Current Biology

Spatiotemporal Group Dynamics in a Long-Distance Migratory Bird

Highlights

- Multisensor loggers reveal the spatiotemporal group dynamics of migrating birds

- European bee-eaters (*Merops apiaster*) can migrate ~14,000 km in the same group

- Groups that separate during migration can reform after ~5,000 km apart

- In the non-breeding grounds, groups repeatedly separate and come back together again

Authors

Kiran L. Dhanjal-Adams, Silke Bauer, Tamara Emmenegger, Steffen Hahn, Simeon Lisovski, Felix Liechti

Correspondence

kiran.dhanjal.adams@gmail.com

In Brief

Dhanjal-Adams et al. report on the spatiotemporal group dynamics of migrating bee-eaters using novel lightweight (1.4 g) multisensor loggers. Using synchronisation in pressure measurements, they show how some birds migrate ~14,000 km together, while others repeatedly separate and come back together, despite separations of days or weeks.

CellPress

Current Biology

Report

CellPress

Spatiotemporal Group Dynamics in a Long-Distance Migratory Bird

Kiran L. Dhanjal-Adams,[1,3,*] Silke Bauer,[1] Tamara Emmenegger,[1,2] Steffen Hahn,[1] Simeon Lisovski,[1] and Felix Liechti[1]
[1]Department of Bird Migration, Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland
[2]Institute of Integrative Biology, ETH Zurich, Universitätstrasse 16, 8092 Zürich, Switzerland
[3]Lead Contact
*Correspondence: kiran.dhanjal.adams@gmail.com
https://doi.org/10.1016/j.cub.2018.06.054

SUMMARY

Thousands of species migrate [1]. Though we have some understanding of where and when they travel, we still have very little insight into who migrates with whom and for how long. Group formation is pivotal in allowing individuals to interact, transfer information, and adapt to changing conditions [2]. Yet it is remarkably difficult to infer group membership in migrating animals without being able to directly observe them. Here, we use novel lightweight atmospheric pressure loggers to monitor group dynamics in a small migratory bird, the European bee-eater (*Merops apiaster*). We present the first evidence of a migratory bird flying together with non-kin of different ages and sexes at all stages of the life cycle. In fact, 49% stay together throughout the annual cycle, never separating longer than 5 days at a time despite the ∼14,000-km journey. Of those that separated for longer, 89% reunited within less than a month with individuals they had previously spent time with, having flown up to 5,000 km apart. These birds were not only using the same non-breeding sites, but also displayed coordinated foraging behaviors—these are unlikely to result from chance encounters in response to the same environmental conditions alone. Better understanding of migratory group dynamics, using the presented methods, could help improve our understanding of collective decision making during large-scale movements.

RESULTS

From zebras [3] to monarch butterflies [4], migratory species undertake some of the most extreme feats of endurance known in the animal kingdom. With the advent of novel tracking technologies, we are gradually completing the picture of where and when they travel [5]. However, without being able to directly observe migration [2], we have very little knowledge of who might migrate with whom.

Migratory species are notable for their propensity to aggregate in large numbers. The stability of migratory groups over time can be important in determining survival [6], navigational accuracy [7], migratory speed [8], transfer of information [7], and new migratory behaviors [2]. However, migrating with others is not without risk, as it can increase both disease prevalence [9] and resource competition [10]. Group size typically fluctuates over time and space, with individuals coming together and separating ([11]; hereafter termed "fission-fusion dynamics") as they trade off the different benefits and costs of cooperation [11, 12]. Indeed, resource patches are distant, seasonal, and often unpredictable. One slow individual could, for instance, force the entire group to slow down and miss peaks in resource availability, creating conflict [11]. Groups can therefore either compromise to remain together or split into subgroups, for example, of different migratory speeds.

Fission-fusion can occur without individuals being able to "recognize" each other per se [11]. The same individuals could encounter each other again and again at the same site as a result of migratory connectivity, simply because it is the only one available to them at a particular period [13–15]. Under such circumstances, resource bottlenecks are likely driving group fusion, not social relationships [14]. On the other hand, where resources occur broadly over a large area, animals must coordinate decisions to fuse into a long-term group—especially if they regularly fissure and must find each other again [13, 16]. Only species with high social cognition, such as elephants [17], dolphins [18], and bats [19], have been found to form long-term social bonds by coordinating decisions, despite separations imposed by migration. In birds, long-term social bonds, despite fission-fusion dynamics, have been observed between non-migratory non-kin [20, 21], migratory kin [22], or migratory bonded pairs [23]. Long-term social bonds, despite fission-fusion dynamics, are poorly understood in non-kin migratory birds.

Here, we use novel lightweight (∼1.4 g) multisensor loggers to track the spatiotemporal pattern of group cohesion between 29 European bee-eaters (*Merops apiaster*; Figure S1A) over the annual cycle. Indeed, European bee-eaters are gregarious. They can breed cooperatively, making complex decisions on whether to help another breeding pair, which pair to help, and how much to help them [24]. The species also forages socially [25] and can cooperate with other bee-eater species to mob predators, preen, and forage [26]. In the non-breeding grounds, they form vocal flocks of 8 individuals (on average with a range of 5–40 individuals based on e-bird data from the non-breeding grounds [27]), 8–39 during stopover [28], and 30–100 during migration [29, 30]. However, what is less well established is
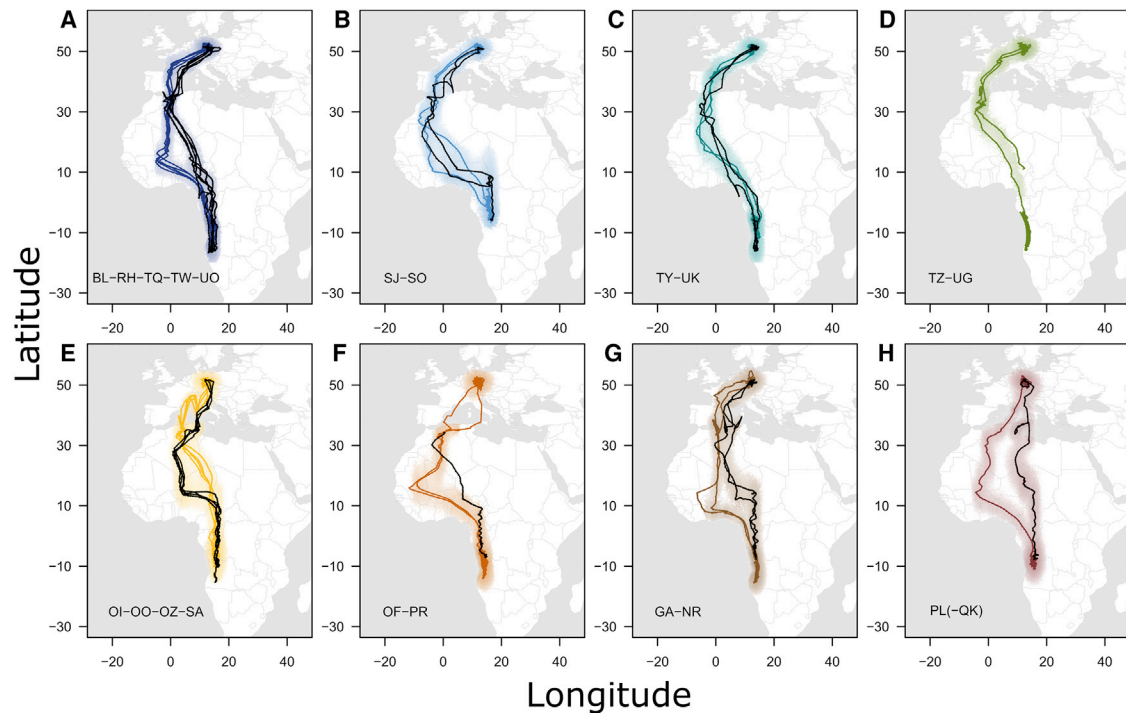
Figure 1. Overlap in Geolocation Estimates

