# Current Biology

# Early and accumulated experience shape migration and flight in Egyptian vultures

## Highlights

- Captive-bred and wild Egyptian vultures' behavior was compared during migration

- Early-life and acquired experiences impacted migratory and flight proficiencies

- Acquired experience helped offset early-life disadvantages

- This can be attributed to possible effects of sensitive periods of learning

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## In brief

Efrat et al. show that early-life and acquired experiences shape migration ontogeny and flight proficiencies. They show that captive-bred Egyptian vultures improve with practice, offsetting initial disadvantages, whereas wild vultures improve at a slower rate.

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**Report**

# Early and accumulated experience shape migration and flight in Egyptian vultures

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## SUMMARY

Two types of experience affect animals' behavioral proficiencies and, accordingly, their fitness: early-life experience, an animal's environment during its early development, and acquired experience, the repeated practice of a specific task.[1–8] Yet, how these two experience types and their interactions affect different proficiencies is still an open question. Here, we study the interactions between these two types of experience during migration, a critical and challenging period.[9,10] We do so by comparing migratory proficiencies between birds with different early-life experiences and explain these differences by testing fine-scale flight mechanisms. We used data collected by GPS transmitters during 127 autumn migrations of 65 individuals to study the flight proficiencies of two groups of Egyptian vultures (*Neophron percnopterus*), a long-distance, soaring raptor.[11,12] The two groups differed greatly in their early-life experience, one group being captive bred and the other wild hatched.[13] Both groups improved their migratory performance with acquired experience, exhibiting shorter migration times, longer daily progress, and improved flight skills, specifically more efficient soaring-gliding behavior. The observed improvements were mostly apparent for captive-bred vultures, which were the least efficient during their first migration but were able to catch up in their migratory performance already in the second migration. Thus, we show how the strong negative effects of early-life experience were offset by acquired experience. Our findings uncover how the interaction between early-life and acquired experiences may shape animals' proficiencies and shed new light on the ontogeny of animal migration, suggesting possible effects of sensitive periods of learning on the acquisition of migratory skills.

## RESULTS

### Complete migration routes, daily progress, and energy expenditure

To test for effects of early-life and acquired experience on the migratory proficiencies of Egyptian vultures, we first compared the behavior of captive and wild vultures during complete migratory journeys and over individual migration days. The early-life experience of the two groups differed in rearing experience and in their age and flight experience at the time of their first migration: wild vultures migrated at the age of 3–5 months, 2–5 weeks after their first flight, whereas captive vultures were released to the wild at the age of 6–18 months, 4–8 months before their first migration.[13,14] Egyptian vultures used similar routes during autumn migration, regardless of their early-life experience (captive or wild upbringing). Moreover, neither early-life nor acquired experience (number of previous migrations) significantly affected migration onset, with a Julian date mean ± SD of 254 ± 22.7 (generalized linear mixed effects model

