

Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight in ibis

Bernhard Voelkl^{a,b,c,1}, Steven J. Portugal^{d,2}, Markus Unsöld^{e,f}, James R. Usherwood^d, Alan M. Wilson^d, and Johannes Fritz^{c,e}

^aEdward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom; ^bInstitute for Ecology and Evolution, University of Bern, 3032 Hinkerkappelen, Switzerland; ^cInstitute for Theoretical Biology, Humboldt University at Berlin, 10115 Berlin, Germany; ^dStructure & Motion Laboratory, Royal Veterinary College, University of London, Herts AL9 7TA, United Kingdom; ^eWaldrappteam, 6162 Mutters, Austria; and ^fOrnithology Section, Bavarian Zoological State Collection, 81247 Munich, Germany

Edited by Raghavendra Gadagkar, Indian Institute of Science, Bangalore, India, and approved January 13, 2015 (received for review July 17, 2014)

One conspicuous feature of several larger bird species is their annual migration in V-shaped or echelon formation. When birds are flying in these formations, energy savings can be achieved by using the aerodynamic up-wash produced by the preceding bird. As the leading bird in a formation cannot profit from this up-wash, a social dilemma arises around the question of who is going to fly in front? To investigate how this dilemma is solved, we studied the flight behavior of a flock of juvenile Northern bald ibis (*Geronticus eremita*) during a human-guided autumn migration. We could show that the amount of time a bird is leading a formation is strongly correlated with the time it can itself profit from flying in the wake of another bird. On the dyadic level, birds match the time they spend in the wake of each other by frequent pairwise switches of the leading position. Taken together, these results suggest that bald ibis cooperate by directly taking turns in leading a formation. On the proximate level, we propose that it is mainly the high number of iterations and the immediacy of reciprocation opportunities that favor direct reciprocation. Finally, we found evidence that the animals' propensity to reciprocate in leading has a substantial influence on the size and cohesion of the flight formations.

formation flight | cooperation | social dilemma | reciprocity

A considerable portion of the worldwide bird population performs biannual long-distance migrations (1, 2). These journeys impose large energetic costs on the animals, and as a consequence, mortality is considerably higher during migration than at any other time of the year (3). Reasons for this increased mortality during migration include suppressed immune response, starvation, and dehydration, among others (4, 5). In greater snow geese (*Chen caerulescens*), for example, mortality during the autumn migration was estimated at 5% for adult birds and up to 35% for juvenile birds (6). At least a part of this increased mortality can be directly or indirectly linked to the physical exertion during migration flights. Consequently, there should be a strong selection pressure—especially on young birds during their first migration—to minimize energy expenditure during migratory flights and increase the chance of survival. Traveling in close, structured groups has been proposed as an energy-saving strategy, with savings being accrued through positive aerodynamic interactions between members of the group (7–10). Flight in V-shaped or echelon formation by birds is perhaps the most prominent example of this. The precise aerodynamic interactions in a flock have been the subject of detailed theoretical and, more recently, empirical studies (2, 7, 11–14). During flight, high-pressure air under the wings flows around the tips to a region of low air pressure above the wings. This flow forms two vortices in the bird's wake, produced by regions of up-wash outboard of the wings, and a central region of downwash immediately behind the bird (7, 13). This up-wash can provide

a following bird with extra lift, reducing their requirements for weight support. Theoretical calculations, based on fixed-wing aerodynamic theory, suggest that by flying in this up-wash region at optimal wing-tip spacing, birds could save more than 50% of their energy costs relative to unaccompanied solo flight (7, 12, 13).

Analyses of photographs of geese formations suggested that birds fly in a position where they can potentially profit from the beneficial up-wash, although their wing-tip spacings were typically away from the optimal position, and energy savings were estimated to be between 10% and 14% only (13, 14). However, photographs taken from the ground will only provide snapshots of information from long-distance migratory flights and crucially lack information about precise positioning and height. Recent advances in bio-logging have now allowed the study of this phenomenon in greater detail. The first study to provide empirical evidence that energetic savings can be garnered from V-formation flight was done by Weimerskirch et al. (15), who demonstrated that heart rate, a proxy for energy expenditure, was lower in those birds flying in the middle of a V-formation compared with the bird positioned at the front. Studying the migratory flight pattern of a group of Northern bald ibises (*Geronticus eremita*), Portugal et al. (16) demonstrated that birds, when flying in

Significance

Cooperation in animals is an enigma because it contravenes the basic notion that evolution favors selfish genes that promote only their own well-being. Bird migration in organized V-shaped or echelon formations constitutes such a cooperation dilemma. We show that juvenile Northern bald ibis (*Geronticus eremita*) cooperate by taking turns and precisely matching times they spend in the advantageous trailing position and in the disadvantageous front position. This time matching is done on a pairwise level. Furthermore, we found evidence that the animals' propensity to reciprocate in leading has a substantial influence on the size and cohesion of the flight formations. This study shows that direct reciprocation can enable cooperation between animals in a natural context.

Author contributions: B.V., A.M.W., and J.F. designed research; B.V., S.J.P., M.U., and J.F. performed research; B.V. and S.J.P. analyzed data; and B.V., S.J.P., M.U., J.R.U., A.M.W., and J.F. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

Data deposition: Complete raw data are provided as [Dataset S1](#).

¹To whom correspondence should be addressed. Email: bernhard.voelkl@zoo.ox.ac.uk.

²Present address: School of Biological Sciences, Royal Holloway, University of London, Surrey TW20 0EX, United Kingdom.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1413589112/-DCSupplemental.

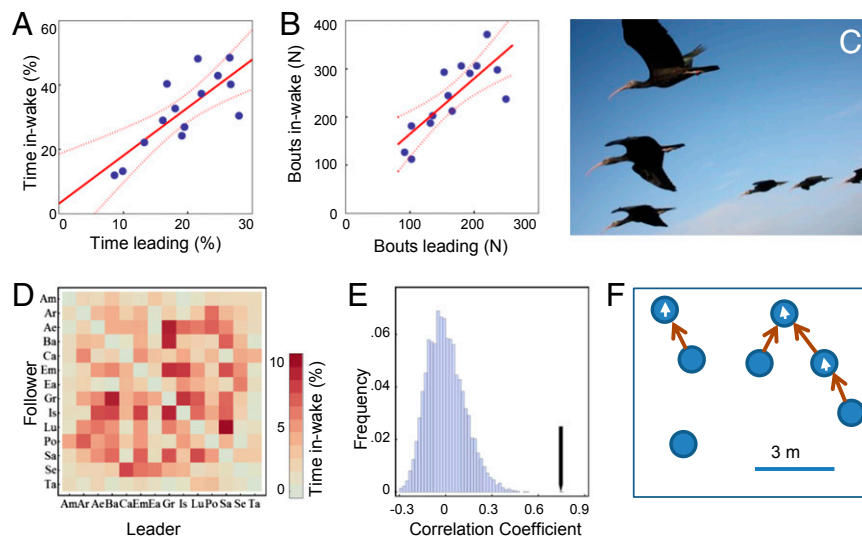


Fig. 1. In-wake flying in Northern bald ibis. (A) Percentage of time leading a formation is plotted against the percentage of time flying in the wake of another bird. (B) Number of bouts leading a formation is plotted against the number of bouts flying in the wake of another bird. (C) Northern bald ibis (*G. eremita*) flying in tight formations. Image courtesy of M. Unsöld. (D) Matrix plot of the percentages of time flying in the wake of a specific bird for all 14 birds. Rows and columns give the 14 subjects (names abbreviated). (E) Histogram for the expected Pearson product moment correlation coefficient assuming random associations based on 10,000 random matrix permutation and the observed value (black arrow). (F) Representation of the flock as a graph where vertices indicate individuals and a direct edge is drawn from vertex i to vertex j if bird i was in the wake of bird j , where “in the wake” is defined as being within an area of 3 m behind and 1.6 m lateral to the preceding bird. Behind and lateral are defined relative to the flight direction of the preceding bird (indicated by white arrows inside the vertices). In this hypothetical example, a flock of seven birds, consisting of one formation of four individuals (an asymmetric V-formation), a separate pair formation of two individuals (echelon formation), and an isolated bird would be represented by a graph consisting of two weakly connected components of sizes four and two, respectively, and one isolated vertex.

formation, favored positions that allowed them to profit from the up-wash. Furthermore, the birds also coordinated their wing flaps with a phase shift mechanism such that their wingtips followed the path of the preceding bird’s wing tips through the air, allowing them to maximize the capture of beneficial up-wash through positive aerodynamic interactions.

