

From local collective behavior to global migratory patterns in white storks

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Soaring migrant birds exploit columns of rising air (thermals) to cover large distances with minimal energy. Using social information while locating thermals may benefit such birds, but examining collective movements in wild migrants has been a major challenge for researchers. We investigated the group movements of a flock of 27 naturally migrating juvenile white storks by using high-resolution GPS and accelerometers. Analyzing individual and group movements on multiple scales revealed that a small number of leaders navigated to and explored thermals, whereas followers benefited from their movements. Despite this benefit, followers often left thermals earlier and at lower height, and consequently they had to flap considerably more. Followers also migrated less far annually than did leaders. We provide insights into the interactions between freely flying social migrants and the costs and benefits of collective movement in natural populations.

In many animal taxa, migrations are performed by large social groups (*I*), providing various benefits to individual group members (*2–6*). In heterogeneous groups, coordinated movements frequently generate leader-follower patterns (*7–10*), and individuals may adopt these behavioral strategies, presumably without knowing their own or their group members' roles (*11*). Given interindividual variation within migratory groups, it is necessary to quantify the relationships between each individual to fully understand group dynamics, social influences, and the resulting overall migration patterns. Despite existing knowledge from theoretical work (*12–14*), studying collective movement in wild migratory species has been a major challenge (*15*) because it is nearly impossible to record the simultaneous movements of freely flying animals in large, natural groups with appropriate spatiotemporal resolution.

We approached this question by tagging large numbers of juvenile white storks (*Ciconia ciconia*) with high-resolution tracking devices (Fig. 1, A to E). We recorded the trajectories of 27 GPS-tagged naturally migrating juvenile storks flying in a flock (together with untagged birds; table S1) over ~1000 km during the first 5 days of their migratory journey. Owing to some birds eventually leaving the flock, the number of tagged birds in the flock was 27, 22,

21, 20, and 17 for the first 5 days, respectively. Using solar GSM (Global System for Mobile Communications)–GPS–accelerometer loggers, we recorded triaxial acceleration (at 10.54 Hz for 3.8 s every 10 min) and high-frequency GPS locations (at 1 Hz for 2 or 5 min every 15 min, synchronized in time between individuals; henceforth, GPS bursts) of each individual during the group flights (Fig. 1, F to I). After these 5 days, we continued to monitor each bird's movements throughout their entire lifetime, using GPS and accelerometer recordings at lower resolution (fig. S1).

Similar to other large-bodied soaring migrants (*16–19*), white storks try to reduce the amount of energetically costly flapping flight by exploiting their atmospheric surroundings (*20*). When comparing movement activity among our tagged juvenile birds of the same flock, we found large differences in the amount of costly flapping. For each bird, we calculated a quantitative measure of animal activity from triaxial acceleration data (henceforth, flapping activity; see the methods) (Fig. 1F) (*21, 22*). Although storks flew in close proximity (figs. S2 and S3), flapping activity ranged from 0.8 to 1.8. Thus, to cover the same distance during the same time, some individuals performed considerably more flapping flight than did others. Flapping activity was not influenced by individual features (e.g., body measures or sex) or conditions before fledging (general linear model, $F_{17,8} = 0.798$, $P = 0.671$; table S2). Within-individual differences in flapping activity were stable across the different migration days (table S3).

First, we examined how these differences in flapping activity relate to birds' positions within the group. Exploring group structure in detail is challenging because of the differ-

