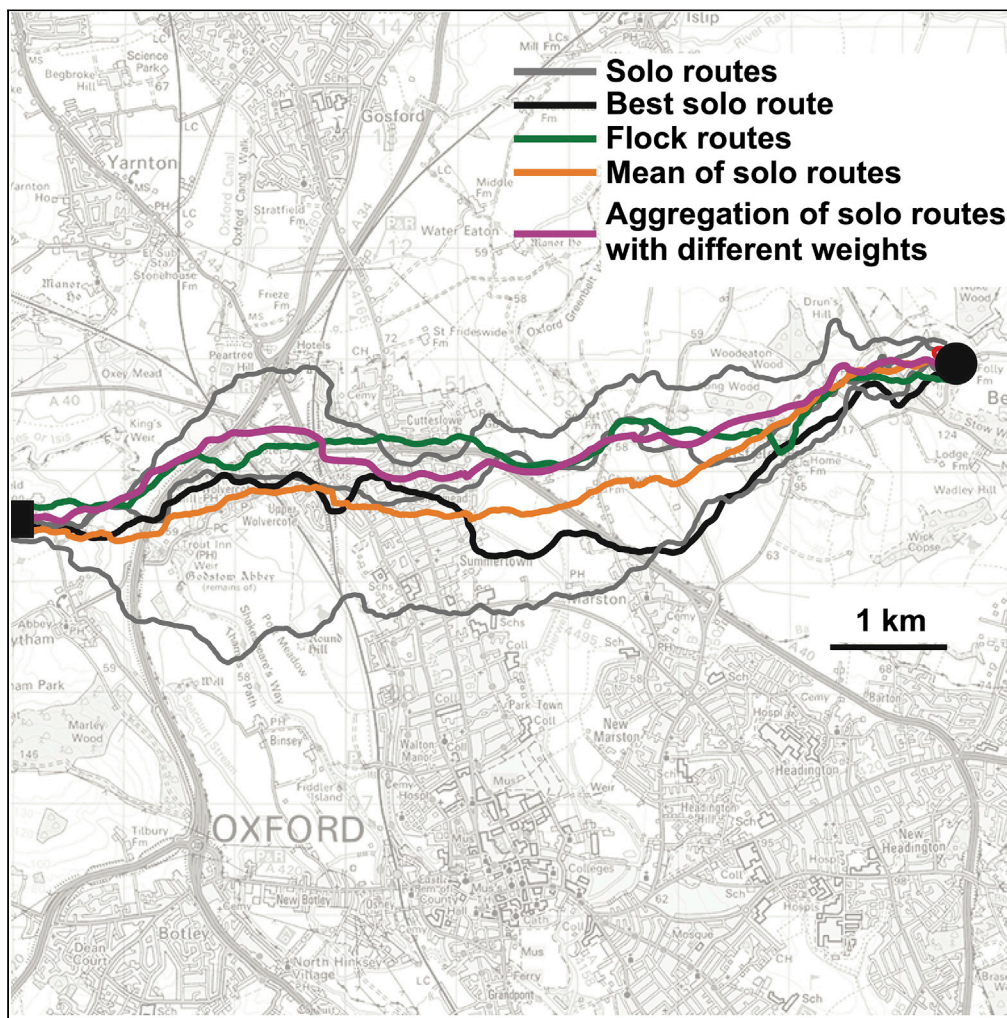


Article

Empirical test of the many-wrongs hypothesis reveals weighted averaging of individual routes in pigeon flocks



Takao Sasaki,
Naoki Masuda,
Richard P. Mann,
Dora Biro

takao.sasaki@uga.edu

Highlights

The ‘many-wrongs hypothesis’ was empirically tested using homing pigeons

Larger flocks had significantly more efficient routes than smaller flocks

Flock routes were not simply averages of individual routes

Individuals with greater route fidelity have more influence on their flocks’ routes

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Article

Empirical test of the many-wrongs hypothesis reveals weighted averaging of individual routes in pigeon flocks

Takao Sasaki,^{1,7,*} Naoki Masuda,^{2,3} Richard P. Mann,⁴ and Dora Biro^{5,6}

SUMMARY

The ‘many-wrongs hypothesis’ predicts that groups improve their decision-making performance by aggregating members’ diverse opinions. Although this has been considered one of the major benefits of collective movement and migration, whether and how multiple inputs are in fact aggregated for superior directional accuracy has not been empirically verified in non-human animals. Here we showed that larger homing pigeon flocks had significantly more efficient (i.e. shorter) homing routes than smaller flocks, consistent with previous findings and with the predictions of the many-wrongs hypothesis. However, detailed analysis showed that flock routes were not simply averages of individual routes, but instead that pigeons that more faithfully recapitulated their routes during individual flights had a proportionally greater influence on their flocks’ routes. We discuss the implications of our results for possible mechanisms of collective learning as well as for the definition of leadership in animals solving navigational tasks collectively.

INTRODUCTION

Collective intelligence—the phenomenon whereby groups improve their decision-making by pooling individual information—has been identified in many taxa (Couzin, 2009; Krause et al., 2010; Sumpter, 2010). One surprising finding in research on collective intelligence is that even when each group member has inaccurate information, groups can still make relatively accurate decisions (Surowiecki, 2005). Francis Galton’s analysis of a weight-guessing competition at a county fair remains one of the best-known examples (Galton, 1907a). His results showed, based on a dataset of approx. 800 people’s independent estimates of the weight of a specific ox, that (i) guessers’ individual estimates ranged widely, but (ii) their mean was extremely close to the ox’s actual weight (1,197 lb vs 1,198 lb, respectively) (Galton, 1907b). The mechanism for this kind of collective intelligence has been mathematically formalized through the Law of Large Numbers: when individual estimates are distributed around the true value, then the mean of these estimates not only tends to be accurate (as individual errors are canceled out) but also becomes increasingly accurate as group size increases (Simons, 2004). These predictions are based on the ‘many-wrongs hypothesis’ (Simons, 2004). Although some past research invokes the many-wrongs hypothesis when there is any improvement in collective performance by pooling individual estimates (e.g. 38, 39), here we apply the definition proposed by Simons (2004), which also posits that the improvement emerges as a result of the group assuming the mean derived from all individual inputs.