However, not all birds in a formation can profit to the same extent. In particular, the leading individual in the front will have no energetic advantage in comparison with flying alone. Consequently, a cooperation dilemma arises around the question of who is going to fly in the front position? From an evolutionary perspective, cooperation between unrelated individuals is difficult to explain as it seems to contravene the basic notion that natural selection favors “selfish” genes that promote only their own well-being. Game theoretic models have been repeatedly applied to explain under which conditions cooperation can be an evolutionary stable strategy (17–19). Formation flight in migrating birds resembles a multiplayer volunteer’s dilemma where at least one individual in a group has to volunteer (by flying in the front position) to produce a public good, from which all other individuals can profit either directly or indirectly (by flying in the wake of the leader or another bird). For the case where individuals play mixed strategies, i.e., they volunteer with a given probability, there exists a certain probability value for volunteering which is an evolutionary stable strategy (20). That is, in a population where all individuals volunteer with a certain probability, single individuals cannot gain higher fitness by volunteering more or less frequently. The value for this probability depends on the group size and the expected benefits and costs (20, 21).

To investigate how this cooperation dilemma can be resolved, we equipped a group of juvenile Northern bald ibis with high-precision global positioning system/inertial measurement unit (GPS/IMU) data loggers (22, 23) that allowed us to monitor the flight behavior of all individuals within the flock during a human-guided autumn migration. In this study, we could, for the first time to our knowledge, determine the relative position of the

birds to each other during free-flying migratory flight—a feat that was made possible due to recent advances in sensor technology. These data enable us to estimate how much time each bird spent leading a formation or trailing another bird.

Results

During the migratory flight, the birds formed a cohesive flock with a median distance to the center of mass of the flock of 5.0 m (range, 3.6–11.2 m; Fig. S1B). Summing up relative positions of the birds over the whole flight, we find a blurred V-shaped formation (Fig. S14 and Movie S1), although the overall formation shape was variable over time (16). Positions of individuals within the flock changed frequently (Fig. S2), but individuals were most often in an area where—according to aerodynamic theory—they can profit from the up-wash produced by the wings of the preceding bird (16). Based on these findings, we defined that a bird was in the wake of another bird if it was at a given time point in a rectangular area of up to 3 m behind and 1.6 m lateral to either side of the preceding bird (see SI Text and Table S1 for a discussion of this criterion). On average, birds spent $32 \pm 12\%$ of their time in the wake of another bird, although bouts of continuous flying in the wake of another bird were relatively short (median, 2 s; interquartile range, 1–4 s; maximum, 41 s), and birds frequently changed the conspecific they followed, resulting in 241 ± 74 bouts of in-wake flying per bird for a flight of 39 km.

Based on our definition of “in-wake,” we can define a formation (in contrast to a flock) as any assemblage of animals consisting of one leading bird and one or more trailing birds flying either in the wake of the leading bird or of one of the other trailing birds (Fig. 1F). Thus, although the size of the flock was constant during the flight ($n = 14$), formation sizes—the number of animals constituting a formation—were highly variable depending on whether individuals were flying close enough to be considered as constituting a formation. We observed pair formations consisting of only two individuals most often, making up 60.7%

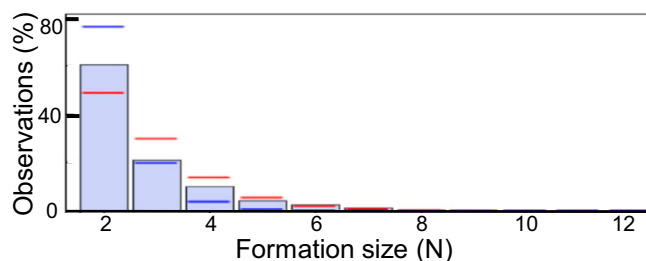


Fig. 3. Observed and predicted formation sizes. Bars give the percentage of observed formation sizes at a sample interval of one second. Red lines indicate predictions based on model I assuming a general individual preference to follow any other bird. Blue lines indicate predicted values based on model II assuming individual preferences for specific birds.

be seen that model I predicts the observed formation sizes reasonably well (Kolmogorov–Smirnov test for goodness of fit: $g_{\max} = 0.23$, $P = 0.89$; Fig. 3), although it underestimates the number of pair formations while slightly overestimating the number of larger formations. In the second model, we assumed additionally that each bird differentiates between conspecifics and has a different propensity for following each individual bird. This time the model overestimates the number of pair formations and underestimates the occurrence of larger formations ($g_{\max} = 0.46$, $P = 0.12$). This result suggests that the observed formation sizes can be largely explained by a mixture of two simple models that assumes that the birds have (i) a certain tendency to fly behind another bird and (ii) preferences for specific individuals. Additional assumptions about group coordination, communication, or other mechanisms to increase group adhesion are not required.

Discussion

Formation flight in migrating birds is a cooperation dilemma, because only the trailing birds can profit from the beneficial up-wash produced by the leading bird. On this migration leg, all birds managed to fly in the wake of another bird for a notable proportion of the whole flight time. This finding and the high correlation on the individual level between leading a formation and flying in the wake of another bird are in line with the notion that the birds actively seek positions in the wake of other birds and that they take turns in leading. However, as a single observational study cannot deliver unequivocal proof that these findings imply cooperation based on direct reciprocity, we would like to discuss potential alternative explanations for the observed patterns before elaborating more on the evidence for direct reciprocity and its potential implications.

First, we have to consider the possibility that birds travel in flocks, where each bird is trying to stay close to the other birds, but without actively seeking to get into an aerodynamically advantageous trailing position. We used a simulation approach to generate predicted values for the proportion of in-wake flying and the correlations for leading and following that we should expect in such a case. As the observed values were much higher than the predicted ones (i.e., 32% of in-wake flying as contrasted to an expected value of 1%; *Results*), we argue that this assumption alone cannot sufficiently explain the reported patterns. A second possibility to consider is that the birds actively try to form formations but that they are indifferent about their position within those formations. Direct swaps of position would simply be a result of the leading bird getting exhausted and falling back. In such a case, we should expect that times of in-wake flying would be distributed more or less evenly over all dyads, but this was clearly not the case. Furthermore, if exhaustion of the leading bird was responsible for swaps of position, we should expect that (i) swaps are initiated by the leading bird by losing speed, (ii) the length of bouts should decrease with time as birds should tire, and

(iii) the average time in the leading position should be correlated with the strength of the birds. We could not find support for any of these predictions (Figs. S4F and S5).

Finally, it could be the case that individuals are not cooperating but competing to be in an advantageous position. Given the high percentage of achieved in-wake flying, strong competition seems implausible; however, as we cannot make quantitative predictions for expected times of in-wake flying under competition, we cannot exclude this possibility. The short duration of bouts of in-wake flying and the high number of switches are, generally, in line with predictions for a competitive scenario. However, under strong competition, the time that a bird can stay in the favorable position should depend on its resource holding potential. As body mass is a good indicator for social dominance and energy reserves (within sex and age class), we would expect that heavier birds will be more often in the favorable position. According to aerodynamic theory, on the other hand, heavier birds should have a slightly higher optimal travel speed and might, therefore, gain less from following lighter birds. However, we could not find any evidence for either of these two opposing effects (Fig. S5).

Andersson and Wallander (25) suggested that formation flight in flocks with intermediate or low levels of relatedness could be established by birds reciprocating in taking the lead. Both theoretical and empirical studies have shown that reciprocity in a multiplayer setting is prone to defection and a rather unstable strategy, because it is based on reputation building or image scoring—that requires detailed book keeping of the actions of all other group members (26–29). Reciprocity is easier to maintain on a dyadic level (30–32). The fact that the majority of observed formations are pair formations consisting of only two individuals and the high correlation of in-wake flying on the dyadic level support the idea that direct reciprocity in terms of mutual leading is the key for solving the cooperation dilemma of formation flight in the ibis. This idea is further corroborated by the high percentage of direct swaps and the finding that the distribution of observed formation sizes closely matched the expected distribution for a model based on dyadic attraction. We must note that there might be also alternative explanations for the observed distribution of formation sizes with its high proportion of pair formations. Modeling formation flight using insights from control theory, Seiler et al. (33) argued that oscillations in the relative lateral positioning of the birds accumulate, making it inherently difficult for birds further back in the line to keep the lateral distance to the preceding bird. The strength of dyadic ties during the flight seems not to be correlated with social proximity on the ground, although this observation is in line with findings in pigeons, where social hierarchies on the ground cannot predict leader-follower relationships in the air (34).

We argue that five characteristics of the migration flight are prone to increase the success of direct reciprocity. First, the payoff structure of in-wake flying resembles the structure of a snowdrift game. In the snowdrift game, a noncooperator meeting a cooperator gains the highest payoff, but a noncooperator meeting another noncooperator earns even less from an interaction than a cooperator meeting a noncooperator (SI Text). The iterated snowdrift game is more favorable for the emergence of cooperation than the infamous iterated prisoner's dilemma (29, 35, 36). In the prisoner's dilemma, a co-operator who is exploited by a defector is worse off than a defector who cannot exploit anyone, though this is not the case in the formation flight, where defectors are effectively free riders, who do profit from co-operators but who do not incur any additional costs on them. Second, repeated bouts of in-wake flying facilitate cooperation. The more often two individuals interact in situations where they can cooperate, the higher the potential gains of mutual cooperation (32). For example, the high numbers of opportunities for cooperation have been put forward as one explanation

PNAS

Methods

Data Processing. For each time point, we calculated the relative position of each bird to every other bird in the flock. If a bird was within a rectangular area of up to 3 m behind and 1.6 m lateral (to either side) of another bird, where behind refers to 180° relative to the current flight direction of the preceding bird and lateral refers to 90° or 270°, respectively, and the difference in the altitude of the two birds was less than 1 m, then we considered the bird as flying in the wake of the preceding bird (see [SI Text](#) for

Voelkl et al.

a discussion of this criterion). If, based on this definition, the bird was in wake of more than one individual, we considered it as being in wake of the closest individual in the front of it. Next, we condensed the temporal resolution from 5 to 1 Hz, by splitting the data stream into time bouts of 1 s each, and considering a bird as in-wake during this second, if it was recorded as in-wake for at least three of the five sample points within that second.