[GLMM], p > 0.14 for each experience type and for their interaction, Table S1), or the vultures' total travel distance, with 1,964 ± 350 km between the vultures' first and last location (linear mixed effects model [LMM], p > 0.22 for experience-related variables, Figure 1A; Table S1). Importantly though, we found a significant effect of both experience types and their interaction on the number of days it took vultures to complete an entire migration route (GLMM, p < 0.05 for experience-related variables, Table S1). Model results show that captive-reared vultures' first migration lasted significantly longer than later migrations, 5.9 and 6.8 days more than during their second and third migrations, respectively. Additionally, captive vultures during their first migration migrated 4.1, 5.4, and 6.2 days more than wild vultures during their first, second, and third migrations, respectively (Tukey-adjusted p < 0.05 for all significant comparisons, Figure 1B; Table S1). No difference in migration time was found between wild vultures' different migrations nor between captive and wild vultures after their first migration, meaning that captive vultures were able to close the performance gap between them and the
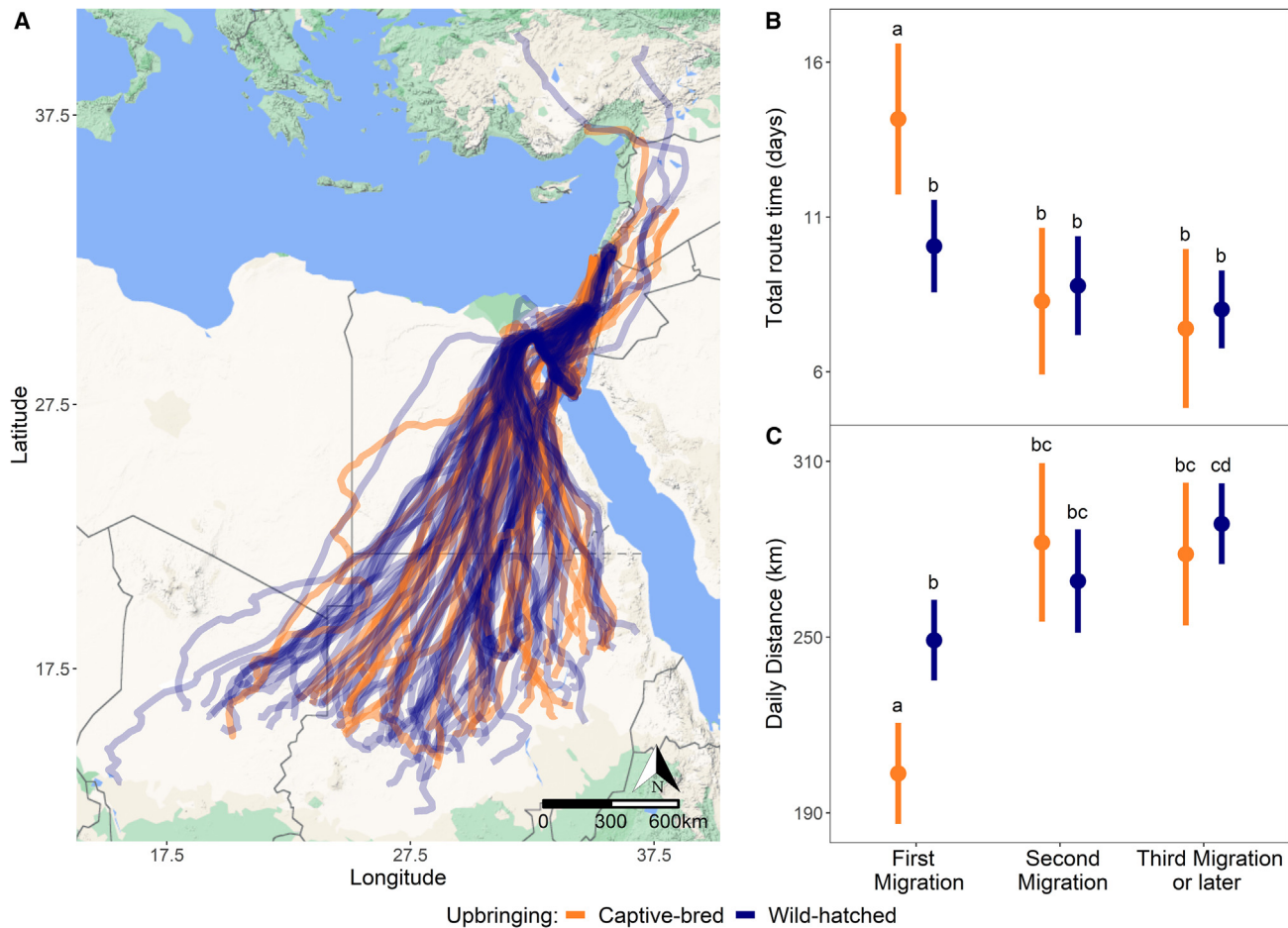
**Figure 1. Complete migration routes and daily progress**

Although captive-bred and wild-hatched Egyptian vultures migrated using the same routes toward the same destination (A), captive-bred vultures during their first migration took longer to reach their destination (B) and progressed less each day (C). These differences disappeared during the second migration, with captive-bred vultures showing faster improvement than wild vultures (B and C). Routes in (A) are semi-transparent to allow the visualization of multiple routes. Dots and lines in (B) and (C) represent model results for mean and 95% confidence intervals. Lowercase letters represent groups with statistically significant differences within each subplot (for example, in subplot C, the groups marked with bc are significantly different from the group marked with a but are not significantly different from each other or from groups marked with b or cd).

See also Tables S1, S3, and S4 and Figure 3.

wild vultures (Tukey-adjusted p > 0.25 for all non-significant comparisons).

Considering daily progress (beeline) during migration, we found an effect of both experience types and their interaction (LMM: p < 0.002 for experience-related variables, Table S1). Model results show that captive-reared vultures during their first migration progressed significantly fewer kilometers toward their migratory destination daily compared with all other groups: 79 and 75 km less than captive vultures during their second and third migrations, respectively, and 46, 66, and 86 km less than wild vultures during their first, second, and third migrations, respectively (Tukey-adjusted p < 0.001, Figure 1C; Table S1). As with total migration time, this shows that captive vultures were able to close the performance gap already during second migration. Additionally, wild-bred vultures progressed significantly less each day (40 km) during their first migration than during their third migration or later (Tukey-adjusted p = 0.0001; no other pairs of groups differed significantly (p > 0.25). In contrast

to daily progress, we did not find a significant effect of either experience type on the overall daily body acceleration (ODBA), a proxy for movement-related energy expenditure. Furthermore, no effect of either experience types was found on hourly probability of flapping, which is the main source of energy expenditure during flight for soaring birds[15,16] (GLMM: p > 0.3 for experience-related variables in both ODBA and flapping, Table S1).

