Overcoming Innate Lateralization Improves Avian Flight Performance

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Abstract

Behavioural lateralization—side-bias or handedness—enhances neurological processing efficiency but creates a dilemma for behaviours requiring symmetry. Flight demands symmetric execution, particularly when optimising energy extraction from atmospheric updrafts during soaring. Using high-resolution biologging of 31 juvenile European honey buzzards from fledging through their first intercontinental migration leg, we show that strong lateralised circling was prevalent immediately after fledging (74%). This proportion declined to parity by migration onset, indicating developmental adjustment with increasing experience. During migration, side-biased circling was linked to wider turns, reduced altitude gain, and daily travel distances shortened by 13%. These findings reveal a direct trade-off between the neurological efficiency of lateralization and the aerodynamic requirements of efficient soaring. Our results challenge the notion that lateralization is universally adaptive and highlight how experience and ontogeny modulate the balance between task difficulty, neural specialization, and ecological performance.

Keywords: Handedness, Side-bias, Bird migration, Soaring, Motor control, behavioural symmetry, Honey buzzard

Introduction

Behavioural lateralization —favouring one side when executing a complex task— is a hallmark of efficient neural processing and considered ubiquitous across the animal kingdom (1, 2). Much of the advantage of lateralization is founded on the notion that the allocation of certain tasks to certain parts of the brain, and hence executed with a side bias, improves performance (3–5). Laterality streamlines cognition and action, as seen in everything from predator detection in chickens to handedness in humans (2). Yet, by restricting an animal's ability to coordinate both sides equally well, this broad evolutionary strategy faces a fundamental dilemma when side bias compromises tasks requiring exquisite bilateral execution (6, 7).

While laterality likely evolved through environmental triggers that were subsequently fixated by genetic assimilation (8), it can also emerge collateral to developmental pathways (9). Bird embryos exemplify this, as they position asymmetrically in eggs with the right eye toward the translucent shell, creating differential light exposure that produces consistent functional asymmetries (2, 10). The differential exposure to light leads to visual lateralization where the left hemisphere (right eye) specializes in detail discrimination and categorization (11, 12), while the right hemisphere (left eye) manages spatial attention and social cognition (10, 12, 13). This developmental mechanism gives rise to the aforementioned performance differences in chickens, where non-lateralized individuals make more mistakes than lateralized individuals in spotting predators while feeding -a potentially fatal trade-off between vigilance and the ability to distinguish grit from grain (5, 11).

One of the main mechanistic foundations of lateralization is that the preferential use of one limb will elicit a life-long learning feedback loop, giving rise to a unilateral improvement that manifests asymmetrical execution through motor and perceptual learning and reinforcement, with consequences on survival and fitness (2, 14). It is suggested that if both hemispheres of the brain processed information in parallel, the efficacy of the neurological task would be reduced due to higher cognitive redundancy (4). As lateralization is commonly associated with benefits in executing complex behaviours (15, 16), it seems counter-intuitive that symmetry is regraded as a phenomenon not in need of justification (8,

17).

However, given the seemingly inescapable mechanism of manifestation of laterality through learning

feedback loops, along with the praised advantages of neurological processing efficiency through lateral-

ization and the pervasiveness of behavioural side-bias across taxa, it seems puzzling that brains achieve

symmetric task performance (*17*). Particularly when it comes to complex behaviours where symmetry

is critical, it remains unclear how and under which circumstances animals suppress side-bias to achieve

symmetry or remain unbiased. Examining challenging behaviours where laterality poses a disadvan-

tage might therefore provide a more dynamic, context-dependent perspective, in which neurological

benefits are weighed against ecological, evolutionary, or energetic costs (*6*, *7*, *17*).

While birds exhibit laterality in contexts ranging from visual processing in pigeons and chickens (*2*, *11*,

13) to footedness in parrots handling seeds (*18–20*), evidence for flight asymmetry remains limited

to extreme experimental conditions (*21–23*). Although hemispheric lateralization might enhance

information processing and motor control, the scarcity of laterality in flight suggests strong selection

against both behavioural lateralization and morphological asymmetry (*24*), likely due to aerodynamic

constraints imposed by efficiency and manoeuvrability (Fig. 1; but see (*25*)).

Flight thus represents an evolutionary paradox, a complex sensorimotor task where symmetry prevails

despite potential neural efficiency gains from lateralization, providing unique opportunities to study

evolutionary pressures that constrain lateralization in biomechanically complex behaviours.

Here, we investigate the ontogenetic development of laterality in soaring flight behaviour in the Eu-

ropean honey buzzard (*Pernis apivorus*), spanning from fledging, when juveniles learn to fly for the

first time, to the completion of the first leg of their continental-scale migration. Large birds incur high

metabolic costs for flapping due to their size, thus they harness energy from atmospheric updrafts,

such as thermals (vertically rising air pockets created by sun-heated surfaces), or orographic and lee

waves (topographically induced rising air masses), to remain airborne and traverse extensive distances

(*26*, *27*). This strategy can reduce their metabolic costs to levels comparable to rest (*28*).