The many-wrongs hypothesis proposes a potential mechanism for increased flight route efficiency by flocks of birds (Bergman and Donner, 1964; Wallraff, 1978). That is, flocks may be able to assume more direct routes to specific destinations by taking the mean of individual birds’ directional estimates. Although past empirical work has shown that route efficiency tends to improve as flock sizes increase (Biro et al., 2006; Dell’Ariccia et al., 2008; Tamm, 1980) (but see (Keeton, 1970; Santos et al., 2016)), consistent with the many-wrongs hypothesis, these studies did not test if this outcome was achieved by flocks taking a “mean route,” or even by pooling individual information. In fact, bird flocks can improve route efficiency without aggregating individual information. For example, the efficiency of a flock route will increase with flock size if the flock selects the best estimate among those of its flock members. Although rare in non-human animal groups (Laland, 2004), this ‘copy the best’ strategy is commonly used during collective decision making and social learning in human groups (King et al., 2012; Laughlin, 2011). Therefore, it is still unknown whether bird flocks achieve higher route efficiency through adopting the mean route according to the

¹Odum School of Ecology, University of Georgia, Athens, GA 30602, USA

²Department of Mathematics, University at Buffalo, State University of New York, Buffalo, NY 14260, USA

³Computational and Data-Enabled Science and Engineer Program, University of Buffalo, State University of New York, Buffalo, NY 14260, USA

⁴Department of Statistics, University of Leeds, Leeds LS2 9JT, UK

⁵Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

⁶Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY 14627, USA

⁷Lead contact

*Correspondence:

takao.sasaki@uga.edu

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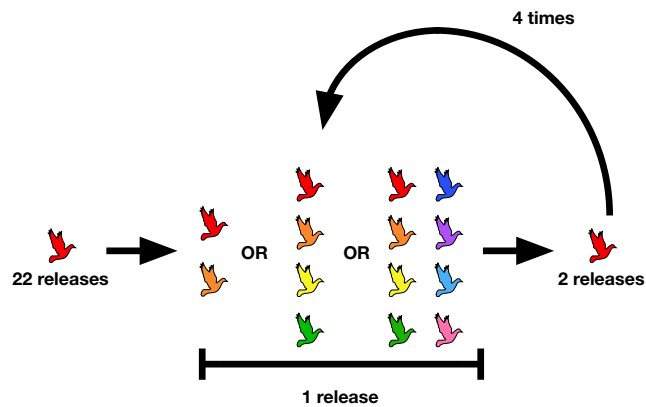


Figure 1. Experimental procedure

All pigeons were first released individually 22 times in succession. They were then assigned to flocks of either 2, 4, or 8 birds, and released once. The flock release was followed by two individual releases, then birds were again assigned to flocks (in new combinations), and the cycle was repeated four more times (i.e. five flock releases were conducted in total). All pigeons experienced all flock sizes at least once.

many-wrongs hypothesis, or even whether they aggregate individual route preferences in any “democratic” way.

The many-wrongs hypothesis has at least two potential problems in terms of its implementation for birds in nature. First, there is typically no central control to calculate the mean of individual inputs. Second, it is difficult for an individual bird to track the positions and flight directions of all the flock members while flying and maneuvering at speed. Collective decisions instead often emerge from local interactions among group members (Camazine et al., 2003; Gordon, 2010; Seeley, 2010). Collective movement in bird flocks is thought to obey a similar decentralized process: individual starlings, for example, attend only to a limited number of nearest neighbors during flock flights (Ballerini et al., 2008a, 2008b). Individuals are also thought to follow local interaction rules, such as attraction, alignment and repulsion, and during flock flights. That is, each individual is assumed to move away from others in closeness, proximity to avoid collisions, to align its motion with other individuals at a somewhat greater distance, and to move toward individuals at larger distances to maintain group cohesion (Couzin et al., 2002; Okubo, 1986; Reynolds, 1987). As such, it may be difficult for bird flocks to discern what the overall mean directional preference is. How, then, do animals aggregate individual opinions in nature? In some animal groups, one or a few individuals with certain characteristics, such as more experience (Flack et al., 2012), larger body size (Krause et al., 2000), faster travel speed (Pettit et al., 2015), higher nutritional needs (Fischhoff et al., 2007; Krause et al., 2000), or greater social dominance (Rands et al., 2006), act as leaders and determine the direction of collective movement (King and Cowlishaw, 2009). In a more subtle variant, multiple group members may contribute to collective movement decisions, but do so with different weights (Nagy et al., 2010).

In this study, we used homing pigeons, *Columba livia*, as a model system that has provided numerous important insights into collective animal movement (Dell’Ariccio et al., 2008; Flack et al., 2013; Santos et al., 2016). Previous work using miniature global positioning system (GPS) tracking has shown that, if birds are released singly, they typically develop idiosyncratic homing routes over a series of releases and, once the routes are developed, they recapitulate them faithfully (Meade et al., 2005). This robust phenomenon allowed us to characterize an individual route preference for each bird. Furthermore, if multiple birds are released together, they will fly home as a flock, even if they have different preferred routes (Watts et al., 2016). Thus, we were able to measure flock routes created by individuals with different route preferences. We first tested the key predictions of collective intelligence in the context of collective movement by constructing flocks of various sizes composed of individuals with idiosyncratic homing routes (Figure 1): do flocks take more efficient homing routes than individuals, and does route efficiency increase as a function of group size? Confirming both these predictions, we next examined the underlying mechanism by testing two hypotheses: groups improve route efficiency according to the ‘many-wrongs’ hypothesis (taking the mean of individual routes; Figure 2) or using the ‘copy the best’ strategy (following the individual that has the most efficient route). Finally, because both hypotheses were rejected, we quantified each flock