**High-resolution flight behavior**

To understand the mechanisms leading to the differences in migratory behavior presented above, we compared the vultures' soaring and gliding proficiencies, using high-resolution (1 Hz) GPS data (Figure 2A). Examining soaring periods, we did not find a significant effect of either experience type on vertical speed or altitude gain (LMM and GLMM, respectively, p > 0.5 for experience-related variables, Table S2). We did find a significant effect of both early-life and acquired experience on the maximum altitude reached during soaring sessions but no significant effect of their interaction (LMM,
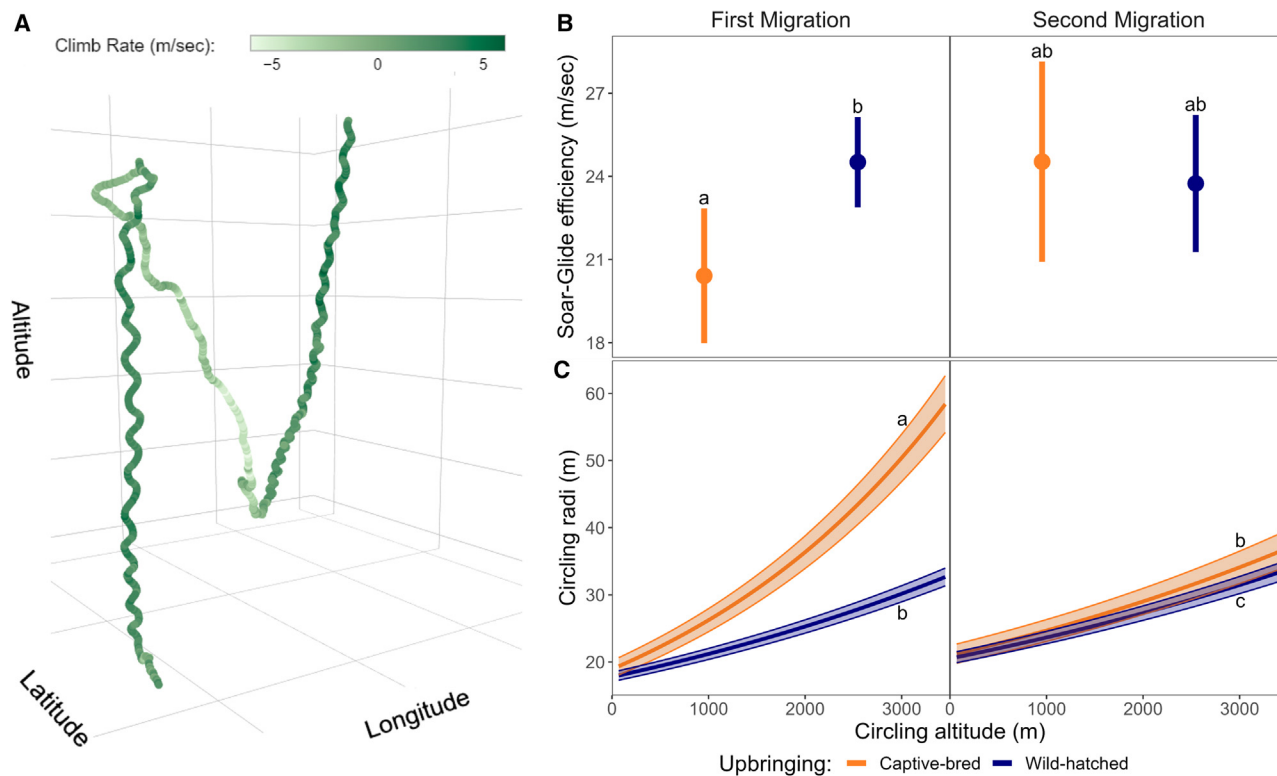
**Figure 2. High-resolution flight behavior**
During soaring-gliding periods (A), captive-bred vultures in their first migration were less efficient, gaining less progress while gliding for each second spent gaining altitude in the preceding soaring event (B). Captive-bred vultures also increased their circling radii faster with increasing altitude in both their first and second migrations (C). Dots in (B) and bold lines in (C) represent model results for mean, and lines in (B) and shaded areas in (C) represent 95% confidence intervals. Lowercase letters represent groups with significant differences within each subplot (for example, in subplot B, the group marked with a is significantly different from the group marked with b but is not significantly different from groups marked with ab).
See also Tables S2 and S4.

p = 0.027, 0.011, and 0.066, respectively, Table S2). Raw data show that soaring peaked at 1,061 ± 414 and 1,175 ± 479 m above ground level for captive vultures and at 1,207 ± 550 and 1,387 ± 614 for wild vultures, during their first and second migrations, respectively. We then tested for soaring-gilding efficiency by calculating the time spent in each soaring event in relation to the distance gained in the following gliding event[17] and found significant effects of both experience types and their interaction (GLMM, p < 0.038 for experience-related variables, Table S2). Captive-reared vultures during their first migration were less effective in soaring-gliding than all other groups. Model estimates suggest that, for every second of soaring, their forward movement while gliding was 4.1, 4.1, and 3.3 m less than that of wild-hatched vultures during their first migration and captive-bred and wild-hatched vultures during their second migration, respectively. Yet, only the difference between first time migrants was significant (Tukey-adjusted p = 0.042, 0.153, and 0.25, respectively, Figure 2B; Table S2). Finally, we found that circling radii, which affects soaring efficiency, increased with increasing altitude at a different rate depending on the two types of experience and their interaction (GLMM, p < 0.001 for the interaction of both experience types and altitude, Table S2), increasing fastest for captive vultures during their first migration and slowest for wild vultures during their second migration, with significant differences among all groups

except for captive vultures during their second migration and wild vultures during their first migration (Tukey-adjusted p < 0.05 for all significant comparisons, Figure 2C; Table S2).