ent flight modes of soaring migrants (*23, 24*). To examine flock organization during all flight modes, we developed a metric that quantifies time advances or delays (Δt) between each pair of birds, allowing us to measure the time that separates two individuals—i.e., how much time a bird needs to reach the current location of the other bird (figs. S4 and S5). Storks with low flapping activity flew ahead of other flock members on average, whereas storks with high flapping activity flew behind (Pearson's $r = -0.778$, $n = 27$, $P = 1.7 \times 10^{-6}$; Fig. 2A). Next, we found that an individual's position within the flock (Δt) correlated with leadership (*25*) during the gliding segments (Pearson's $r = 0.846$, $n = 27$, $P = 2.7 \times 10^{-8}$; Fig. 2B). Further, following birds tended to have higher flapping activity than did leaders (Pearson's $r = -0.770$, $n = 27$, $P = 2.6 \times 10^{-6}$; figs. S6 and S7). Because leader and follower roles are respectively reflected in the front and back positions in the flock, we refer to birds that are ahead of the flock on average as leaders and those behind as followers (supplementary text and figs. S8 and S9).

Followers not only spent considerably more time flapping their wings, but also spent less time thermalling than did leaders (Pearson's $r = -0.688$, $n = 27$, $P = 7.2 \times 10^{-5}$; Fig. 2C). Followers finished thermalling earlier, at a lower altitude, likely to avoid being isolated from others—thus seemingly failing to exploit the full potential of thermals (fig. S10). In addition, followers flew farther behind, and at lower altitudes, than leaders during glides (Fig. 2D and figs. S11 to S13). Given that the tagged juveniles migrated together with untagged storks, it is likely that the motion of the observed leaders was in fact affected by other, possibly more experienced, adult birds. Juveniles have higher flight costs than adults, but their ability to use thermals effectively improves throughout their journey (*26*). Collective movements may also partly arise from identical reactions to the same environmental features, but in this study we cannot distinguish between responses to environmental and social cues (*27*).

Leaders and followers differed in their path “tortuosity” while flying within the thermals. Leading birds showed irregular circling while thermalling (calculated as the absolute value of the time derivative of the horizontal curvature, $|d\kappa/dt|$), demonstrating that they make considerable adjustments to their flight paths, consistent with a need to locate the center of the complex thermal structures. In contrast, followers circled more regularly, indicating that, as theory has suggested (*24*), followers can benefit from social information to reach the center of thermals; Δt correlates highly with $|d\kappa/dt|$ for individual averages (Pearson's $r = 0.570$, $n = 27$, $P = 0.002$; Fig. 3A). Because every bird spent some time in the front and back half of the flock, we determined each individual's thermalling performance when ahead and behind the center of the flock (Fig. 3B). Almost all exhibited more regular circling and faster