Models for the Expected Formation Size and Direct Swaps. We compare the distribution of observed formation sizes with the expected distributions for two null models. For model I, we make the assumption that individuals have given propensities to fly in the wake area of another bird. As estimates for these propensities, we take the observed frequencies of in-wake flying. For model II, we make the additional assumption that birds have individual preferences for other birds. As estimates for these preferences, we take the observed frequencies of dyadic in-wake flying. We define a direct swap as a change of position in a formation where a bird *i* flying in the wake of bird *j* is subsequently flying in front of bird *j* such that bird *j* is in the wake of bird *i*, without any other bird being in the wake of bird *i* between these bouts of in-wake flying. We compared the observed number of direct swaps with expected numbers based on two different models. For the first null model, we assumed choice of the leading individual proportional to individual preferences. For the second null model, we assumed that the choice of the leading bird is influenced by spatial proximity at the time of switching (see [SI Text](#) for details for all models).

Matrix Correlation. For dyadic in-wake data, we calculated the Pearson product moment correlation coefficient. As dyadic data involving the same individuals are not statistically independent, we used a nonparametric matrix permutation procedure introduced by Mantel (49) to produce a null distribution for the correlation coefficient. For partialing out the effect of spatial

proximity, we performed an additional partial matrix correlation (50) by calculating the partial correlation coefficient as

$$r_{xy,z} = \frac{r_{xy} - (r_{xz} \times r_{yz})}{\sqrt{1 - r_{xz}^2} \times \sqrt{1 - r_{yz}^2}},$$

where $r_{xy,z}$ is the correlation between the time spent leading (*x*) and the time spent trailing (*y*) for each pair of birds with the effect of average spatial distance of the birds removed, r_{xy} is the correlation between the time spent leading (*x*) and the time spent trailing (*y*) for each pair of birds, and r_{xz} and r_{yz} are the correlations between the average spatial distance of the birds with the time spent leading or following, respectively. To account for relatedness or common rearing environment, we made additional hierarchical matrix permutations, where the interaction matrix was rearranged as to group related individuals (or individuals with common rearing history) and permutations were made only within groups and on the group level.

Throughout the text, CI₉₅ indicates the 95% parametric CI and \pm is the SD.

ACKNOWLEDGMENTS. We thank all members of the Waldrappteam who provided logistical support. Suggestions by B. Sheldon, R. Noë, C. Kasper, M. Taborsky, members of the Behavioral Ecology group at the University Bern, and three anonymous reviewers improved the paper significantly. J. Lowe, K. Roskilly, and S. Amos assisted with the production and design of the data loggers. Funding was provided by Deutsche Forschungsgemeinschaft Research Grant VO1806/1-1 (to B.V.), Engineering and Physical Sciences Research Council Grant EP/H013016/1 (to A.M.W., J.R.U., and S. Hailes), Biotechnology and Biological Sciences Research Council Grant BB/J018007/1 (to A.M.W.), and LIFE+ Grant of the EU LIFE+—BIO-AT-000143. B.V. was supported by European Research Council Grant AdG 250164 during preparation of the work.

1. Alerstam T (1990) *Bird Migration* (Cambridge Univ Press, Cambridge, UK).
2. May RM (1979) Flight formations in geese and other birds. *Nature* 282(5741):778–780.
3. Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* 71(2):296–308.
4. Bairlein F (1992) Recent prospects on trans-Saharan migration of songbirds. *Ibis* 134(Suppl 51):41–46.
5. Owen JC, Moore FR (2006) Seasonal differences of immunological condition of three species of thrushes. *Condor* 108(2):389–398.
6. Menu S, Gauthier G, Reed A (2005) Survival of young Greater Snow Geese (Chen caerulescens atlantica). *Auk* 122(2):479–496.
7. Lissaman PBS, Shollenberger CA (1970) Formation flight of birds. *Science* 168(3934):1003–1005.
8. Liao JC, Beal DN, Lauder GV, Triantafyllou MS (2003) Fish exploiting vortices decrease muscle activity. *Science* 302(5650):1566–1569.
9. Bill RG, Herrnkind WF (1976) Drag reduction by formation movement in spiny lobsters. *Science* 193(4258):1146–1148.
10. Fish FE (1995) Kinematics of ducklings swimming in formation: Consequences of position. *J Exp Biol* 273(1):1–11.
11. Badgerow JP, Hainsworth FR (1981) Energy savings through formation flight? A re-examination of the Vee formation. *J Theor Biol* 93(1):41–52.
12. Pennycuik CJ (1969) The mechanics of bird migration. *Ibis* 111(4):525–556.
13. Cutts C, Speakman J (1994) Energy savings in formation flight of pink-footed geese. *J Exp Biol* 189(1):251–261.
14. Hainsworth FR (1988) Induced drag savings from ground effect and formation flight in brown pelicans. *J Exp Biol* 135(1):431–444.
15. Weimerskirch H, Martin J, Clerquin Y, Alexandre P, Jiraskova S (2001) Energy saving in flight formation. *Nature* 413(6857):697–698.
16. Portugal SJ, et al. (2014) Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* 505(7483):399–402.
17. Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246(5427):15–18.
18. Gadagkar R (1997) *Survival Strategies: Cooperation and Conflict in Animal Societies* (Harvard Univ Press, Cambridge, MA).
19. Dugatkin LA (1997) *Cooperation Among Animals. An Evolutionary Perspective* (Oxford Univ Press, Oxford, UK).
20. Diekmann A (1985) Volunteer's dilemma. *J Conflict Resolut* 29(4):605–610.
21. Diekmann A (1993) Cooperation in an asymmetric volunteer's dilemma game. *Int J Game Theory* 22(1):75–85.
22. Wilson AM, et al. (2013) Locomotion dynamics of hunting in wild cheetahs. *Nature* 498(7453):185–189.
23. Usherwood JR, Stavrou M, Lowe JC, Roskilly K, Wilson AM (2011) Flying in a flock comes at a cost in pigeons. *Nature* 474(7352):494–497.
24. Jarman PJ (1974) The social organisation of antelope in relation to their ecology. *Behaviour* 48(1):215–267.
25. Andersson M, Wallander J (2003) Kin selection and reciprocity in flight formation? *Behav Ecol* 15(1):158–162.
26. Nowak MA, Sigmund K (1998) Evolution of indirect reciprocity by image scoring. *Nature* 393(6685):573–577.
27. Nowak MA, Sigmund K (2005) Evolution of indirect reciprocity. *Nature* 437(7063):1291–1298.
28. Leimar O, Hammerstein P (2001) Evolution of cooperation through indirect reciprocity. *Proc Biol Sci* 268(1468):745–753.
29. Noe R (2006) Cooperation experiments: Coordination through communication versus acting apart together. *Anim Behav* 71(1):1–18.
30. Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 211(4489):1390–1396.
31. Boyd R, Richerson PJ (1988) The evolution of reciprocity in sizable groups. *J Theor Biol* 132(3):337–356.
32. Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46(1):35–57.
33. Seiler P, Pant A, Hedrick JK (2003) A systems interpretation for observations of bird V-formations. *J Theor Biol* 221(2):279–287.
34. Nagy M, et al. (2013) Context-dependent hierarchies in pigeons. *Proc Natl Acad Sci USA* 110(32):13049–13054.
35. Doebeli M, Hauert C (2005) Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. *Ecol Lett* 8(7):748–766.
36. Voelkl B (2010) The 'Hawk-Dove' game and the speed of the evolutionary process in small heterogeneous populations. *Games* 1(2):103–116.
37. Bshary R, Grutter AS (2006) Image scoring and cooperation in a cleaner fish mutualism. *Nature* 441(7096):975–978.
38. Stevens JR, Stephens DW (2008) Patience. *Curr Biol* 18(1):R11–R12.
39. Fruteau C, Voelkl B, van Damme E, Noë R (2009) Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc Natl Acad Sci USA* 106(29):12007–12012.
40. Hart BJ, Hart LA (1992) Reciprocal allogrooming in impala, *Aepyceros melampus*. *Anim Behav* 44(6):1073–1083.
41. Connor RC (1995) Impala allogrooming and the parcelling model of reciprocity. *Anim Behav* 49(2):528–530.
42. Connor RC (1995) Altruism among non-relatives: Alternatives to the 'Prisoner's Dilemma'. *Trends Ecol Evol* 10(2):84–86.
43. Pfeiffer T, Rutte C, Killingback T, Taborsky M, Bonhoeffer S (2005) Evolution of cooperation by generalized reciprocity. *Proc Biol Sci* 272(1568):1115–1120.
44. Rutte C, Taborsky M (2007) Generalized reciprocity in rats. *PLoS Biol* 5(7):e196.
45. Wilkinson GS (1984) Reciprocal food sharing in the vampire bat. *Nature* 308(5955):181–184.
46. Hamilton WD (1964) The genetical evolution of social behaviour. I. *J Theor Biol* 7(1):1–16.
47. White CR, et al. (2013) Implantation reduces the negative effects of bio-logging devices on birds. *J Exp Biol* 216(Pt 4):537–542.
48. King AJ, et al. (2012) Selfish-herd behaviour of sheep under threat. *Curr Biol* 22(14):R561–R562.
49. Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* 27(2):209–220.
50. Smouse PE, Lang JC, Sokal RR (1986) Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Syst Zool* 35(4):627–632.