However, the effective use of atmospheric updrafts presents considerable challenges: updrafts are in-

Figure 1: Soaring flight and its quantification using multi-sensor biologging technology. **a**: In the depicted scenario, two birds with a left-turning bias encounter a thermal updraft; only the bird whose turning direction aligns with the updraft's position can immediately enter the core and begin extracting energy. The other, due to its turning bias, must complete a full 360° turn, losing altitude before potentially entering the updraft at a lower height. Given the ephemeral and spatially limited nature of thermals, this manoeuvrer comes at the risk of missing the updraft entirely, forcing energy-intensive flapping flight (metabolic cost $\approx 10\times$ higher than soaring) (*28*) or landing. Optimal exploitation of an updraft requires circling with minimal radii (typically 20–26 m) to remain within the updraft's core maximum vertical velocity (2–5 m s^{-1}). Small radii require sustained high roll angles (15°–45°) and rapid sensory-motor adjustments to compensate for turbulence. While wider circles reduce control demands and allow slower roll corrections, they decrease climb efficiency by 30–50%. Very wide circles increase exposure to peripheral downdrafts and turbulence-induced injury risks (shear forces > 5 g) (*29*). Failed centering attempts –especially in wind-shifted updrafts, which are more common than the idealized scenario shown– can eject birds into subsiding air, necessitating emergency flap-glide transitions. Cumulative height deficits from suboptimal circling strategies reduce potential energy extraction from updrafts and, consequently, cross-country travel range. **b**, Biologging devices used in this study were equipped with accelerometer, magnetometer, and gyroscope sensors, enabling characterization of soaring flight in wild European honey buzzards. These data were used for calculating rotation along three axes, quantifying roll, yaw, and pitch, which correspond to the degree of banking, the width of the thermal, and the strength of the thermal, respectively.

⁷⁷ visible and occur unpredictably in both space and time, with their strength ranging from insufficient

⁷⁸ to support flight to, in rare cases, levels that can endanger even experienced fliers (*29*). Rather than

⁷⁹ forming coherent columns, updrafts are typically transient, irregular pockets of rising air, which can be

⁸⁰ difficult for inexperienced birds to exploit consistently (*30*). These updrafts also vary in spatial extent,

⁸¹ structure, and persistence, with turbulence often more pronounced at their peripheries than at the core

⁸² (*29*). Climbing within dynamic air masses requires a sophisticated interplay of sensory perception and

⁸³ motor control to maximize energy gain (*29*). Theoretically, approaching updrafts without a lateral

preference should be more efficient, as side bias could force a bird to adjust its trajectory, potentially resulting in lost opportunities and/or in unnecessary energy expenditure (Fig. 1).

Such inefficiencies may have substantial fitness consequences, as demonstrated in white storks (*Ciconia ciconia*), where differences in soaring performance have been linked to long-term migratory success and survival (*30*, *31*). Against this background, we examined whether juvenile honey buzzards exhibit lateralized circling behaviour during soaring, and how such side-biases relate to age, the acquisition of flight experience, and the physical characteristics and complexity of the updrafts encountered (Fig. 1).

Methods

By equipping 31 young honey buzzards (*Pernis apivorus*) prior to fledging with biologging devices (E-obs GmbH, Munich, Germany) in breeding grounds in Finland (25 in 2022 and 6 in 2023), we collected longitudinal data at high resolution. Permit to trap and deploy GPS-tracking devices on buzzards in Finland were issued by the Centre for Economic Development, Transport and the Environment in Southwestern Finland (VARELY/8915/2022). All individuals were returned to their nest immediately after the deployment of the biologging devices. The devices weighed 25 grams ($<3\%$ of the birds' body mass) and were deployed on the upper back of the birds using a backpack harness. The individuals were on average 31.7 days old (range = 27–38) at the time of tagging. Feather samples were collected for DNA sexing. All samples remained and were analysed in the country of origin (Finland).

GPS fixes (at $1\,\mathrm{Hz}$) were received in bursts over a period of $120\,\mathrm{s}$ every 900 s. In case of a full battery, the burst length was set to extend to $240\,\mathrm{s}$ collecting positions at 1 Hz. When battery was low, the inter-burst interval was reduced to $3600\,\mathrm{s}$ and the burst length to 1 s. The devices included a 9 axis Inertial Measurement Unit (IMU) collecting accelerometer (ACC), gyroscope (GYR), and magnetometer (MAG) at $20\,\mathrm{Hz}$ in bursts of $8\,\mathrm{s}$ and a inter-burst interval of $600\,\mathrm{s}$. We thus obtained three-dimensional position (via GPS) and body posture (through 9-axes inertial measurement sensors) from the birds' first attempts of flight in Finland over the completion of their migratory journeys into their wintering sites for as far as to Southern Africa (Fig. 2a). Overall, our dataset contained up to

109 620 days of tracking, but 90% of the data were collected within the first 284 days after tagging, which

110 we used as cut-off to subset the data to be included in our analyses.

Inertial Measurement Unit (IMU) data processing

We used multi-sensor data to quantify the fine-scale changes in the birds' body posture during flight and

to estimate the characteristics of soaring flight performance, including lateralization. We calculated

yaw (rotation around the z axis– head to tail), roll (rotation around the y axis – from wingtip to

wingtip), and pitch (rotation around the x axis – up and down through the center of the bird) (Fig.

1) using quaternion values computed on-board the biologging devices using sensor fusion of ACC and

GYR.

The calculation of yaw, roll, and pitch (eqn 1,2,3) followed the instructions of the tag manufacturer

where

$$\text{yaw} = \psi = -\arctan \frac{2(q_x q_y - q_w q_z)}{1 - 2(q_x^2 + q_z^2)} \tag{1}$$

$$\text{roll} = \phi = -\arctan \frac{2(q_w q_y - q_x q_z)}{1 - 2(q_x^2 + q_y^2)} \tag{2}$$

$$\text{pitch} = \theta = 2\arctan \sqrt{\frac{1 + 2(q_w q_x + q_y q_z)}{1 - 2(q_w q_x + q_y q_z)}} - \frac{\pi}{2} \tag{3}$$

$$= \arcsin \left(2(q_w q_x + q_y q_z)\right)$$

q_w is the scalar (real) part of the quaternion, q_x, q_y, and q_z are the vector (imaginary) parts of the

quaternion, representing the rotation around the x, y, and z axes, respectively.

To summarize the original 20 Hz data in each 8 s burst, we calculated the sum of yaw angles (hereafter

total yaw; corresponding to how many degrees of rotation around the z axis was recorded during 8 s),

average pitch (corresponding to the average tilt in the body during 8 s), and the sum of roll angles

(corresponding to how many degrees of rotation around the y axis was recorded during 8 s). For the

six individuals tagged in 2023, the IMU burst length was set to 240 s, collected simultaneously with

GPS, in addition to the 8 s burst lengths. When battery was low, the burst interval automatically

changed to 1800 s. For these longer bursts, we split up the long bursts into 8 s chunks for consistency when summarizing the IMU data. We sub-sampled these data to make sure consecutive bursts were at least 2 min apart. This was done to ensure that each burst was more likely to represent flight in a unique thermal.