**Associations between mortality and migratory proficiencies**
To ascertain that our results, indeed, represent the effects of gained migratory experience and are not affected by the mortality of less proficient individuals, we reran the models predicting the number of days it took vultures to complete an entire migration route and their daily progress, including only vultures for which we had data during their first three migrations (i.e., vultures that survived at least three migratory journeys). For both models, we found the same between-groups significant differences as in the original models. Moreover, we did not find any evidence suggesting that vultures that survived their first three migrations performed better than those that did not survive this period or parts of it, although conclusions are limited due to the small sample size and large confidence intervals (Figure 3; Table S3).

**DISCUSSION**

In this study, we examined the effects of early-life experience and acquired experience on migratory and flight proficiencies.
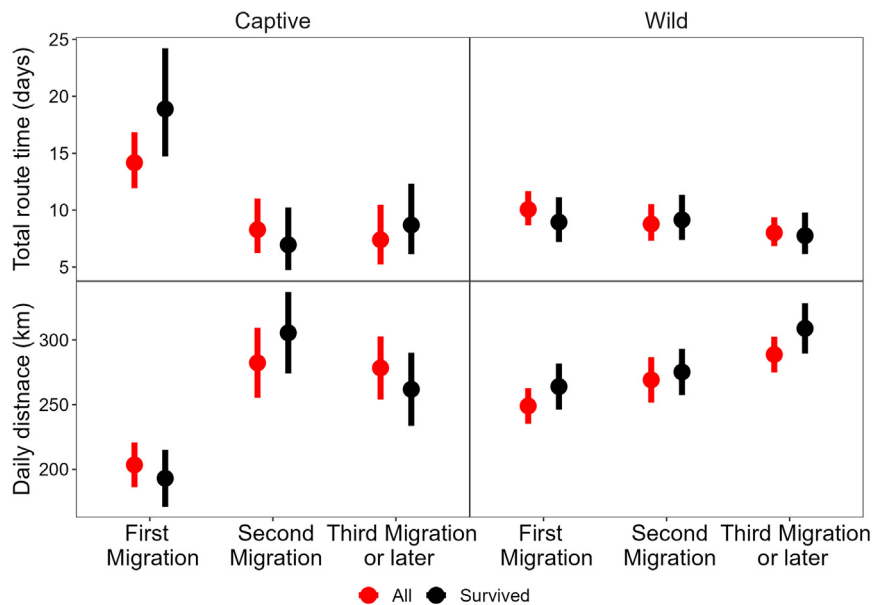
**Figure 3. Tested mortality effects**
Comparisons of migration time (top) and of daily migration distance (bottom) between models including all vultures (red) and those including only vultures with data during their first three migratory journeys. Dots and lines represent model results for mean and 95% confidence intervals.
See also Tables S3 and S4.

Overall, we found strong effects of early-life experience on these proficiencies, whereas effects of acquired experience were mainly apparent for birds that were negatively affected by early-life experience. This means that acquired experience allowed the captive-bred Egyptian vultures to close the gap in migratory proficiencies created by their early-life experience, leading to similar performance already during second migration. More specifically, we show that despite similar migration routes and distances, captive-bred Egyptian vultures during their first migration took longer to complete their autumn migration and traveled less each day compared with captive vultures during later migrations or wild vultures during all migrations. We also show a stronger improvement with acquired experience for captive vultures compared with wild vultures in daily distances traveled, soaring-gliding efficiency, and circling radii, whereas soaring altitude was only affected by early-life experience. Finally, and somewhat surprisingly, we did not observe an effect of either of the two experience types on movement-related energy expenditure or the probability of using flapping flight.

Because we found major effects of early-life experience, it is important to describe the differences between the studied groups and their possible consequences in detail. The two groups had three main differences in early-life experience: captive-bred vultures were reared in captivity, their delayed release (released in spring or winter) meant they had months instead of weeks before their first migration, and they made their first flight out of the cage at least 3 months older than their wild conspecifics.[13,14] Our finding that early-life experience had negative effects on captive-bred vultures conforms with previous research that showed inferior behaviors and fitness of reintroduced captive-bred animals, compared with wild animals.[18,19] Yet, considering the captive vultures' prolonged periods in the wild prior to their first migration, our findings of inferior flight skills during that migration are surprising because the birds had more time to practice flight. One possible explanation for this discrepancy is that prolonged flight experience did not significantly contribute to the vultures' flight skills during

migration.[14] A comparison of the period between first flight and first migration of these captive and wild vultures was thoroughly discussed by Hertel et al.[14] This paper showed a strong influence of the time available before first migration on the ontogeny of movement behavior but no effect on the vultures' flight performance immediately prior to first migration.[14] Exploratory analyses of the same dataset did not uncover any effects of individuals' pre-migration flight experience on their migratory behavior (unpublished data). This implies that migratory flight proficiencies are different from those required during other periods of the annual cycle, in which birds fly much shorter daily distances and usually in more familiar environments. Alternatively, it is possible that being reared in captivity had strong negative consequences for the development of the birds' flight skills, masking the positive effects of practice.[20,21] One such factor could be related to the older age at which the captive vultures flew for the first time, which might have affected their ability to best acquire flight skills because they missed a sensitive period of learning.[22,23]

