

# Supporting Information

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## 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  $\varepsilon$  (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. 1*F*). 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  $k = 1..n$ , 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 fictions 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.

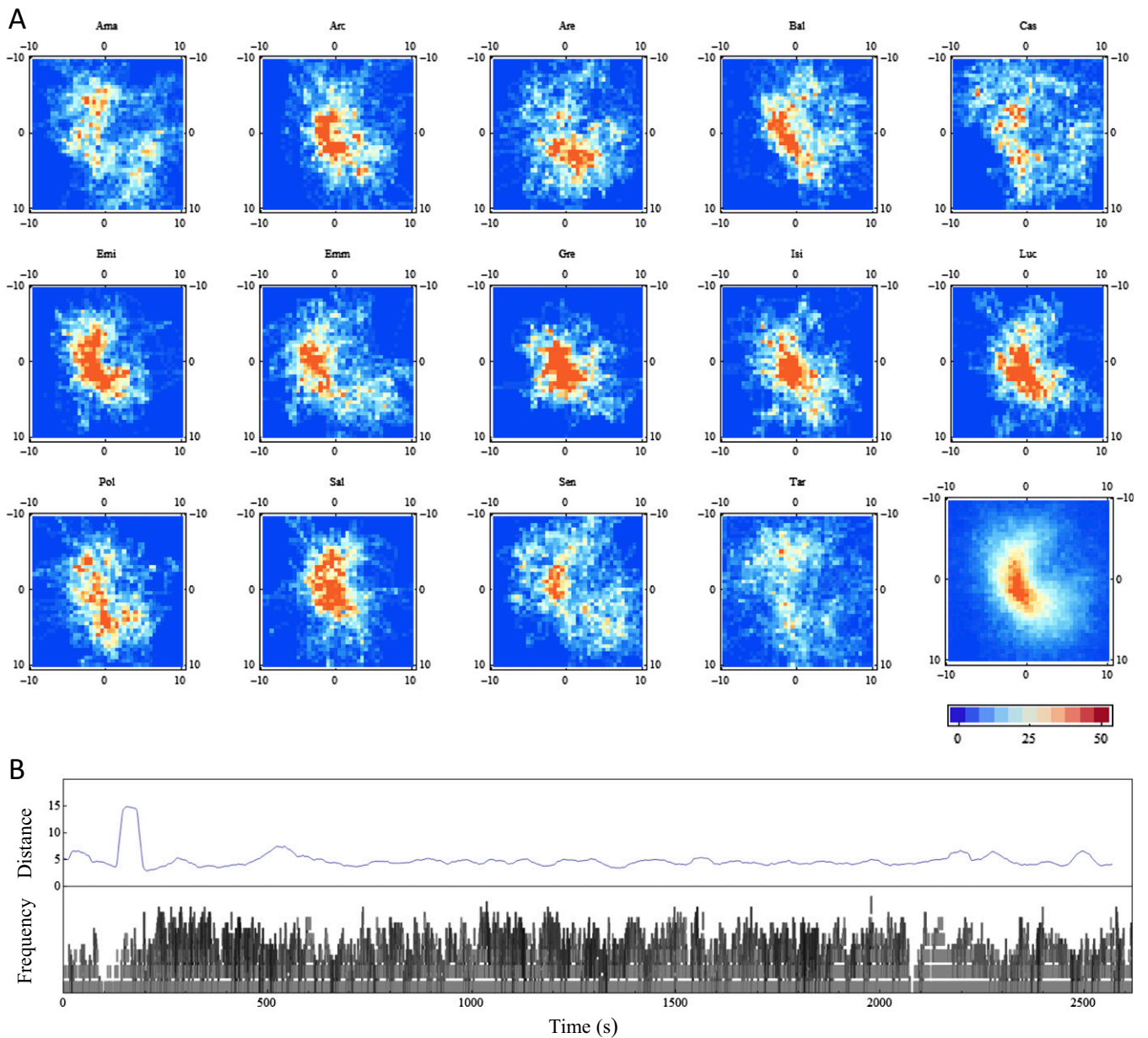
- i) Aerodynamics during the flight: For most of the time during the human-guided migration, the birds flew at a relatively large distance to the paraplane. It even happened, from time to time, that the distance between paraplane and birds was that great that the pilot lost sight of the birds (which 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

allowed us to optimize the flight technique of the pilots and to fit it to the requirements of the birds.