Lateralization at burst and daily scales

We quantified lateralization in flight from the roll angle time series by calculating a laterality index (LI, eqn 4) (32, 33):

$$\text{LI} = \frac{R_t - L_t}{R_t + L_t + N_t} \tag{4}$$

where R_t and L_t are the counts of right and left turns, respectively, and N_t is the count of no-turns.

To restrict the analysis to circling flight, we retained only 8 s IMU bursts in which the bird completed at least one-eighth of a full circle, that is, bursts with an absolute total yaw $\geq 45°$. For each such circling burst, we classified the turning direction at 1 Hz based on roll angle: positive roll indicated a right turn (increasing yaw), and negative roll indicated a left turn (decreasing yaw). Seconds with roll values below the turning threshold were classified as no-turns. Using these second-wise classifications, we computed LI at two temporal scales:

- **IMU burst scale**: Each 8 s burst was treated as a separate circling burst. Within a burst (which was separated from neighbouring bursts by at least 2 min), each second contributed one classification (right turn, left turn, or no-turn), and the corresponding counts R_t, L_t, and N_t were entered into eqn 4 to obtain a burst-level LI. Within an 8 s burst, LI therefore captures the balance of turning directions across the 1 Hz observations: values near 0 indicate that left and right turns occurred with similar frequency, whereas values approaching -1 or 1 indicate bursts composed almost exclusively of left or right turns, respectively.

- **Daily scale**: All circling bursts within a day were aggregated by summing R_t, L_t, and N_t across bursts, and a single daily LI was then computed from these daily totals using eqn 4 (Fig. 2b).

Following commonly used LI thresholds for handedness (*20*, *33–35*), we categorized each burst and each day as right-biased (LI = 0.25 to 1), left-biased (LI = −1 to −0.25), or unbiased (LI = −0.25 to 0.25).

To assess whether individual variation in lateralization influenced migratory performance, we summarized flight characteristics at the daily scale during migration. For each day, we averaged total yaw and average pitch over all 8 s bursts. To estimate daily energetic costs of movement, we calculated vectorial dynamic body acceleration (VeDBA) from the tri-axial accelerometer (ACC) data, a proxy for oxygen consumption (*36*) widely used as a measure of energy expenditure in biologging studies (*37*). For each individual, we then computed daily mean VeDBA.

Identifying life stages

Using the biologging data, we first distinguished between the three different life stages: post-fledging, migration, and wintering (Fig. 2a). To identify the start and end of pre-fledging, post-fledging, migration, and wintering stages, we used discrete-time Hidden Markov Models (HMMs) for behavioural segmentation based on hourly step lengths and turning angles (*38*). We first obtained three behavioural states: stationary, local movement, and migration. For the stationary state, we chose a step length distribution range of $0 - 0.5$km. The local movement state covered short-distance movements such as exploratory flights, with the step length distribution between $0.5 - 22$km. Step lengths above 22km were attributed to migration. For turning angle, we categorized directed movement (stationary, migration) with a turning angle range of $-0.5 - 0.5$ radians, and non-directed movements (local movement) with turning angles outside the range of $-0.5 - 0.5$ radians. These were then used to calculate the initial parameters for each individual for fitting the HMM model. We removed any data corresponding to the pre-fledging period, defined as the time between tagging and the first exploratory flight for each bird, as the birds did not perform long flight bouts and their movement was limited to the nest and the immediate surroundings. The post-fledging period defined the onset of the first exploration away from the nest site, which was selected for analysis based on the first occurrence of local movement state for each individual. To determine the migration period, we selected the start of migration by

filtering for migration state. When migration state was detected, the following conditions were tested: 1) whether at least two other migration states occurred within the following three days; 2) whether there were at least three migration states within one day. In other words, if the individual performed frequent long-distance movements within a period of three days or at least three hours in a day. If either condition applied, we considered it as the onset of migration. We used the GPS data to quantify a set of metrics related to performance during migration. We first sub-sampled the data to hourly intervals for the migration period. For each individual, we then only retained days that had 12-14 hours of movement data and calculated total distance (sum of hourly distances) and maximum flight altitude (using the height above ellipsoid collected by the biologging devices). The end of migration was assigned when there was an absence of migration state for three consecutive days following the migration period marking the beginning of movements in the wintering areas (*39*).

Wind annotation

To account for the difficulty associated with soaring flight in windy conditions(*30*), we associated the flight characteristics of the birds with the experienced wind speed. We therefore matched each IMU burst with its closest GPS record in time (within one hour, which matched the temporal resolution of the wind data). Then, at each GPS location, we extracted the eastward and northward components of wind at the 900mbar pressure level from the ERA5 reanalysis provided by the European Centre for Medium-Range Weather Forecasts (ECMWF) (*40*). This data was available at an hourly temporal resolution and a spatial resolution of $-0.25° \times 0.25°$. We used a bilinear interpolation method to associate each GPS point with its nearest wind component values. Subsequently, we calculated wind speed using the eastward and northward wind components following the Pythagorean Theorem.

Analysis

We investigated laterality separately at the burst and daily scales. At the burst scale, we modelled the probability of lateralization as a function of difficulty of soaring/turning and age. We considered difficult thermals as those that were smaller in diameter, stronger in terms of vertical velocity, and

those occurring in stronger horizontal wind speeds. For each 8 s burst, we calculated the absolute total yaw as a proxy for the diameter of the thermal column and average pitch as a proxy for thermal strength. Before modelling, we z-transformed the values of absolute total yaw, average pitch, wind speed, and days since tagging. We modelled the binary outcome of lateralization (1 if $|LI| \geq 0.25$, 0 otherwise) using a binomial generalized linear mixed effect model with logit link. Fixed effects included z-transformed absolute total yaw, average pitch, wind speed. We including individual ID as a random effect on the slopes of these fixed effects. We also added a penalized smooth term for days since tagging to account for the tendency of laterality to vary with age.