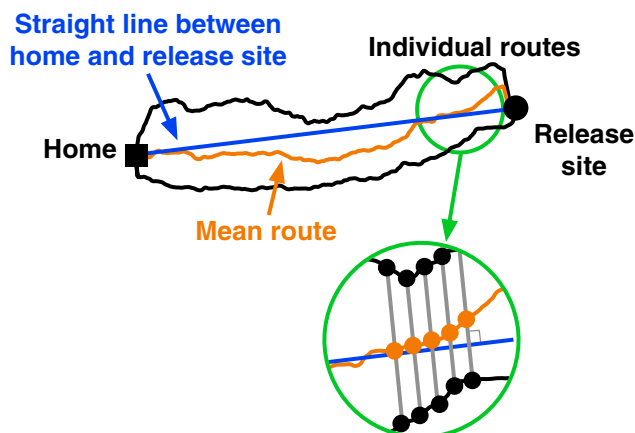


Figure 2. Schematic illustration of how the hypothetical mean route for a flock was calculated based on the established solo routes of individuals within the flock

We first defined a series of equidistant target points along the straight line connecting the release site with the home loft (blue line and blue points in the inset), and measured the orthogonal distance from these points to each individual trajectory (black lines and black points in the inset; two individuals). We defined the mean route (orange line and orange points in the inset) as the mean of these displacements for each target point.

member's contribution to the collective route through a heuristic optimization procedure and examined if certain individual traits (fine-scale leadership rank, flight speed, route efficiency, and route fidelity) correlated with the level of influence that that individual had. Note the original many-wrongs hypothesis used the deviations of birds from a singular target location as the destination (e.g., a small island). In our experiment, we instead considered the beeline (the blue line in Figure 2) as the destination and calculated the deviation from it for each positional fix along a flight track, as pigeons take diverse routes to reach the home loft. In other words, we assumed that pigeons continuously make local, spatially specific estimates about the best direction toward the home loft.

RESULTS

Larger flocks have more efficient routes but do not use the mean of individual routes

As flock sizes increased, homing routes became more efficient (i.e. closer to the beeline; Theil-Sen regression: $v = 2056$, $p < 0.01$; Figures 3 and 4). The efficiency of the flock routes was, however, lower than that of the hypothetical mean routes calculated from all flock members' solo routes, especially for large flock sizes (Nemenyi test: $p = 0.49, 0.03, 0.02$ for flock sizes = 2, 4, and 8, respectively; Figure 3), in conflict with the many-wrongs hypothesis. These discrepancies in route efficiency between the empirical flock routes and the hypothetical mean routes suggest that flocks were not using the mean of the individual routes. Interestingly, overall, the performance of flocks was at least as good as that of their best member (i.e. the individual with the most efficient solo route). The median route efficiency tended to be higher for flocks than for their best member, especially at flock size two, although the differences were not significant (Nemenyi test: $p = 0.26, 0.86, 0.99$ for flock sizes = 2, 4 and 8, respectively; Figure 3). Thus, the flock route was not only different from the mean route, but was also likely not simply the best flock member's route. In fact, the route of the best flock member was not significantly better than that of a random flock member for predicting the flock's route (see Data S1 and Figure S1). Figure 4B shows an example of a set of solo routes, the resultant flock route, and the hypothetical mean route calculated from the solo routes.

How do flocks aggregate their members' routes?

We next tested if larger flocks performed better because we inadvertently assigned more efficient individuals to the larger flocks than to the small flocks. This test confirmed that average solo route efficiency was not different for different flock sizes (Kruskal-Wallis test: $\chi^2 = 1.68$, $df = 2$, $p = 0.43$; Figure S2). This result thus rejected the possibility that the high performance of the larger flocks could be explained by their 'elite' flock members.

Given that neither a strict many-wrongs model nor solo leadership appeared to account for the structure of flock routes, we further investigated how flocks aggregated their members' different routes. To do so, we

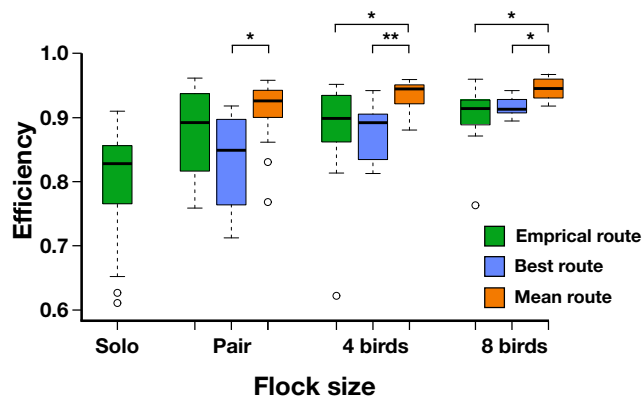


Figure 3. Route efficiency for different flock sizes

Each box extends between the lower and upper quartiles; the horizontal line within the box indicates the median, and whiskers show the range of the data, except for outliers indicated by open circles. * indicates $p < 0.05$ and ** indicates $p < 0.01$ based on Nemenyi test. (Because it would be too conservative, Bonferroni correction was not performed; see (Perneger, 1998) for details).

first calculated the influence of each pigeon on the flock route by running a heuristic optimization procedure: the flock route was assumed to be a weighted sum of the solo routes, where we sought to assign individuals with different degrees (weights) of influence. We determined the weight for each bird by minimizing the difference between the actual flock route and the hypothetical flock route based on the weighted sum of the solo routes across all of its flock flights. In other words, each bird had an ‘intrinsic’ weight, which was calculated based on all flock flights it had participated in, but, because the weight for each bird was standardized separately for each flock release, the same bird could have different weights in different flock releases (Note that this calculation of the weight for each individual required data from multiple of its flock releases so that accurate weights could not be obtained based on a single data point during a flock flight, or even on one flock release; see STAR Methods for details). We found that the hypothetical routes based on these different individual weights were, indeed, significantly more similar to the empirical flock routes than the ones based on equal individual weights (i.e., the many-wrongs model; Wilcoxon signed-rank test: $V = 493$, $p < 0.01$). An example of such a hypothetical route based on optimal individual weights is shown in Figure 4B (the purple line), for comparison with the observed flock route (the green line). In line with our conclusions based on the analysis of route efficiency, the distributions of weights in flocks of different sizes showed that neither did just a single bird determine the flock route nor did all birds contribute equally (Figure 5). Instead, individuals possessed a range of different weights, with a limited subset of flock members having the greatest influence on flock routes. To confirm the rejection of the many-wrongs model, we looked at the individual weights. Under the many-wrongs model the weight for each bird in each group is expected to be identical; however, given that we also expect some degree of noise in the data we do not expect to see absolutely identical inferred weights. Instead, if this hypothesis were true we would expect to see inferred weights that are closely and symmetrically distributed around a central mean value, rather than being dominated by a subset of individuals. This hypothesis was tested with a sign test, constrained to 78 flights out of 142 as each flock must contain at least one weight above the mean and one below by definition. Of these, only 19 flights had weights above the mean, and thus we rejected the hypothesis (two-tailed sign test: $n = 78$, $x = 19$, $p = 6.4 \times 10^{-6}$). We further showed that the most ‘influential’ individuals in flocks had higher weights of influence than expected if the weights of influence were distributed either uniformly (and thus symmetrically around the mean as expected under the many-wrongs hypothesis) or exponentially (corresponding to a maximum-entropy Boltzmann distribution, representing maximum ignorance about the distribution of weights subject to the constraint that they are positive and have a fixed sum) (Figure S3). These results showed that the weights of influence were neither uniformly nor exponentially randomly distributed and thus confirmed that some flock members had more influence on flock routes than others.