Supporting Information

Voelkl et al. 10.1073/pnas.1413589112

SI Text

Cooperation Dilemma. Most cases of animal cooperation can be analyzed in game theoretic terms as a game where actors engaged in social interactions pursue certain strategies. The payoff from an interaction is conditional on their own strategies and the strategies of their interaction partners (1–3). In-wake flying can be paraphrased as a dyadic game where two individuals meet and have to decide how to continue their flight. This game has the following properties: individuals are traveling from one point to another and traveling is associated with some costs c , but reaching the destination brings along a large benefit b . The benefit b of reaching the destination is always larger than the cost c —otherwise traveling would not be a profitable action (3, 4). However, if one individual can travel in the wake of another individual and use the aerodynamic up-wash, this individual can reduce its travel costs by an amount s .

We envisage two strategies: volunteers (V) are individuals who accept if another individual is flying in their wake and do not take any measures either to shake off an individual flying in their wake or to fall back behind another individual to get into its wake; free-riders (F), on the other hand, are individuals who always strive to be in the wake of another individual. If two volunteers meet, flying in approximately the same direction, the one who is slightly ahead of the other will become the leader and the one slightly behind will become the follower who can fly in the leader's wake. Which individual is initially ahead is governed by chance, so that in the long run average of repeated interactions each volunteer will be follower in half of the cases. If a volunteer and a free-rider meet, it is always the volunteer who will take on the leading position and the free-rider will become the follower. If two free-riders meet, both individuals will strive to get into the follower position. We assume that individuals will realize quickly that this does not work and continue their flight separately. However, their initial attempt to get into the rear position is associated with a minimal cost ε (as individuals might slow down in an attempt to get behind the other bird and have to accelerate again afterward). We can summarize this in the following payoff matrix:

$$\begin{pmatrix} P_{V|V} & P_{V|F} \\ P_{F|V} & P_{F|F} \end{pmatrix} = \begin{pmatrix} b - \frac{c}{2} - \frac{c-s}{2} & b - c \\ b - (c-s) & b - c - \varepsilon \end{pmatrix},$$

where $P_{X|Y}$ is the payoff for an individual playing strategy X , whereas the other individual is playing strategy Y , and by definition $b \gg c \gg s > \varepsilon > 0$.

Without loss of generality we can subtract the term $(b - c)$ from this payoff matrix, retrieving

$$\begin{pmatrix} s/2 & 0 \\ s & -\varepsilon \end{pmatrix},$$

which shows that the structure of this game is equivalent to the structure of the snowdrift game in terms that the payoffs are ordered as $P_{F|V} > P_{V|V} > P_{V|F} > P_{F|F}$.

Expected Formation Sizes. To estimate the expected distribution for formation sizes, we calculated for each possible formation the conditional probability for its occurrence given the observed individual preferences for in-wake flying. To estimate the expected distribution for formation sizes, we represent a formation as a

directed graph where vertices represent individuals and a directed edge is pointing from vertex i to vertex j if bird i is flying in the wake area of bird j (Fig. 1F). Based on accumulated observational data on the shape of migratory formations (5–7), we make the following assumptions: (i) a bird can only be in the wake area of one preceding bird, i.e., the maximal out-degree of a vertex is one; (ii) no more than two birds can fly in the wake of a leading bird, i.e., the maximal in-degree of a vertex is two; (iii) lambda-shaped formations which are very rarely observed in nature are excluded, i.e., the sum of in- and out-degree of a vertex cannot exceed two; and (iv) graphs are circle free. All graphs that fulfill all four points are called possible formation graphs.

Summing up over all rows of the adjacency matrix of the graph, we get a binary column vector v , with $v_i = 1$ if bird i is flying in the wake of another bird and 0 otherwise. We define an out-isomorphism class as the class of all possible formation graphs with the same column vector v . Making no further assumptions other than that individuals have given propensities for flying behind some other bird (model I), the expected frequency for out-isomorphism class C_j is given by $P(C_j) = \prod_{i=1}^n \{v_j(i) \times p_i + [1 - v_j(i)] \times (1 - p_i)\}$, where n is the size of the graph (giving the number of individuals) and p_i is the probability of observing individual i flying in the wake of another animal at a given time point. Within each out-isomorphism class, all graphs are equally likely to occur, and the probability for observing a specific graph $G_i \in C_j$ is, therefore, given by $P(G_i) = P(C_j)/|C_j|$. For each graph, we count the number of weakly connected components, which represent separate formations, of size k , with $k = 1 \dots n$, and multiply their frequencies with the probability of observing the respective graph. Adding up the resulting frequencies for all possible formation graphs, we get the expected frequency estimates for model I for observing formations of size k . For model II, where we assume individual preferences, the probability of observing a specific graph G_i is given by $P(G_i) = \prod_{j=1}^n \prod_{k=1}^n \{a_{j,k}(i) \times p_{j,k} + [1 - a_{j,k}(i)] \times (1 - p_{j,k})\}$, where $a_{j,k}$ is the element at position j, k of the adjacency matrix A of graph G , and $p_{j,k}$ is the estimated preference of individual j for flying behind individual k , based on the observed frequencies. Expected frequency estimates for formations of size k are calculated in the same way as for model I.

Expected Direct Swaps. To estimate the expected number of direct swaps, we took for each bird the observed bouts of in-wake flying and randomly reshuffled the identity of the leading birds between bouts. Repeating this randomization procedure 1,000 times and counting each time the number of direct swaps, we get expected numbers of direct swaps assuming individual preferences, as the reshuffling procedure only changes the order but not the original observed frequencies for following specific birds. For the second null model, we assumed that the choice of the leading bird is influenced by spatial proximity at the time of switching. For this model, we first estimated the likelihood for selecting a bird at a given distance as the next leading bird conditional on the length of the time gap between bouts, by fitting gamma distributions to the observed frequencies for time gaps of 0–10 s in increments of 1 s and time gaps larger than 10 s. Thereafter, we calculated for each bout of in-wake flying the distance of the trailing bird to all other birds at the end of the bout and the time gap to the next bout, where the respective bird was following another bird, and randomly selected one bird as the future leading bird proportional to the probability for the given time gap that a bird chooses a bird at such a distance.

Definition of the In-Wake Area. As much of the analysis of this study hinges on the definition of the in-wake area, it is of interest how the choice of the threshold values influences the resulting picture of in-wake flying. The definition of in-wake flying used throughout the main text was based on the expectation that the optimal position of a birds' wing tip would be only a few centimeters in-board of the wingtip of the preceding bird. Adding 0.4 m to the wingspan (roughly equivalent to the measurement error plus 0.1 m), we ended up with a maximal distance of 1.6 m lateral. The resulting area might give an overestimation of effective in-wake flying, although we were more concerned about losing valid times of in-wake flying than about adding random noise to the data. Thus, to see how a more stringent criterion would have influenced the results, we compared some fundamental statistics of in-wake flying with those based on different definitions of the in-wake area (Table S1). As expected, the average time the birds spend per definition in-wake increases with the size of the in-wake area, and so does the maximal length of in-wake bouts. However, the correlation between flying in the wake of another bird and having another bird in one's wake seems to be a very robust relationship that stays at a very high level for all probed in-wake areas—the smallest one comprising only 17% of the original area.