- iii) Group composition: In free-living Northern bald ibis populations the juveniles from different families group together. The data from the European population indicate that during their first autumn migration they do not preferably join their parents but other experienced conspecifics. Thus, the group composition and constellation during the human-guided migration is overall very similar to the natural situation, with the following deviations: (a) hand-raised juveniles were separated from their biological parents already after hatching, whereas under natural conditions, they separate from the parents after fledging; and (b) the flock of hand raised juveniles contains no experienced conspecifics, thus there can be no vertical social learning concerning details of the flight technique. Nevertheless, during their first autumn migration, the hand-raised birds show the same individual and social flight techniques as their free-living conspecifics; i.e., V-formation flight during calm periods of the day and soaring and gliding if thermals are available.
- iv) Social behavior: The bird group for hand raising was composed of chicks from different zoo breeding groups. Chicks were collected with an age of 2–8 d after hatching; the maximum age difference in the group was 10 d. The chicks were divided into four nest with three to four chicks each nest and

an age-graduation with a mean of 2 d. This nest composition resembles the natural situation (10). Physiological parameters (body weight, food quantity) and social parameters (agonistic interactions, socio-spatial behavior using nearest-neighbor protocols) were collected from fledging until arrival in the wintering area. All parameters were in a regular range, compared with previous year groups, zoo colonies, and nonmigrating free-living colonies. As far as we can judge, the birds developed normal social behavior toward their group members, as we could not see any obvious differences in their social behavior in comparison with zoo populations or the free flying colonies in Tierpark Rosegg and Cumberland Wildpark Grünau, both in Austria. Throughout the whole migration, the birds were provisioned with sufficient amounts of food. This means that we potentially reduced within-group competition for food resources. However, as Northern bald ibis feed on small invertebrates that they swallow at once, their foraging style creates scramble competition, which is less prone to lead to social conflict over food. During resting times, birds were confined to a 6 × 9-m aviary. Although this aviary was rather spacious, it is still possible that the restricted space influenced, e.g., nearest-neighbor data collected on the ground (which might be an alternative explanation why we could not find a correlation between social proximity on the ground and in the air).