To understand the influence of laterality on migratory flight performance at the daily scale, we built separate models for each of the following response variables: average daily VeDBA, daily distance, daily average absolute total yaw, daily average pitch, and daily maximum flight altitude. We built separate linear mixed models (Gaussian family, except gamma with log-link for VeDBA) for each response. Fixed effects were maximum daily wind speed and absolute daily LI (both z-transformed), with random intercepts by individual ($response \sim wind + abs(LI) + (1|ID)$). Each model included maximum wind speed and the laterality index for each day as predictor variables as well as individual ID as a random effect on the intercept. Only days with at least 12 hours of data were included in these models.

Results

Honey buzzards began their independent life after leaving their nests, remaining in natal territories for an average of 17 (SD=±4.62) days before initiating their unassisted migration, which on average took 24 (SD=±8.84) days to complete. The birds then remained in their wintering areas for an extended period and from where we collected data for an average duration of 108 (SD =±127.40) days.

In natal territories during the post-fledging period, a majority of individuals (n=16; 52%) preferentially circled in updrafts turning right (LI between 0.25 and 1), 8 individuals (26%) were non-lateralized (with LI values between -0.25 and 0.25), and 7 individuals (22%) preferentially turned left (LI between -0.25

and -1) (Fig. 2b) based on their daily laterality indices (LI). Thus, 74% of the juveniles exhibited side

bias in circular soaring early in life. At migration onset the ratio dropped to 1:1 (16 individuals with

a side-bias vs. 15 without) (Fig. 2b).

Figure 2: Lateralisation of circling flight in European honey buzzards across the different life stages. **a**, Map of movement trajectories of 31 juvenile birds migrating from Finland to Sub-Saharan Africa. Colours indicate the three life stages: post-fledging (blue), migration (green), and wintering (teal). **b**, Distribution of daily laterality index for each individual during different life stages. Lateralisation at each life stage corresponds to the laterality index calculated for that stage: right bias (LI = 1.0 to 0.25), left bias (LI = -1 to -0.25), or no bias (LI = -0.25 to 0.25). Wintering data is missing for individuals that stopped transmitting data during or shortly after migration (n = 7). During migration one bird (D225_231) switched from non-lateralised (at a mean LI -0.18) to a left turning bias (mean LI -0.3 during migration and -0.56 during wintering respectively), all other instances were birds that transitioned from lateralised to non-lateralised.

During wintering period, 12 of 24 individuals, which from the initial 31 continued to send data, re-

mained side biased (8 right versus 4 left). We observed 11 side bias changes between life-stages: 8 losses

of laterality between post-fledging and migration, one loss of laterality between migration and winter-

ing, and two gains of laterality (1 between post-fledging and migration and 1 reversion to the previous

side preference in its wintering area) (Fig. 2b). Notably, none of the individuals changed preferences

from a left turning bias to right or vice-versa. To our knowledge, this is the first documentation of side

bias in flight and ontogenetic decline of laterality.

We found that during pre-migration, the likelihood of lateralized circling behaviour decreased signifi-

cantly with each additional day until the onset of migration (Fig. 3a). With the onset of migration,

age no longer influenced the likelihood of biased turning behaviour (Fig. 3b). Overall, laterality at the scale of single turns correlated with wider turning circles (lower total yaw), indicating poorer flight skills, and higher pitch and wind speed values, reflecting challenging atmospheric conditions (Fig. 3c-e). Lateralized individuals continued to display side bias during difficult tasks regardless of age (Fig. 3a) - suggesting residual persisting bias when the flight conditions were challenging and/or the pressure on the birds for peak performance was lowered (such as in wintering).

Cost of side-bias

During migration increased laterality reduced daily flight performance (Fig. 3f-i). After accounting for the wind conditions, more lateralized execution lead to lower daily distances achieved on a given day of migration (Fig. 3i). Daily lateralization resulted in lower flight heights (Fig. 3g), affecting flight efficiency, since height achieved translates in distance available for gliding (for details see also supplementary table 1). However, lateralization was also associated with slightly lower daily energy expenditure (less flapping in lateralized compared to non-lateralized individuals, Fig. 3h). These results suggest that while lateralization helped to avoid energetically costly flapping, presumably by taking updrafts from the preferred side, the expression of a side bias *per-se* accumulated over a day into a disadvantage at the cost of not being able to climb as high and/or omitting opportunities to extract energy from rising air columns as optimally as less biased individuals could. The maximum wind speeds measured in a day increased the likelihood of having to flap and thus the energy the birds spent, as updrafts dissipate in high winds, forcing the birds to flap to remain aloft on windy days.

Discussion

Our study demonstrates that ontogenetic loss of lateralization in soaring flight was associated with improved migration efficiency in honey buzzards, revealing a trade-off between neural specialization and biomechanical flight performance. Laterality at daily scale during migration, like at the single turn scale, correlated with wider circles flown (lower total yaw) and higher pitch (Fig. 3i-j)- consistent with association of laterality with perceived (skill based) and actual (environmentally induced) task