A Null Model for Expected Times for In-Wake Flying. The average time that individual birds spent in the wake of another bird was 825 s, which was ~32% of the whole flight time. This amount seems to be a substantial proportion, suggesting that individuals actively seek to fly in these in-wake areas of other birds. However, even if birds do not actively pursue such a strategy, it will happen from time to time that a bird crosses the flight path of another bird and will be in its wake area for a short time. Here, we will estimate the expected time of accidental wake flying that is due to chance alone. This value would be the expected value of a null model contrasting our hypothesis that animals actively establish in-wake flying. For this null model we make following assumptions. (i) Individuals travel in flocks that have approximately the same overall flock cohesion as we observed on this migration leg. This assumption is important because without any spatiotemporal restrictions the probability that a bird would get into the wake area of another bird during its migration from Austria to Italy would be effectively zero. As a measure for the cohesion of the flock, we take the average distance of all birds to the center of mass of the flock at any given time point. (ii) Birds fly on average with the same speed and at the same average altitude as observed. This assumption is again necessary for constructing a valid null model for this specific flight. (iii) Birds have specific acceleration patterns that are close to those observed. This assumption adds biological realism to the null model: there are limits how fast birds can accelerate or slow down, and even within these limits very abrupt changes in speed and direction might be relatively rare. There are two possible ways how to arrive at a useful null model. The first one would be to simulate flights using agent based simulations where birds fly along a given route and random changes in their flight direction and speed are based on likelihood functions, parameterized with values from the observed flight. This approach has two disadvantages. First, the number of parameter to include remains speculative (e.g., how many higher moments for the probability distributions for speed and directional changes to include). Second, it requires a mechanism that preserves the group cohesion. As we do not know how this mechanism works in the birds, we could only suggest an arbitrary mechanism; however, such a mechanism might have side effects on the overall patterns that are difficult to fathom. We therefore opted for an alternative approach that relies on resampling from the original data. This method works as follows. (i) We take the positional data of all birds with a temporal resolution of 5 Hz and calculate their relative position to the

center of mass to the flock. (ii) For each bird, we take the stream of relative positional data, cut off a bout of positions from the end of the data stream, and prepend it at the start. The length of this bout is a uniform random variable of minimum 60 and maximum 13,021 (which is the length of the data stream minus 60). (iii) This procedure is repeated five times and basically shuffles substrings like a deck of cards. (iv) We take the reshuffled relative positions and the position of the original center of mass for the flock and calculate fictitious absolute positions for the birds. The aim of this procedure is to destroy spatiotemporal correlations between pairs of birds that go beyond those produced by their overall flocking tendency. This procedure has two potential issues. First, we introduce unnatural jumps in the position of the birds at those places where we concatenate the substrings. Although this is an intrinsic problem of this method, we tried to keep its effect minimal by splitting the original data stream only five times. As a result, we get a data stream of length 13,081 out of which the transition between five pairs of consecutive data points (0.038% of the data) are compromised. We argue that this proportion is so small, that we can safely ignore its effect on the overall data. The second question arising is, whether five random cuts are sufficient to speak of a randomized data stream. Here, we can look at the correlation of the original data stream with the randomized version to convince ourselves that this randomization is sufficient (Fig. S5C). The advantage of this method is that within each substream of the randomized data version, the relative positions are unchanged and hence all of the properties with respect to altitude, direction and speed changes are conserved.

Effects of Human-Guided Migration and Hand Rearing. We considered the effects of a human-guided migration on (i) the aerodynamics during the flight, (ii) the general flight pattern, (iii) group composition, and (iv) the social behavior of the birds.

- i) Aerodynamics during the flight: For most of the time during the human-guided migration, the birds flew at a relatively large distance to the paraplane. It even happened, from time to time, that the distance between paraplane and birds was that great that the pilot lost sight of the birds (which had repeatedly led to interruptions of the flight, although not during the data collection). During the flight reported here, the average distance of the flock to the paraplane was 147 m (8). That is, it is highly unlikely that the birds could gain any aerodynamic advantage from the paraplane.
- ii) General flight pattern: We tried to mimic the natural migration patterns in terms of leg-length (average 225 km), flight speed (average active air speed 42 km/h), altitude (0–2,200 m a.s.l.), flight time (mean 4:50 h; maximum 8:00 h), and flight/rest ratio (1:3) as closely as possible. Our understanding of the natural migration patterns of Northern bald ibis are primarily based on the following. (a) Observations of the migratory behavior of a wild relict population in the Middle East. The data show that before start of their first autumn migration, the juveniles join together and follow one or more adult conspecifics southward. Data from satellite tags indicate an average daily flight length of 240 km, which resembles the flight length during the human-guided migrations (9). (b) GPS tracking records from the reintroduced migratory Northern bald ibis population in Europe over the last years. The findings confirm and complement the data from the Middle East; also, the European juveniles flock together and follow adult conspecifics to the south. The flights usually start in the later morning, with daily leg lengths up to 300 km and a flight duration of up to 8 h/d. (c) Experience gathered during seven previous human-guided migrations. During these migrations we gained considerable experience that

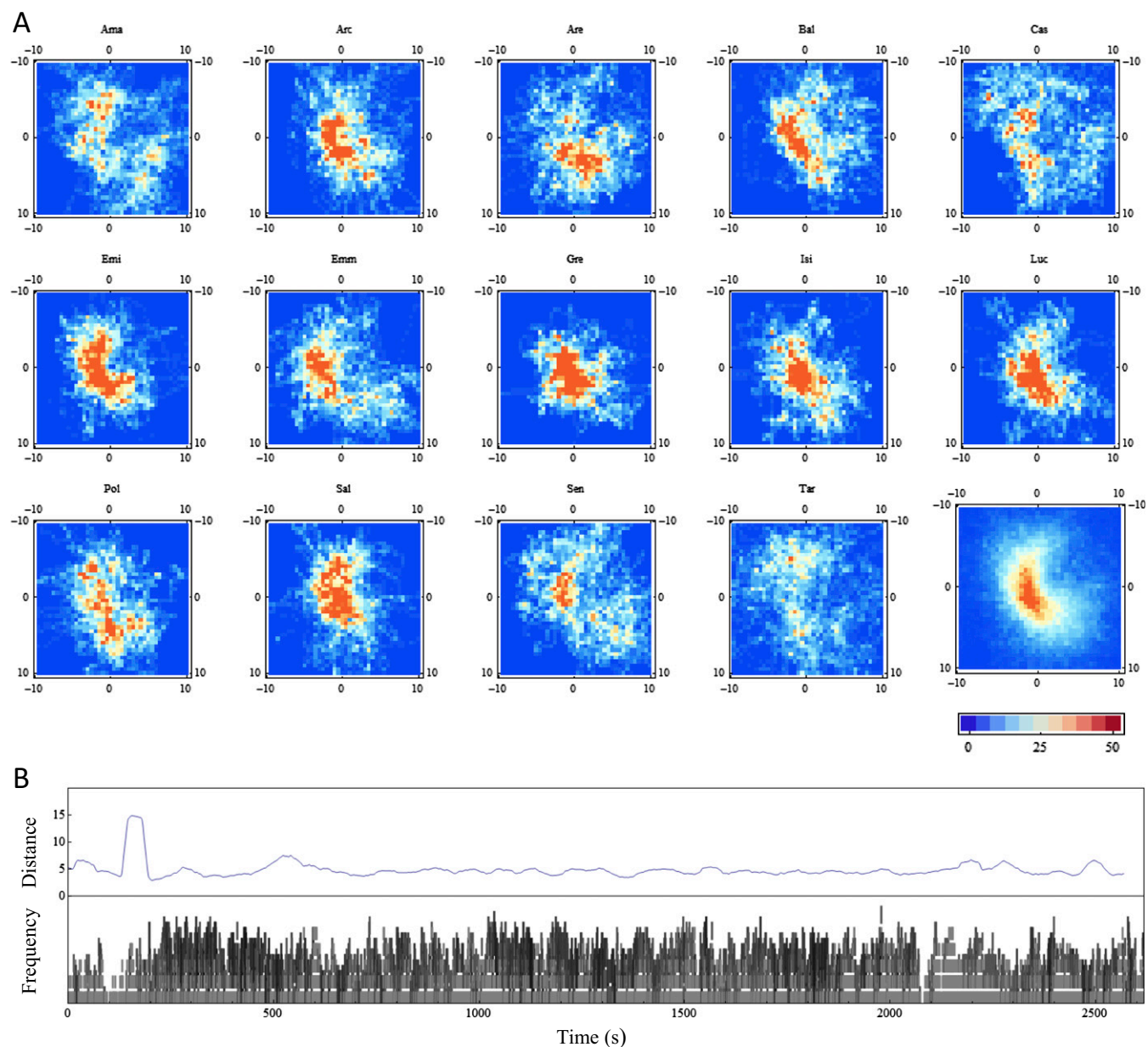


Fig. S1. (A) Position of the 14 birds in relation to the centroid of the bird flock. For each second of the flight, we determined the position of each bird. Plots show area and area of 20×20 m surrounding the centroid. The area is split into cells of 0.5×0.5 m, and colors indicate how often a bird was observed in each cell at a sampling rate of 1 s. The centroid of the flock is the center of mass of the position of all 14 birds at a given time. The panel in the lower right corner shows the overlay of the data from all 14 birds. Overall flight direction was toward the left side. (B) Median distance of all birds from the centroid of the flock and occurrence of formations during the migration. The centroid of the flock is the center of mass of the position of all 14 birds at a given time. Bars indicate the existence of a formation at a given time point. Length and color indicate the size of the formation (large formations in dark gray). Multiple independent formations at a given time are depicted as staged bars.



