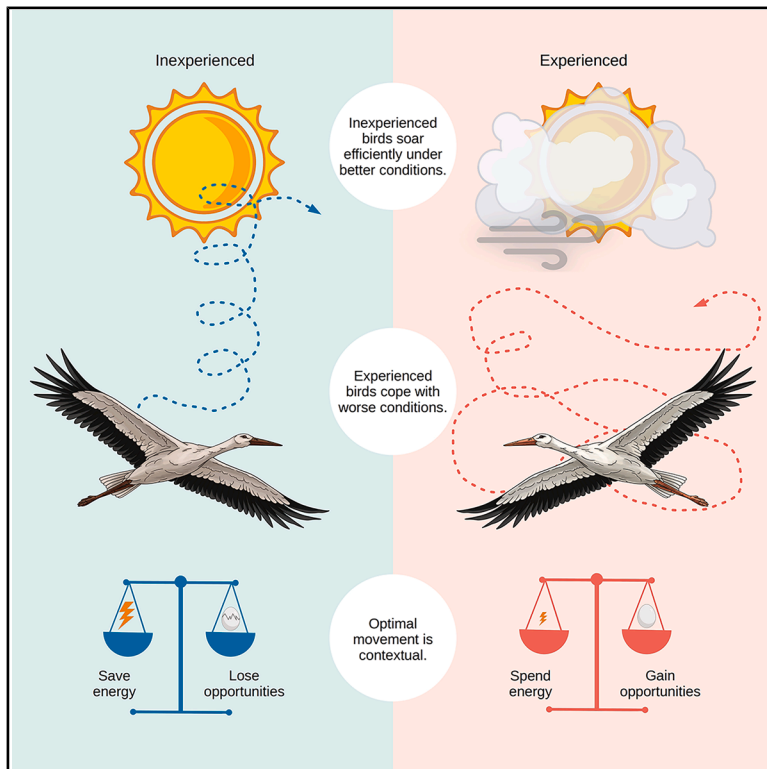


Current Biology

Experience and motivation shape the flight performance of white storks migrating long-distance

Graphical abstract



Authors

Hester Brønnevik, Andrea Flack

Correspondence

hbronnvik@ab.mpg.de (H.B.),
aflack@ab.mpg.de (A.F.)

In brief

Individual animals make decisions to balance their costs and benefits. This balance can be affected by experiences gained with age but also by breeding pressure. Brønnevik and Flack show that age reduces soaring performance in white storks. This demonstrates one way that age can rebalance a trade-off by changing the costs and payoffs to an individual.

Highlights

- Age mediates movement decisions because it can affect both learning and motivation
- Older storks had lower vertical speeds and used much more expensive flapping flight
- Adults appeared to perform more poorly because they coped with greater difficulty
- Optimality is not just saving time and energy but accounts for all costs and benefits



Brønnevik & Flack, 2025, *Current Biology* 35, 3736–3744
August 4, 2025 © 2025 The Authors. Published by Elsevier Inc.
<https://doi.org/10.1016/j.cub.2025.06.044>



Report

Experience and motivation shape the flight performance of white storks migrating long-distance

Hester Brønsvik^{1,2,3,5,*} and Andrea Flack^{1,2,4,*}

¹Collective Migration Group, Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany

²Department of Migration, Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany

³Department of Biology, University of Konstanz, 78464 Konstanz, Germany

⁴Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78468 Konstanz, Germany

⁵Lead contact

*Correspondence: hbrønsvik@ab.mpg.de (H.B.), aflack@ab.mpg.de (A.F.)

<https://doi.org/10.1016/j.cub.2025.06.044>

SUMMARY

Movement allows animals to access resources and pursue fitness.^{1–4} Yet, this requires balancing movement costs against other potential benefits. These trade-offs can change over lifetimes, as optimality is contextual and depends on ability and need.^{5–16} For migratory soaring birds, efficient movement requires exploiting atmospheric uplift—a challenging task that negates the cost of flight.^{17–19} Due to this link between costs and the environment, soaring birds are limited in when and where they fly. Thus, soaring performance goes beyond movement skills and also involves coping with potentially imperfect conditions to reduce time or competition. Here, we asked whether, over repeated migrations, white storks (*Ciconia ciconia*) improve their ability to soar. Using high-resolution lifetime tracking data from 151 storks, we found that juveniles outperformed adults under supportive conditions, but, with age, migration difficulty increased and adults performed well under challenging conditions. Adults traveled in less-supportive conditions and spent more energy on flight, indicating a change in ability and motivation. Thus, understanding how animals improve is not simply described by a learning curve but requires a multifaceted perspective on individual needs and skills.

RESULTS

Movement is fundamental to organisms seeking shelter, energy, and mates, from chemotactic foraging in bacteria² to conspicuous animal migrations. Individual animals must make decisions about how to maximize their payoffs based on their internal state, their environment, and their knowledge of these. Ultimately, performance is measured in fitness. Proximately, the question of how well an individual performs can be defined as how well it maximizes its payoffs, which requires minimization of its costs (energetic, time, and opportunity) and maximization of its benefits at the scale of individual decisions. Because decisions are made across a range of environmental conditions and internal states, optimal movement is contextual and may be different for every individual. Such a dynamic, individual perspective has historically been difficult to integrate with broader ecological theory.^{1,3,4}

Age is one example of an individual-level variable that can affect the value of movement by altering an individual's physiology, knowledge, and skill.^{5–7} In some cases, juveniles have more restricted movements than adults because they lack movement capacity^{20,21} or face greater predation risk than adults.²² Alternatively, young animals may move more, investing in exploration during dispersal²³ or migration²⁴ and using experience to settle and become resident²⁵ or to migrate more

directly²⁶ and efficiently.²⁴ It has been shown that experience can improve movement performance, allowing adults to outperform juveniles in navigation,^{11,12} timing,²⁷ innovation,²⁸ and fine-scale time efficiency¹³ or energy savings.¹⁴ These improvements can allow adults to access resources that juveniles could not simply because they lacked movement capacity.^{15,16} For migratory animals, movement skills may also affect when they can travel and how much energy that travel costs.

Soaring flight is a type of movement that is limited by the environment because the availability and strength of uplifts vary in space and time. Soaring flight is riding atmospheric uplifts, using the environment to pay the cost of transport for the soaring animal.^{4,17} Thus, soaring flight can allow large, heavy birds, for which flapping flight is exhausting, to cross vast distances over land and sea with only trivial energetic expenditure.^{29,30} Thermal soaring requires birds to locate and enter invisible thermal uplifts, turn in the direction of the core, and then constantly adjust their banking angles to remain inside of the thermal. Thermals are turbulent, highly variable, and often shared by flocks of birds. Because thermal soaring is challenging, we expected soaring to be learned and to improve over time.

Using high-resolution GPS data from 151 white storks (*Ciconia ciconia*), we recorded soaring in 55,643 thermals and were able to scrutinize fine-scale changes in soaring flight over up to eight consecutive migrations. We investigated pre-migration flight