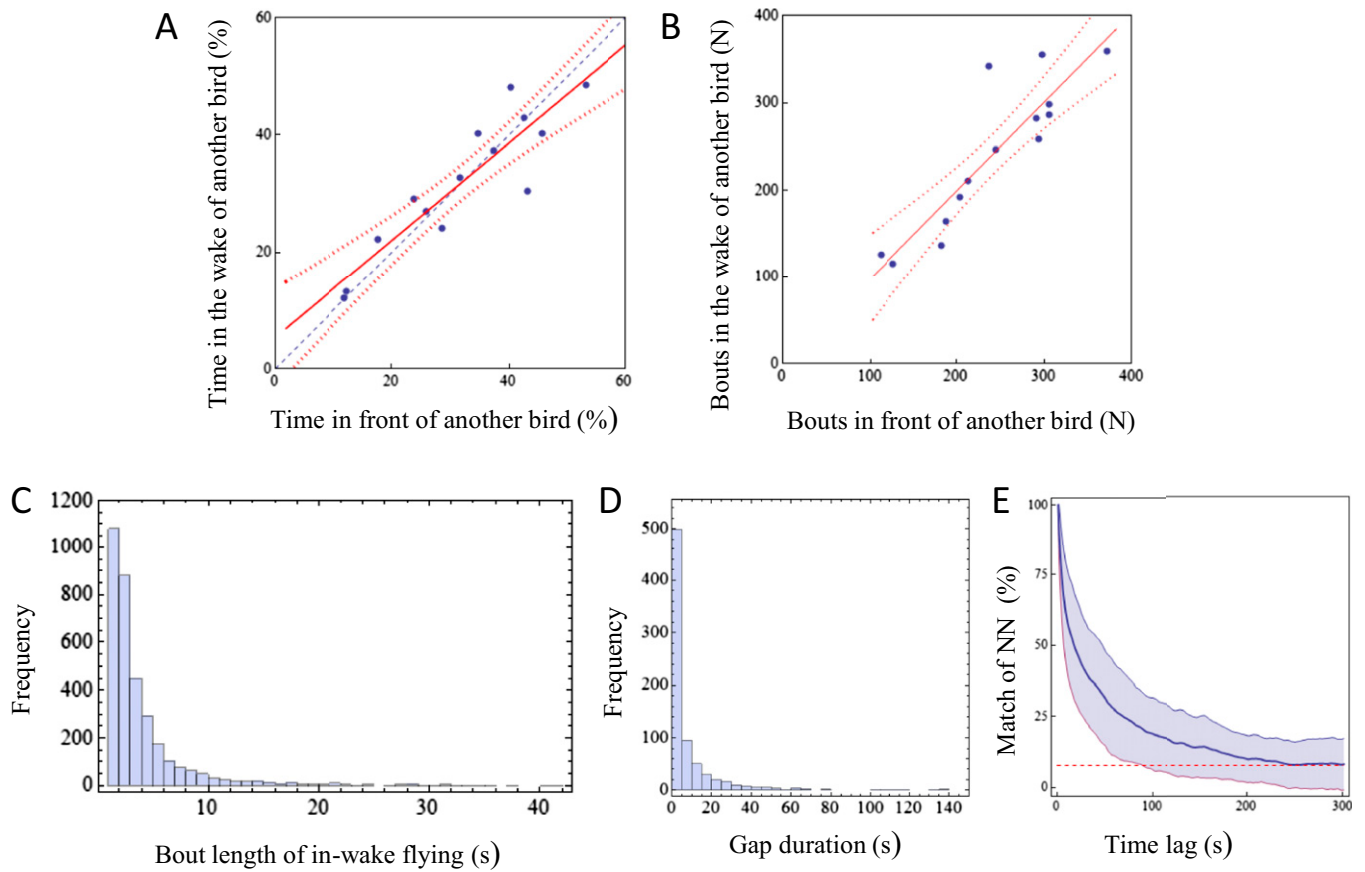
1. Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31(2):295–311.
2. Rands SA, Cowlishaw G, Pettifor RA, Rowcliffe JM, Johnstone RA (2003) Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423(6938):432–434.
3. Guttal V, Couzin ID (2010) Social interactions, information use, and the evolution of collective migration. *Proc Natl Acad Sci USA* 107(37):16172–16177.
4. Sumpter DJT (2010) *Collective Animal Behavior* (Princeton Univ Press, Princeton).
5. Badgerow JP, Hainsworth FR (1981) Energy savings through formation flight? A re-examination of the Vee formation. *J Theor Biol* 93(1):41–52.
6. Newton I (2010) *Bird Migration* (Harper Collins Publishers, London).
7. Gould LL, Heppner FH (1974) The vee formation of Canada geese. *Auk* 91(3):494–506.
8. Portugal SJ, et al. (2014) Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* 505(7483):399–402.
9. Serra G, et al. (2014) Accounting for the low survival of the critically endangered northern bald ibis *Geronticus eremita* on a major migratory flyway. *Oryx*, 10.1017/S0030605313000665.
10. Tintner A, Kotrschal K (2002) Early social influence on nestling development in Waldrapp ibis (*Geronticus eremita*). *Zoo Biol* 21(5):467–480.