Fig. S2. In-wake flying during the 43 min of the migration stage. x axis, time (s); y axis, individual leading birds (abbreviated names). Bold bars indicate that a bird was flying in the wake of the leading bird. The identity of the trailing bird is color coded. Thin colored lines connect the in-wake bouts of an individual bird and indicate times where the bird was not flying in the wake of any other bird.

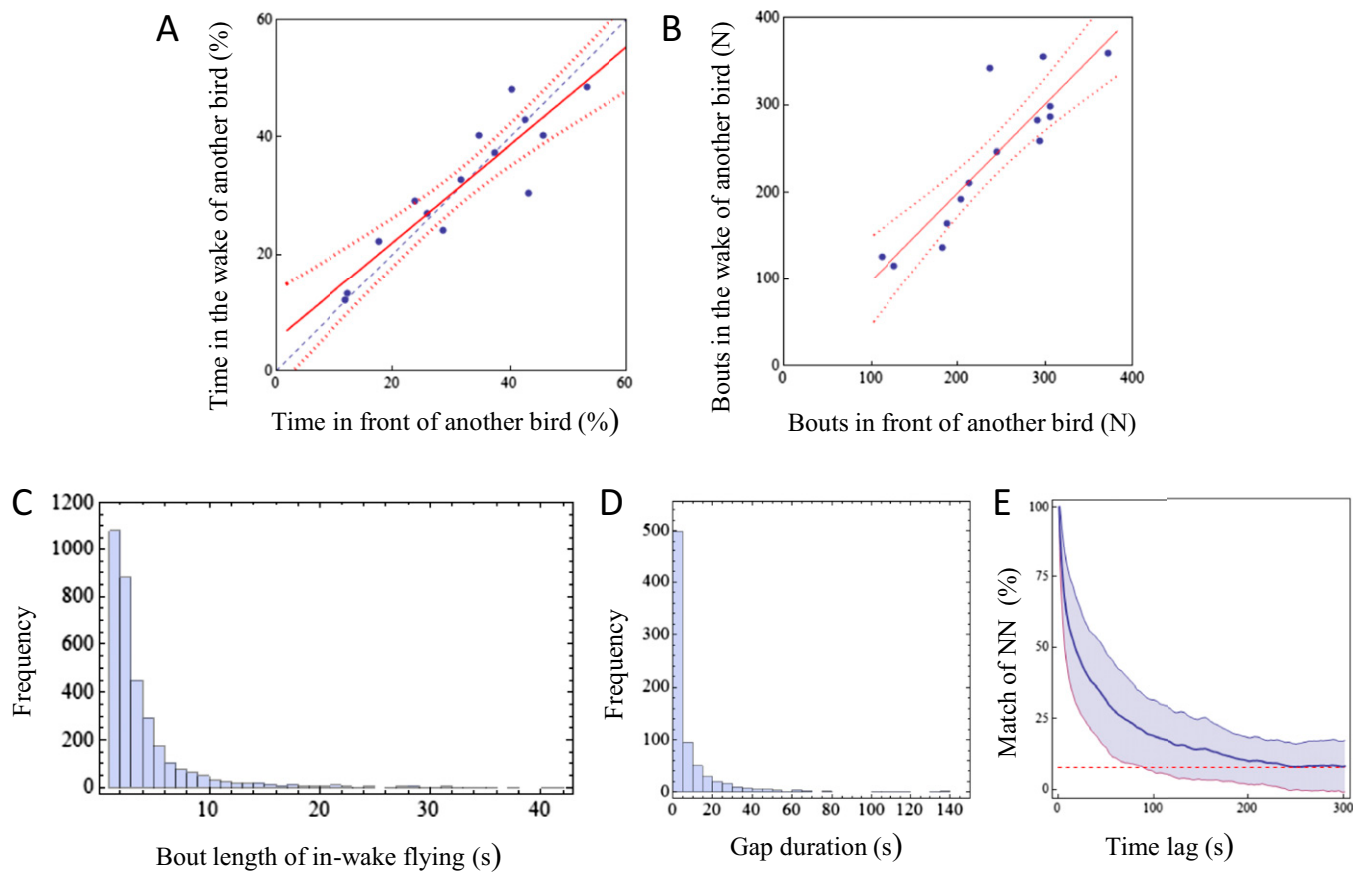


Fig. S3. (A) Relation of the time an individual is flying in front of another bird and the time this individual is flying in the wake of another bird; Pearson product moment correlation coefficient, $r = 0.91$, $CI_{95}[0.72, 0.97]$. The diagonal (blue dashed line) gives the expected value for perfect time matching. This expected value is within the 95% CI for the observed data. (B) Relation of the number of bouts where an individual is flying in front of another bird and the number of bouts where this individual is flying in the wake of another bird; Pearson product moment correlation coefficient, $r = 0.89$, $CI_{95}[0.69, 0.97]$. (C) Distribution for the duration of bouts of in-wake flying, pooled for all individuals. (D) Duration of the time gap between the end of the first bout of in-wake flying and the start of the second bout of in-wake flying for direct swaps (all dyadic swaps pooled). (E) Temporal autocorrelation of nearest neighbors (NN). The mean concordance of nearest neighbors of the 14 birds at any time point in intervals of 10 s with the nearest neighbors at a time lag of k seconds for time lags of 0–600 s. Thin lines give the SD and the dotted red line gives the expected concordance for completely random associations.

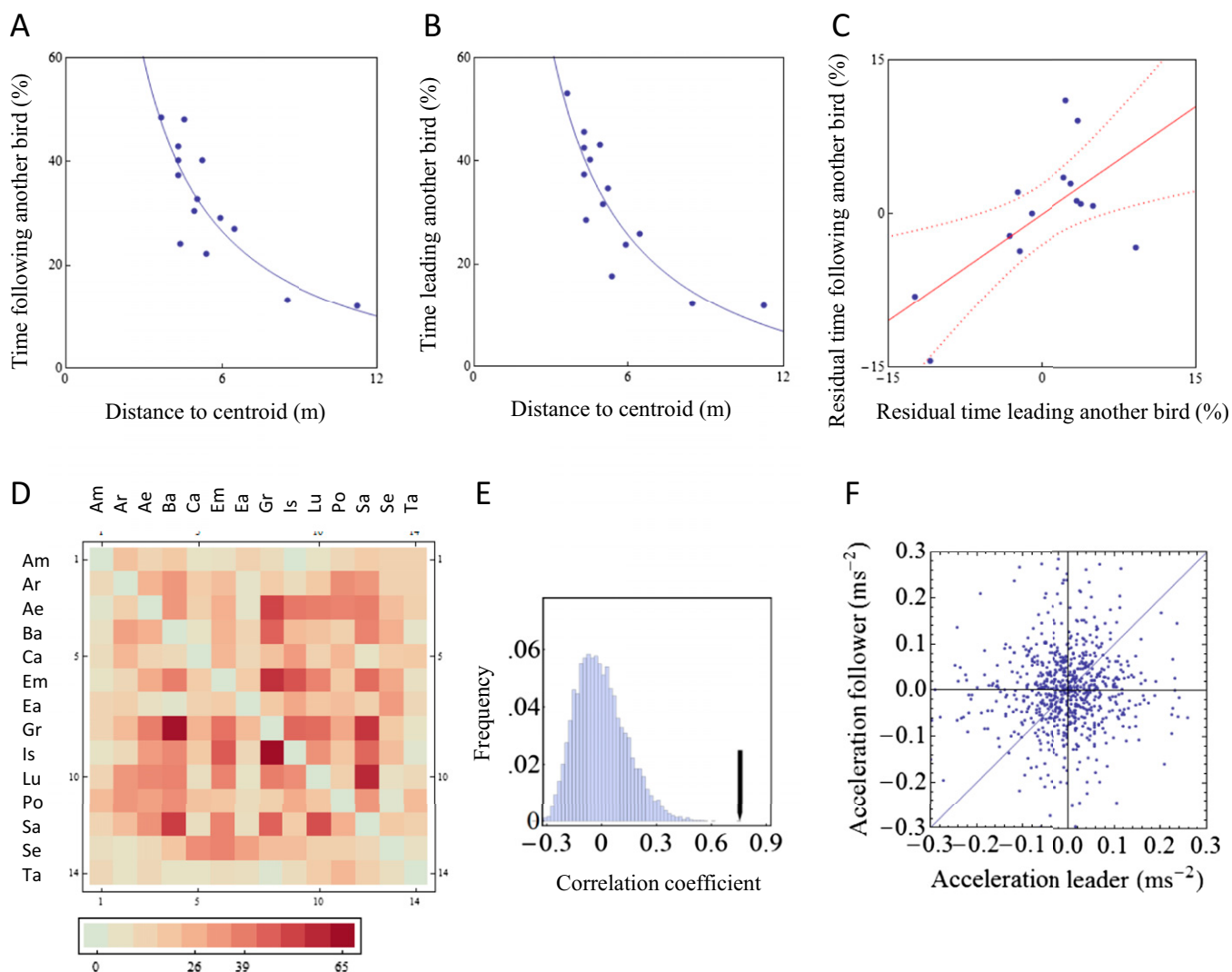


Fig. 54. Both the overall time of being in wake of another individual (A) and being in front of another individual (B) are correlated with the average distance to the centroid of the flock (Pearson product moment correlation: $r = -0.79$, $CI_{95}[-0.93, -0.46]$ and $r = -0.80$, $CI_{95}[-0.93, -0.47]$, respectively). (C) Partialing out closeness to the centroid of the flock from the time of in-wake flying and the time of being in front of another bird, we get a correlation for the residual values of $r = 0.65$, $CI_{95}[0.18, 0.88]$. (D) Matrix plot of the number of bouts of flying in the wake of a specific bird for all 14 birds. (E) Histogram for the expected Pearson product moment correlation coefficient assuming random associations based on 10,000 random matrix permutation and the observed value (black arrow). (F) Acceleration of leading and trailing birds during direct swaps measured at the time point at which the first bout breaks up. Points above the main diagonal indicate that the leading bird slowed down relative to the trailing bird; points below the main diagonal indicate that leading birds became faster relative to the trailing bird.