(A–H) For (A) group1: BL-TH-TQ-TW-OU, (B) group 2: SJ-SO, (C) group 3: TY-UK, (D) group 4: TZ-UG, (E) group 5: OI-OO-OZ-SA, (F) group 6: OF-PR, (G) group 7: GA-NR, and (H) group 8: PL-QK. Colored tracks represent migration southward, and black tracks migration northward. Note that QK did not record light, so we have no geolocation estimate for it. Individuals named TW, TZ, UG, and OF stopped recording light during southward migration.

(A), (B), (C), and (D) were all tagged 2016–2017 and (E), (F), (G), and (H) in 2015–2016. See also Figure S1.

how gregariousness might change over time. More specifically, we aim to determine (1) whether birds from the same colony have similar migratory routes, (2) whether they remain together during migration, (3) what the stability of these groups might be, and (4) what the composition of these groups might be.
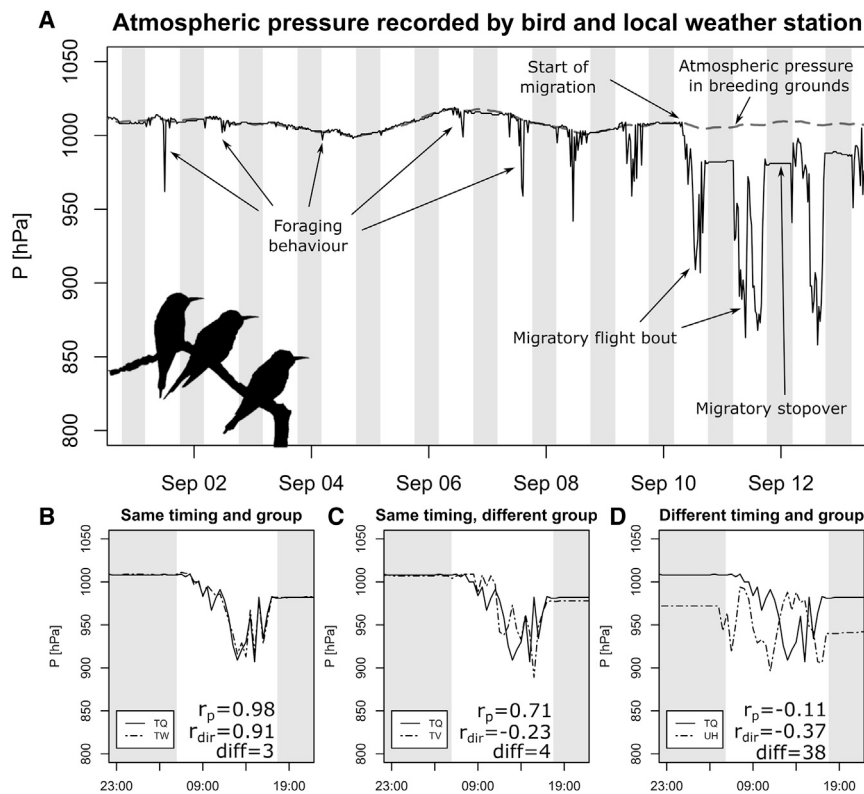
We used novel multisensor loggers to measure both light for geolocation and ambient air pressure for altitudinal changes during the annual cycle (2015–2016 and 2016–2017). To confirm potential groups suggested by geolocation overlap (Figures 1 versus S1B), we applied a hidden Markov model (HMM) to ambient air pressure measurements and identified periods of synchronization in altitudinal changes between birds (Figures 2 and S2). Indeed, altitudinal changes can easily be identified from the pressure measurements: background variations in pressure driven by weather are less than 2 hectopascals (hPa) per hour, while those caused by flight range from 2–205 hPa per hour (equivalent to a change in altitude of 16.89–1934.97 m, assuming a starting pressure of 1000 hPa at 15°C; Figures 2, S2E, and S2F). We assume that if these highly dynamic altitudinal changes are synchronous, then the decisions to fly/not fly or go up/down and how high/low to go are coordinated between individuals. Thus, if some individuals made the same decision at the same time repeatedly, especially over weeks or months, the decision must have been shared between individuals flying within the same flock.

To test the method, we then compared birds within the same breeding colony (Figure 3A) and found that even birds that were

nesting within 500 m from each were not always classified as having similar pressure signatures (Figures 3A and 3E). Thus, the observed patterns are likely driven by behavior and not overestimated due to geographic proximity or weather fronts (Figures S2E and S2F).