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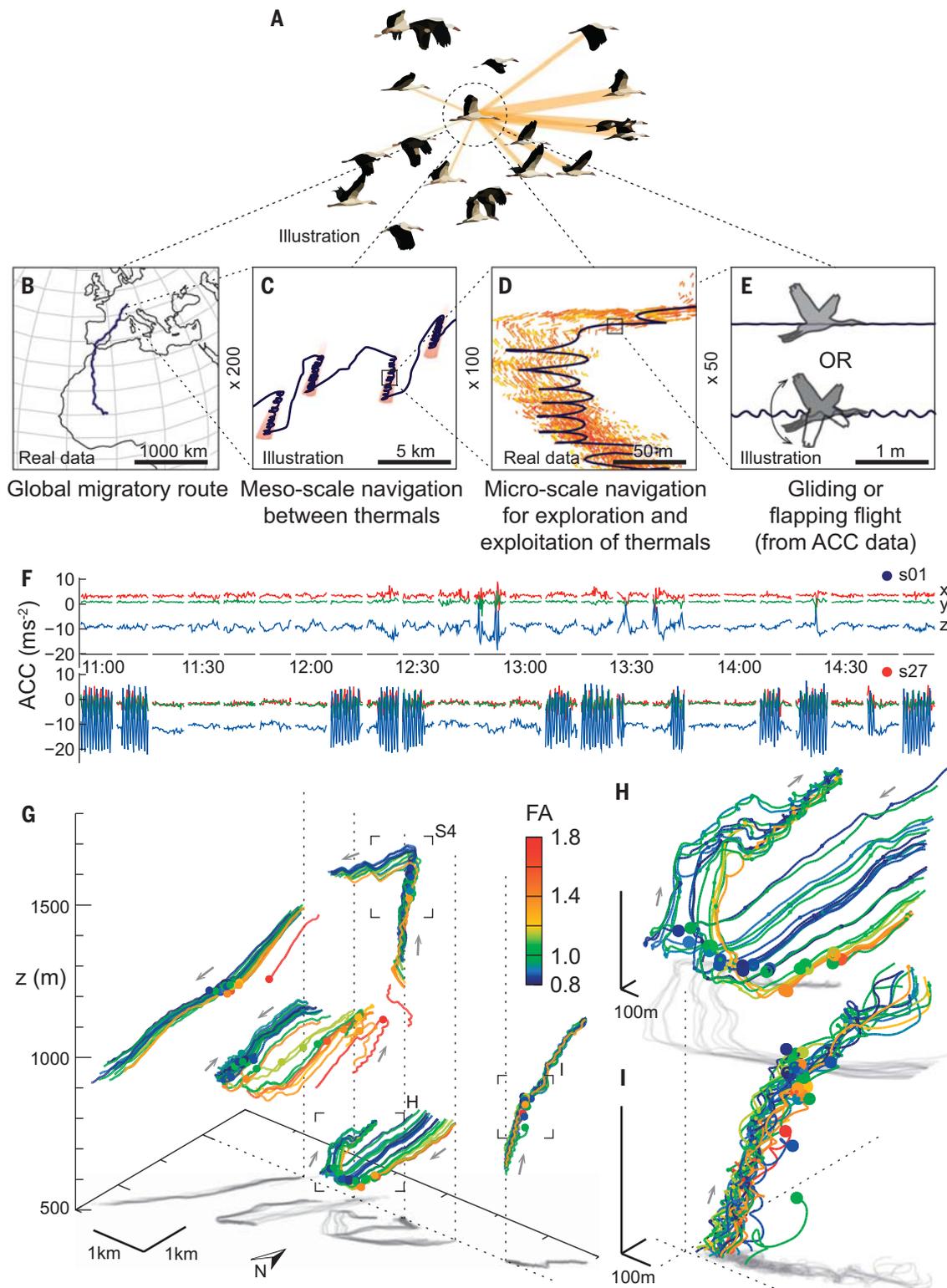
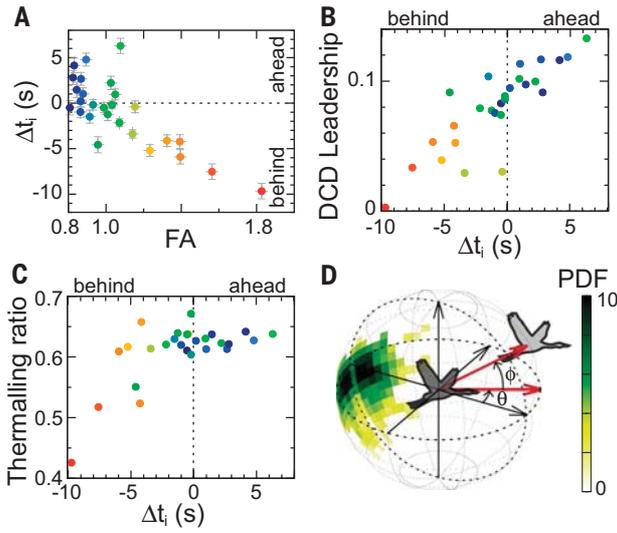