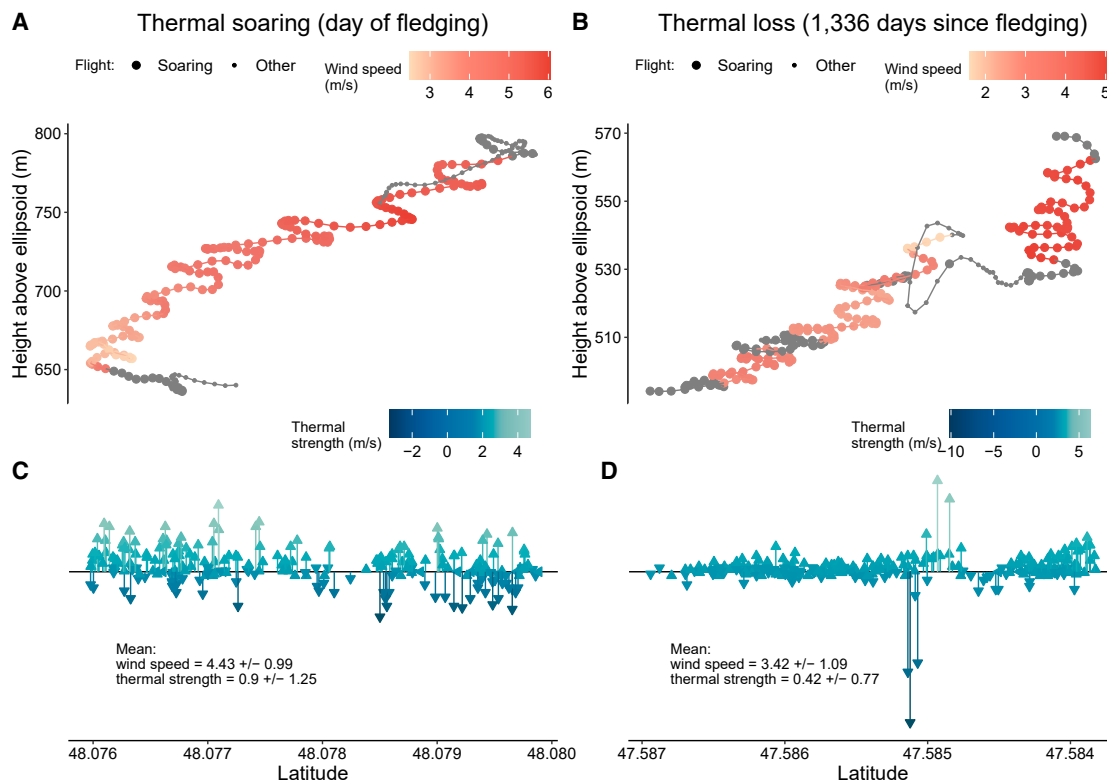


Figure 1. Thermal soaring trajectories with thermal strength and wind speed estimates

(A) Stork trajectory on first flight day.

(B) Stork trajectory during fourth spring migration. Point size indicates flight classification, color scale corresponds to wind speeds (m/s).

(C and D) Vertical speeds (m/s) of the trajectories above colored by thermal strength. Means \pm standard deviation.

See also [Figures S1](#) and [S2](#).

performance in a subset of 27 individuals, all of which were tagged in 2024. Out of these 27 individuals, we detected soaring from nine storks on the day they fledged ([Figure S1](#)) and another 12 birds within a week of fledging ([Figure 1](#); [Figure S2A](#)). An initial increase in time spent thermaling was matched by a decrease in detected flapping flight ([Figure S2](#)).

Although differences were marginal, white storks on their first migrations tended to perform slightly better than they did in later migrations. Younger storks soared with smaller circling radii and higher vertical speeds, indicating that they were soaring near the cores of the thermals where uplift is strongest ([Figure S3](#); [Table S1](#)). Younger storks also showed a slightly smaller standard deviation of the turning angles in thermals, which indicates that they circle smoothly with few corrections ([Figure S3](#); [Table S1](#)). Although strong wind can pose a challenge to thermal soaring as it tilts and shifts thermals, younger storks flew in marginally stronger and more variable winds than older storks did ([Figure S3](#); [Table S1](#)).

Ultimately, the goal of performing well in terms of turning angles, circling radii, vertical speeds, and appropriate responses to wind is to remain inside of a thermal and avoid losing it. We defined losing a thermal as any time that a stork spent at least 10 and fewer than 60 s not thermal soaring between two thermal soaring bouts each lasting at least 30 s. The data contained 48,491 thermals in which we did not detect thermal loss and

7,152 thermals that were lost ([Figures 1A](#) and [1B](#)). Storks lost between 11% and 14% of the thermals they rode each migration, with marginally more losses in spring than in fall ([Figures 2E](#) and [2F](#)). Losing thermals was associated with weak thermals and wind gusts (fall root mean square error [RMSE] = 0.32, spring RMSE = 0.33). In both seasons, thermal strength and age had significant negative effects on thermal loss and deviation in wind speed had a positive effect ([Figures 2G](#) and [2H](#)). Thus, storks were more likely to lose thermals in which they were climbing slowly and experiencing gusty winds, and younger storks were more likely to lose thermals than older storks.

To determine the consequences of these thermal losses for time minimization, we estimated per-hour soaring-gliding efficiency in meters per second. In hours that contained thermal loss, storks of all ages experienced lower soaring-gliding efficiency ([Figures 3A](#) and [3B](#)), gaining less distance per second spent soaring. Thermal loss had a significant negative effect on soaring-gliding efficiency and older storks had lower soaring-gliding efficiency ([Figures 3C](#) and [3D](#), fall RMSE = 0.98, spring RMSE = 0.97).

Finally, we identified flapping—the most energetically costly form of flight—using triaxial accelerometer data. We found that older storks flapped more than younger ones in both seasons (fall $\chi^2(3) = 90$, $p < 2.2e-16$ and spring $\chi^2(3) = 120$, $p < 2.2e-16$, [Table S2](#); [Figure 4](#)). This pattern of older storks

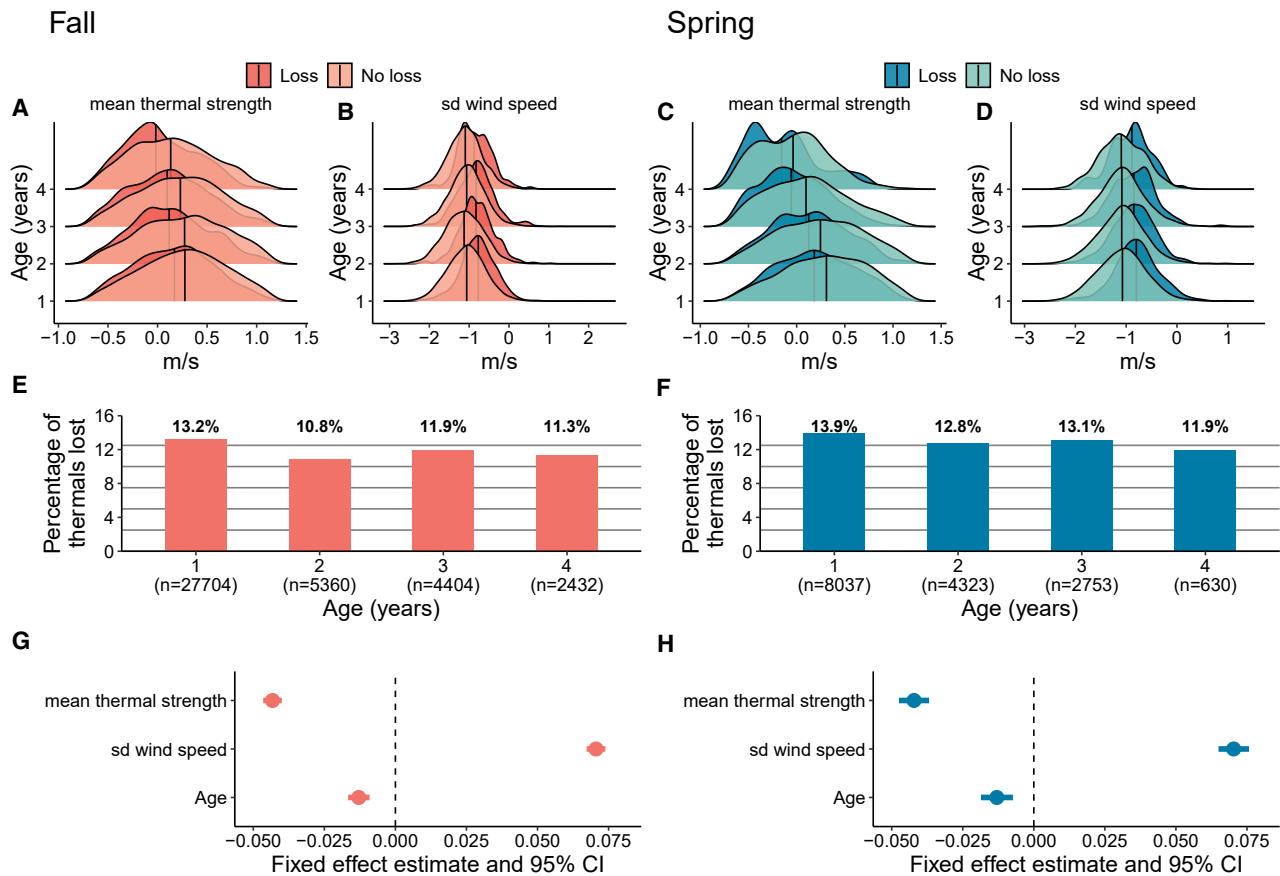


Figure 2. Storks lose weak, windy thermals, especially when young

(A–F) Distributions of mean thermal strength (A) and (C) and deviation in wind speed (B) and (D) in fall (A) and (B) and spring (C) and (D) across different ages, classified by thermal loss or no thermal loss (Box-Cox transformed). Percentages of thermal loss across ages in fall (E) and spring (F). (G and H) Posterior means (centered, scaled) and 95% confidence intervals for fixed effects in linear mixed-effects models. See also [Figures S3](#) and [S5](#) and [Table S1](#).

flapping more was correlated with route straightness ([Figure S4](#)) and strongest in spring, when pressure to rush to the breeding grounds is highest. Flapping was also correlated with time of year, and storks traveling earlier in spring and later in fall tended to flap more ([Figure S5](#)).