Even within a relatively small sample size of 29 tagged individuals recaptured between 2016 and 2017, 89% formed long-term groups with one or more other tagged individuals outside the breeding grounds (Figures 3, 4, S3, and S4). Many groups formed in the breeding grounds prior to migration (Figures 3A and 4), with none of the recaptured individuals having bred together before (Table S1). In total, we identified one group of five individuals (group 1), one group of four (group 5), and six groups of two (groups 2, 3, 4, 6, 7, and 8; Figures 1, 3, and 4). The group of four (group 5; i.e., 19% of grouped birds) persisted throughout the annual cycle, covering 14,000 km together (Figures 1, 3, and 4). HMMs never classified these individuals as having separated during migration (Figure 4). Only during the non-breeding residency period did we observe individuals breaking into subgroups for short periods of no longer than 5 days (e.g., November 2–6, 2016; Figure S3K).

For two groups (1 and 6; i.e., 33% of grouped birds), fission occurred during southward migration for 5 and 4 days, respectively (Figures S4A, S4B, S4M, and S4N). Group 1 fissured into two subgroups while crossing France, while group 6 fissured while crossing Algeria (Figures S4A and S4M). Both groups fused again to remain stable during the rest of migration, crossing the

A Atmospheric pressure recorded by bird and local weather station

Start of migration

Atmospheric pressure in breeding grounds

Foraging behaviour

Migratory flight bout

Migratory stopover

B Same timing and group

$r_p = 0.98$
$r_{dir} = 0.91$
diff=3

C Same timing, different group

$r_p = 0.71$
$r_{dir} = -0.23$
diff=4

D Different timing and group

$r_p = -0.11$
$r_{dir} = -0.37$
diff=38

Figure 2. Examples of Raw Air Pressure Measurements in Hectopascals

(A–D) For bird (A) TQ in September 1–13, 2016 compared with pressure for (B) TW, (C) TV, and (D) UH on September 10. Gray shading represents nighttime periods for TQ derived from geolocation. We only consider pressure during daytime because this is the period when birds are actively changing altitude and is therefore less likely to be similar when birds are not together. Indeed, looking at raw atmospheric temperature measurements in (A) for TQ (in black), we can see that they follow the same background pressure variations recorded at the local weather station (in red) until the start of migration. The change in atmospheric pressure during flight bouts is much higher than that of background fluctuations in atmospheric pressure driven by weather (September 1–9 in A) or by geography and topography (September 10–11). It is therefore possible to distinguish between pressure changes caused by flight (during daytime), weather (during nighttime), and geography (from one night to the next). Birds classified as migrating together (B) are birds whose raw pressure measurements are highly correlated (r_p), whose direction and amplitude of altitudinal changes is correlated (r_{dir}), and whose difference in pressure measurements between birds is low (diff). High synchronization occurs between individuals migrating together (B). However, birds can experience similar background pressure conditions while following similar migratory routes without having synchronized behavior (C). Finally, some birds record completely different atmospheric pressure, indicating their migratory behaviors are different (D).

See also Figure S2.

Sahara and spending their non-breeding residency repeatedly coming together and separating (Figures 4A and 4F). Group 1 occasionally formed subgroups for a maximum of 9 days before fusing again (Figure S3G). Group 6 only separated for 1 or 2 days at a time (Figure S3L). Group 1 then migrated north to the breeding grounds as a stable group without separating (Figures 3 and 4). For group 6, fission-fusion dynamics remain unknown, because the pressure logger on individual OF failed during the non-breeding season (Table S1).

All other groups (2, 3, 4, 7, and 8; i.e., 48% of grouped birds) started migration from their breeding grounds to their non-breeding grounds together (Figure 4). Of these bonded birds, 80% (groups 2, 3, 4, and 7) parted from their flight partner while crossing the Sahara (Figures 4 and S4). Of these separated birds, 80% (groups 2, 3, and 4) then came back together, having migrated up to 5,000 km over 1 month separately, in their non-breeding grounds spread across Cameroon, Equatorial Guinea, Gabon, Congo, Democratic Republic of Congo, and Angola (Figures 3, 4, S3, S4D, S4E, and S4I). Pressure loggers failed on both individuals in group 4; however, groups 2 and 3 then started migrating north to the breeding grounds together but separated after crossing the Sahara, only meeting again in the breeding colony (Figures 4, S4H, and S4L).

Also, 17% of birds did not migrate with any tagged birds but repeatedly joined a group in the non-breeding grounds (Figures 3C and S3A–S3F; UT and TV joined TY-UK, AA sometimes joined

TY-UK and sometimes joined TZ-UG, and SH and RZ joined BL-RH-TQ-TW-UO). In fact, two groups (3 and 4) occasionally foraged together in the non-breeding grounds, particularly with UG foraging more often with AA than with its migratory partner, TZ (Figures 3 and S3F), and AA in turn foraging with TY-UK-UT (Figures 3C, S3B, and S3E). Most of these birds were already classed as having foraged together in the breeding grounds prior to migration (Figure 3).