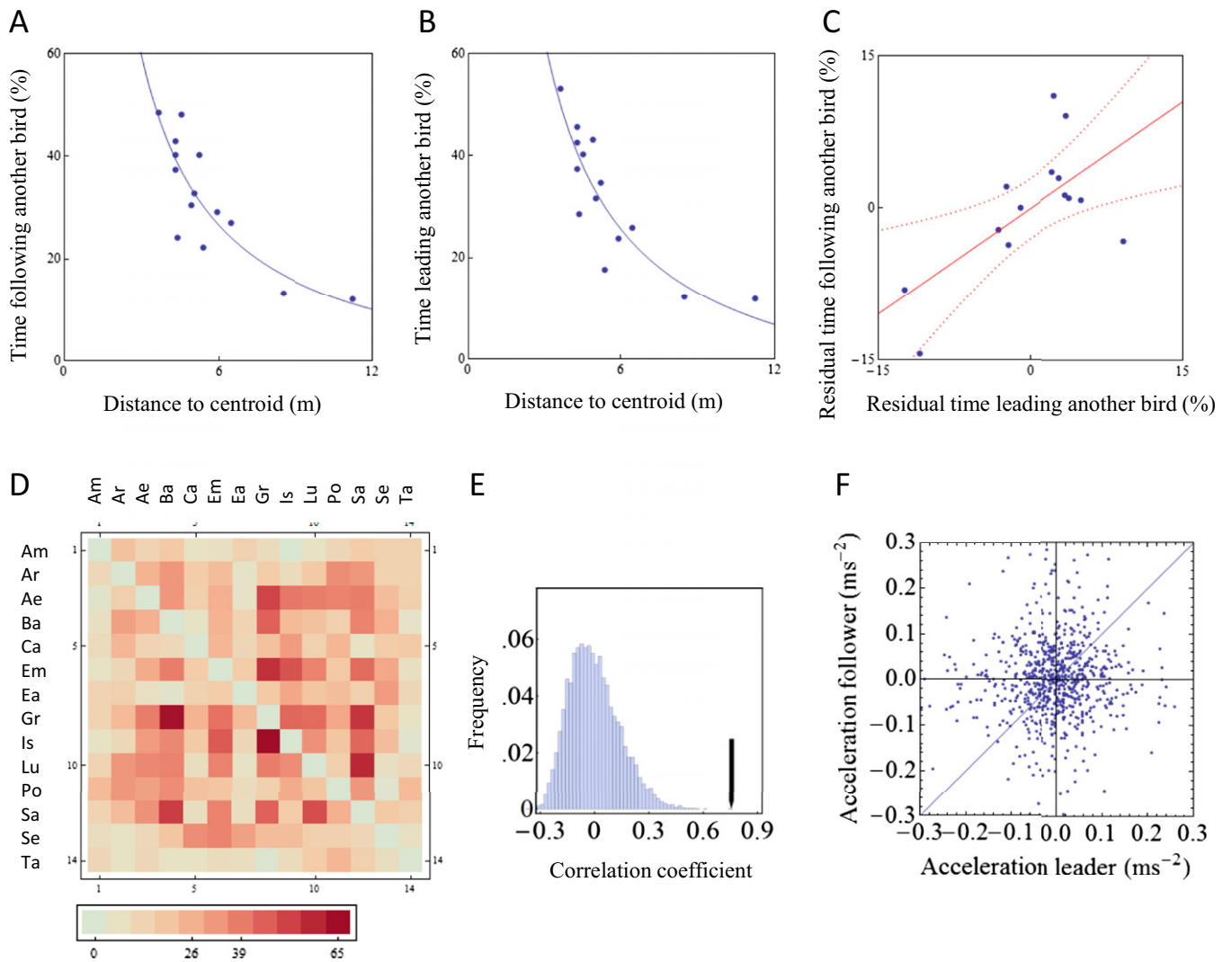
**Fig. S1.** (A) Position of the 14 birds in relation to the centroid of the bird flock. For each second of the flight, we determined the position of each bird. Plots show and area of  $20 \times 20$  m surrounding the centroid. The area is split into cells of  $0.5 \times 0.5$  m, and colors indicate 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.