Fig. 1. Collective migration on different spatial scales, recorded using accelerometers and high-resolution GPS. (A to E) Social interactions during migration (A) shape the global migratory route (B) by influencing small-scale navigational decisions [flight behavior between (C) and within (D) thermals] and individual flight performance (E). Arrow color and size in (D) represent coarse-grained local air velocities estimated from the birds' tracks (29). ACC, accelerometer. (F) Sample of triaxial accelerometer data used to calculate flapping activity, defined as the

standardized mean of daily overall dynamic body acceleration. Plots show data for the birds with the lowest (s01; top) and highest (s27; bottom) flapping activity. (G) Five flock trajectories (1-Hz GPS bursts) of migrating storks during thermalling and gliding flight. Bursts are shifted by 1 km for visualization. Gray arrows indicate flight direction. Filled circles show the positions of all individuals at 2 min. Track color corresponds to flapping activity (FA). (H and I) Enlarged view of the tracks marked in (G). The third area marked in (G) is shown in fig. S4.

Fig. 2. Relationship of time advance or time delay (Δt) to leadership and flapping activity and relative positions of leaders and followers.



in a spherical coordinate system during gliding. We placed the focal bird (dark gray; one of the five birds with the lowest flapping activity) at the center of the coordinate system and measured the relative position of another bird (light gray; one of the five birds with the highest flapping activity) using the polar (θ) and elevation angle (ϕ) measured from the focal bird's horizontal flight direction. The probability density function (PDF) shows the relative locations of these birds when both were gliding and $\Delta t \in (2.5 \text{ s}, 7.5 \text{ s})$.

climb rates in thermals when following others than when flying ahead (paired t test, $n = 22$, $P = 0.030$ and 0.018 , respectively; Fig. 3C and figs. S13 and S14).

Examining the complete migratory paths of the 27 birds (at lower temporal resolution) revealed considerable differences in migratory distance, with some birds remaining within Europe and others traveling several thousand kilometers to Africa (Fig. 4). Migratory distance was strongly correlated with the birds' migratory flight behavior; birds that exhibited a high proportion of (costly) flapping activity migrated less far than birds that occupied frontal positions and exhibited low flapping activity when within the flock (Pearson's $r = -0.66$, $n = 20$, $P = 0.001$; Fig. 4, inset). These differences in long-term migration behaviors can be predicted using only a few minutes of movement data from the flock's first migration day (supplementary text and fig. S15). Furthermore, flight time before migration (i.e., total number of GPS bursts in which each bird was found to be flying, before migrating) was also highly correlated with flapping activity (Pearson's $r = -0.648$, $n = 27$, $P = 2.6 \times 10^{-3}$; fig. S16) and migratory distance (Pearson's $r = 0.619$, $n = 20$, $P = 0.004$). The differences in flight performance between leaders and followers suggest that juvenile storks may differ in their aerodynamic features and/or their behavioral strategies, which may affect their migration and group behavior over multiple scales. Nevertheless, birds can compensate for