Two breeding pairs formed after migration together: TQ-UO from group 1 and OO-OI from group 5 (Table S1). In fact, UO switched colonies from 2016 to 2017 to breed with TQ, though both birds already foraged together in the breeding grounds in 2016, as did OO and OI in 2015 (Figure 3 and Table S1). Neither pair bred together in the year before they were tagged, suggesting that these migratory groups formed independently from pair formation the previous year (Table S1). In total, eight birds switched breeding colonies, five of which moved to the colony of their travel companion (i.e., UO-TW to the breeding colony of BL-TQ-RH, SJ to SO, TY to UK, and TZ to UG; Figures 3A and 3E and Table S1). All in all, group formation was not consistent with age or sex, and no birds were ever ringed or tagged within the same burrow before this study, indicating they were not likely kin or previously bonded pairs (Table S1). Indeed, roughly 80% of the juveniles from these colonies have been ringed since 2003, and over 95% have been since 2007 [31].
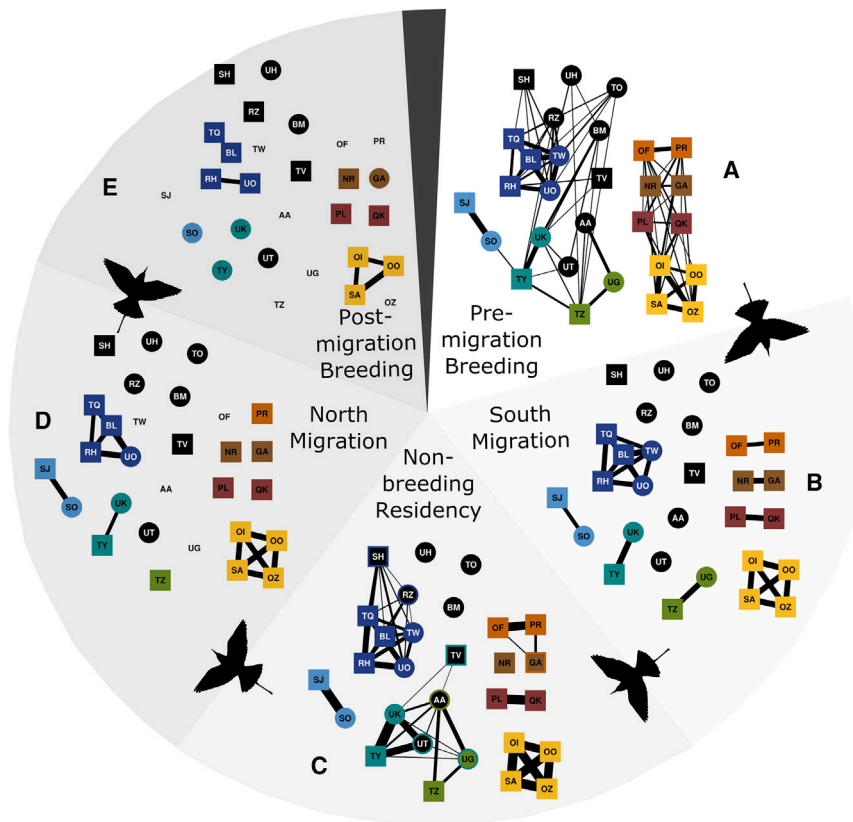
Figure 3. Network Representationn of Interactions between All Tagged Birds

(A–E) Nodes represent individuals and edges represent pairs of birds that were classified as together by a hidden Markov model during (A) pre-migration breeding (i.e., capture), (B) southward migration, (C) non-breeding residency and (D) northward migration, and (E) post-migration breeding (i.e., recapture). In all networks, the thickness of the edges indicates the proportion of time within the season where these bird pairs were classified as together. Warm colors (red/orange/yellow) represent birds tagged in 2015 and recaptured in 2016, while cold colors (blue/green/black) represent birds tagged in 2016 and recaptured in 2017. All nodes are colored according to group, and node shapes represent the breeding colony at which the birds were caught. Note that the air pressure loggers on TW, UG, AA, and OF stopped working before north migration and are therefore not represented as nodes in the network in (D), as were TZ, SJ, OF, PR and OZ in (E). See also Figures S3 and S4.

DISCUSSION

Without physically following birds with an ultralight aircraft [7], it has previously been impossible to monitor spatiotemporal group dynamics in small migrating birds. Here, we show how novel lightweight multisensor loggers can be used to better understand who migrates with whom at all stages of the annual cycle. Indeed, our analyses provide strong evidence for long-term group formation in a small migratory bird both during migration and in the non-breeding grounds between non-kin of mixed age and sex. Though our results do not exclude the possibility of tagged birds forming groups with non-tagged kin, our sample size only included non-kin. This is particularly rare between non-kin, as there is no direct genetic benefit to be gained from remaining together over long periods. In fact, this is some of the first evidence of migratory birds remaining in long-term non-kin groups throughout all stages of the annual cycle. Despite evidence of waterbirds migrating in non-kin groups, most research indicates that these groups still separate into family or same-sex and same-age subgroups, most frequently unpaired juvenile, in the non-breeding grounds [2, 7, 32, 33].

During migration, theory suggests that stable groups may arise as a result of environmental bottlenecks or social interactions [34], with the importance of sociality increasing with decreasing group size [34, 35]. Given that hundreds of bee-eaters migrate simultaneously in flocks of 5–39 individuals [27–30] and that they encounter difficult flight conditions [36], we expected high fission-fusion [11, 34]. Indeed, soar gliding

requires birds to identify suitable thermal updrafts, adjust their speed to navigate within the updraft, and then find the right moment to leave with enough momentum to get to the next updraft [37]. Older individuals are therefore better at navigating this challenge than younger individuals [37], and species such as storks rarely remain together long term despite short-term coordination [38, 39]. It is therefore surprising that all birds remained together during these periods of rapid altitudinal changes for a minimum of 3 weeks, and 45% remained during the entire migratory period, hinting at some social aspects to group stability [34]. Though our data cannot directly measure sociability, it is well documented in the species at different stages of the annual cycle [24–26, 36].