Sensitive periods of learning are periods in which the effects of experience are unusually strong, leading to a change in behavior.[23] Sensitive periods have been studied extensively in humans and model animals, and to a lesser extent in wild animals. Yet, to the best of our knowledge, they have not been studied in the context of migratory behavior.[22,23] Although some sensitive periods are termed "critical" for their irreversible effects on the learned behavior, other periods are not final, and the learning of some behaviors can be achieved outside these periods.[23] However, learning at an older age (i.e., outside a sensitive period) can be slower and less efficient.[20,24,25] Wild Egyptian vultures start their first migration a few weeks after their first flight, forcing them to acquire flight skills in a short period.[14] This means that if a sensitive period for learning migratory-related flight skills exists for Egyptian vultures, it most likely occurs during the first weeks of their life. We thus suggest that our results, showing a negative effect of early-life experience that is compensated by acquired experience, stem from the late start of the learning process in captive-reared Egyptian vultures, forcing their learning to occur outside a sensitive period.

Our study examined differences in behavior during consecutive migratory journeys, starting from the vultures' first migration, and thus sheds new light into the ontogeny of animal migration, a research field that was recently described as having major knowledge gaps.[26] Moreover, migration provides a unique opportunity to separate early-life (pre-first migration) and acquired (during

migrations) experiences and thus presents a key period to study their interaction and its effects on animal proficiencies. Our findings regarding the lack or minimal effect of acquired experience on wild birds' total migration time and daily distance are surprising, contradicting previous studies in other species.[2,27–30] Specifically, steep improvements in these migratory properties were found for two species of soaring long-distance migrants, Black kites (*Milvus migrans*) and White storks (*Ciconia ciconia*).[27,28] White storks also showed reduced energy-expenditure-related proxy and flapping flight with gained experience,[28] an effect we did not find in Egyptian vultures. This last contradiction may be explained by differences in social structure: unlike Egyptian vultures that migrate individually, White storks might expend more energy attempting to "keep up" with their flock.[28,31] Another study that showed somewhat contradicting results to our findings tested the effects of acquired experience on soaring-gliding behavior of Griffon vultures (*Gyps fulvus*).[17] Interestingly, inexperienced Griffon vultures were found to have smaller circling radii and lower vertical speeds while soaring compared with adults, whereas we found opposite effects on circling radii and no differences in vertical speed.[17] These might stem from the differences in species morphology, Griffon vultures being much larger, and from the different seasons and flight motivations in which the vultures' flights were studied because the Griffon vultures were not studied during migration.[17,32,33]

Aside from the abovementioned study of Griffon vultures, very few studies measured high-resolution flight proficiencies, and, to the best of our knowledge, no previous study tested the effects of experience on soaring-gliding performance during migration. Studies that have measured or modeled circling radius showed an expected increase with altitude due to the weaker thermal strength at these altitudes which requires a shallower bank angle, allowing a larger wing surface to be pushed by the rising air.[34,35] However, increasing the radius also means flying further from the thermal center, where uplift is strongest, eventually reaching a position where the uplift is no longer strong enough to push the bird up.[17,34,35] We found a faster increase in circling radii with increasing altitudes for captive-bred vultures and for less experienced vultures. The different between-groups effect of altitude on circling efficiency alongside the lower soaring peak altitude we found for captive-bred vultures mean that the different experience types mainly affected the vultures when flying conditions were less ideal (i.e., at higher altitudes). Importantly, both experience types influenced soaring-gliding efficiency, providing an explanation for the differences found in the larger scale migratory proficiencies: migratory time and daily distance.

To conclude, our study presents an example of how the interaction between early-life experience and acquired experience can shape the development of animal behavior. Specifically, we found that this interaction shaped Egyptian vultures' migratory behavior by affecting the flight proficiencies of a migrating animal. We show that the negative effects of early-life experience, as found for captive-reared vultures, can be offset by acquired experience after a relatively short period, with captive and wild birds behaving similarly already during their second migration. The fact that we did not find a correlation between survival and less efficient migratory or flight behaviors contradicts findings from previous studies.[2,27,28] Yet, it is in agreement with the weak effects we found for acquired experience on wild birds and also with the

lack of difference in survival between captive and wild Egyptian vultures found in previous studies.[12,13] Importantly, sub-optimal behavior at one stage of an animal's life, and specifically during migration, might have effects other than short-term survival.[36–38] We therefore suggest that future research will study the effects of early-life and acquired experience and their interaction on other behaviors, such as foraging and breeding. Finally, our study is one of a few that compared post-release captive and wild conspecific behavior, presenting captive breeding effects, which should be studied more thoroughly and likely require further consideration in conservation interventions.[19,39,40]

## STAR★METHODS

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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.10054543 |
| GPS data | This study | https://doi.org/10.5441/001/1.298 |
| **Experimental models: Organisms/strains** | | |
| Egyptian vulture (*Neophron percnopterus*, n = 65, 2013–2022) | Israel | N/A |
| **Software and algorithms** | | |
| R Software version 4.1.2 | https://www.r-project.org/ | N/A |

## RESOURCE availabilitY

### Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Ron Efrat (ronef@post.bgu.ac.il).