Figure 3: Probability of lateralisation of circling flight in different soaring conditions and the influence of lateralisation on migration performance. Data were analysed at two temporal scales: **a-e**, at the scale of 8 s bursts, we modelled the probability of lateralisation as a function of difficulty of soaring and age. Absolute total yaw is a proxy for the width of the thermal where larger values represent tighter turns (more rotation in accumulated in 8s) and average pitch corresponds to the strength of the updraft (larger values being stronger updrafts). **a**, The coefficient estimates of the linear predictors (centred and scaled) of the model with 95% credible intervals. Individual-specific coefficients are presented in Extended Data Figure 1. **b**, The effect size of age as a smooth term in the model. The first dashed line represents the onset of migration and the second the arrival at the wintering grounds. **c-e**, Predicted probabilities of laterality under different levels of interacting predictors. **f-j**, at the daily scale for the duration of autumn migration, we modeled various movement metrics, that represent migration performance, as a function of wind speed encountered and absolute daily laterality shown. The predictors were included in the model in their original scale. The 95% credible intervals are shown. Complete model results, including the intercept values, are reported in Supplementary File 1. Individual-specific intercepts are shown in Fig. 3-figure supplement 1.

difficulty. In thermals, maximizing energy extraction requires tight centring in the updraft core (*29*). Wider radii, as also seen in juvenile Griffon vultures (*30*), are indicative of inefficient thermal exploitation attributed to inexperience. Steeper pitch angles, meanwhile, reflect the biomechanical, motor, and sensory strain of navigating strong updrafts -causing the high pitch values measured and requiring or being more exclusive to side-biased execution (*30*). Consequently, as juveniles gained experience, both

the proportion displaying a side-bias and its individual degree decreased, fostering a more balanced bilateral skilled soaring behaviour execution.

While lateralization optimizes neural processing (2), when it comes to optimal energy extraction during flight, selection favours bilateral proficiency, which the honey buzzards acquired through learning. This parallels the evolutionary selection for morphological symmetry in flight-critical structures like wings (24). Hence, tasks requiring bilateral motor coordination potentially represent neurologically expensive solutions, necessitated by environmental demands. Hence, in contrast to prevailing views, a bilateral execution of complex tasks should be considered exceptional.

During migration, the missed opportunities and reduced efficiency in extracting atmospheric energy from updrafts made the lateralized execution of flight manoeuvrers in the context of soaring less advantageous. A disadvantage that possibly could plausibly represent the proximate mechanism for natural selection on symmetric execution of soaring behaviour. The ontogenetic trajectory of laterality in honey buzzards also indicated that early-life biases can take long to overcome -if they ever can be- and resurface later, when encountering difficult conditions or when performance pressure is relaxed, evidenced by some individuals regaining their prior side-bias after completion of migration. Thus, despite individually gaining experience and mastering flight with age, the emergence of lateral execution can be elicited as a response to a naturally, or artificially induced exceptionally demanding challenge (21, 23).

Beyond the perceived difficulty, the cost-benefit ratio of displaying side-biased behavioural execution of soaring in the honey buzzards could be context-dependent and contain an element of affordability. Missing an updraft and/or extracting atmospheric energy not at peak efficiency in the natal territories or wintering areas may have had negligible consequences, however as migration bears substantial risks including high energy expenditure, increased predation risk, and time constraints (41), efficiently covering large distances can become critical adding pressure on efficient execution of circling behaviour. This pressure on peak in-flight efficiency during migration is likely to intensify as global change increasingly disrupts long-distance migration (42) putting lateralized individuals possibly at a higher

risk of failure. Deterioration of stopover site quality (*43*), increased migration distances due to shifting ranges (*44*), altered wind patterns (*45*), and rising mortality from human-made obstacles (*46*), among others, compound the challenges migratory birds face in a rapidly changing world exacerbating the vital importance of flight efficiency.

More generally, the acquisition of bilaterality as a marker of experience and task mastery required a shift from lateralized execution to bilateral processing, suggesting some degree of neurological redundancy. Critical functions such as memory (*47–49*), attention (*50*), language (*51*), and motor control (*52*) retain bilateral redundancy to balance efficiency with robustness. This redundancy is mediated by structural (e.g., commissural pathways) (*53*) and functional (e.g., interhemispheric co-activation) mechanisms (*54*), ensuring resilience against damage or cognitive load. For instance, while language use in humans is highly lateralized (*3, 55*), the brain retains a basic level of bilateral redundancy, with highly familiar words eliciting bilateral processing (*56*). Neurological redundancy may provide the substrate for acquired bilaterality through learning, potentially explaining the reduction in hemispheric specialization observed in children raised bilingually (*57, 58*). Similarly, this redundancy underlies the finding that professional musicians process music bilaterally, while non-musicians show right-hemispheric dominance (*59*).

Our work establishes flight efficiency as a vital selective pressure shaping both neural plasticity and ontogenetic behavioural adaptation. Honey buzzards resolve a fundamental evolutionary trade-off by learning to suppress innate lateralization, achieving bilateral flight proficiency. Ecological demands thus supersede neurological optimizations for hemispheric specialization. By linking developmental skill acquisition to biomechanical efficiency gains during migration, we provide a novel framework for understanding experience-dependent neural plasticity in wild animals, emphasizing the underappreciated fitness benefits of bilateral motor control in tasks demanding symmetry. These findings clearly challenge the assumption that neural and motor lateralization is always advantageous in the animal kingdom. Instead, we show that selection for behavioural and morphological symmetry also impacts neural resource allocation, favouring bilateral motor redundancy —an adaptive strategy that might be

especially important for the long distance migratory birds- which must consistently perform at their peak and are increasingly exposed to and further challenged by human-induced threats.

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Author contributions

KS conceived the study. EN and PB collected the data. EN and EYY processed and analysed the data. KS and EN wrote the first draft of the manuscript. All authors critically contributed to the drafts and gave their final approval for publication.

Data availability

The processed biologging data sets are available at the Edmond repository "soaring_lateralization _European_honey_buzzards", (`https://doi.org/10.17617/3.HKLBET`). The raw data are stored under the study "European Honey Buzzard_Finland" on `https://www.movebank.org`.

Code availability

All R scripts necessary to reproduce the results of this study can be accessed at `https://doi.org/10.5281/zenodo.18399784`.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information This manuscript does not include Supplementary Information. **Correspondence and requests for materials** should be addressed to Kamran Safi (ksafi@ab.mpg.de).