Surprisingly, of the separated migratory groups, 89% reformed again in the Congo Basin [40], an area of roughly 4 million km², with individuals they had previously interacted with in the breeding grounds or on migration Figures 3 and 4). To some degree, non-breeding range can be genetically driven [41], forcing birds into the same region where they form groups due to proximity. For this population, however, the non-breeding ranges are not necessarily overlapping (Figures S1C–S1J) and are sparsely spread out over thousands of kilometers between Gabon and Angola [40]. Given (1) the lack of resource bottlenecks in the region that might force all birds into the same tree or waterhole [11, 34], (2) the fact that non-breeding flocks are relatively small (average size of 8 [27]) [35], and (3) that separated individuals primarily reunited with individuals they had previously spent time with, these reunions may not have occurred by chance. Indeed, the only individual that was tagged over 2 years (OO in 2016 and TO in 2017) returned to the same breeding site both years, suggesting that individuals could be returning to sites that they had used with other flock members in the past. However, the mechanisms by which
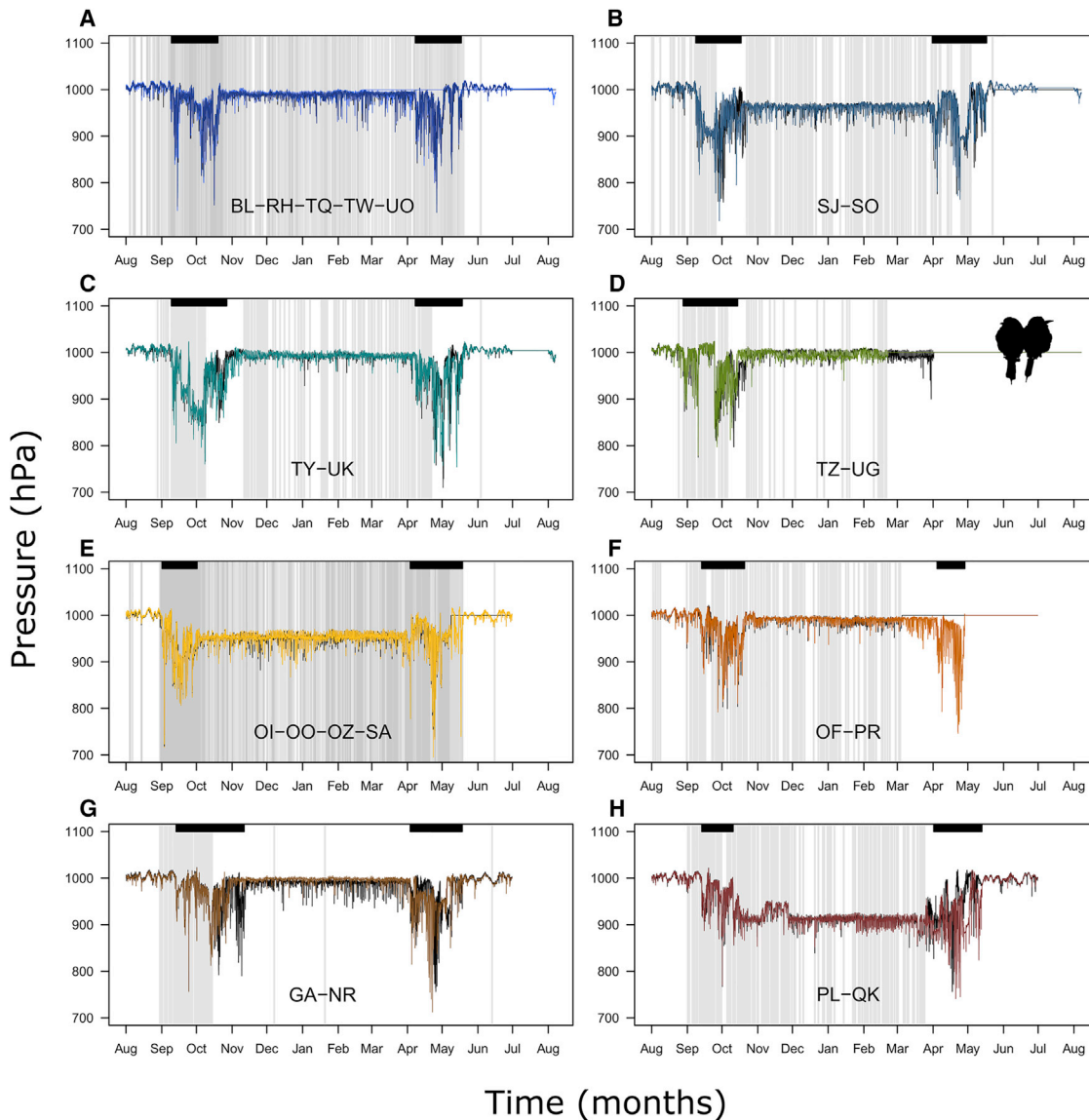
Figure 4. Raw Air Pressure Measurements in Hectopascal for All Groups across the Annual Cycle

(A–H) These illustrate fission-fusion for (A) group1: BL-TH-TQ-TW-OU, (B) group 2: SJ-SO, (C) group 3: TY-UK, (D) group 4: TZ-UG, (E) group 5: OI-OO-OZ-SA, (F) group 6: OF-PR, (G) group 7: GA-NR, and (H) group 8: PL-QK, where the gray background represents periods when the birds were classified as "together." For (A) and (E), there are five and four birds, respectively, within the groups; darker gray represents days when all birds are classed as together and lighter gray when only some birds within the group are classed as together. Black bars represent migratory periods, with the left bar indicating south (post-breeding) migration and the right bar north (pre-breeding) migration.

Note that (A), (B), (C), and (D) were tagged in 2016–2017, and (E), (F), (G), and (H) in 2015–2016. See also Figures S3 and S4.

separated individuals reunited despite long separations remains to be elucidated.

The benefits of cooperation, both in the non-breeding grounds and during migration, may explain the need to reach consensus decisions by maintain long-term groups with non-kin. Indeed, within the non-breeding grounds, grouping can help with predator detection and competition for prime feeding areas, thus increasing fitness and reducing stress levels [33]. Not only can this increase survival, but it can also help maintain a better body condition during migration and increase later reproductive success. During migration, flocking can increase naviga-

tional accuracy [7, 42] either through social learning, where experienced individuals guide less-experienced individuals [2], or through collective learning, where groups pool their knowledge to generate better migratory decisions than solitary individuals [43].

Whether through collective or social learning, being able to transfer information within a group to identify new non-breeding sites allows birds to respond to environmental changes [2, 7]. This could potentially be the case for our study population, whose migratory range has rapidly expanded, with new breeding and non-breeding sites appearing in Europe and the Congo

Basin, respectively [40] (when birds were previously only known to migrate to Western and Southeastern Africa [41]). Given the stability of these non-kin groups, and the rapid emergence of new migratory routes, it is possible that social transfer of information could, in combination with phylogenetic plasticity, be affecting this change. Indeed, though phylogenetic plasticity can allow populations to change migratory routes over generations, behavioral plasticity can allow these changes to occur within the lifespan of an individual.

Overall however, migratory birds are declining more severely than non-migratory birds [44]. Given the current rate and extent of anthropogenic driven changes, adaptability could be key in averting population declines. Disentangling the relative roles of genetic, social, and environmental factors in migration could help understand how collective decision making affects large-scale movements and how new migratory routes might (or might not) arise from social transfer of information and thus how adaptable a species might be to a changing environment.

Conclusions

In conclusion, we find that birds from the same colony do not always follow the same migratory routes but will in fact join with birds from nearby colonies post-breeding to form groups that migrate together. Groups are generally stable during migration. However, if groups separate, they can reunite in the non-breeding grounds to form dynamic groups that repeatedly forage together, sometimes separating for 1–5 days at a time before migrating back to the breeding grounds together. Most surprisingly, these groups showed no age or sex structure and consisted of non-kin. Our research is the first to show such behavior between migratory non-breeding non-kin bird groups, displaying rare spatiotemporal group dynamics more often observed in mammals [17, 19].

STAR★METHODS

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

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Geolocation
  - Ambient air pressure
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and one table and can be found with this article online at https://doi.org/10.1016/j.cub.2018.06.054.