DISCUSSION

The development of soaring flight is a fast process that involves multiple steps. Strikingly, soaring flight occurred right after fledging, allowing storks to exhibit efficient flights already in their first migration. Our longitudinal data of the same individuals show that juveniles even slightly outperformed older individuals with regard to simple movement characteristics. This is likely because, with age and the onset of reproduction, storks shifted their migration timing ([Figure S5](#)) and thus encountered deteriorating environmental conditions. However, the decrease in environmental support was not matched by an equal decrease in soaring performance. From early in life, storks were able to locate and ride thermals. Yet, as they gained experience, they were increasingly able to avoid losing thermals under challenging conditions. Thermal loss was strongly influenced by

wind gusts and thermal strength, such that migratory storks encountering weak, wind-blown thermals had higher probabilities of losing those thermals. This was especially true for younger storks, even though they travel under overall superior environmental conditions³¹ ([Figures 2A](#) and [2C](#)). Because thermal loss is associated with reduced soaring-gliding efficiency, successfully remaining inside thermals has a strong effect on the total effort required to complete a migration.

Depending on supportive thermaling conditions limits the movements of soaring birds in space and time.^{32,33} As they gain experience, young storks improve in their use of thermals under sub-optimal environmental conditions. This improvement may allow storks to broaden the set of conditions available to them and shift their migrations. By performing migrations later in fall, older storks may gain a chance to recover from their breeding efforts and defend their nests for as long as possible. By advancing the spring migration, breeding adults can compete to arrive early at the breeding grounds, which can help them to recover from migration, prepare for breeding, and potentially increase the number of young fledged.^{34–36} But because environmental conditions, particularly thermal strength and wind regimes, change over the year, storks on early spring migrations

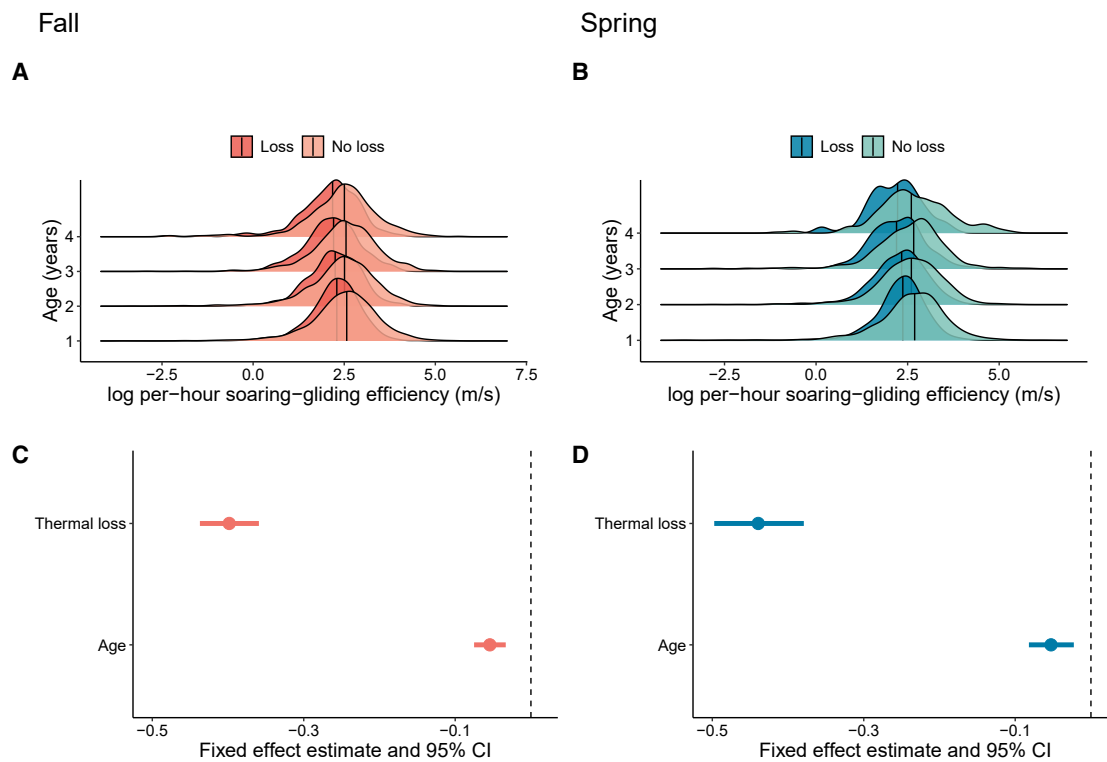


Figure 3. Thermal loss corresponds to reduced soaring-gliding efficiency (meters gained in gliding per soaring second)
(A and B) Distributions of soaring-gliding efficiency in fall (A) and spring (B) across different ages, classified by thermal loss or no thermal loss.
(C and D) Posterior means (centered, scaled) and 95% confidence intervals for fixed effects in lmer model.
See also [Figures S3](#) and [S5](#) and [Table S1](#).

and late fall migrations are faced with less-supportive weather than migrations closer to summer.^{31,37,38} Thus, the task of migration is more difficult for older storks than for young ones, yet we found that their rate of thermal loss (i.e., failure rate) is not higher. This suggests that adults have learned to cope with difficult soaring conditions and that adults choose to migrate at times when they will likely encounter difficult soaring conditions ([Figure S5](#)).

Although flapping flight is energetically expensive and can be exhausting for large birds, older storks flapped more than young ones ([Figure 4](#)). The amount of flapping flight that storks used was particularly high in spring and correlated positively with the straightness of the routes they traveled, delayed fall departure, and advanced spring arrival ([Figures S4](#) and [S5](#)). This relationship between flapping and direct routes traveled at less-supportive times suggests that older birds avoided being limited by supportive soaring conditions by flapping instead, allowing them to select their routes and timing rather than follow patterns of up-lifts. By taking more direct routes, older storks also reduce their migration durations,³⁸ apparently choosing to invest energy to save time. Like soaring, flapping efficiently may be a learned skill. For example, homing pigeons adjust their wing beat frequency and amplitude in response to turbulence.³⁹ Whether that is a learned response and whether it is true of much larger birds have not been addressed, but it is possible that more experienced birds are better at flapping. The increasing flapping rates for older storks could also be supported by superior fueling rates as adults may be more efficient in prey capture⁴⁰ and be able to

out-compete juveniles for access to food resources.⁴¹ This could mean that adults are heavier and have higher costs of transport.⁴² But, if adults have more energy when they begin their migrations, they may not have as much need to save energy and be able to afford more time in energetically expensive flight. As with our findings regarding soaring, these results suggest that adults are choosing to migrate under difficult conditions and coping with that choice.