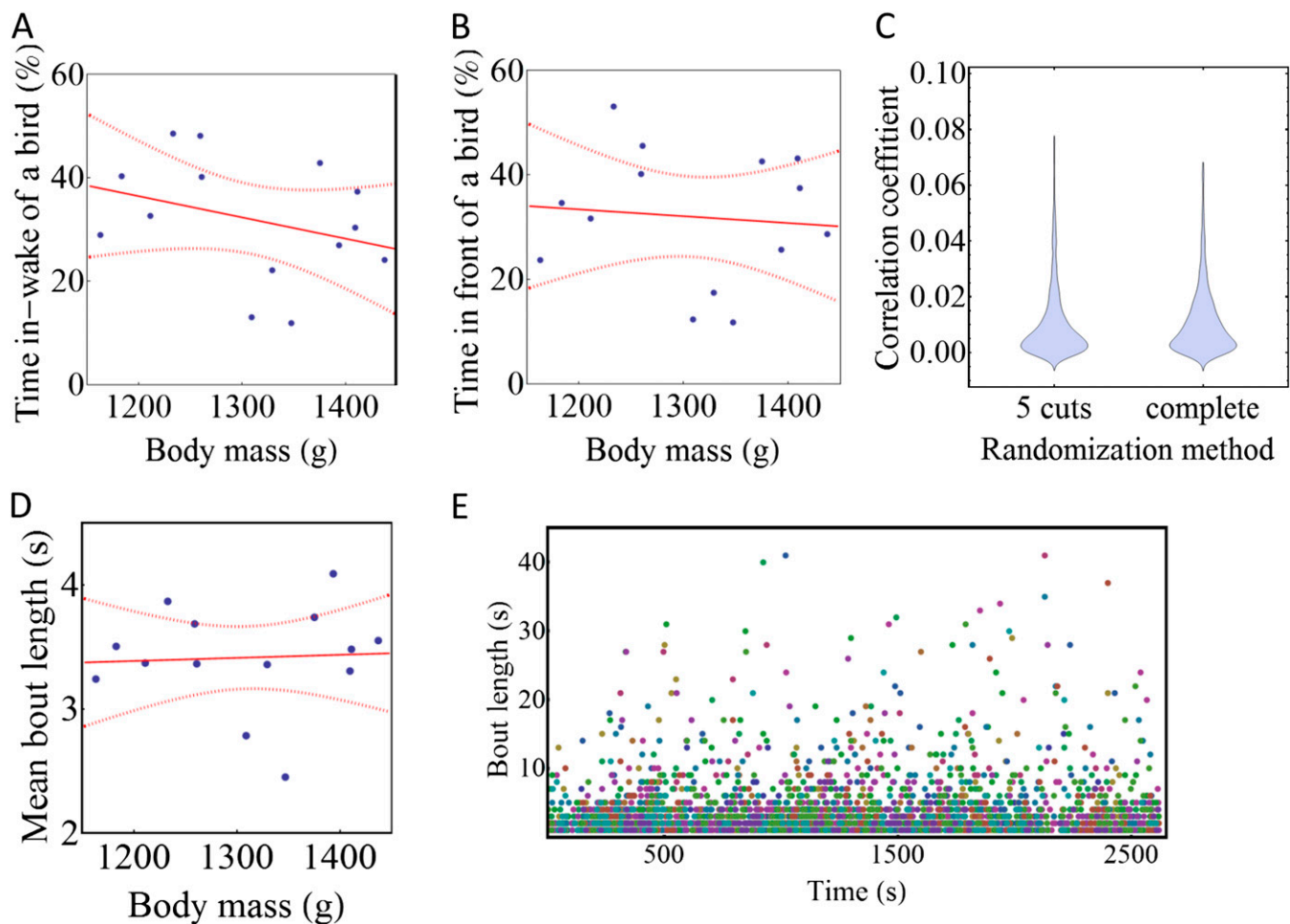


Fig. S5. (A) The time for each individual (in percent of the total flight time) of being in the wake of another bird is plotted against individual body mass before departure for the second migration leg, $r = -0.32$, $CI_{95}[-0.73, 0.25]$. (B) Time for each individual of being in the front of another bird against individual body mass, $r = -0.09$, $CI_{95}[-0.59, 0.46]$. (C) Distributions of Pearson product moment correlation coefficients (r) between the distance of birds to the center of mass of the observed data and randomized versions. The randomization method used for generating a null model for expected times of in-wake flying is, here, termed "5 cuts" as it involved splitting the original data stream five times into substrings of random length. The resulting correlation can be compared with the correlation one gets by creating new data streams by randomly sampling single data points from the observed data stream (complete randomization). Sampling was repeated 1,000 times for each method. The median correlation coefficient for the 5-cut method was with $r = 0.006$ (interquartile range: 0.002–0.015) both very low and very similar to the one for the complete randomization method with $r = 0.007$ (interquartile range: 0.003–0.016), suggesting that splitting and rearranging the original data stream five times is sufficient for generating uncorrelated data while preserving the main characteristics of the flight behavior. (D) Mean length for bouts of leading a formation for each individual plotted against body mass: $r = 0.05$, $CI_{95}[-0.49, 0.57]$. (E) Bout length for each bout plotted against the time of the flight, $r = 0.04$, $CI_{95}[-0.50, 0.56]$. Colors indicate bird identity.