AUTHOR CONTRIBUTIONS

F.L. came up with the initial concept of the paper, K.L.D.-A. performed the analysis and wrote the first draft of the manuscript, T.E. and S.H. collected data, and S.L. and K.L.D.-A. wrote code. K.L.D.-A., S.B., T.E., S.H., S.L., and F.L. developed the concepts of the paper and edited final version of manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Robinson, R.A., Crick, H.Q.P., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F., Forchhammer, M.C., Francis, C.M., Gill, J.A., Godley, B.J., et al. (2009). Travelling through a warming world: climate change and migratory species. Endangered Species Res. 7, 87–99.

2. 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.

3. Naidoo, R., Chase, M.J., Beytell, P., Du Preez, P., Landen, K., Stuart-Hill, G., and Taylor, R. (2016). A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. Oryx 50, 138–146.

4. Urquhart, F., and Urquhart, N. (1978). Autumnal migration routes of the eastern population of the monarch butterfly (Danaus p. plexippus L.; Danaidae; Lepidoptera) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. Can. J. Zool. 56, 1759–1764.

5. Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L., et al. (2011). Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90.

6. Caro, T. (2005). Antipredator defenses in birds and mammals (University of Chicago Press).

7. 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.

8. Portugal, S.J., Hubel, T.Y., Fritz, J., Heese, S., Trobe, D., Voelkl, B., Hailes, S., Wilson, A.M., and Usherwood, J.R. (2014). Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. Nature 505, 399–402.

9. Altizer, S., Bartel, R., and Han, B.A. (2011). Animal migration and infectious disease risk. Science 331, 296–302.

10. Hopcraft, J.G.C., Morales, J.M., Beyer, H.L., Borner, M., Mwangomo, E., Sinclair, A.R.E., Olff, H., and Haydon, D.T. (2014). Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. Ecol. Monogr. 84, 355–372.

11. Sueur, C., King, A.J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C.M., Williams, L., Zinner, D., and Aureli, F. (2011). Collective decision-making and fission–fusion dynamics: a conceptual framework. Oikos 120, 1608–1617.

12. Silk, M.J., Croft, D.P., Tregenza, T., and Bearhop, S. (2014). The importance of fission–fusion social group dynamics in birds. Ibis 156, 701–715.

13. Krause, J., and Ruxton, G.D. (2002). Living in groups (Oxford University Press).

14. Conradt, L., and Roper, T.J. (2005). Consensus decision making in animals. Trends Ecol. Evol. 20, 449–456.

15. Myers, J.P. (1983). Space, time and the pattern of individual associations in a group-living species: Sanderlings have no friends. Behav. Ecol. Sociobiol. 12, 129–134.

16. Krause, J., James, R., and Croft, D.P. (2010). Personality in the context of social networks. Philos. Trans. R. Soc. B Biol. Sci. *365*.

17. Wittemyer, G., and Getz, W.M. (2007). Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. Anim. Behav. *73*, 671–681.

18. Fox, K.C.R., Muthukrishna, M., and Shultz, S. (2017). The social and cultural roots of whale and dolphin brains. Nat. Ecol. Evol. *1*, 1699–1705.

19. Kerth, G. (2008). Causes and Consequences of Sociality in Bats. Bioscience *58*, 737–746.

20. Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F., and Bugnyar, T. (2017). Fission-fusion dynamics over large distances in raven non-breeders. Sci. Rep. *7*, 380.

21. Aplin, L.M., Farine, D.R., Morand-Ferron, J., and Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. Proc. Biol. Sci. *279*, 4199–4205.

22. Scheiber, I.B., Kotrschal, K., Weiß, B.M., and Hemetsberger, J. (2013). The social life of Greylag Geese (Cambridge University Press).

23. Stutchbury, B.J.M., Fraser, K.C., Silverio, C., Kramer, P., Aeppli, B., Mickle, N., Pearman, M., Savage, A., and Mejeur, J. (2016). Tracking mated pairs in a long-distance migratory songbird: migration schedules are not synchronized within pairs. Anim. Behav. *114*, 63–68.

24. Jones, C.S., Lessells, C.M., and Krebs, J.R. (1991). Helpers-at-the-nest in European Bee-eaters (Merops apiaster): a Genetic Analysis. In DNA Fingerprinting: Approaches and Applications, T. Burke, G. Dolf, A.J. Jeffreys, and R. Wolff, eds. (Basel: Birkhäuser Basel), pp. 169–192, 10.1007/978-3-0348-7312-3_13.

25. Campobello, D., and Hare, J.F. (2007). Information transfer determined by association of neighbours in European bee-eater (*Merops apiaster*) colonies. Ethol. Ecol. Evol. *19*, 237–243.

26. Kossenko, S.M., and Fry, C.H. (1998). Competition and coexistence of the European Bee-eater Merops apiaster and the Blue-cheeked Bee-eater Merops persicus in Asia. Ibis *140*, 2–13.

27. ebird (2018). eBird: An online database of bird distribution and abundance (Cornell Lab of Ornithology, Cornell Univeristy).

28. Yosef, R. (2010). Thermoregulatory behavior in migratory European bee-eaters (*Merops apiaster*). Wilson J. Ornithol. *122*, 378–380.

29. Sapir, N., Wikelski, M., Avissar, R., and Nathan, R. (2011). Timing and flight mode of departure in migrating European bee-eaters in relation to multi-scale meteorological processes. Behav. Ecol. Sociobiol. *65*, 1353–1365.

30. López-Gordo, J.L. (1975). Sobre la migración postnupcial del Abejaruco (*Merops apiaster*) en el Estrecho de Gibraltar. Ardeola *21*, 615–625.

31. Arbeiter, S., Schulze, M., Tamm, P., and Hahn, S. (2016). Strong cascading effect of weather conditions on prey availability and annual breeding performance in European bee-eaters *Merops apiaster*. J. Ornithol. *157*, 155–163.

32. Frigerio, D., Weiss, B., and Kotrschal, K. (2001). Spatial proximity among adult siblings in greylag geese (Anser anser): evidence for female bonding? Acta Ethol. *3*, 121–125.

33. Scheiber, I.B.R., Kotrschal, K., and Weiss, B.M. (2009). Benefits of family reunions: social support in secondary greylag goose families. Horm. Behav. *55*, 133–138.