In comparing storks of different ages, we could not account for the aerodynamic effects of wing and feather morphology. Different parts of a wing serve different purposes and are acted on by different forces.⁴³ The shape of a wing affects lift and drag⁴⁴ and, if adults and juveniles differ in their wing shape,^{45–48} that could explain differences in their soaring performance. For example, juvenile and adult frigatebirds differ in wing shape and soaring performance,⁶ which may be evidence for age-specific optima in flight performance. Whereas some measures of wing morphology have been published for adult white storks,⁴⁴ data from juveniles are not available for comparison. The permeability of individual feathers also affects lift and drag.^{49,50} If individuals or ages differ in the quality of their feathers, that difference could affect comparisons of soaring performance. White storks replace their flight feathers in the breeding season,⁵¹ and individuals that have molted (1+ years old) may have better feathers for harnessing lift.^{52,53} Adults may also groom their feathers more.⁴⁰ However, if older birds do have better feathers, this would not explain our findings that younger birds tended to

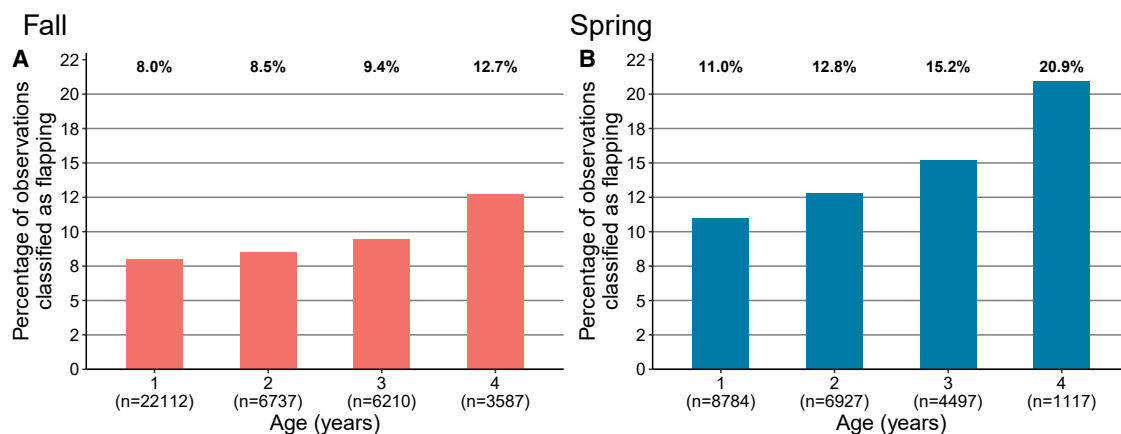


Figure 4. Older birds flap more

Proportion of flight classified as flapping against age in fall (A) and spring (B). See also [Figures S3–S5](#) and [Table S2](#).

have higher vertical speeds. Finally, wing loading is the ratio of a bird's mass to its wing area, and, if ages have consistently different weights,⁵⁴ that could also affect soaring performance. Heavier birds, even with identical wings, have to use larger circling radii and experience lower lift in thermals. White stork weights vary within and between ages, and whether there are consistent differences is unclear (see [STAR Methods](#)).

Our analysis of flight skills in the days following fledging revealed that storks learn remarkably quickly to soar. That some storks soared on their first day outside the nest contrasts with findings from raptors that require 2 weeks or more.^{55–59} White storks probably stay on the nest until later in their development. Many raptors have a post-fledging dependence period during which they are fed by their parents outside the nest. Thus, some raptors may be able to leave the nest more than a week before they are prepared to fly and forage,^{60–62} whereas storks may only fledge once they are developmentally closer to independence. In addition, white storks in this population migrate within 2 months of fledging, potentially motivating them to perform more long-distance flight behaviors than resident birds would,^{59,63} and they are not in a territorial system that would limit their movements through aggression. Regardless of the reason for the difference between fledging in raptors and storks, it is clear that, in principle, soaring is not too difficult a task for fledging storks.

Our results highlight the contradictory pressures on animals of different ages.³⁸ The inherent value of movement is not a fixed quantity. Value is decided by the cost and the benefit of a movement; thus, the same movement can have different payoffs for animals of different ages. The energetic expenditure of flapping between weak thermals may reward adult storks with better breeding opportunities and fewer conflicts but is probably not outweighed for younger individuals that may still have lower success or fail to breed at all.^{35,64} To understand the different performances of age groups, we need first to understand whether and how the value of that performance varies.^{7,24,65–67}

In fact, it is not age groups that make decisions but individuals. Each individual must assess its own needs and whether its internal state and external environment meet those needs. Each

individual will have its own optimal performance based on what maximizes its payoffs, even if that does not reflect the best payoff for another individual. This is rooted in fundamental behavioral ecology, with optimal clutch size⁶⁸ used to demonstrate that optimal strategies (how many eggs to lay) depend on individual variation (territory quality).⁶⁹ Similarly, improvement in a task is itself contextual and individual specific. Here, we found that as they gained experience storks used worse conditions and spent more energy. Yet, defining what constitutes improvement depends on defining the costs to an individual at the time a decision is made and afterward.^{70,71} This cannot be done by examining only one cost (e.g., time, energy, opportunity, and exposure to pathogens or predators) and requires a holistic approach^{4,72–75} to account for the fact that what constitutes the greatest cost to an individual at one point in its life may not cost as much later.^{76,77} This is essentially an n-dimensional reaction norm,⁷⁸ considering that a single genotype (individual) can express different behavioral traits in different internal environments (ages), thus changing the set of optimal solutions to external environmental conditions (weather).^{79,80} This can be extended to consider other behaviors; for example, red deer decrease their social connectedness as they age in response to reduced value of social information and increased infection risk.⁸¹

Across up to eight consecutive migrations, white storks improved in their use of deteriorating weather conditions. Although older storks encountered weaker thermals, they did not lose thermals more than younger birds. However, older storks did have lower soaring-gliding efficiency and use more energetically expensive flapping flight than juveniles did, especially in the pre-breeding spring migration. Our results indicate that the motivation underlying a decision drives what is perceived as the optimal balance of costs and benefits. Experienced storks investing in breeding effort choose to cope with more difficult migratory journeys and inexperienced storks without this pressure choose easier, more energetically rewarding migrations. This demonstrates an ontogenetic rebalancing of movement trade-offs from juveniles saving energy to adults spending energy on opportunities. Thus, defining performance is not as simple as measuring the energetic cost of a

behavior or the time invested in it; rather, whether or not an animal is improving its performance at a task can only be determined in the context of that task.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to, and will be fulfilled by, the lead contact, Hester Brønnevik (hbronnvik@ab.mpg.de).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All raw data necessary to replicate the findings of this study are available on Movebank.org. Files containing only the processed data used in this study have been deposited in an Edmond repository at: <https://doi.org/10.17617/3.9B8VCK>.
- R scripts used for all data acquisition, analyses, and figures are available on GitHub at: https://github.com/hesterbronnvik/stork_flight_performance_public.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

ACKNOWLEDGMENTS

We thank the members of the Collective Migration research group at the Max Planck Institute of Animal Behavior. We thank Alain Chauffoureaux, who provided helpful suggestions. We sincerely thank Wolfgang Fiedler and everyone who helped with the extensive tagging efforts. We thank Elham Nourani, Emily Shepard, and Kamran Safi for several helpful discussions. We also thank Martin Wikelski for his support. Josephina Amaru encouraged the writing. Finally, two anonymous reviewers donated their time to provide helpful comments. Icons in the graphical abstract were created in BioRender. Brønnevik, H. (2025) <https://BioRender.com/1so5nm>. H.B. was supported by the German Research Foundation (DFG, Emmy Noether Fellowship 463925853 awarded to A.F.). A.F. was supported by the German Research Foundation (DFG, Emmy Noether Fellowship 463925853), the Hans und Helga Maus-Stiftung, and the James Heineman research award of the Minerva Stiftung. This research was supported by the Max Planck Society.

AUTHOR CONTRIBUTIONS

A.F. and H.B. designed the study; H.B. performed all analyses; H.B. wrote the first draft of the manuscript, and both authors contributed substantially to revisions.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

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

- [KEY RESOURCES TABLE](#)
- [EXPERIMENTAL MODEL AND SUBJECT DETAILS](#)
- [METHOD DETAILS](#)
 - Tracking data
 - Classifying fledging and migration
 - Classifying flight
 - Estimating wind speed
 - Estimating thermal strength
- [QUANTIFICATION AND STATISTICAL ANALYSIS](#)
 - Quantifying thermal soaring performance
 - Classifying flapping
 - Statistical analysis

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2025.06.044>.