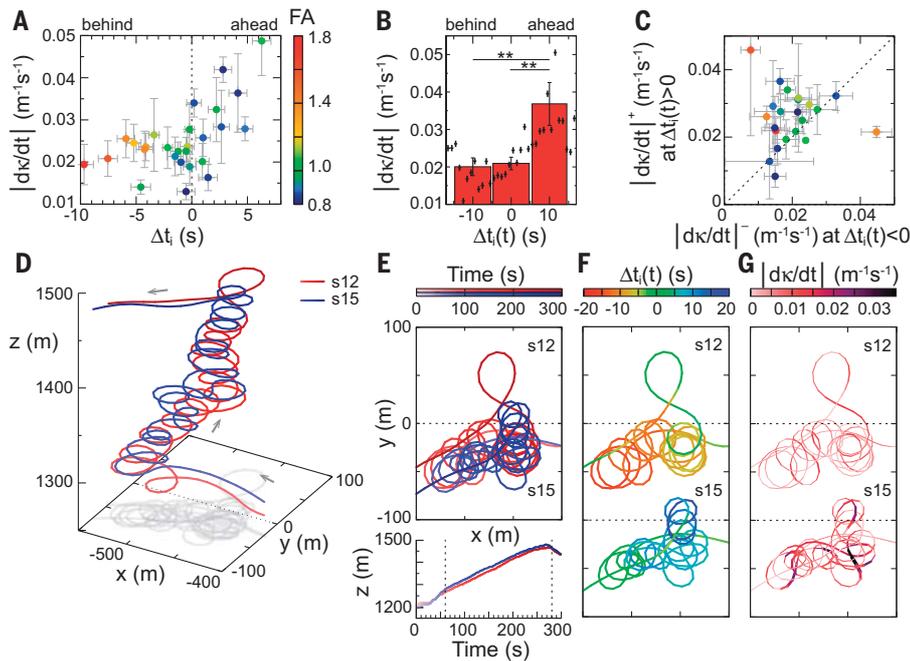


Fig. 3. Derivative of curvature during thermalling flight for leaders and followers. (A) Relationship between the absolute value of the time derivative of horizontal path curvature ($|dk/dt|$) and Δt , averaged for each individual over the first migration day. Error bars, SEM. (B) $|dk/dt|$, calculated using Δt as 1-s (crosses) and 10-s (bars) bins. Error bars represent the standard deviation of the mean (two-tailed t test, $**P < 0.01$, $n = 27$). (C) Relationship between $|dk/dt|$ while flying ahead of ($\Delta t > 0$) and behind ($\Delta t < 0$) the average of the flock. Line, $y = x$. Error bars, SEM. (D) Example trajectories for illustrating the derivative of curvature. Of all bursts that contained thermalling and had a small wind drift, we chose one random example and depicted the most leading (blue) and following (red) individuals, identified on the basis of their Δt (highest and lowest value of that burst, respectively). (E) Horizontal (top) and vertical (bottom) movement components of these tracks. (F and G) Tracks color-coded to show Δt (F) and $|dk/dt|$ (G) (s15 is shifted down for better visualization). $|dk/dt|$ is also indicated by line width.

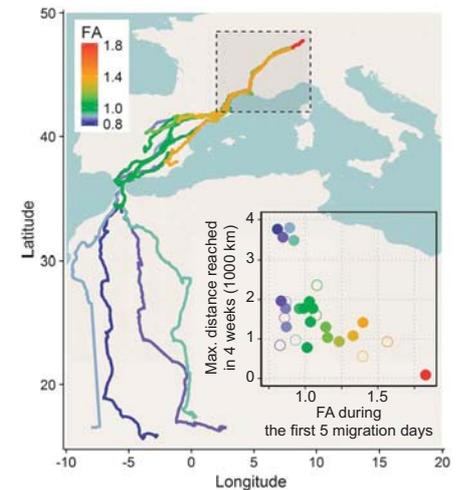


Fig. 4. Relationship between migratory distance and flapping activity. Migration routes of storks during the first 4 weeks of migration. Tracks are color-coded on the basis of the overall flapping activity measured during the high-resolution data acquisition period (black dashed rectangle). The inset shows the relationship between flapping activity and maximum distance reached within 4 weeks. Color corresponds to flapping activity; open circles show birds that died within the first 4 weeks.

their inferior flight skills [e.g., lower glide ratio (ratio of forward speed to sink speed) and more flapping flight] by following others, which enables them to rise faster within thermals (figs. S13 and S14).

Unlike storks, which form large groups with spatiotemporally dynamic structures, other species have been suggested to improve social information usage by flying in V-formation (28). Although the number of studies that use advanced tracking technologies to examine collective migration is increasing (3, 4, 29), the consequences of social behavior and social organization are still largely unknown, especially in wild, freely moving animals. We identified two different behavioral strategies in a flock of migrating white storks, a finding that agrees with theoretical predictions (2). We unraveled mechanisms of collective migration in a natural environment by showing how local-scale leader-follower strategies emerge through a differential exploitation of the atmosphere. We suggest that integrating intraspecific interactions into the study of animal movements will enable a better, more mechanistic understanding of broad-scale ecological processes.