Of the four measured individual traits, fine-scale leadership rank, flight speed, route efficiency, and route fidelity, only route fidelity was positively correlated with individual weights of influence on flock routes (Figure 6A). That is, pigeons that recapitulated their routes more closely during solo flights had a higher

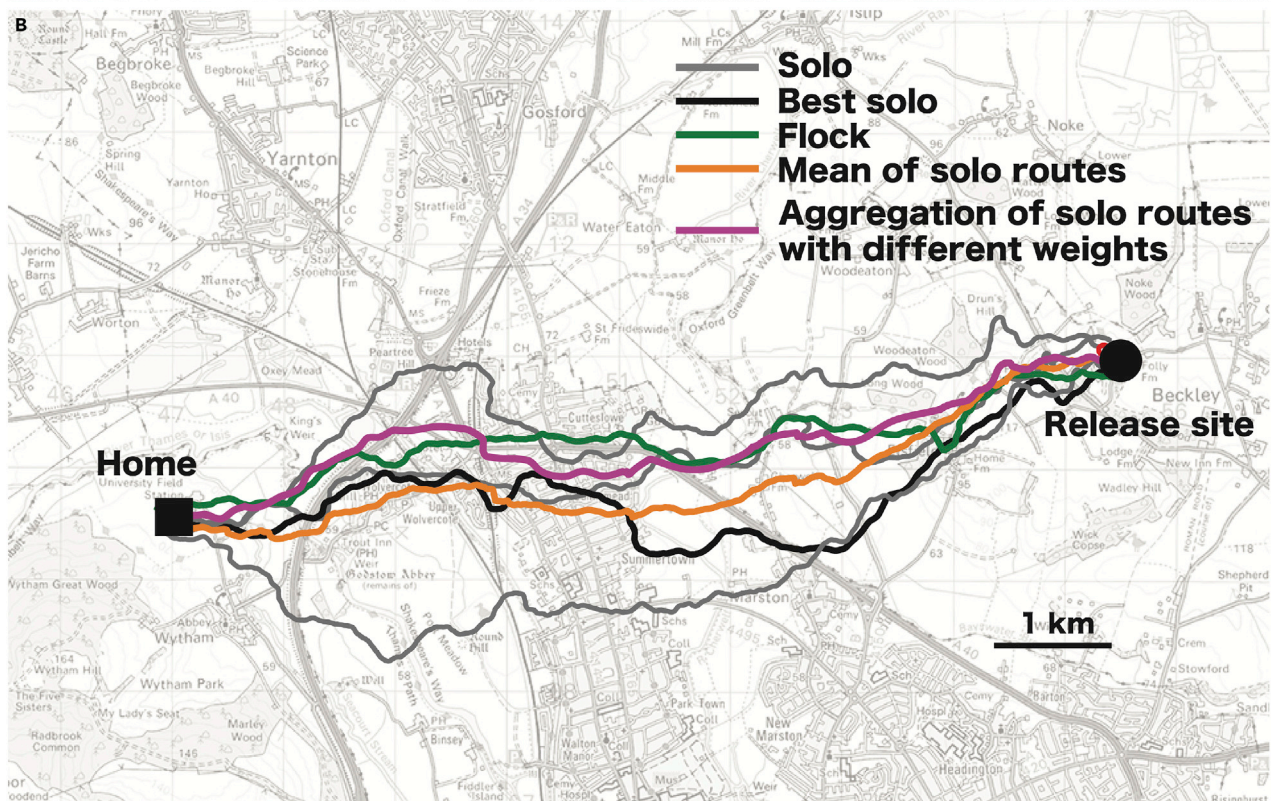
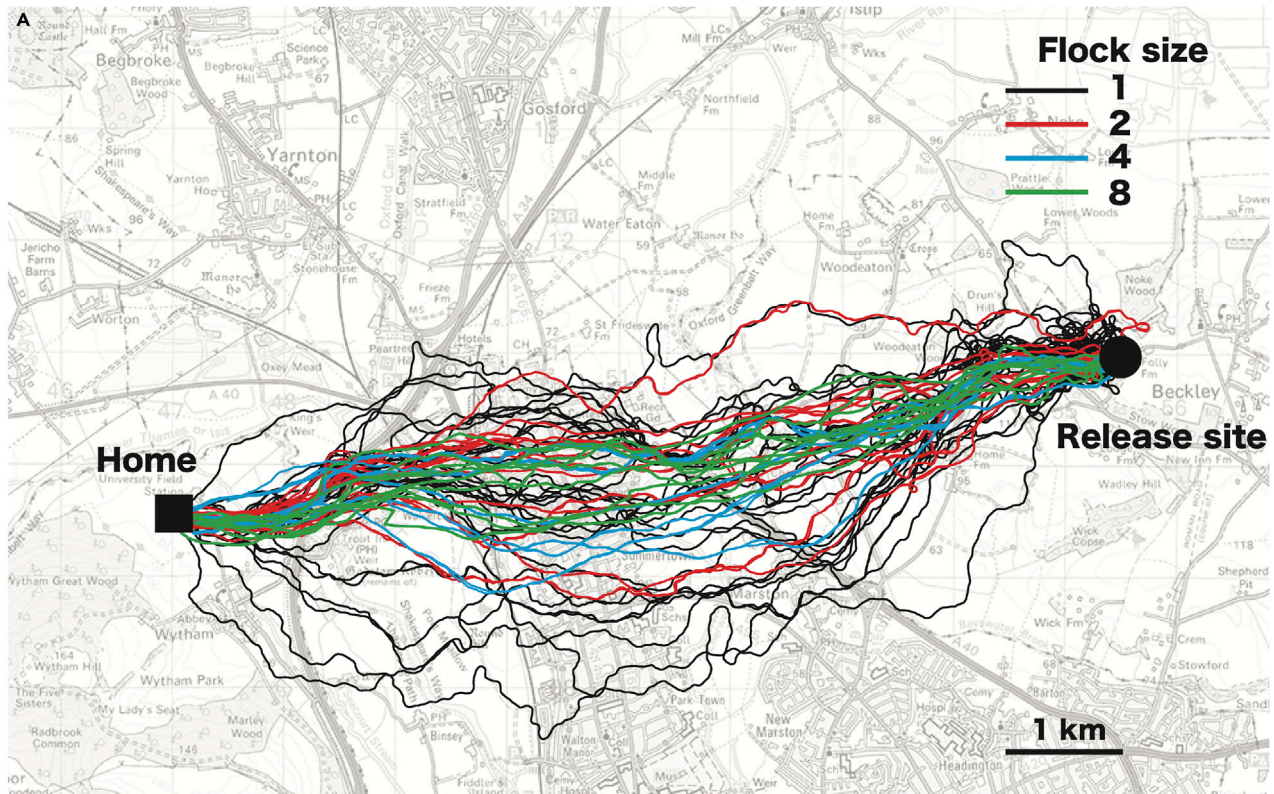