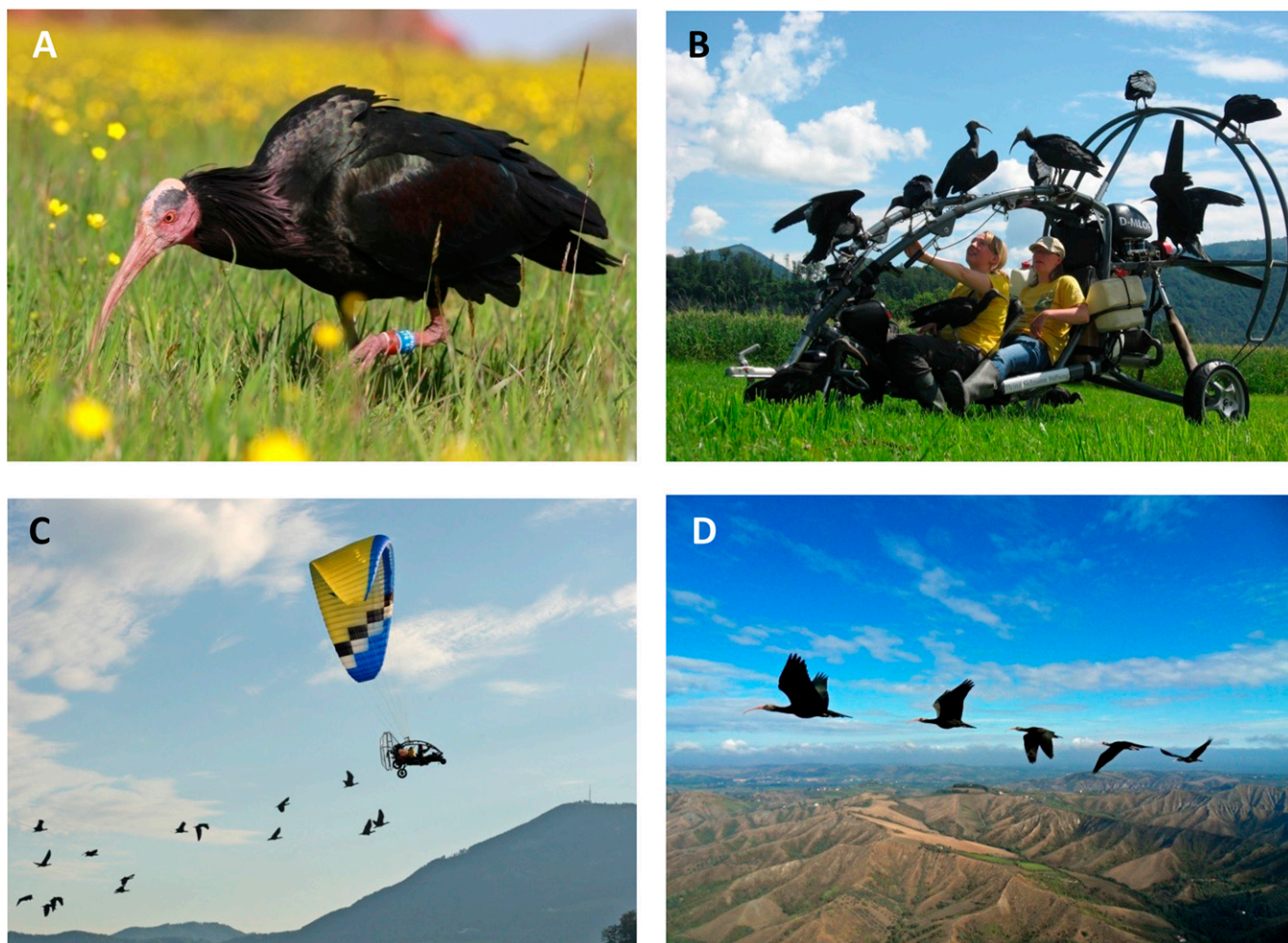


Fig. 56. (A) Northern bald ibis (*G. eremita*) foraging. (B) Juvenile bald ibis are habituated to the paraplanes by their foster parents. (C) Juvenile bald ibis following the paraplane shortly after takeoff. (D) Echelon formation of five bald ibis during the migration. Images courtesy of J. Fritz (A–C) and M. Unsöld (D).

Table S1. Comparison of in-wake areas

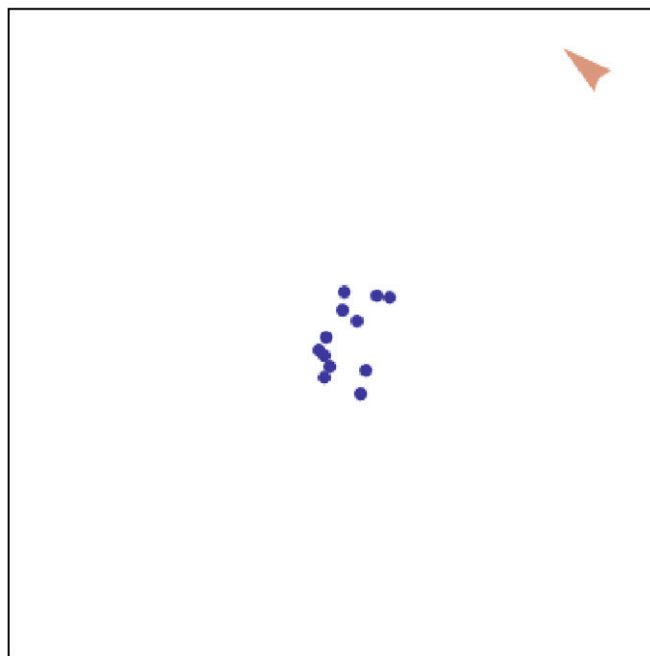
In-wake area behind (m)		In-wake area sideways (m)		In-wake time (%)	In-wake bouts (N)	Bout duration (s) (maximum)	Typical group size		Correlation in-wake flying	
Minimum	Maximum	Minimum	Maximum				Minimum	Maximum	<i>r</i>	CI ₉₅
0	3	0	1.6	32.0	3,374	41	2.6	3.3	0.90	0.72–0.97
0	3	0	1.4	29.0	3,146	40	2.5	3.3	0.90	0.73–0.97
0	2	0	1.6	23.0	2,650	33	2.3	3.0	0.88	0.66–0.96
0	2	0.8	2.0	17.0	2,581	42	2.3	3.1	0.86	0.60–0.95
0	3	1	1.6	11.3	2,060	22	2.1	2.6	0.85	0.59–0.95
0	2	1	1.6	8.4	1,516	22	2.0	2.5	0.85	0.59–0.95
0	2	0.8	1.6	12.0	1,982	32	2.1	2.8	0.85	0.57–0.95
0	3	0.8	2.0	22.4	3,401	42	2.4	3.2	0.85	0.58–0.95
0	3	0.8	1.6	16.0	2,651	32	2.2	2.9	0.84	0.57–0.95
0	3	1	1.4	7.2	1,437	11	2.1	2.4	0.83	0.55–0.95
0	2	1	1.4	5.3	1,059	11	2.1	2.4	0.81	0.50–0.94

Summary statistics for in-wake flying for different in-wake areas. In-wake time gives the mean percentage of time birds were spending in the in-wake area of another bird, bout duration gives the maximum length of an uninterrupted bout of in-wake flying, typical group size gives the minimum and maximum of the typical group size per individual, and correlation in-wake flying gives the Pearson correlation coefficient and its 95% CI for the correlation of the time spent in the wake of another bird and the time a bird was in the wake of the respective bird.

Table S2. Individual data

Individual	Ama	Arc	Are	Bal	Cas	Emi	Emm	Gre	Isi	Luz	Pol	Sal	Sen	Tar
Sex	Male	Male	Female	Male	Male	Male	Male	Male	Female	Male	Female	Female	Female	Male
Nest number	3	4	3	1	2	2	1	3	3	4	2	1	1	2
Hatch day	25.4.	22.4.	23.4.	21.4.	23.4.	25.4.	22.4.	24.4.	20.4.	23.4.	26.4.	20.4.	23.4.	27.4.
Weight (g)	1,309	1,437	1,183	1,409	1,393	1,375	1,329	1,233	1,259	1,411	1,211	1,261	1,163	1,347
Ground speed	53.7	53.7	53.5	53.7	53.6	53.7	53.6	53.6	53.5	53.6	53.6	53.6	53.8	53.4
% in-wake	13.2	24.2	40.3	30.4	27.0	42.9	22.2	48.6	48.2	37.4	32.7	40.3	29.1	12.0
% in-front	12.3	28.6	34.7	43.2	25.8	42.6	17.6	53.1	40.3	37.5	31.7	45.6	23.8	11.8
% leading a formation	9.9	19.1	16.8	28.0	19.4	24.6	13.2	26.5	21.6	22.1	18.1	26.6	16.1	8.6
N of bouts in-wake	127	213	293	237	188	306	182	372	306	291	245	298	203	113
N bouts in front	116	211	259	342	165	298	137	359	286	282	246	355	192	126
Bout length in-wake (s)	2.7	3.0	3.6	3.4	3.8	3.7	3.2	3.4	4.1	3.4	3.5	3.5	3.8	2.8
Bout length in-front (s)	2.8	3.6	3.5	3.3	4.1	3.7	3.4	3.9	3.7	3.5	3.4	3.4	3.2	2.5
Typical group size	2.6	3.0	3.3	3.1	2.7	3.1	2.7	3.3	3.2	3.1	3.2	3.2	2.7	2.7
Distance to centroid (m)	5.8	3.6	4.7	4.3	6.2	3.6	4.9	3.1	3.9	3.7	4.6	3.6	5.8	6.9

Summary statistics for the 14 individuals of the flock. Individuals were hand-raised in four different nests numbered 1–4. Weight is the body weight at the day of the migratory flight. Ground speed is the average ground speed (km/h) over 43 min of flight from the start to the stop over point, % in-wake: percentages of time an individual spends in the wake (maximal 3m behind and 1.6m lateral) of another bird, % in-front: percentage of time bird spends in the wake (maximal 3m behind and 1.6m lateral) of the individual, % leading a formation: percentage of time an individual spends at the front position of a formation of two or more birds, N of bouts in-wake: number of bouts an individual was in the wake of another bird, N of bouts in front: number of bouts another bird was in the wake of the individual; bout length in wake: mean duration in seconds of the bouts where the individual was in the wake of another bird; bout length in front: mean duration in seconds of the bouts where another bird was in the wake of the individual; Typical group size: mean typical size of the formation an animal was observed in given by $1/(\sum_{i=1}^k n_i) \times \sum_{i=1}^k n_i^2$, where k is the number of times an individual was flying in a formation and n_i is the number of animals in formation i . The distance to the centroid is median distance in meters from the individual to the center of mass of the positions of all individuals over all one-second time frames.



Movie S1. This animation shows the position of the birds in the horizontal plane relative to the center of mass of the flock for a 43-min phase of the second migratory stage. The first 3 min of the flight, which the birds spent circling to gain height, were omitted. The frame captures an area of 100×100 m, with the center of mass of the flock in the center of the frame. The animation runs at 80x time lapse, and the arrow in the upper right corner indicates the average travel direction of the 14 birds.

[Movie S1](#)

Dataset S1. This file contains the data on which Movie S1 is based

[Dataset S1](#)

It provides the GPS coordinates (northing, easting, altitude) in meters for all 14 birds at time intervals of 0.2 s. The data are saved as .csv file of 13,089 rows and 42 columns, where columns 1–3 give northing, easting, and altitude for bird 1, respectively, columns 4–6 give northing, easting, and altitude for bird 2, etc.