Received: May 9, 2025

Revised: May 9, 2025

Accepted: June 18, 2025

Published: July 11, 2025

REFERENCES

1. Alerstam, T., and Lindström, Å. (1990). Optimal bird migration: the relative importance of time, energy, and safety. In *Bird Migration* (Springer), E. Gwinner, ed. (Springer Berlin Heidelberg), pp. 331–351. https://doi.org/10.1007/978-3-642-74542-3_22.
2. Passino, K.M. (2002). Biomimicry of bacterial foraging for distributed optimization and control. *IEEE Control Syst.* 22, 52–67. <https://doi.org/10.1109/MCS.2002.1004010>.
3. Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., Schröder, B., Buchmann, C.M., Mueller, T., Blaum, N., et al. (2013). Integrating movement ecology with biodiversity research—exploring new avenues to address spatiotemporal biodiversity dynamics. *Mov. Ecol.* 1, 6. <https://doi.org/10.1186/2051-3933-1-6>.
4. Williams, H.J., and Safi, K. (2021). Certainty and integration of options in animal movement. *Trends Ecol. Evol.* 36, 990–999. <https://doi.org/10.1016/j.tree.2021.06.013>.
5. McKinnon, E.A., Fraser, K.C., Stanley, C.Q., and Stutchbury, B.J. (2014). Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. *PLoS One* 9, e105605. <https://doi.org/10.1371/journal.pone.0105605>.
6. Corbeau, A., Prudor, A., Kato, A., and Weimerskirch, H. (2020). Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. *J. Anim. Ecol.* 89, 20–28. <https://doi.org/10.1111/1365-2656.13121>.
7. Penteriani, V., Lamamy, C., Kojola, I., Heikkinen, S., Vermeulen, C., and Delgado, M.M. (2022). Age Ain't Nothing But a Number: factors other than age shape brown bear movement patterns. *Anim. Behav.* 183, 61–67. <https://doi.org/10.1016/j.anbehav.2021.10.020>.
8. Pape Moller, A. (2001). Heritability of arrival date in a migratory bird. *Proc. R. Soc. Lond. B* 268, 203–206. <https://doi.org/10.1098/rspb.2000.1351>.
9. Daunt, F., Afanasyev, V., Adam, A., Croxall, J.P., and Wanless, S. (2007). From cradle to early grave: juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biol. Lett.* 3, 371–374. <https://doi.org/10.1098/rsbl.2007.0157>.
10. Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L.L., Blas, J., Tavecchia, G., Preatoni, D., and Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature* 515, 410–413.
11. Mueller, T., O'Hara, R.B., Converse, S.J., Urbanek, R.P., and Fagan, W.F. (2013). Social learning of migratory performance. *Science* 341, 999–1002. <https://doi.org/10.1126/science.1237139>.
12. Bracis, C., and Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proc. R. Soc. B* 284, 20170449. <https://doi.org/10.1098/rspb.2017.0449>.
13. Efrat, R., Hatzofe, O., Mueller, T., Sapir, N., and Berger-Tal, O. (2023). Early and accumulated experience shape migration and flight in Egyptian vultures. *Curr. Biol.* 33, 5526–5532.e4. <https://doi.org/10.1016/j.cub.2023.11.012>.
14. Harel, R., Horvitz, N., and Nathan, R. (2016). Adult vultures outperform juveniles in challenging thermal soaring conditions. *Sci. Rep.* 6, 27865. <https://doi.org/10.1038/srep27865>.
15. Leung, E.S., Chilvers, B.L., Nakagawa, S., and Robertson, B.C. (2014). Size and experience matter: diving behaviour of juvenile New Zealand