References

1. L. J. Rogers, Laterality in Animals. *International Journal of Comparative Psychology* **3** (1989), DOI `10.46867/C48W2Q`.

2. O. Güntürkün, F. Ströckens, S. Ocklenburg, Brain Lateralization: A Comparative Perspective. *Physiological Reviews* **100**, 1019–1063 (2020), DOI `10.1152/physrev.00006.2019`.

3. S. Knecht, B. Dräger, M. Deppe, L. Bobe, H. Lohmann, A. Flöel, E.-B. Ringelstein, H. Henningsen, Handedness and hemispheric language dominance in healthy humans. *Brain* **123**, 2512–2518 (2000), DOI `10.1093/brain/123.12.2512`.

4. H. Cochet, R. W. Byrne, Evolutionary origins of human handedness: evaluating contrasting hypotheses. *Animal Cognition* **16**, 531–542 (2013), DOI `10.1007/s10071-013-0626-y`.

5. L. J. Rogers, P. Zucca, G. Vallortigara, Advantages of having a lateralized brain. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, S420–S422 (2004), DOI `10.1098/rsbl.2004.0200`.

6. D. Topalli, B. G. Eyüboğlu, N. E. Cagiltay, Understanding the Effect of Handedness on Both-Handed Task Performance: An Experimental Study based on a Haptic-Controlled, Simulation-Based Surgical Skill Training Scenario. *International Journal of Human–Computer Interaction* **35**, 478–482 (2019), DOI `10.1080/10447318.2018.1464283`.

7. M. A. Whiteside, M. M. Bess, E. Frasnelli, C. E. Beardsworth, E. J. G. Langley, J. O. van Horik, J. R. Madden, Low survival of strongly footed pheasants may explain constraints on lateralization. *Scientific Reports* **8**, 13791 (2018), DOI `10.1038/s41598-018-32066-1`.

8. A. R. Palmer, From symmetry to asymmetry: Phylogenetic patterns of asymmetry variation in animals and their evolutionarysignificance. *Proceedings of the National Academy of Sciences* **93**, 14279–14286 (1996), DOI `10.1073/pnas.93.25.14279`.

9. D. Marzoli, G. Prete, L. Tommasi, Perceptual asymmetries and handedness: a neglected link? *Frontiers in Psychology* **5** (2014), DOI `10.3389/fpsyg.2014.00163`.

10. M. Manns, F. Ströckens, Functional and structural comparison of visual lateralization in birds – similar but still different. *Frontiers in Psychology* **5** (2014), DOI `10.3389/fpsyg.2014.00206`.

11. L. J. Rogers, Light experience and asymmetry of brain function in chickens. *Nature* **297**, 223–225 (1982), DOI `10.1038/297223a0`.

12. J. N. Daisley, E. Mascalzoni, O. Rosa-Salva, R. Rugani, L. Regolin, Lateralization of social cognition in the domestic chicken (Gallus gallus). *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 965–981 (2008), DOI `10.1098/rstb.2008.0229`.

13. M. Manns, O. Güntürkün, Dual coding of visual asymmetries in the pigeon brain: the interaction of bottom-up and top-down systems. *Experimental Brain Research* **199**, 323–332 (2009), DOI `10.1007/s00221-009-1702-z`.

14. J. Cho, K.-S. Park, M. Kim, S.-H. Park, Handedness and Asymmetry of Motor Skill Learning in Right-handers. *Journal of Clinical Neurology* **2**, 113–117 (2006), DOI `10.3988/jcn.2006.2.2.113`.

15. A. Vergallito, L. J. Romero Lauro, R. Bonandrini, L. Zapparoli, L. Danelli, M. Berlingeri, *What is difficult for you can be easy for me*. Effects of increasing individual task demand on prefrontal lateralization: A tDCS study. *Neuropsychologia* **109**, 283–294 (2018), DOI `10.1016/j.neuropsychologia.2017.12.038`.

16. A. Brechmann, N. Angenstein, The impact of task difficulty on the lateralization of processing in the human auditory cortex. *Human Brain Mapping* **40**, 5341–5353 (2019), DOI `10.1002/hbm.24776`.

17. I. G. Johnston, K. Dingle, S. F. Greenbury, C. Q. Camargo, J. P. K. Doye, S. E. Ahnert, A. A. Louis, Symmetry and simplicity spontaneously emerge from the algorithmic nature of evolution. *Proceedings of the National Academy of Sciences* **119**, e2113883119 (2022), DOI `10.1073/pnas.2113883119`.

18. C. Brown, M. Magat, The evolution of lateralized foot use in parrots: a phylogenetic approach. *Behavioral Ecology* **22**, 1201–1208 (2011), DOI `10.1093/beheco/arr114`.

19. C. Brown, M. Magat, Cerebral lateralization determines hand preferences in Australian parrots. *Biology Letters* **7**, 496–498 (2011), DOI `10.1098/rsbl.2010.1121`.

20. H. Friedmann, M. Davis, "Left-Handedness" in Parrots. *The Auk* **55**, 478–480 (1938).

21. J. T. Mandel, J. M. Ratcliffe, D. J. Cerasale, D. W. Winkler, Laterality and Flight: Concurrent Tests of Side-Bias and Optimality in Flying Tree Swallows. *PLOS ONE* **3**, e1748 (2008), DOI `10.1371/journal.pone.0001748`.

22. P. S. Bhagavatula, C. Claudianos, M. R. Ibbotson, M. V. Srinivasan, Behavioral Lateralization and Optimal Route Choice in Flying Budgerigars. *PLOS Computational Biology* **10**, e1003473 (2014), DOI `10.1371/journal.pcbi.1003473`.

23. I. Schiffner, M. V. Srinivasan, Behavioural Lateralization in Budgerigars Varies with the Task and the Individual. *PLOS ONE* **8**, e82670 (2013), DOI `10.1371/journal.pone.0082670`.