### Materials availability
This study did not generate new unique reagents.

### Data and code availability
Data received have been deposited at Movebank Data Respiratory and is publicly available.[41] All original code has been deposited at Zenodo and is publicly available.[42] DOIs are listed in the key resources table. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

## EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

### Deployment of GPS devices
We used solar powered satellite tracking devices (hereafter "tags") to collect GPS and tri-axial acceleration data. Tags weighed < 2.5% of the vultures' body mass[43] and were attached to Egyptian vultures using a backpack (one captive-bred vulture) or leg-loop (all other vultures) harness configuration.[44] Between 2013 and 2022 we tracked captive-bred and wild Egyptian vultures that were all tagged in Israel (see Efrat et al.[13] for details regarding captive-breeding). All but one captive-bred vultures were tagged before their release to the wild and most wild-hatched vultures were tagged as chicks before their first flight. Other vultures were caught and tagged as freely flying birds, during their second calendar year or later (aged by plumage). We used data of vultures that completed at least one full day of autumn migration. Additionally, while most vultures migrated through Egypt, a few vultures migrated through Saudi Arabia, a route different in length, direction and geographical features, and thus these birds were left out of the analyses. Overall, we used data from 21 captive-bred and 44 wild-hatched Egyptian vultures. See Table S4 for individual vulture information.

## METHOD DETAILS

### Analytical approach
We tested the effects of early-life (i.e., upbringing: captive or wild origin) and acquired experience (i.e., number of previous migrations) on different flight related proficiencies, at different time scales. Migratory journeys of captive- and wild-hatched vultures were divided into three acquired experience groups: first, second and third or later autumn migration. Vultures that were tagged in the wild during their third calendar year migrated either once or twice before being tagged (Egyptian vultures migrating through Israel often stay at the wintering grounds for 1.5 years before heading back for the first time), and thus their first migration following tagging was removed from the data. Migratory journeys of vultures tagged during their fourth calendar year or later were treated as third or later.

We sub-sampled the data to include only days during autumn migration. Daily data included GPS locations starting at the first location after which the vulture left the night's roost and ending in the first location at the next night's roost. Migration was defined as the period which started and ended in a directional long flight (>50 km) towards the migratory destination (i.e., southwards during autumn migration). In some rare cases, vultures stopped their migration for several days (i.e., moved less than 50 km towards the migratory destination) before continuing towards the migratory destination. These stops were visually examined and considered as migratory-stopovers, and not as the end of migration, if the movement following them was clearly directional (and not exploratory) in the same migratory direction.

### Used GPS and acceleration data

Tags collected GPS data at 1-second to 1-hour intervals, depending on predefined geographic areas and decreasing with reduced battery voltage. For analyses of complete routes, we excluded vultures for which we did not have data for at least one complete migration due to tag failure or mortality. For the analyses of daily data, we first sub-sampled the data to 1-hour interval, except for the last location of each day which was kept regardless of the time that passed between it and the previous location, to avoid losing data. Additionally, we considered days in which the vultures moved in the opposite direction to their migratory destination as stopover days and consequently removed these days from all analyses besides the count of days it took the vultures to migrate.

Acceleration data was collected at 4 second 10 Hz bursts during 2.5- or 5-minute intervals; all 2.5-minute data were then sub-sampled to a 5-minutes interval. We used acceleration data to calculate overall dynamic body acceleration (ODBA), a proxy for movement-related energy expenditure[45] and to test whether flapping occurred in each acceleration burst during flight.[46] We identified flapping and soaring-gliding flight (the two possible flight modes for Egyptian vultures) by first finding the local maxima and minima of the acceleration values in the z axis and calculating the differences between each pair. We then visually inspected >500 figures displaying the four second bursts of acceleration data collected during flight. Following these observations, we defined a flapping event as any pair of minimum and maximum with a difference of 8 m/sec$^2$ or higher. To prevent biases created by ununiform data collection, we plotted the calculated daily ODBA median in relation to the number of acceleration bursts measured each day and did not find a correlation between the two factors. Yet, because the number of days with less than 125 bursts was very low, we could not ascertain that no correlation exists during these days, thus we omitted them from the data.

GPS data collected at 1 Hz interval was used to identify soaring and gliding periods and to calculate vertical speed, altitude gain (altitude difference between start and end of a soaring event), maximum altitude for each soaring event, circling radii during soaring and soaring-gliding efficiency, calculated as the progress made in each glide divided by the time spent in the thermal preceding it.[17] For the analyses of acceleration and 1 Hz GPS data, we only used data collected during flight and limited our analyses to include data from first and second migrations due to the small sample size of third and later migrations for these measurements. Moreover, most of the tags only collected 1 Hz data between latitudes 21 and 30 north, not including the Sinai Peninsula, an area with high environmental similarity (low-altitude desert habitat). Thus, to avoid biases arising from different environmental factors and different stages of migration, we removed the few data that was collected outside this range. When flying over this area, all birds made long, directional flights towards their migratory destination. This allowed maximum battery charging, because the solar panel is exposed to the sun most ideally when the wings are spread in flight, allowing the tags to sample 1 Hz GPS data without losing much battery. Eventually, tags collected 1 Hz data at bursts ranging in length from a few seconds to over five hours. We then removed segments shorter than two minutes, which we found to be the minimal time frame required to identify soaring-gliding events.