- sea lions (*Phocartos hookeri*). *Polar Biol.* 37, 15–26. <https://doi.org/10.1007/s00300-013-1405-6>.
16. Nourani, E., Faure, L., Brønnvik, H., Scacco, M., Bassi, E., Fiedler, W., Gruebler, M.U., Hatzl, J.S., Jenny, D., Roverselli, A., et al. (2024). Developmental stage shapes the realized energy landscape for a flight specialist. *eLife* 13, RP98818. <https://doi.org/10.7554/eLife.98818>.
 17. Spaar, R., and Bruderer, B. (1997). Optimal flight behavior of soaring migrants: a case study of migrating steppe buzzards, *Buteo buteo vulpinus*. *Behav. Ecol.* 8, 288–297. <https://doi.org/10.1093/beheco/8.3.288>.
 18. Reddy, G., Celani, A., Sejnowski, T.J., and Vergassola, M. (2016). Learning to soar in turbulent environments. *Proc. Natl. Acad. Sci. USA* 113, E4877–E4884. <https://doi.org/10.1073/pnas.1606075113>.
 19. Scacco, M., Flack, A., Duriez, O., Wikelski, M., and Safi, K. (2019). Static landscape features predict uplift locations for soaring birds across Europe. *R. Soc. Open Sci.* 6, 181440. <https://doi.org/10.1098/rsos.181440>.
 20. Fowler, S.L., Costa, D.P., and Arnould, J.P. (2007). Ontogeny of movements and foraging ranges in the Australian sea lion. *Mar. Mamm. Sci.* 23, 598–614. <https://doi.org/10.1111/j.1748-7692.2007.00134.x>.
 21. Grecian, W.J., Stenson, G.B., Biuw, M., Boehme, L., Folkow, L.P., Goulet, P.J., Jonsen, I.D., Malde, A., Nordøy, E.S., Rosing-Asvid, A., et al. (2022). Environmental drivers of population-level variation in the migratory and diving ontogeny of an Arctic top predator. *R. Soc. Open Sci.* 9, 211042. <https://doi.org/10.1098/rsos.211042>.
 22. Matich, P., and Heithaus, M.R. (2015). Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). *Oecologia* 178, 347–359. <https://doi.org/10.1007/s00442-015-3253-2>.
 23. Delgado, M.d.M., Penteriani, V., Nams, V.O., and Campioni, L. (2009). Changes of movement patterns from early dispersal to settlement. *Behav. Ecol. Sociobiol.* 64, 35–43. <https://doi.org/10.1007/s00265-009-0815-5>.
 24. Campioni, L., Dias, M.P., Granadeiro, J.P., and Catry, P. (2020). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: timings and destinations change progressively during maturation. *J. Anim. Ecol.* 89, 29–43. <https://doi.org/10.1111/1365-2656.13044>.
 25. Greenwood, P.J., and Harvey, P.H. (1982). The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13, 1–21. <https://doi.org/10.1146/annurev.es.13.110182.000245>.
 26. Chan, Y.C., Kormann, U.G., Witczak, S., Scherler, P., and Gruebler, M.U. (2024). Ontogeny of migration destination, route and timing in a partially migratory bird. *J. Anim. Ecol.* 93, 1316–1327. <https://doi.org/10.1111/1365-2656.14150>.
 27. Abrahms, B., Teitelbaum, C.S., Mueller, T., and Converse, S.J. (2021). Ontogenetic shifts from social to experiential learning drive avian migration timing. *Nat. Commun.* 12, 7326. <https://doi.org/10.1038/s41467-021-27626-5>.
 28. Teitelbaum, C.S., Converse, S.J., Fagan, W.F., Böhning-Gaese, K., O'Hara, R.B., Lacy, A.E., and Mueller, T. (2016). Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nat. Commun.* 7, 12793. <https://doi.org/10.1038/ncomms12793>.
 29. Duriez, O., Kato, A., Tromp, C., Dell'Omo, G., Vyssotski, A.L., Sarrazin, F., and Ropert-Coudert, Y. (2014). How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PLoS One* 9, e84887. <https://doi.org/10.1371/journal.pone.0084887>.
 30. Watanabe, Y.Y. (2016). Flight mode affects allometry of migration range in birds. *Ecol. Lett.* 19, 907–914. <https://doi.org/10.1111/ele.12627>.
 31. Brønnvik, H., Nourani, E., Fiedler, W., and Flack, A. (2024). Experience reduces route selection for conspecifics by the collectively migrating white stork. *Curr. Biol.* 34, 2030–2037.e3. <https://doi.org/10.1016/j.cub.2024.03.052>.
 32. Shepard, E.L., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A., and Vosper, S.B. (2013). Energy landscapes shape animal movement ecology. *Am. Nat.* 182, 298–312. <https://doi.org/10.1086/671257>.
 33. Williams, H.J., Shepard, E.L.C., Holton, M.D., Alarcón, P.A.E., Wilson, R.P., and Lambertucci, S.A. (2020). Physical limits of flight performance in the heaviest soaring bird. *Proc. Natl. Acad. Sci. USA* 117, 17884–17890. <https://doi.org/10.1073/pnas.1907360117>.
 34. Tryjanowski, P., Sparks, T.H., Ptaszyk, J., and Kosicki, J. (2004). Do White Storks *Ciconia ciconia* always profit from an early return to their breeding grounds? *Bird Study* 51, 222–227. <https://doi.org/10.1080/00063650409461357>.
 35. Vergara, P., Aguirre, I., and Fernández-Cruz, M. (2007). Arrival date, age and breeding success in white stork *Ciconia ciconia*. *J. Avian Biol.* 38, 573–579. <https://doi.org/10.1111/j.0908-8857.2007.03983.x>.
 36. Belabed, B.E., Athamnia, M., Touati, L., Samraoui, F., Bouchecker, A., and Samraoui, B. (2019). The early bird catches the worm: Age-specific arrival time influences reproductive performance in the White Stork *Ciconia ciconia*. *Bird Study* 66, 121–129. <https://doi.org/10.1080/00063657.2019.1618240>.
 37. Acácio, M., Catry, I., Soriano-Redondo, A., Silva, J.P., Atkinson, P.W., and A.M. Franco, A.M.A. (2022). Timing is critical: consequences of asynchronous migration for the performance and destination of a long-distance migrant. *Mov. Ecol.* 10, 28. <https://doi.org/10.1186/s40462-022-00328-3>.
 38. Aikens, E.O., Nourani, E., Fiedler, W., Wikelski, M., and Flack, A. (2024). Learning shapes the development of migratory behavior. *Proc. Natl. Acad. Sci. USA* 121, e2306389121. <https://doi.org/10.1073/pnas.2306389121>.
 39. Lempidakis, E., Ross, A.N., Quetting, M., Krishnan, K., Garde, B., Wikelski, M., and Shepard, E.L. (2024). Turbulence causes kinematic and behavioural adjustments in a flapping flier. *J. R. Soc. Interface* 21, 20230591. <https://doi.org/10.1098/rsif.2023.0591>.
 40. Rotics, S., Kaatz, M., Resheff, Y.S., Turjeman, S.F., Zurell, D., Sapir, N., Eggers, U., Flack, A., Fiedler, W., Jeltsch, F., et al. (2016). The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality. *J. Anim. Ecol.* 85, 938–947. <https://doi.org/10.1111/1365-2656.12525>.
 41. Martins, B.H., Soriano-Redondo, A., Franco, A.M., and Catry, I. (2024). Age mediates access to landfill food resources and foraging proficiency in a long-lived bird species. *Anim. Behav.* 207, 23–36. <https://doi.org/10.1016/j.anbehav.2023.10.011>.
 42. Schmidt-Nielsen, K. (1972). Locomotion: energy cost of swimming, flying, and running. *Science* 177, 222–228. <https://doi.org/10.1126/science.177.4045.222>.
 43. Osváth, G., Vincze, O., David, D.C., Nagy, L.J., Lendvai, Á.Z., Nudds, R.L., and Pap, P.L. (2020). Morphological characterization of flight feather shafts in four bird species with different flight styles. *Biol. J. Linn. Soc.* 131, 192–202. <https://doi.org/10.1093/biolinnean/blaa108>.
 44. Eder, H., Fiedler, W., and Neuhäuser, M. (2015). Evaluation of aerodynamic parameters from infrared laser tracking of free-gliding white storks. *J. Ornithol.* 156, 667–677. <https://doi.org/10.1007/s10336-015-1176-7>.
 45. Mueller, H.C., Berger, D.D., Mueller, N.S., Robichaud, W., and Kaspar, J.L. (2004). Age differences in wing loading and other aerodynamic characteristics of Red-tailed Hawks. *Wilson Bull.* 116, 272–274. <https://doi.org/10.1676/03-070>.
 46. Lish, J.W., Domenech, R., Bedrosian, B.E., Ellis, D.H., and Payton, M. (2016). Wing loading in North American golden eagles (*Aquila chrysaetos*). *J. Raptor Res.* 50, 70–75. <https://doi.org/10.3356/rapt-50-01-70-75.1>.
 47. Graves, G.R. (2017). Sexual monomorphism in wing loading and wing aspect ratio in Black Vulture (*Coragyps atratus*) and Turkey Vulture (*Cathartes aura*). *Proc. Biol. Soc. Wash.* 130, 240–249. <https://doi.org/10.2988/17-00018>.
 48. Cabodevilla, X., Pérez-Tris, J., Moreno-Zarate, L., Pérez-Rodríguez, A., Lima-Barbero, J.F., Camacho, M.C., Villanua, D., Ibáñez, R., Gerboles, A., and Arroyo, B. (2020). Age-related variation in wing shape differs between bird orders: implications for interpretation of the pointedness index (C2 axis) in a Size-Constrained Principal Component Analysis (SCCA). *Ardeola* 67, 341–354. <https://doi.org/10.13157/arla.67.2.2020.ra7>.

