.

An iSSA allowed us to better understand the decision-making of the tracked eagles by comparing their movements to other possible movements in the study area. Because we only used migratory days (as defined by the HMM) in this analysis, our data was divided into short segments consisting of a few consecutive days of migration. These segments were too short to model separately using iSSA. Therefore, we joined the data from all eagles and modeled them together using the amt package in R.[83]Using the amt package allowed us to treat every segment separately, avoiding the inclusion of false steps connecting between segments. In the model, we compared each daily movement to 100 available steps. We created these available steps by finding the location an eagle would have reached if it was starting from the same onset location of the real step and moving in a direction and distance taken

randomly from given distributions. We used the distributions of step lengths and turning angles of the real steps, applying a gamma distribution and a von Mises distribution,[26,83] respectively. We assumed that eagles will not land in large water bodies,[52] and that once they crossed the mountain ridges defining the northern border of the study area, they will not cross them again northwards in their southbound autumn migration. Thus, to create our 100 available steps, we first created 1000 random steps for each real step, then removed the steps that ended in water or north of the study area and randomly chose 100 available steps for each real step from those that remained. We then calculated the value of all explanatory variables used in the iSSF for all real and available steps.

We predicted that the measured daily movements made by the eagles will differ from the simulated (available) steps with respect to several variables. First, we expected that the eagles would choose to fly towards their destination, which we defined as the last location of each individual in the study area in each tracking year. This meant that the destination was almost identical for the eagles that left the study area during the tracking year, as they all used the same route. For the eagles that did not leave the study area during a tracking year, we defined the destination at their wintering site. We evaluated this by including the (cosine-transformed) angular deviation between the azimuth of each step and the azimuth to the destination in the model. We also included the interaction between this predictor and the age of the bird (a proxy for experience, see *Used data* for details) because we expected that experienced eagles would fly more directly toward the destination.[14] Third, we included in the model the interaction between tailwind and eagle age, as we expected that eagles will choose favorable tailwinds and that this choice will differ between experienced and inexperienced eagles.[14,68] We also included the interaction of tailwind and step length and of tailwind and log step length to account for the expected positive effect of tailwind on the distribution of step lengths.[55,67] Finally, we evaluated whether the eagles moved toward or away from human-altered habitats, expecting that experienced eagles would choose different feeding sources compared with inexperienced eagles.[38,40] To this end, we included in the model the interaction of eagle experience with the proportion of human-altered habitat at the $0.25^{\circ}\times0.25^{\circ}$ square surrounding the step's endpoint (the roost). To allow inference of the iSSF model, we plotted the relative selection strength (RSS) of variables of interest compared with their means.[84]