Figure 4. Visualization of homing routes recorded in the experiment

(A) Homing routes of flocks of different sizes (1, 2, 4, and 8).

(B) Examples, from a single flock of four, of flock members' solo routes recorded immediately preceding the flock flight (gray and black), the flock route (green), and the mean route calculated from the solo routes (orange). The black route shows the best (most efficient) solo route. The purple route shows the hypothetical flock route based on optimal individual degrees (weights) of influence (see text for details).

influence on flock routes. No significant correlations were found for the other three traits (Figures 6B, 6C and 6D).

DISCUSSION

We investigated collective navigation—specifically, if and how animals improve navigational accuracy by traveling together as a group (Berdahl et al., 2018)—using homing pigeons as our model system. This study elucidates how groups larger than two combine idiosyncratic individual routes to produce consensus over the collective route (Biro et al., 2006). We tested two hypotheses for how improvements might accrue in groups: the many-wrongs hypothesis and the copy-the-best hypothesis. Our results showed that the efficiency of pigeons' homing routes increased with flock size: the larger the flock, the better the collective performance. However, this was not a consequence of flocks taking the overall mean route as the many-wrongs hypothesis predicts; neither did the flocks use the best of their flock members' routes. Therefore, flock routes emerged neither in an egalitarian nor in a fully despotic way.

How, then, do flocks aggregate diverse individual routes? We used a heuristic optimization procedure, which has never been used in the field of collective animal behavior, to quantify precisely each flock member's contribution to the final flock route. Our results show that rather than obeying a "pure" many-wrongs averaging of inputs, the emergence of the flock route can be conceptualized as a weighted many-wrongs process. Crucially, we are able to further show that these weights correlate with a specific individual trait, route fidelity: birds that recapitulate their solo routes more closely have greater influence on flock routes. These results confirm and extend past findings that individuals with greater route fidelity have more influence on the combined flight paths of pairs of pigeons flying together (Freeman et al., 2011). Here we use a more sensitive method of assigning leadership during homing and also show that the effect scales up to larger flock sizes. Although our study does not directly investigate how these 'high-fidelity' individuals achieve higher influence on flock routes, we propose two possibilities, both predicated on the suggestion that high route fidelity and high input into flock routes are rooted in the same phenomenon: the bird's lack of willingness to stray from established routes. In other words, these birds' loyalty to their own routes makes them less likely to follow others during flock flights, and, as a consequence, flock routes are more similar to routes of high-fidelity individuals than to those of low-fidelity individuals. First, high route fidelity may be an indicator of perceived route safety (or, conversely, perceived danger associated with any adjacent routes). In such a case, route fidelity, and the consequent lack of the bird's willingness to stray, may even be utilized as a cue by other flock members, increasing their willingness to follow. Second, route fidelity may indicate a bird's "confidence" in its own navigational solution, making it less willing to follow others. A similar pattern has been found in humans: the more confident individuals are in their own opinions, the less likely they are to be influenced by information from others (Deutsch and Gerard, 1955), and as a result, group opinions tend to be similar to the opinions of individuals with high self-confidence (Laughlin and Ellis, 1986; Zarnoth and Sniezek, 1997). Of course, route fidelity in pigeons and confidence in humans do not necessarily derive from similar phenomena. For example, human studies have shown that groups can make optimal collective decisions by combining opinions according to individual confidence levels (Bang et al., 2017; Marshall et al., 2017). This conforms to the mathematical result that accurate estimation requires weighting differing information in proportion to its precision (Marshall et al., 2017). Our data, however, show that pigeon flocks could in fact reach better routes by weighting individual opinions equally than by doing so according to fidelity levels. Although this difference is likely owing to the fact that while confidence is often correlated with accuracy in humans (Bang et al., 2017; Marshall et al., 2017), this is not the case for route fidelity and efficiency in pigeons; individuals with higher solo route efficiency are not necessarily the ones with higher route fidelity, as our data show (Figure S4). Indeed, it would be interesting to investigate further what determines route fidelity at the individual level (whether, for example, route fidelity reflects individual differences in navigational styles or in exploratory tendency, or differences in the landscape individuals happen to have formed their routes over) and how differences among individuals in such traits affect collective decisions in different animal groups.