49. Geyer, T., Sarradj, E., and Fritzsche, C. (2010). Measurement of the noise generation at the trailing edge of porous airfoils. *Exp. Fluids* 48, 291–308. <https://doi.org/10.1007/s00348-009-0739-x>.
50. Eder, H., Fiedler, W., and Pascoe, X. (2011). Air-permeable hole-pattern and nose-droop control improve aerodynamic performance of primary feathers. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* 197, 109–117. <https://doi.org/10.1007/s00359-010-0592-7>.
51. Hall, M.R., Gwinner, E., and Bloesch, M. (1987). Annual cycles in moult, body mass, luteinizing hormone, prolactin and gonadal steroids during the development of sexual maturity in the white stork (*Ciconia ciconia*). *J. Zool.* 211, 467–486. <https://doi.org/10.1111/j.1469-7998.1987.tb01546.x>.
52. Jovani, R., and Blas, J. (2004). Adaptive allocation of stress-induced deformities on bird feathers. *J. Evol. Biol.* 17, 294–301. <https://doi.org/10.1111/j.1420-9101.2003.00680.x>.
53. Jovani, R., and Rohwer, S. (2017). Fault bars in bird feathers: mechanisms, and ecological and evolutionary causes and consequences. *Biol. Rev. Camb. Philos. Soc.* 92, 1113–1127. <https://doi.org/10.1111/brv.12273>.
54. Berthold, P., van den Bossche, W., Fiedler, W., Gorney, E., Kaatz, M., Leshem, Y., Nowak, E., and Querner, U. (2001). Der Zug des Weißstorchs (*Ciconia ciconia*) eine besondere Zugform auf Grund neuer Ergebnisse. *J. Ornithol.* 142, 73–92. <https://doi.org/10.1007/BF01651740>.
55. Johnson, S.J. (1986). Development of hunting and self-sufficiency in juvenile red-tailed hawks (*Buteo jamaicensis*). *J. Raptor Res.* 20, 29–34.
56. Bustamante, J., and Hiraldo, F. (1989). Post-fledging dependence period and maturation of flight skills in the Black Kite *Milvus migrans*. *Bird Study* 36, 199–204. <https://doi.org/10.1080/00063658909477025>.
57. Ferrer, M. (1992). Regulation of the period of postfledging dependence in the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* 134, 128–133. <https://doi.org/10.1111/j.1474-919X.1992.tb08389.x>.
58. Bustamante, J. (1993). Post-fledging dependence period and development of flight and hunting behaviour in the red kite *Milvus milvus*. *Bird Study* 40, 181–188. <https://doi.org/10.1080/00063659309477181>.
59. Ruau, G., Lumineau, S., and de Margerie, E. (2020). The development of flight behaviours in birds. *Proc. Biol. Sci.* 287, 20200668. <https://doi.org/10.1098/rspb.2020.0668>.
60. Bortolotti, G.R. (1984). Physical development of nestling bald eagles with emphasis on the timing of growth events. *Wilson Bull.* 524–542.
61. Penteriani, V., Delgado, M.d.M., Maggio, C., Aradis, A., and Sergio, F. (2005). Development of chicks and dispersal behaviour of young in the Eagle Owl *Bubo bubo*. *Ibis* 147, 155–168. <https://doi.org/10.1111/j.1474-919X.2004.00381.x>.
62. Delgado, M.M., Penteriani, V., and Nams, V.O. (2009). How fledglings explore surroundings from fledging to dispersal. A case study with Eagle Owls *Bubo bubo*. *Ardea* 97, 7–15. <https://doi.org/10.5253/078.097.0102>.
63. Hertel, A.G., Efrat, R., Reznikov, K., Sapir, N., Berger-Tal, O., and Mueller, T. (2023). Time constraints may pace the ontogeny of movement behaviour. *Proc. R. Soc.* 290, 20222429.
64. Barbraud, C., Barbraud, J.C., and Barbraud, M. (1999). Population dynamics of the White Stork *Ciconia ciconia* in western France. *Ibis* 141, 469–479. <https://doi.org/10.1111/j.1474-919X.1999.tb04416.x>.
65. Gustin, M., and Pizzari, T. (1998). Migratory pattern in the genus *Circus*: sex and age differential migration in Italy. *Ornis Svecica* 8, 23–26. <https://doi.org/10.34080/os.v8.22957>.
66. Martínez-Curci, N.S., Isacch, J.P., D'Amico, V.L., Rojas, P., and Castresana, G.J. (2020). To migrate or not: drivers of over-summering in a long-distance migratory shorebird. *J. Avian Biol.* 51. <https://doi.org/10.1111/jav.02401>.
67. Tavera, E.A., Stauffer, G.E., Lank, D.B., and Ydenberg, R.C. (2020). Oversummering juvenile and adult Semipalmated sandpipers in Peru gain enough survival to compensate for foregone breeding opportunity. *Mov. Ecol.* 8, 42. <https://doi.org/10.1186/s40462-020-00226-6>.
68. Lack, D. (1947). The significance of clutch-size. *Ibis* 89, 302–352. <https://doi.org/10.1111/j.1474-919X.1947.tb04155.x>.
69. Högestedt, G. (1980). Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210, 1148–1150. <https://doi.org/10.1126/science.210.4474.1148>.
70. McNamara, J.M., and Houston, A.I. (1986). The common currency for behavioral decisions. *Am. Nat.* 127, 358–378. <https://doi.org/10.1086/284489>.
71. Houston, A.I., Fromhage, L., and McNamara, J.M. (2024). A general framework for modelling trade-offs in adaptive behaviour. *Biol. Rev. Camb. Philos. Soc.* 99, 56–69. <https://doi.org/10.1111/brv.13011>.
72. MacArthur, R.H., and Pianka, E.R. (1966). On optimal use of a patchy environment. *Am. Nat.* 100, 603–609. <https://doi.org/10.1086/282454>.
73. Alerstam, T. (2011). Optimal bird migration revisited. *J. Ornithol.* 152, 5–23. <https://doi.org/10.1007/s10336-011-0694-1>.
74. Riekkola, L., Andrews-Goff, V., Friedlaender, A., Zerbini, A.N., and Constantine, R. (2020). Longer migration not necessarily the costliest strategy for migrating humpback whales. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 30, 937–948.
75. Boyles, J.G., Johnson, J.S., Blomberg, A., and Lilley, T.M. (2020). Optimal hibernation theory. *Mamm. Rev.* 50, 91–100. <https://doi.org/10.1111/mam.12181>.
76. Senner, N.R., Conklin, J.R., and Piersma, T. (2015). An ontogenetic perspective on individual differences. *Proc. Biol. Sci.* 282, 20151050. <https://doi.org/10.1098/rspb.2015.1050>.
77. Wille, M., and Klaassen, M. (2023). Should I stay, should I go, or something in between? The potential for parasite-mediated and age-related differential migration strategies. *Evol. Ecol.* 37, 189–202. <https://doi.org/10.1007/s10682-022-10190-9>.
78. Woltereck, R. (1909). Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden. *Verh. Dtsch. Zool. Ges.* 1909, 110–172. https://www.zobodat.at/pdf/Verh-dtsch-zool-Ges_19_0107-0252.pdf.
79. Westneat, D.F., Stewart, I.R., and Hatch, M.I. (2009). Complex interactions among temporal variables affect the plasticity of clutch size in a multi-brooded bird. *Ecology* 90, 1162–1174. <https://doi.org/10.1890/08-0698.1>.
80. Araya-Ajoy, Y.G., Mathot, K.J., and Dingemans, N.J. (2015). An approach to estimate short-term, long-term and reaction norm repeatability. *Methods Ecol. Evol.* 6, 1462–1473. <https://doi.org/10.1111/2041-210X.12430>.
81. Albery, G.F., Clutton-Brock, T.H., Morris, A., Morris, S., Pemberton, J.M., Nussey, D.H., and Firth, J.A. (2022). Ageing red deer alter their spatial behaviour and become less social. *Nat. Ecol. Evol.* 6, 1231–1238. <https://doi.org/10.1038/s41559-022-01817-9>.
82. Profus, P. (2006). Population changes and breeding ecology of the White stork *Ciconia ciconia* L. in Poland against a background of the European population. *Synth Studia Nat* 50, 1–155. 9.
83. Kwiecieński, Z., Tryjanowski, P., and Zduniak, P. (2024). Intersexual patterns of the digestive tract and body size are opposed in a large bird. *Sci. Rep.* 14, 15039. <https://doi.org/10.1038/s41598-024-66022-z>.
84. Pennycuik, C.J. (1972). Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* 114, 178–218. <https://doi.org/10.1111/j.1474-919X.1972.tb02603.x>.
85. Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., Aghababian, K., Fakriadis, I., Makrigianni, E., Jerzak, L., et al. (2016). Costs of migratory decisions: a comparison across eight white stork populations. *Sci. Adv.* 2, e1500931. <https://doi.org/10.1126/sciadv.1500931>.
86. Reed, C.A., and Lovejoy, T.E. (1969). The migration of the white stork in Egypt and adjacent areas. *Condor* 71, 146–154. <https://doi.org/10.2307/1366076>.
87. Becciu, P., Panuccio, M., Dell'Omo, G., and Sapir, N. (2021). Groping in the fog: soaring migrants exhibit wider scatter in flight directions and respond differently to wind under low visibility conditions. *Front. Ecol. Evol.* 9. <https://doi.org/10.3389/fevo.2021.745002>.