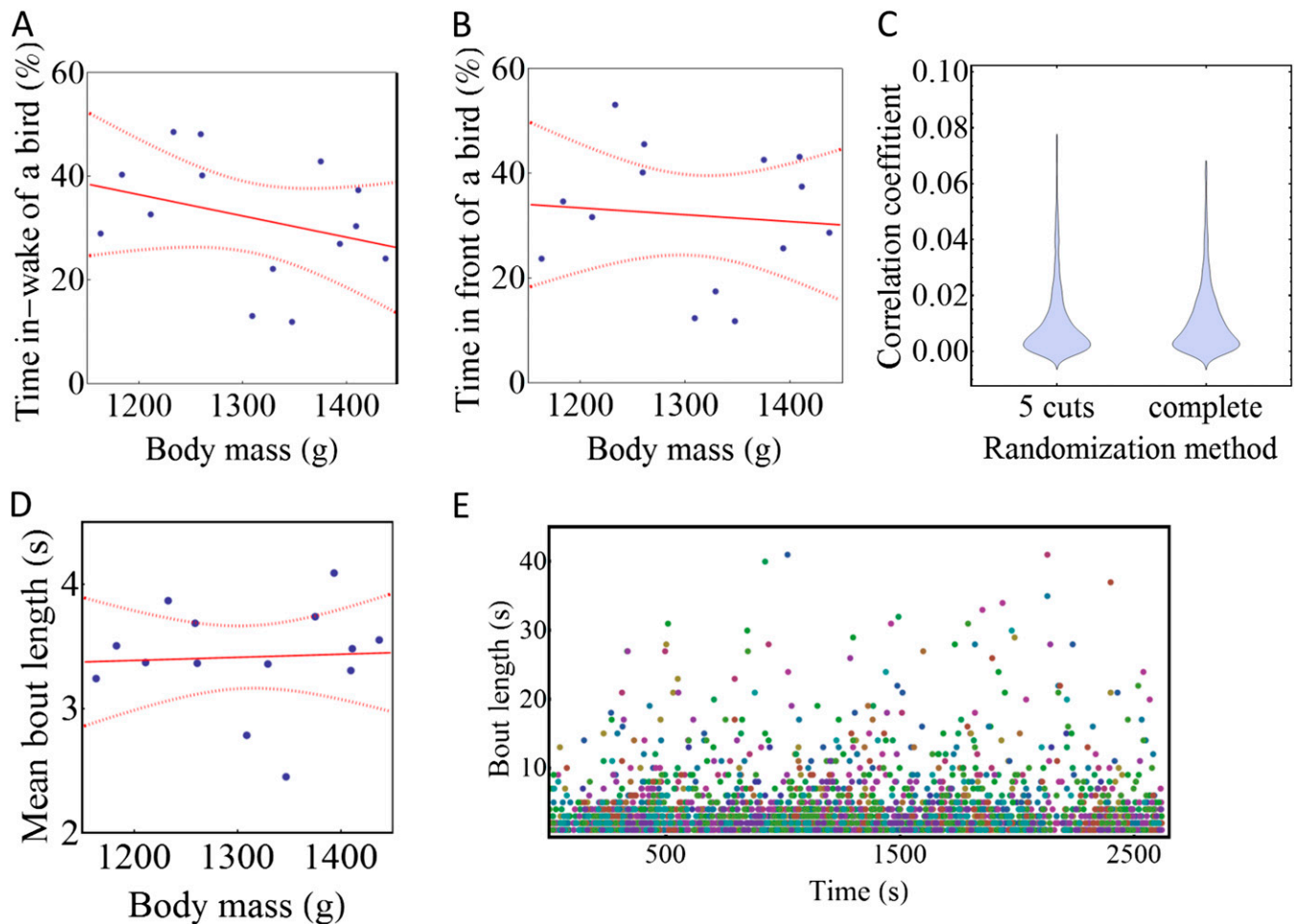
**Fig. S2.** In-wake flying during the 43 min of the migration stage. x axis, time (s); y axis, individual leading birds (abbreviated names). Bold bars indicate that a bird was flying in the wake of the leading bird. The identity of the trailing bird is color coded. Thin colored lines connect the in-wake 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.