Soaring (gaining altitude by circling in thermals) and gliding (losing altitude while moving forward) periods were identified using 1 Hz data during daily migration flights. For each segment of continuous 1 Hz data sampling during flight, we first subsampled the data to obtain a GPS location every 10 seconds and calculated the vertical speed using a moving average of 2 (a mean of the speed in the current location, the speed two locations prior to the current one and two locations after the current one). We then identified peaks and valleys by locating a change in the sign of vertical speed (from + to – or vice versa). Finally, we used the original 1 Hz data to search for the true peak and valley between each two valleys or peaks, respectively. We annotated every segment between a valley and a peak as a soaring period and every segment between a peak and a valley as a gliding period.[47]

To ascertain that the identified soaring events were thermal and not orographic soaring, we first calculated the mean turning angle in each segment, assuming that thermal soaring will be characterized by high means. Plotting the distribution of these means presents a fat-tail below a mean of 8 degrees turning angle, implying that these measurements might be produced by a different behavior, being either orographic soaring or strongly drifted thermal soaring. To further identify Orographic soaring, we calculated the maximum height above ground level during each soaring event. We assumed that along the low elevations of the vulture's autumn migration routes over the Sahara Desert, rarely reaching 500 m above sea level, any flight higher than 250 m above ground level could not result from orographic uplift (250 m being 10 times higher than the altitude used to identify Orographic soaring over the Netherlands[48]). Adding the two factors: mean turning angle of 8 deg or lower and altitude above ground of less than 250 meters, we found only 13 soaring events that are suspected of being orographic soaring and not thermal soaring. We consequently removed these soaring events from our data.

To identify circling events, we used a Gaussian filter ($\sigma = 1$ s) to smooth GPS data during soaring segments. We then calculated the azimuth of flight between each two locations and categorized each azimuth by the cardinal direction it is closest to (e.g., flight directions of 350°, 300° and 270° were categorized as north, west and west, respectively). Finally, a circling event was considered as consecutive GPS locations which direction of flight included all four cardinal directions, in an order that depicts a circle (e.g., north-east-south-west or east-north-west-south).

To calculate circling radius, we summed the distances between each two locations in the circle to get an approximation of the circle's circumference and divided them by $2*\pi$. Because a vulture progresses both upwards and forward while circling, we calculated the distance between each two locations as the square root of the sum of the square geodesic distance and the square of the altitude difference between each two locations.

### Environmental variables

To account for the effects of different weather variables, we downloaded weather data from the Copernicus Data Climate Store using the ecmwfr R package.[49] We used ERA5 hourly data to obtain data at 0.25-degree spatial resolution and 1-hour temporal resolution, annotating each GPS location with the spatiotemporally closest weather data and acceleration data using the GPS location taken at the closest time. Wind data was obtained as west-to-east and south-to-north wind components at 900 hPa, corresponding to about 1000 m above sea level, the typical flight altitude of Egyptian vultures during migration. We calculated parallel (positive values being tail and negative values being head wind) and perpendicular (cross) wind vectors relative to the bird's flight direction, calculated as the azimuth between each two consecutive locations. We used the absolute cross-wind speed values, assuming that the direction to which the vulture is pushed (leftward or rightward relative to its flight direction) is irrelevant to its decision-making. We also obtained the boundary layer height, a proxy for convection, i.e., soaring (thermal) conditions.[50] The maximum correlation coefficient among the three weather variables was 0.12, thus we treated them as uncorrelated.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### General approach

We tested our hypothesis that early-life and acquired experience affect different proficiencies of migrating Egyptian vultures, by fitting Linear Mixed Effects Models (LMM) or Generalized Linear Mixed Effects Models (GLMM) including these two variables, their interaction and random intercepts for individual identity. To account for the known effects of different weather variables on birds' flight and migratory performance, we considered these variables as covariates in each model except for the models explaining migration onset timing, total migration distance and total migration time, which have a large spatiotemporal scale that makes testing weather effects irrelevant. As weather effects were not the focus of our study questions, we do not discuss the found effects in the main text, and instead present them in the summary tables included in the supplementary. Weather variables used in each model are detailed below. Models were fitted using the glmmTMB package in R[51] and for each model, we used the DHARMa package[52] to determine the best distribution and link function by comparing QQ plots and residual plots among different options. Continuous explanatory variables were centered by subtracting the variable mean from each data point and scaled by dividing each point by the variable's standard deviation, except for cases in which these variables were part of an interaction, then they were not centered, and were scaled by dividing them by the variable's root mean square. Predicted model results were calculated and plotted according to model estimates by keeping all continuous variables for which the prediction was not calculated at their means. When an interaction's term effect was significant, we used a Tukey-adjusted post-hoc test to test whether the estimated marginal (least square) means of the different groups are significantly different.[53]