88. Cheng, Y., Fiedler, W., Wikelski, M., and Flack, A. (2019). "Closer-to-home" strategy benefits juvenile survival in a long-distance migratory bird. *Ecol. Evol.* 9, 8945–8952. <https://doi.org/10.1002/ece3.5395>.
89. Kranstauber, B., Smolla, M., and Scharf, A.K. (2017). *move: Visualizing and Analyzing Animal Track Data* (R package version 3.0.1).
90. Brønsvik, H., Scacco, M., Chimento, M., Bassi, E., Hatzl, J.S., Sumasgutner, P., Tschumi, M., Wikelski, M., Zimmermann, S., Safi, K., et al. (2025). Timing of independence is explained by movement ability, but depends on how independence is defined for a long-lived raptor. Preprint at bioRxiv. <https://doi.org/10.1101/2025.04.21.649390>.
91. Weinzierl, R., Bohrer, G., Kranstauber, B., Fiedler, W., Wikelski, M., and Flack, A. (2016). Wind estimation based on thermal soaring of birds. *Ecol. Evol.* 6, 8706–8718. <https://doi.org/10.1002/ece3.2585>.
92. R Core Team (2024). *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing).
93. Hijmans, R.J. (2022). *Geosphere: Spherical Trigonometry*. R package version 1.5-18.
94. Scharf, A. (2021). *moveACC: Visualisation and analysis of acceleration data (mainly for eObs tags)*. R package version 0.1.
95. Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed- Effects Models Using lme4. *J. Stat. Software* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Processed GPS and ACC data	Edmond repository	https://doi.org/10.17617/3.9B8VCK
Experimental models: Organisms/strains		
White stork (<i>Ciconia ciconia</i>)	See https://doi.org/10.1016/j.cub.2024.03.052	See https://doi.org/10.1016/j.cub.2024.03.052
Software and algorithms		
R code	Github repository	https://github.com/hesterbronnvik/stork_flight_performance_public.git

EXPERIMENTAL MODEL AND SUBJECT DETAILS

White storks are large birds. Adults have wingspans of 2.02 ± 0.10 m^{44, 82} and weigh

$3.22\text{--}3.43$ kg in Poland⁸³ and 3.53 ± 0.53 kg in Southwestern Germany⁴⁴ during the breeding season. Data for wild juveniles are sparse, but juveniles kept in a care center in Northern Germany (and thus assumed to represent healthy individuals) weighed 3.37 ± 0.38 kg⁵⁴. White storks make seasonal, long-distance migrations. To accomplish these long-distance flights in spite of their large size, storks rely on exploiting thermal uplifts,^{84,85} which results in avoiding inclement weather.^{86,87} As they age and begin to breed (at around age 3–4⁶⁴), white storks alter their migration timing, distance, and duration so that they can arrive earlier and stay longer at their breeding sites.^{31,38,40} Whether these broader changes are accompanied by improvements in soaring flight has remained unclear.

Permits for tagging and tracking the white storks were issued by the authorities of the Federal States (G-13/28 and G-268 15/47 by Regierungspräsidium Freiburg, 54- 2532.1-14/14 by Regierung von Mittelfranken, MPI269 O-1/14 by Regierungspräsidium Tübingen, G15-20-032 by LUA Rheinland-Pfalz, ROB-55.2Vet-270 2532.Vet_02-17-95 by Regierung von Oberbayern).

METHOD DETAILS

Tracking data

We used existing data from tracking of white storks (*Ciconia ciconia*) from southwestern Germany. 494 juvenile white storks were tagged on the nest with solar GSM-GPS- ACC tags between 2013 and 2024 (e-obs GmbH, for details see^{38,85,88}). GPS data were transmitted in 1 Hz bursts lasting 300 or 600 seconds and separated by 5 to 15 minutes. Triaxial acceleration (ACC) data were collected in four-second bursts of 10 Hz per axis immediately following the GPS bursts. In total, 151 storks transmitted 1 Hz GPS data over up to four years, generating data from 290 migration tracks as well as 10 Hz ACC data from 223 tracks (Table S3).

Classifying fledging and migration

We defined fledging as the first time the bird flew out of the nest horizontally. Because the radius of GPS error can be larger than the distance of these first flights, we determined fledging times manually to exclude any error.

We identified migration dates using two ground speed thresholds³¹. We defined migratory days as those on which a stork showed at least a 70 km displacement between 02:00 and 20:00. Because young storks tend to start and end their migrations at relatively lower speeds, we then included any days with at least a 40 km displacement within one week of a migratory (70 km) day.

Classifying flight

We used 1 Hz bursts of GPS data to classify thermal soaring and gliding flight. First, we calculated the turning angles and vertical speeds between consecutive flight locations (using the R package *move*⁸⁹). We applied a *k*-means clustering algorithm with *k* = 2 on the average vertical speed to distinguish between soaring (rising) and gliding (sinking) flight. When riding thermals, birds turn in circles to remain inside the pockets of rising air. We defined soaring as thermal soaring if the bird turned at least 10 degrees per second for at least 20 seconds. We then applied three steps of smoothing based on the duration of consecutive behaviors to reclassify behaviors lasting \leq five seconds using the behaviors before and after them. For details see Bronnvik et al.⁹⁰ and supplemental code.

Our classification of flight behaviors yielded 65,071 thermal soaring events that lasted at least 30 seconds and were separated by at least 60 seconds.¹⁹

Estimating wind speed

We estimated the velocity of the wind in each thermal event following Weinzierl et al.⁹¹ (using the package *moveWindSpeed*). The approach assumes that individuals are trying to turn perfect circles to maintain a constant bank angle. Thus any distortion in the observed track from a perfect circle is assumed to be due to wind. The wind speed is estimated as the vector needed to produce the observed distortion from a circle. Estimating wind speeds this way requires that individuals turn consistent circles that last more than 29 seconds, thus not all of the thermal soaring events we identified were useful for wind estimates. Of the 65,071 thermal soaring events that we identified, we obtained wind estimates for 58,413.

Estimating thermal strength

We proxied thermal strength using the vertical speed of a stork at the 1 Hz scale.¹⁹ The vertical speed of a bird inside an uplift is not powered by the bird, but it is affected by the bird's morphology, banking angle, and location within the uplift. In fact, the uplift intensity varies within an uplift and soaring birds will never be in the strongest part of a thermal (angles of bank too high cause sink) or in the weakest (areas not strong enough to carry a bird cause sink). But, assuming that birds are attempting to maximize their realized lift, vertical speed represents the strength of the part of the thermal the bird was in given the physical properties of the bird. For each thermaling event, we took the mean of the 1 Hz vertical speeds to represent the overall uplift strength experienced in that thermal.

QUANTIFICATION AND STATISTICAL ANALYSIS

We performed all statistical analyses in R 4.4.1 ("Race for Your Life"),⁹² with criteria for significance set at $p < 0.05$. Sample size and the other relevant statistical details are provided in the supplemental tables.

Quantifying thermal soaring performance

To describe how individuals used thermals, we took descriptive metrics of each thermal event. We extracted the mean of the wind-corrected circling radii,⁹¹ the standard deviation and the mean of the wind speeds, and the overall vertical speed (total height gained over total time spent) of each thermal.

For each individual in each hour, we estimated soaring-gliding efficiency as the distance of all glides (on the ellipsoid,⁹³) divided by the total seconds classified as thermal soaring.

We defined losing a thermal as any time that a stork spent at least 10 and fewer than 60 seconds not thermal soaring between two thermal soaring bouts each lasting at least 30 seconds. This allowed us to use only soaring that lasted long enough to have wind estimates, and to consider only times that the animals were certainly not moving as they would inside a thermal (Figure 1).

Classifying flapping

For each burst of GPS data that was classified as flight, we classified the following ACC burst as either containing flapping or not. We used the *moveACC*⁹⁴ package to apply a Fast Fourier Transform to the ACC data and then to cluster them using the variance in the largest peak of the wave and the eigenvalue of the wave of the first principle component (see supplemental code for details). This provided us with a True/False identification of flapping in each ACC burst.

Statistical analysis

We used linear mixed-effects models⁹⁵ to explore the effect of age on soaring performance. We used only thermals with thermal strengths in the middle 95% of the data (between 0.20 m/s and 2.63 m/s) to exclude outliers (-0.11 m/s to 0.20 m/s and 2.63 m/s to 8.22 m/s). This left us with 55,643 thermals. For each season, we predicted whether a thermal was lost or not (1/0) using the estimated thermal strength, the standard deviation of the 1 Hz wind speeds, and the age of the stork. We Box Cox transformed both speeds (thermal strength $\lambda = 0.14$, wind speed $\lambda = 0.34$) and standardized all variables by calculating their z-scores. We included individual as a random effect on the intercept.

We explored how changes in flight affect time minimization by comparing soaring-gliding efficiency across ages. We used linear mixed-effects models predicting log-normalized, scaled per-hour soaring-gliding efficiency using whether that hour contained thermal loss (1/0) and scaled age with individual as a random effect on the intercept.

Finally, we explored how changes in flight affect energy minimization by comparing flapping across ages. We used χ^2 proportion tests⁹² to determine whether significant differences existed in the amount of flapping each age transmitted. All the R code used in our analyses is available as a GitHub repository.