24. A. L. R. Thomas, The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **254**, 181–189 (1997), DOI `10.1098/rspb.1993.0144`.

25. H. O. Holliday, Observations of directional thermal soaring preference in vultures. *Ibis* **130**, 300–301 (1988).

26. G. Bohrer, D. Brandes, J. T. Mandel, K. L. Bildstein, T. A. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, J. A. Tremblay, Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters* **15**, 96–103 (2012), DOI `https://doi.org/10.1111/j.1461-0248.2011.01713.x`.

27. T. Carrard, E. Nourani, L. Jansing, T. Zimmermann, P. Sumasgutner, M. Tschumi, D. Jenny, M. Wikelski, K. Safi, M. Sprenger, M. Scacco, Golden eagles regularly use gravity waves to soar: new insights from high-resolution weather data. *Journal of The Royal Society Interface* **22**, 20240891 (2025), DOI `10.1098/rsif.2024.0891`.

28. O. Duriez, A. Kato, C. Tromp, G. Dell'Omo, A. L. Vyssotski, F. Sarrazin, Y. Ropert-Coudert, How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PLOS ONE* **9**, e84887 (2014), DOI `10.1371/journal.pone.0084887`.

29. H. J. Williams, E. L. C. Shepard, M. D. Holton, P. A. E. Alarcón, R. P. Wilson, S. A. Lambertucci, Physical limits of flight performance in the heaviest soaring bird. *Proceedings of the National Academy of Sciences* **117**, 17884–17890 (2020), DOI `10.1073/pnas.1907360117`.

30. R. Harel, N. Horvitz, R. Nathan, Adult vultures outperform juveniles in challenging thermal soaring conditions. *Scientific Reports* **6**, 27865–27865 (2016), DOI `10.1038/srep27865`.

31. A. Flack, M. Nagy, W. Fiedler, I. D. Couzin, M. Wikelski, From local collective behavior to global migratory patterns in white storks. *Science* **360**, 911–914 (2018), DOI `10.1126/science.aap7781`.

32. J. T. E. Richardson, How to measure laterality. *Neuropsychologia* **14**, 135–136 (1976), DOI `10.1016/0028-3932(76)90015-4`.

33. A. Bennison, B. L. Clark, S. C. Votier, J. L. Quinn, J. Darby, M. Jessopp, Handedness and individual roll-angle specialism when plunge diving in the northern gannet. *Biology Letters* **19**, 20230287 (2023), DOI `10.1098/rsbl.2023.0287`.

34. A. a. S. Weir, B. Kenward, J. Chappell, A. Kacelnik, Lateralization of tool use in New Caledonian crows (Corvus moneduloides). *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, S344–S346 (2004), DOI `10.1098/rsbl.2004.0183`.

35. R. M. R. Rodgers, K. E. Cain, No evidence for side preference or handedness in a New Zealand rail species with habitual foot-usage, the pukeko. *Behavioural Processes* **167**, 103910 (2019), DOI `10.1016/j.beproc.2019.103910`.

36. L. Qasem, A. Cardew, A. Wilson, I. Griffiths, L. G. Halsey, E. L. C. Shepard, A. C. Gleiss, R. Wilson, Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector? *PLOS ONE* **7**, 1–8 (2012), DOI `10.1371/journal.pone.0031187`.

37. R. P. Wilson, L. Börger, M. D. Holton, D. M. Scantlebury, A. Gómez-Laich, F. Quintana, F. Rosell, P. M. Graf, H. Williams, R. Gunner, L. Hopkins, N. Marks, N. R. Geraldi, C. M. Duarte, R. Scott, M. S. Strano, H. Robotka, C. Eizaguirre, A. Fahlman, E. L. C. Shepard, Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology* **89**, 161–172 (2020), DOI `https://doi.org/10.1111/1365-2656.13040`.

38. B. T. McClintock, T. Michelot, momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution* **9**, 1518–1530 (2018), DOI `10.1111/2041-210X.12995`.

39. W. M. Vansteelant, J. Shamoun-Baranes, W. van Manen, J. van Diermen, W. Bouten, Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic Flyway. *Journal of Animal Ecology* **86**, 179–191 (2017), DOI `10.1111/1365-2656.12593`.

40. H. Hersbach, B. Bell, P. Berrisford, G. Biavati, A. Horányi, J. Muñoz Sabater, J. Nicolas, C. Peubey, R. Radu, I. Rozum, D. Schepers, A. Simmons, C. Soci, D. Dee, J.-N. Thépaut, *ERA5 hourly data on pressure levels from 1940 to present*, 2023, DOI `10.24381/cds.bd0915c6`.

, 41. A. Hedenström, Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 287–299 (2008), DOI `10.1098/rstb.2007.2140`.

42. S. P. Saunders, W. V. DeLuca, B. L. Bateman, J. L. Deppe, J. Grand, E. J. Knight, T. D. Meehan, N. L. Michel, N. E. Seavy, M. A. Smith, L. Taylor, C. J. Witko, C. B. Wilsey, Multispecies migratory connectivity indicates hemispheric-scale risk to bird populations from global change. *Nature Ecology & Evolution* **9**, 491–504 (2025), DOI `10.1038/s41559-024-02575-6`.

43. C. Both, C. A. M. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, R. P. B. Foppen, Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences* **277**, 1259–1266 (2009), DOI `10.1098/rspb.2009.1525`.

44. D. Zurell, C. H. Graham, L. Gallien, W. Thuiller, N. E. Zimmermann, Long-distance migratory birds threatened by multiple independent risks from global change. *Nature climate change* **8**, 992–996 (2018), DOI `10.1038/s41558-018-0312-9`.

45. E. Nourani, N. M. Yamaguchi, H. Higuchi, Climate change alters the optimal wind-dependent flight routes of an avian migrant. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20170149 (2017), DOI `10.1098/rspb.2017.0149`.