### Migration routes, daily and acceleration data

First, we tested the effects of the two experience types on large-scale migratory characteristics: migration onset, total migratory distance and migratory duration. We measured migration onset as the Julian date – the number of days since the beginning of the calendar year. We calculated total migratory distance as the geodesic distance (beeline, in km) between the first location on the first day of migration and the last location of the last day of migration and migratory duration as the number of days passed between these two events. We only used data from migratory journeys with a known start date for the migration onset analysis and only complete migratory journeys for total distance and duration analyses. For all three analyses we used only the first migration of each individual in the third or later migrations group.

Next, we tested the effects of the two experience types on the daily migration distance (daily beeline, in km) including the daily mean of each of the three weather variables. Then, we tested the effects of experience on daily proxy of movement-related energy expenditure (mean ODBA),[45] and on the probability that a vulture will flap its wings during an hour of migratory flight.[46] An hour in which flapping was identified during at least one of the 12 measured acceleration bursts was considered as an hour in which flapping occurred. In these models we included daily (for mean ODBA) and hourly (for flap probability) means of the three weather variables.

We used GLMM with a Gamma distribution and a log link function for the analysis of migration onset (n = 21, 8 and 6 captive and 29, 19 and 26 wild vultures' migrations during first, second and third or later migrations, respectively), LMM for total migratory distance and GLMM with a Poisson distribution and a log link function for migratory duration (n = 14, 7 and 5 captive and 24, 17 and 25 wild vultures' complete migrations during first, second and third or later migrations, respectively). We did not find significant overdispersion (dispersion = 1.34, p = 0.072) for the model explaining migratory duration.

We used LMM for the analysis of daily distance (n = 170 (during 19 migratory journeys), 53 (8) and 84 (12) captive and 242 (29), 127 (17) and 283 (42) wild vultures' complete migratory days during first, second and third or later migrations, respectively). We used GLMM with a Gamma distribution and a log link function for ODBA (n = 98 (during 12 migratory journeys) and 41 (6) captive and

215 (27) and 121 (17) wild vultures' complete migratory days during first and second migrations, respectively) and a binomial distribution with a logit link function for flapping probability (n = 445 (12) and 228 (6) captive and 838 (27) and 654 (17) wild vultures' flight hours during first and second migrations, respectively).

### High-resolution flight-behavior

Following the results of the abovementioned analyses, we used 1 Hz GPS data to test the effects of the two experience types on a high-resolution flight behavior. First, we analyzed soaring-gliding performance by testing the effects of experience on vertical speed, altitude gain and maximum altitude reached during soaring periods. In these analyses, we accounted for the possible effects of boundary layer height and lateral drift, calculated as the horizontal distance divided by the duration of each soaring event.[17] Next, we tested for among-group differences in soaring-gliding efficiency which we calculated by dividing the time spent in each soaring event by the distance gained in the following gliding event.[17] In this model, we included boundary layer and drift during the soaring period and absolute cross wind speed during the gliding period as predictors. We did not use tail-wind during gliding periods for this analysis, because it was highly correlated with drift during soaring periods. Then, we tested for experience effects on circling radii. For this model we accounted for the possible effects of boundary layer height and drift, and also included the interaction of the two experience types and altitude during each circling event, because we expected circling radii to change with altitude.[34]

We used LMM for the analysis of vertical speed and maximum altitude reached during soaring periods and GLMM with a Gamma distribution and a log link function for altitude gain (n = 537 (during 8 migratory journeys) and 261 (6) captive and 1636 (26) and 559 (12) wild vultures' soaring events during first and second migrations, respectively). We used a GLMM model with a Gamma distribution and a log link function explaining soaring-gliding efficiency (n = 498 (during 8 migratory journeys) and 235 (6) captive and 1484 (26) and 517 (12) wild vultures' soaring-gliding pairs during first and second migrations, respectively) and for circling radii (n = 10190 (during 8 migratory journeys) and 5077 (6) captive and 40614 (26) and 15696 (12) wild vultures' circling events during first and second migrations, respectively).

### Mortality and migratory proficiencies

Finally, we wanted to test whether the improvement found with acquired experience is indeed a result of experience and not of the removal of less proficient individuals from the data following mortality during or after the first or second migration. To do so, we used the same models presented above for the number of days it took vultures to complete an entire migration route and their daily progress, removing data from vultures for which we did not have complete data during their first, second and third migration, thus including only vultures that survived at least their first three migratory journeys. We compared these models with the original models by looking for differences in the variables that were found to have a significant effect and comparing the predicted model results. We assumed that an effect of mortality will result in a removed or reduced effect of acquired experience, meaning that either acquired experience will not show a significant effect, or that the predicted results will show lower improvement with increased acquired experience. We did not find significant overdispersion (dispersion = 1.34, p = 0.056) for the model explaining migratory duration. Both mortality-related models included 4 captive and 10 wild vultures.