REFERENCES AND NOTES

1. E. J. Milner-Gulland, J. M. Fryxell, A. R. E. Sinclair, *Animal Migration: A Synthesis* (Oxford Univ. Press, 2011).
2. V. Guttal, I. D. Couzin, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 16172–16177 (2010).
3. S. J. Portugal *et al.*, *Nature* **505**, 399–402 (2014).
4. T. Mueller, R. B. O'Hara, S. J. Converse, R. P. Urbanek, W. F. Fagan, *Science* **341**, 999–1002 (2013).
5. N. Chernetsov, P. Berthold, U. Querner, *J. Exp. Biol.* **207**, 937–943 (2004).
6. A. Berdahl, C. J. Torney, C. C. Ioannou, J. J. Faria, I. D. Couzin, *Science* **339**, 574–576 (2013).
7. J. W. Jolles, N. J. Boogert, V. H. Sridhar, I. D. Couzin, A. Manica, *Curr. Biol.* **27**, 2862–2868.e7 (2017).
8. I. D. Couzin, J. Krause, N. R. Franks, S. A. Levin, *Nature* **433**, 513–516 (2005).
9. A. Strandburg-Peshkin, D. R. Farine, I. D. Couzin, M. C. Crofoot, *Science* **348**, 1358–1361 (2015).
10. A. Flack, B. Pettit, R. Freeman, T. Guilford, D. Biro, *Anim. Behav.* **83**, 703–709 (2012).
11. A. J. King, D. D. P. Johnson, M. Van Vugt, *Curr. Biol.* **19**, R911–R916 (2009).
12. A. M. Simons, *Trends Ecol. Evol.* **19**, 453–455 (2004).
13. E. A. Codling, J. W. Pitchford, S. D. Simpson, *Ecology* **88**, 1864–1870 (2007).
14. C. Torney, Z. Neufeld, I. D. Couzin, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 22055–22060 (2009).
15. R. Kays, M. C. Crofoot, W. Jetz, M. Wikelski, *Science* **348**, aaa2478 (2015).
16. H. Weimerskirch, C. Bishop, T. Jeanniard-du-Dot, A. Prudor, G. Sachs, *Science* **353**, 74–78 (2016).
17. S. Sherub, G. Bohrer, M. Wikelski, R. Weinzierl, *Biol. Lett.* **12**, 20160432 (2016).
18. G. Bohrer *et al.*, *Ecol. Lett.* **15**, 96–103 (2012).
19. C. M. Bishop *et al.*, *Science* **347**, 250–254 (2015).
20. A. Hedenstrom, *Philos. Trans. R. Soc. London B Biol. Sci.* **342**, 353–361 (1993).
21. A. C. Gleiss, R. P. Wilson, E. L. C. Shepard, *Methods Ecol. Evol.* **2**, 23–33 (2011).
22. A. Flack *et al.*, *Sci. Adv.* **2**, e1500931 (2016).
23. C. J. Pennycuik, *Ibis* **111**, 525–556 (1969).
24. Z. Ákos, M. Nagy, T. Vicsek, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 4139–4143 (2008).
25. M. Nagy, Z. Ákos, D. Biro, T. Vicsek, *Nature* **464**, 890–893 (2010).
26. S. Rotics *et al.*, *J. Anim. Ecol.* **85**, 938–947 (2016).
27. N. W. Bode *et al.*, *Am. Nat.* **179**, 621–632 (2012).
28. B. Voelkl, J. Fritz, *Philos. Trans. R. Soc. London B Biol. Sci.* **372**, 20160235 (2017).
29. M. Nagy, I. D. Couzin, W. Fiedler, M. Wikelski, A. Flack, *Philos. Trans. R. Soc. London B Biol. Sci.* **373**, 20170011 (2018).

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