34. Guttal, V., and Couzin, I.D. (2010). Social interactions, information use, and the evolution of collective migration. Proc. Natl. Acad. Sci. USA *107*, 16172–16177.

35. Kao, A.B., and Couzin, I.D. (2014). Decision accuracy in complex environments is often maximized by small group sizes. Proc. Biol. Sci. *281*.

36. Sapir, N., Horvitz, N., Wikelski, M., Avissar, R., Mahrer, Y., and Nathan, R. (2011). Migration by soaring or flapping: numerical atmospheric simulations reveal that turbulence kinetic energy dictates bee-eater flight mode. Proc. Biol. Sci. *278*, 3380–3386.

37. Harel, R., Horvitz, N., and Nathan, R. (2016). Adult vultures outperform juveniles in challenging thermal soaring conditions. Sci. Rep. *6*, 27865.

38. Nagy, M., Couzin, I.D., Fiedler, W., Wikelski, M., and Flack, A. (2018). Synchronization, coordination and collective sensing during thermalling flight of freely migrating white storks. Philos. Trans. R. Soc. B Biol. Sci. *373*.

39. Flack, A., Nagy, M., Fiedler, W., Couzin, I.D., and Wikelski, M. (2018). From local collective behavior to global migratory patterns in white storks. Science *360*, 911–914.

40. Arbeiter, S., Schulze, M., Todte, I., and Hahn, S. (2012). Das Zugverhalten und die Ausbreitung von in Sachsen-Anhalt brütenden Bienenfressern (Merops apiaster). Ber Vogelwarte Hiddensee *21*, 33–40.

41. Ramos, R., Song, G., Navarro, J., Zhang, R., Symes, C.T., Forero, M.G., and Lei, F. (2016). Population genetic structure and long-distance dispersal of a recently expanding migratory bird. Mol. Phylogenet. Evol. *99*, 194–203.

42. Sumpter, D., Buhl, J., Biro, D., and Couzin, I. (2008). Information transfer in moving animal groups. Theory Biosci. *127*, 177–186.

43. Sasaki, T., and Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. Nat. Commun. *8*, 15049.

44. Kirby, J.S., Stattersfield, A.J., Butchart, S.H.M., Evans, M.I., Grimmett, R.F.A., Jones, V.R., O'Sullivan, J., Tucker, G.M., and Newton, I. (2008). Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conserv. Int. *18*, S49–S73.

45. Keil, D. (1995). Der Bienenfresser – Brutvogel im Landkreis Hettstedt. Apus *9*, 1–5.

46. Langen, T.A. (2000). Prolonged offspring dependence and cooperative breeding in birds. Behav. Ecol. *11*, 367–377.

47. Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W., and Hahn, S. (2012). Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol. Evol. *3*, 603–612.

48. Wotherspoon, S., Sumner, M., and Lisovski, S. (2016). TwGeos: Basic data processing for light-level geolocation archival tags.

49. Wotherspoon, S., Sumner, M., and Lisovski, S. (2013). R package SGAT: solar/satellite geolocation for animal tracking.

50. Lisovski, S., and Hahn, S. (2012). GeoLight – processing and analysing light-based geolocator data in R. Methods Ecol. Evol. *3*, 1055–1059.

51. Visser, I., and Speekenbrink, M. (2010). depmixS4: An R Package for Hidden Markov Models. J. Stat. Softw. *36*, 1–21.

52. Galeotti, P., and Inglisa, M. (2001). Estimating predation impact on honeybees Apis mellifera L. by European bee-eaters Merops apiaster L. Rev. Ecol. Terre Vie *56*, 373–388.

53. Killick, R., and Eckley, I.A. (2014). changepoint: An R Package for Changepoint Analysis. J. Stat. Softw. *58*, 1–19.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Merops apiaster	Leipzig, Germany	N/A
Software and Algorithms		
R code available on Mendeley	Mendeley	https://doi.org/10.17632/wrwhbbptg8.2
Datasets		
Raw light and pressure data in addition to modeled tracks	Movebank study 502110670	https://www.movebank.org/panel_embedded_movebank_webapp?gwt_fragment=page%3Dstudies,path%3Dstudy502110670

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Kiran L. Dhanjal-Adams (kiran.dhanjal.adams@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

During July 2015 and 2016, we fitted 77 and 92 multi-sensor loggers (Figure S1; respectively; SOI-GDL3pam, Swiss Ornithological Institute) on European bee-eaters (*Merops apiaster*). These loggers recorded both light for geolocation, and atmospheric pressure for altitudinal changes. Due to the nature of the tag, individuals needed to be recaptured for data to be downloaded. All birds were tagged and recaptured in two breeding colonies (51°36'N, 11°93'E) belonging to a wider population which has established in Saxony-Anhalt since 1990, in the northern expanding front of the species' distribution in Germany [45]. With roughly 30 breeding pairs in 2003, the population is currently estimated at 800 breeding pairs [40], which migrate to non-breeding sites spread out between Gabon and Angola [40]. Being at the expanding front of the species distribution, this population has not yet reached carrying capacity. Breeding is therefore less likely to fail for individuals in this population, than for more southern populations, reducing the pool of potential helpers and therefore the number of cooperatively-breeding groups [46]. In fact, none of the recaptured birds in 2016 and 2017 had bred cooperatively in 2015 and 2016.

We aimed to tag an even mix of males and females, both second year and older adults, with individuals that bred together and individuals that did not breed together. Due to high dispersal and mortality, we did not tag any first-year juveniles. For the same reasons, we recaptured 10 birds in July 2016, and 19 in July 2017 (Table S1). Unfortunately, we were not able to recapture any birds which had bred together in the previous year, though some birds which had not bred together when fitted with loggers did breed with another tagged bird when recaptured (Table S1). Finally, none of the recaptured individuals were caught together within the same burrow in the years before the analysis (roughly 80% of birds have been ringed since 2003 and > 95% since 2007), indicating they were not likely kin, or previously pair-bonded.

