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 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 ($\Delta$) correlated with leader ($\Delta$) during the gliding segments (Pearson’s $r = 0.846$, $n = 27$, $P = 2.7 \times 10^{-10}$; Fig. 2B). Further, following birds tended to have higher flapping activity than did leaders (Pearson’s $r = -0.770$, $n = 27$, $P = 2.6 \times 10^{-4}$; 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, $|\delta/dt|$) and $25$ to $17$ 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 fludging (general linear model, $F_{3,26} = 0.798$, $P = 0.671$; 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 different 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 ($\Delta$) 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 $r = -0.779$, $n = 27$, $P = 1.7 \times 10^{-6}$; Fig. 2A). Next, we found that an individual’s position within the flock ($\Delta$) correlated with leader ($\Delta$) during the gliding segments (Pearson’s $r = 0.846$, $n = 27$, $P = 2.7 \times 10^{-10}$; Fig. 2B). Further, following birds tended to have higher flapping activity than did leaders (Pearson’s $r = -0.770$, $n = 27$, $P = 2.6 \times 10^{-4}$; 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).

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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.
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 \( r = -0.648 \), \( n = 27 \), \( P = 2.6 \times 10^{-4} \); 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
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 (29). 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 predictions (ratio of forward speed to sink speed) and their inferior flight skills [e.g., lower glide ratio (48)].

REFERENCES AND NOTES