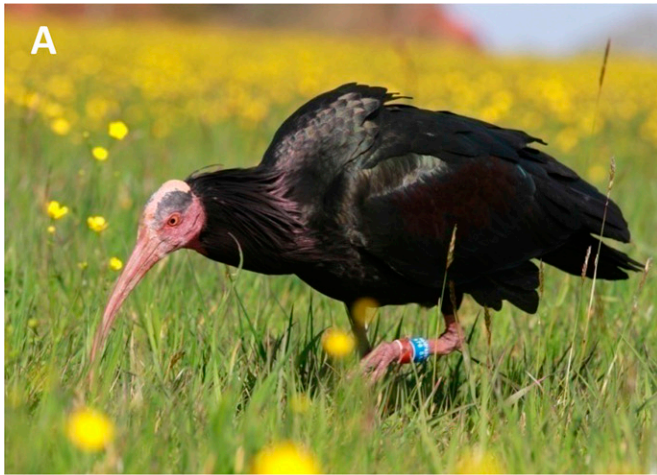


Fig. S6. (A) Northern bald ibis (*G. eremita*) foraging. (B) Juvenile bald ibis are habituated to the paragliders by their foster parents. (C) Juvenile bald ibis following the paraglider shortly after takeoff. (D) Echelon formation of five bald ibis during the migration. Images courtesy of J. Fritz (A–C) and M. Unsöld (D).

**Table S1. Comparison of in-wake areas**

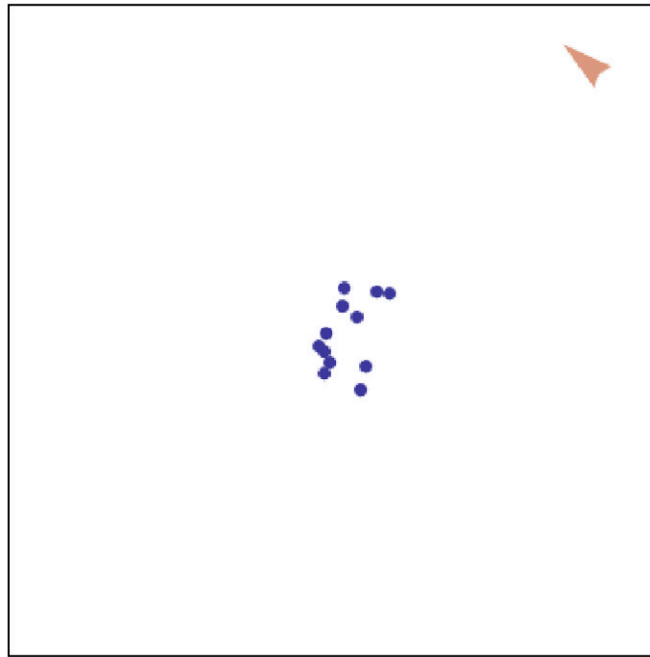
In-wake area behind (m)		In-wake area sideways (m)		In-wake time (%)	In-wake bouts (N)	Bout duration (s) (maximum)	Typical group size		Correlation in-wake flying	
Minimum	Maximum	Minimum	Maximum				Minimum	Maximum	r	CI <sub>95</sub>
0	3	0	1.6	32.0	3,374	41	2.6	3.3	0.90	0.72–0.97
0	3	0	1.4	29.0	3,146	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  $100 \times 100$  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.