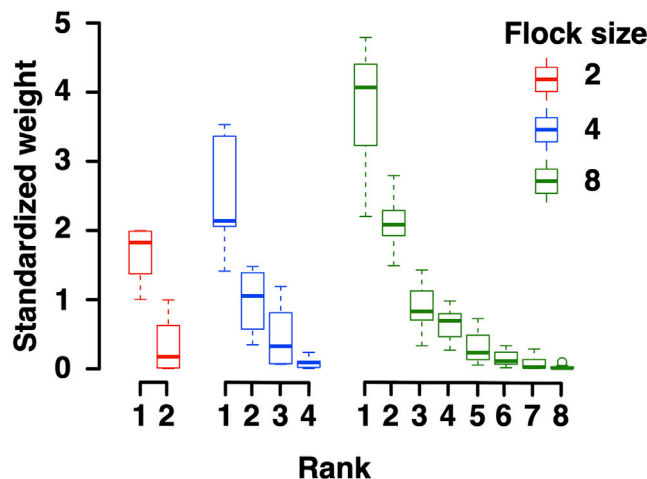


Figure 5. Distributions of standardized weights of influence on flock routes at each flock size

In each flock, the weights were ranked from highest to lowest. Flocks that had a bird missing owing to GPS errors were not included because these flocks would lack a data point for the lowest rank. Each box extends between the lower and upper quartiles; the horizontal line within the box indicates the median, and whiskers show the range of the data. See [supplemental information](#) for further analyses.

If, as we have shown, pigeon flocks could improve their performance further by taking the mean route, then why do we not see a more egalitarian system of decision-making in these flocks? One reason may be that it is difficult for individuals to effectively contribute equally. Because flock routes are typically determined through local interactions among flock members (Ballerini et al., 2008a, 2008b), it may be difficult to scale contributions from each flock member. An alternative consideration is that the mean route may not be the “best” route: on the one hand, pigeons benefit from returning to the loft as quickly as possible (i.e. via the shortest route), but on the other hand this can be traded off against the potentially greater safety of a longer route. For example, if the beeline to the loft traverses terrain with areas that may harbor predators, then a detour around this area will lengthen the route but also reduce risk. In addition, there may be benefits, in terms of cognitive load, to sub-optimal routes: homing pigeons are known to follow linear features such as roads, railway lines, and rivers, when these lead roughly in the homeward direction (Meade et al., 2005), and even incorporate them into their established solo routes (Biro et al., 2004; Mann et al., 2014). Although this can lead to longer-than-the-beeline routes, the detours are potentially favored because they reduce the attentional, computational, and memory requirements of navigating in a visually complex terrain. In short, it remains unclear whether pigeon flocks are unable to take a theoretically more efficient “true mean” route because mechanisms for pure averaging are not in place, or because the mechanisms that are in place have evolved to favor routes superior in structure or location over the mean.

Interestingly, our results show that ‘leaders’—individuals with high hierarchical leadership ranks, whose changes in flight direction are copied by others in the flock over short time scales (Nagy et al., 2010)—do not have higher influence on the overall structure of flock routes than followers (those with lower hierarchical leadership ranks). At first glance, this seems counterintuitive: essentially, small-scale leader-follower interactions appear not to scale up to large-scale route-level effects. However, this contradiction highlights that leadership may operate differently or mean different things at different spatial/temporal scales. For example, while a given individual may be followed more than others at small spatial scales, if this individual’s movement is not consistently in a specific direction then it will be less likely to appear as a leader in a larger-spatial-scale analysis than an individual that is followed relatively less but travels with a strong directional preference. In other words, if an individual is followed by its flock members but does not recapitulate its homing route during flock flight, the small-scale analysis categorizes this individual as a leader while the large-scale analysis does not do so. Similar counterintuitive patterns have been found in research on leadership in other animals. For example, while one study in baboons demonstrated largely democratic decision-making over the course of consecutive time-steps in high-resolution tracking of group movements (Strandburg-Peshkin et al.,

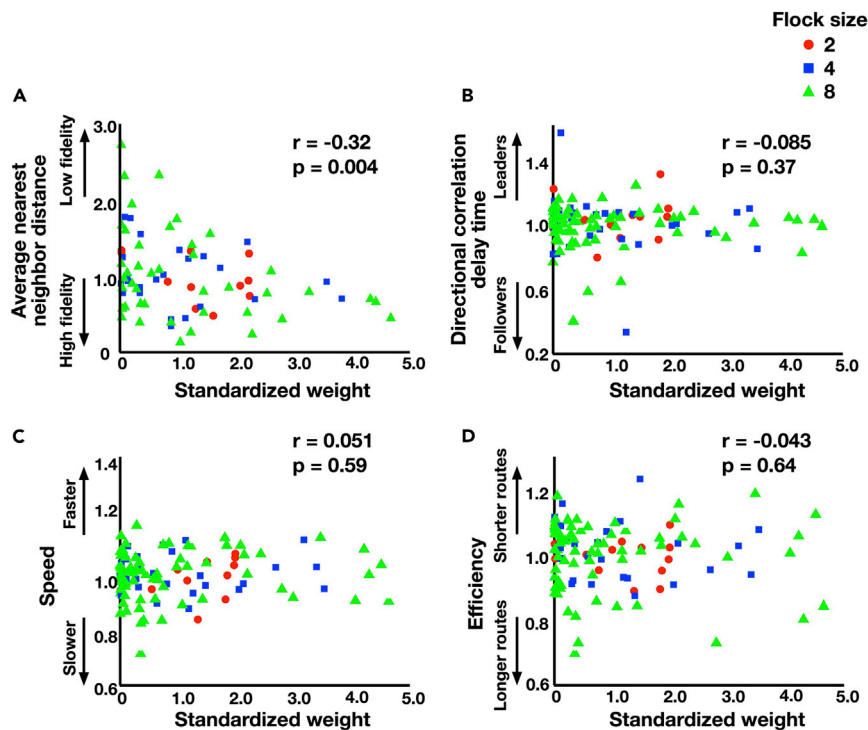


Figure 6. Relationship between selected individual traits and weights of individual influence on flock routes

(A–D) (A) Route fidelity, measured based on the average nearest neighbor distance (Guilford and Biro, 2014; Meade et al., 2005) between two consecutive solo routes of a given bird, (B) hierarchical leadership rank, determined through directional correlation delay analysis (Nagy et al., 2010), (C) flight speed, and (D) route efficiency. Route fidelity was the only trait that significantly predicted individual influence; individuals with high fidelity were more likely to affect flock routes. Both traits and weights were standardized (the weight for each bird was standardized for each flock release). See supplemental information for further detail on this analysis.