METHOD DETAILS

Geolocation

Light-intensity data were recorded at 5 minute intervals and analyzed using a threshold method [47]. Sunrise and sunset events were identified (using the *R package TwGeos* [48] on log transformed light data) and a threshold of 0 (arbitrary units). To define the error distribution of sunrise/sunset times caused by shading (e.g., clouds, habitat) we used the recordings from the beginning of the time series (a day after it was fitted on the bird), until the day before the start of migration (as defined in the next sesction using *changepoint*) as a calibration dataset with known location. The defined error distributing (gamma density distribution with shape = 3.83 ± 1.49 and rate = 0.23 ± 0.07) was then used within the R package *SGAT* [49] to refine track estimates. *SGAT* provides a Bayesian framework which allows us to combine prior information on (i) twilight error distribution, (ii) the flight speed distribution (defined using a relaxed gamma distribution of shape = 1.6 and rate = 0.27), and (iii) a spatial probability mask to ensure birds spend more time on land than at sea with the location estimates. This allows us to refine locations based on a Markov chain Monte Carlo (MCMC) simulations and provide a probability distribution around each estimate (two locations per day). The first and last location was fixed to the breeding site because all birds were captured and recaptured at the same breeding colony (51°36'N and 11°93'E). We first ran a

modifiedGamma model (relaxed assumptions) for 250 iterations to initiate the model, before tuning the model with final assumptions/priors (three runs with 300 iterations). Finally, the model was run for 2000 iterations to ensure convergence.

We then investigated the overlap in the spatial distribution of tracks between all birds. Distributions were first converted to raster format, and grid cell values normalized to sum up to one. We then defined the overlap as the sum of the minimum values of each overlapping grid cell. This was performed for overall tracks, and for each migratory stage, between pairs of birds where tracks were available.

Ambient air pressure

Ambient air pressure data were recorded at 30-minute intervals. Indeed, air pressure varies as a function of weather conditions, geographic location and altitude, creating a unique signature for each bird at a fine temporal resolution. Because background variations in air pressure linked to weather do not exceed 8 hPa per day and 1hPa per hour (Figure S4), while variations in air pressure linked to changes in altitude (i.e., bird flight) range from 2-331 hPa per day and 1-205 hPa per hour (Figure S4), we can identify individual flight events - when they started and stopped, as well as altitudinal variations (Figures 2 and S4). Assuming a starting pressure of 1000 hPa at 20°C for example, the hourly range in pressure during flight of 1-205 hPa is equivalent to an hourly change in altitude of 8.6-1968.6 m. Thus, not only is the range of altitudinal changes observed in these birds high, but so is the rate.

Indeed, bee-eaters are diurnal migrants and preferentially soar-glide as a migratory strategy by manoeuvring from one thermal updraft to the next [36], creating a unique pattern of altitudinal changes at a fine temporal resolution (Figure 2). It is therefore possible to identify whether two birds make the decision at the same time to fly or not fly, to go up or down, and how high or low to fly (Figures S2A–S2E). We assume that if two individuals repeatedly make the same decision at the same time during daytime (Figure 2), especially over weeks or months, then this decision is shared between the two individuals. Indeed, bee-eaters often display complex social interactions, breeding cooperatively [24], mobbing predators, preening and foraging socially (even with other species [26]), as well as socialising on migration with flock members [29].

QUANTIFICATION AND STATISTICAL ANALYSIS

We used a hidden Markov model (HMM) to identify birds with synchronized flight decisions. The HMM classified three variables derived from daytime atmospheric pressure (daytime was identified using the light data by applying the *twilightCalc* function in the package *Geolight* [50]). First, we derived the correlation in atmospheric pressure at time t minus atmospheric pressure at time t+1. This variable represents the synchronization in the direction and amplitude of flight. Second, we derived the correlation in raw atmospheric pressure. This variable is broadly used to find synchronized birds (similar to the latter, but does not distinguish well when birds might have a similar overall patterns, but may not be going in the same direction at a fine temporal scale as seen in Figure 2C). Finally, we derived the median absolute pressure difference between pairs of birds. This is used to ensure that birds in different pressure zones are not classed as together, and that birds whose pressure varies in parallel are classed similarly.

We then used the R package *depmixs4* [51] to classify the three variables into 5 states assuming a gamma distributions for each of the pressure-derived variables. These can be seen in figure S2A with (i) "high difference in pressure between birds," (ii) "medium pressure difference, low correlation in raw pressure and altitudinal changes," (iii) "medium pressure difference, high correlation in raw pressure and altitudinal changes," (iv) "low pressure difference, low correlation in raw pressure and altitudinal changes," (v) "low pressure difference, high correlation in raw pressure and altitudinal changes." The latter was used to class birds as together (Figure S2). Thus, if birds are in a same pressure region, have similar pressure patterns, and are synchronize in the direction in which they are flying, then we assume that the decision to change altitude is synchronized, and that birds must be within the same flock.

It is important to note that although daytime pressure was used to infer coordinated decisions, it cannot be directly correlated to geographic proximity. Indeed, even birds nesting within 500 m of each other in the same breeding colony were not always classified as flying (and therefore foraging socially) together during daytime hours (Figure 3A). In fact, we observed similar numbers of foraging interactions between birds from different colonies (6 km apart) as from birds within the same colony. This is consistent with known bee-eater behavior, where birds forage socially within 3 to 12 km from the colony [52], sometimes even with other bee-eater species [26]. In fact, many birds from our study have been captured in both colonies, even within the same breeding season (e.g., OO in Table S1). The fact that birds from within the same colony are classified as apart despite their close proximity indicates that the classification is not overestimating "togetherness" as a result of geographic proximity, or weather (Figures S2E and S2F).

We then classified the air pressure timeseries for each birds into periods of "migration" and "non-migration," using the R package *changepoint* [53]. This allowed us to identify change points where the standard deviation in ambient air pressure changed state (i.e., changes in state: "not migrating" and "migrating"). Once migration periods were identified for each bird, we defined the overall migration period from when the first bird started migrating to when the last bird stopped migrating. Using these periods, we then broke the air pressure readings for each bird into life cycle stages for the analysis (breeding before migration, southward migration, non-breeding, northward migration and breeding after migration.

CellPress

DATA AND SOFTWARE AVAILABILITY

Code for geolocation and raw pressure data visualization can be viewed as an R markdown html document at https://doi.org/10.17632/wrwhbbptg8.2. Interactive pressure graphics allow the user to explore the raw pressure measurements by zooming in along both the x and y axes by clicking and dragging the mouse over different regions. Double-clicking allows the user to zoom out again. Furthermore, modeled track estimates, raw light and pressure data are stored in Movebank project number 502110670 and are available upon request (https://www.movebank.org/panel_embedded_movebank_webapp?gwt_fragment=page%3Dstudies,path%3Dstudy502110670).