46. A. T. Marques, C. D. Santos, F. Hanssen, A.-R. Muñoz, A. Onrubia, M. Wikelski, F. Moreira, J. M. Palmeirim, J. P. Silva, Wind turbines cause functional habitat loss for migratory soaring birds. *Journal of Animal Ecology* **89**, 93–103 (2020), DOI `10.1111/1365-2656.12961`.

47. B. E. Sherman, N. B. Turk-Browne, E. V. Goldfarb, Multiple Memory Subsystems: Reconsidering Memory in the Mind and Brain. *Perspectives on Psychological Science* **19**, 103–125 (2024), DOI `10.1177/17456916231179146`.

48. H. Li, K. Matsumoto, H. Watanabe, Different effects of unilateral and bilateral hippocampal lesions in rats on the performance of radial maze and odor-paired associate tasks. *Brain Research Bulletin* **48**, 113–119 (1999), DOI `10.1016/s0361-9230(98)00157-9`.

49. M. G. Packard, R. Hirsh, N. M. White, Differential effects of fornix and caudate nucleus lesions on two radial maze tasks: evidence for multiple memory systems. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience* **9**, 1465–1472 (1989), DOI `10.1523/JNEUROSCI.09-05-01465.1989`.

50. A. S. Dakos, E. M. Walker, H. Jiang, B. E. Stein, B. A. Rowland, Interhemispheric visual competition after multisensory reversal of hemianopia. *The European Journal of Neuroscience* **50**, 3702–3712 (2019), DOI `10.1111/ejn.14554`.

51. B. Mohr, T. Endrass, O. Hauk, F. Pulvermüller, ERP correlates of the bilateral redundancy gain for words. *Neuropsychologia* **45**, 2114–2124 (2007), DOI `10.1016/j.neuropsychologia.2007.01.015`.

52. J. Merel, M. Botvinick, G. Wayne, Hierarchical motor control in mammals and machines. *Nature Communications* **10**, 5489 (2019), DOI `10.1038/s41467-019-13239-6`.

53. A. Griffa, M. Mach, J. Dedelley, D. Gutierrez-Barragan, A. Gozzi, G. Allali, J. Grandjean, D. Van De Ville, E. Amico, Evidence for increased parallel information transmission in human brain networks compared to macaques and male mice. *Nature Communications* **14**, 8216 (2023), DOI `10.1038/s41467-023-43971-z`.

54. Z. Ghulam-Jelani, J. Barrios-Martinez, A. Eguiluz-Melendez, R. Gomez, Y. Anania, F.-C. Yeh, Redundancy circuits of the commissural pathways in human and rhesus macaque brains. *Human Brain Mapping* **42**, 2250–2261 (2021), DOI `10.1002/hbm.25363`.

55. J. Packheiser, J. Schmitz, L. Arning, C. Beste, O. Güntürkün, S. Ocklenburg, A large-scale estimate on the relationship between language and motor lateralization. *Scientific Reports* **10**, 13027 (2020), DOI `10.1038/s41598-020-70057-3`.

56. Sangyub Kim, Joonwoo Kim, Kichun Nam, Familiarity with words modulates interhemispheric interactions in visual word recognition. *Frontiers in Psychology* **13**, 1–11 (2022), DOI `10.3389/fpsyg.2022.892858`.

57. L. Marin-Marin, M. Korenar, C. Pliatsikas, Dynamic Effects of Immersive Bilingualism on Cortical and Subcortical Grey Matter Structures. *Frontiers in Psychology* **13**, 886222 (2022), DOI `10.3389/fpsyg.2022.886222`.

58. E. Blanco-Elorrieta, L. Pylkkänen, Bilingual language control in perception versus action: MEG reveals comprehension control mechanisms in anterior cingulate cortex and domain-general control of production in dorsolateral prefrontal cortex. *Journal of Neuroscience* **36**, 290–301 (2016), DOI `10.1523/JNEUROSCI.3009-15.2016`.

59. K. Ono, A. Nakamura, K. Yoshiyama, T. Kinkori, M. Bundo, T. Kato, K. Ito, The effect of musical experience on hemispheric lateralization in musical feature processing. *Neuroscience Letters* **496**, 141–145 (2011), DOI `10.1016/j.neulet.2011.04.002`.

 Supplementary File 1

Supplementary File 1: Output of linear models predicting migration metrics (at the daily scale) as a function of maximum wind speed and daily laterality index. All models include individual ID as a random effect on the intercept.

Factor	Estimate	sd	Lower	0.5quant	Upper
Daily distance					
Intercept	198.35	5.09	188.37	198.35	208.34
daily_max_wind_z	43.49	5.04	33.60	43.49	53.38
daily_abs_LI_z	-25.46	5.05	-35.36	-25.46	-15.56
Daily maximum flight altitude					
Intercept	1123.70	24.55	1075.56	1123.70	1171.84
daily_max_wind_z	-8.31	19.41	-46.38	-8.32	29.76
daily_abs_LI_z	-73.37	19.46	-111.49	-73.38	-35.15
Daily average absolute total yaw					
Intercept	176.68	1.58	173.57	176.68	179.78
daily_max_wind_z	3.81	1.58	0.69	3.81	6.91
daily_abs_LI_z	-10.70	1.58	-13.80	-10.70	-7.58
Daily average pitch					
Intercept	14.93	1.09	12.77	14.93	17.09
daily_max_wind_z	-0.27	0.23	-0.72	-0.27	0.17
daily_abs_LI_z	1.66	0.29	1.09	1.66	2.23
Daily average VeDBA					
Intercept	0.16	0.00	0.15	0.16	0.16
daily_max_wind_z	0.01	0.00	0.01	0.01	0.02
daily_abs_LI_z	-0.01	0.00	-0.02	-0.01	0.00

Figure 3- figure supplement 1: Individual-specific coefficients for the model predicting laterality (binary) as a function of total yaw (a proxy for thermal tightness), average pitch (a proxy for thermal strength), and age (days since tagging) as a smooth term (Fig. 3).