2015), another study had previously shown clear despotic leadership by the alpha male when considering the final outcome of a group’s movement (arrival at a specific foraging site) (King et al., 2008). These observations, including ours, have important implications for the definition of ‘leadership’ in animal groups and suggest that caution needs to be exercised when generalizing from data at one level to conclusions at others. Further work to understand the nature of scaling from small-to large-scale patterns, and quantifying the scale at which their effects may reverse, will be an important avenue for future research.

In our study, birds did not have an opportunity to fly with the same flock members more than once, so we were not able to observe how the collective route might have changed if flocks had had multiple opportunities to solve a given navigational task together. For example, research on humans has shown that group members improve their collective decisions after sharing social information (i.e. initial individual guesses) (Jayles et al., 2017). Past research with pigeons has also shown that naive individuals improve homing routes faster over successive releases when they fly as a pair than when flying solo (Flack and Biro, 2013). However, when pairs fly together repeatedly, they acquire information both individually and socially, and as yet we know little about the relative contributions of each in the improvement of collective routes over time. The gradual improvement of collective performance has been hypothesized to represent a case of ‘collective learning’, defined as the process of generating and disseminating knowledge in a group setting (Berdahl et al., 2018; Biro et al., 2016; Flack and Biro, 2013; Sasaki and Biro, 2017). Future research should investigate how groups exchange and aggregate different individual opinions over time, as many animal groups, including humans (Page, 2008, 2011), often have to make consensus decisions that collate diverse individual input (Conradt and Roper, 2005), and do so repeatedly. The role of feedback from the quality of previous consensus decisions on future decisions may be key in elucidating longitudinal changes in collective performance, allowing individuals to gradually

adjust, for example, the weight of their reliance on social vs individual information. A comparison of individual and collective route development in homing pigeons will provide a promising context for this under-researched area of collective animal behavior.

Limitations of the study

We recognize at least two limitations in our work. First, the performance was measured solely based on the travel distance. However, there are other factors that could affect the performance. For example, if the beeline to the loft traverses terrain with areas that may harbor predators, then a detour around this area will lengthen the route but also reduce risk. Furthermore, homing pigeons tend to follow linear features such as roads, railway lines, and rivers. This behavior can make the route longer but may reduce the attentional, computational, and memory requirements during homing. Second, the homing distance was relatively short (8.1 km) so it is still unknown if the findings in this study are consistent for longer homing flights.

STAR★METHODS

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

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.105076>.

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AUTHOR CONTRIBUTIONS

Study conception and design: T.S. and D.B.; data collection: T.S.; Analysis and interpretation of results: M.N., R.P.M., T.S., and D.B.; draft article preparation: T.S., D.B., R.P.M., and M.N.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Empirical data	https://doi.org/10.17632/6zjmy4wp3v.1	
Experimental models: Organisms/strains		
Homing pigeons, <i>Columba livia</i>	University of Oxford	Unknown
Software and algorithms		
Matlab (2018b)	https://www.mathworks.com/?s_tid=gn_logo	
Matlab code	10.17632/6zjmy4wp3v.1	

RESOURCE AVAILABILITY

Lead contact

Further information and requests regarding the methods or data used should be directed to the lead contact, Takao Sasaki (takao.sasaki@uga.edu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All the original data have been deposited at Mendeley Data and are publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- All original code has been deposited at Mendeley Data and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We used 32 homing pigeons, *Columba livia*, bred at the Oxford University Field Station, Wytham, UK (51°46'58.34"N, 1°19'02.40"W). The pigeons lived in one of two lofts at the station, and each loft had approximately 40 pigeons. Subjects were between three and eight years of age (mean = 5.5 years) and weighed between 379 g and 475 g (mean = 433.6 g). Their sex was unknown. They had participated in experiments in previous years, but had never been released from the vicinity of the release site used in this study. All were equipped with an elastic harness "backpack" carrying a plasticine dummy weight (15 g) a week prior to the start of experiment. Dummy weights were replaced by GPS devices in specific releases during the experiment (see below). All the experiments were approved by the local Ethics Committee of the Department of Zoology at the University of Oxford and conformed the relevant regulatory standards.

METHOD DETAILS

Experimental procedures

All releases were conducted from the same site, Beckley (51°47'36.46"N, 1°11'50.97"W; distance to home: 8.1 km, direction to home: 260°). All subjects were first individually released 22 times ("solo" flights), a sufficient number for pigeons to develop stable homing routes (Meade et al., 2005), except one bird, which did not return on its 5th release. Neither the age nor the body weight of the subject had a significant effect on efficiency (see below for the definition) of solo routes (Data S1), confirming previous findings (Sasaki et al., 2018). Thirty of the remaining 31 birds (with the 31st bird held in reserve) were then randomly assigned to groups with either two, four or eight birds, and released as a flock. Each flock flight was followed by two solo releases to confirm that birds' individual routes had not changed substantially as a result of the flock flight (Figure S5). We repeated this cycle (i.e. one flock release followed by two individual releases) four more

times. Thus, each bird participated in a total of 32 solo releases and five flock releases (Figure 1). On the 24th solo flight (i.e., after the first flock flight), one bird did not return, and was replaced by the reserve bird for the remainder of the experiment. Because we were only interested in the stable solo routes of each bird (rather than the development of these routes) and the flock routes, we replaced the backpack dummy weights with a GPS device only on the 15th and after the 20th solo flight. All birds participated in flock flights with each group size at least once. Within a given release, solo birds and flocks were released at 5–10 min intervals, and all birds experienced similar weather conditions during each release. Up to two releases per bird were conducted per day, with a minimum of 2 h between consecutive releases, in dry weather and at wind speeds $<10 \text{ ms}^{-1}$.

Data logging

Flight tracks of individual birds were recorded using 5 Hz GPS loggers (15 g; BT-Q1300ST, Qstarz, Taiwan) and downloaded to a computer using Qtravel (Qstarz) software. We analyzed the tracks in MATLAB (R2018b), after converting raw positional data from degrees to meters using a Universal Transverse Mercator grid. In order to focus on the choice of homing route, segments of track within a 200 m radius of the loft were excluded because birds typically circled around the loft immediately prior to landing.

QUANTIFICATION AND STATISTICAL ANALYSIS

In total, 630 flights were recorded: 484 solo flights, and 146 (13, 11 and 10 releases for flock size of two, four and eight, respectively) as flocks. Of these, 21 (4%) and four (2%) flights, respectively, failed to provide full track data due to GPS device failure. Therefore, these flights were missing from the analysis.

Measurement of route efficiency and route similarity

We extracted two measures from each flight's GPS data: route efficiency and route similarity (to specific other flights; see below). Route efficiency was defined by the Euclidean distance between the release site and home loft divided by the actual distance flown (Meade et al., 2005). Route similarity between a focal track and a chosen reference track was calculated as follows. For each point on the focal track, the distance to the closest point on the reference track (e.g. a previous flight) was measured. Then, the distance to the reference track was averaged over all the points on the focal track. Smaller means of this nearest neighbor distance therefore correspond to greater similarities between tracks (see 2,3 for details of this analysis).

We first examined how route efficiency varied with flock size. Because the residuals were not normally distributed (Shapiro-Wilk normality test: $W = 0.92$, $p < 0.01$), we used the Theil-Sen regression test as the nonparametric equivalent of a simple linear regression. Route efficiency was the dependent variable, and flock size (1, 2, 4 or 8) the independent variable.

Testing the 'many-wrong' and 'copy the best' best hypotheses

We then tested the 'many-wrongs' and the 'copy the best' hypotheses by comparing the route efficiencies of flock flights with: 1) the hypothetical mean route calculated from all flock members' solo routes, and 2) the most efficient solo route among those of the flock's members. The mean route of a group of trajectories can be defined in a variety of ways (see discussions in (Mann, 2010)). Since we were interested in distance, we chose to define a mean with respect to the orthogonal displacement of the trajectories around the straight line from the release site to the home loft (Figure 2). For the most efficient route, we calculated distances of the solo flights of flock members in the release immediately preceding the flock flight, and chose the shortest.

How do flock members aggregate their individual different routes?

Because flock routes were neither simply those of the best flock members nor the means of all routes (see results), we further investigated how flocks aggregated flock members' different routes. To do so, we first calculated a single flock route for each flock as the trajectory of the mean coordinate of the flight paths of the pigeons during that particular flock release. Then, we assumed that the flock route was a weighted linear sum of the solo routes of its members recorded immediately before the flock release. We denoted the weight (i.e., degree of influence on flock route) of pigeon i by w_i (where $w_i > 0$) and calculated w_i for all pigeons by running a heuristic optimization procedure. The objective function to be minimized was the square sum of the difference between the coordinates of the actual flock route and those of the hypothetical flock route obtained as the weighted linear sum of the solo routes, summed over all the flock releases.

Weight of influence w_i is pigeon-specific such that the same value of w_i is used for calculating the different hypothetical flock routes involving pigeon i . However, because the weight for each bird was then standardized for each flock release, the same bird can have different weights in different flock releases, depending on the weights of other flock members (Data S1). We then tested if birds with certain traits had higher weights w_i (i.e. had more influence on flock routes) than others by calculating correlations between the weights and each of the traits.

We considered the following four traits for each bird: hierarchical leadership rank, flight speed, route efficiency and route fidelity. Hierarchical leadership rank was obtained based on the flock flight data, while speed, efficiency and fidelity were calculated using the solo flight data immediately preceding the flock flight. Homing pigeons are known to establish leadership hierarchies during flock flights, which can be measured as consistent time-delays in directional changes in pairwise comparisons between flock members (Nagy et al., 2010; Pettit et al., 2015; Sasaki et al., 2018). Hierarchical leadership ranks were calculated using a statistical method previously developed for this purpose, called directional correlation delay analysis (Nagy et al., 2010). In short, we measured leadership by quantifying how frequently and how soon a bird was followed by others in the flock whenever it changed its flight direction. We also examined flight speed and route fidelity because past research has suggested that these traits influence hierarchical leadership ranks, and thus flock routes (Freeman et al., 2011; Pettit et al., 2015). The speed of a bird was calculated as the mean flight speed over an entire solo flight. Route fidelity was calculated as route similarity (i.e. an additive inverse of the mean nearest neighbor distances (Guilford and Biro, 2014; Meade et al., 2005)) between consecutive solo flights (Meade et al., 2005). If GPS data of the solo flight immediately preceding the flock flight were missing, we used the solo flight before this final solo flight instead – this occurred 11 times out of 302 solo releases (3%). For route fidelity, because this calculation required data from two consecutive solo routes, these 11 data points were missing. See Data S1 for details on the analysis of correlations between these individual traits and the weights of individual influence on flock routes.

Statistical analysis

Flock sizes were not always stable: birds sometimes split from their flocks during homing. If at any point a bird was more than 250 m away from the center of the flock (or the partner during paired flight), it was considered to have left its flock. At least one member left its flock in 1, 7, and 8 flights for flock sizes of 2, 4, and 8, respectively. We thus considered not only the original flock size (i.e. the flock size when released) but also the ‘average flock size’ over the entire flight. For example, if a flock of eight birds flew together for the first quarter of the flight, then one bird split away, then another at the halfway point, leaving only six birds to complete the journey together, then the average flock size was calculated as $6.75 (= 8 \times 0.25 + 7 \times 0.25 + 6 \times 0.5)$. We re-analyzed our data using this average flock size. Because only one or two birds typically left a flock, average flock sizes were relatively close to the original flock sizes: the means of the average group sizes were 1.94, 3.50, and 6.42 for original flock sizes of 2, 4 and 8, respectively. In fact, results using average flock sizes showed the same patterns as those based on original flock sizes (see Figures S6).

The statistical package R (v. 3.2.1) and MATLAB (v. 2020a) were used for the analyses.