Title

Speed determines leadership and leadership determines learning during pigeon flocking

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Summary

A key question in collective behavior is how individual differences structure animal groups, affect the flow of information, and give some group members greater weight in decisions [1–8]. Depending on what factors contribute to leadership, despotic decisions could either improve decision accuracy or interfere with swarm intelligence [9, 10]. The mechanisms behind leadership are therefore important for understanding its functional significance. In this study, we compared pigeons' relative influence over flock direction to their solo flight characteristics. A pigeon's degree of leadership was predicted by its ground speeds from earlier solo flights, but not by the straightness of its previous solo route. By testing the birds individually after a series of flock flights, we found that leaders had learned straighter homing routes than followers, as we would expect if followers attended less to the landscape and more to conspecifics. We repeated the experiment from three homing sites using multiple independent flocks, and found individual consistency in leadership and speed. Our results suggest that the leadership hierarchies observed in previous studies could arise from differences in the birds' typical speeds. Rather than reflecting social preferences that optimize group decisions, leadership may be an inevitable consequence of heterogeneous flight characteristics within self-organized flocks. We also found that that leaders learn faster and become better navigators, even if leadership is not initially due to navigational ability. The roles that individuals fall into during collective motion might therefore have far-reaching effects on how they learn about the environment and use social information.

Highlights

- Pigeons with faster ground speeds during solo flights become flock leaders.
- Solo homing efficiency does not predict leadership.
- After flocking, leaders take straighter solo routes, indicating enhanced learning.

Results and Discussion

In a moving flock, shoal, or herd, there are many types of heterogeneity that potentially give some individuals more influence than others over the group's direction. Social indifference [1, 11], knowledge [12–16], spatial position within the group [17, 18], and position in the group's affiliation network [5, 19] have all been found to be associated with leadership. However, a key question concerns whether these traits are a cause or a consequence of leading: do they govern the self-organizing process underlying the emergence of leadership, or do they result from leadership once it has arisen through another mechanism? Leadership and followership may have long-term consequences at the individual level, for example by affecting spatial learning, predation risk, or indeed the overall benefits of group living. In order to determine the functional consequences of leadership in a particular species, we must first determine how it arises from individual differences.

A wide range of bird species potentially gain informational benefits by travelling in flocks, either by pooling information from a large number of individuals [20, 21] or by following the most experienced group members [6, 22]. Homing pigeon flocks allow us to study how individual differences structure moving animal groups and affect information transfer in a field setting. Pigeons' navigation and spatial learning capabilities have been studied extensively, they are relatively easy to handle and to manipulate experimentally, and their flight trajectories can be tracked in high spatio-temporal resolution with onboard GPS devices. Analysis of pairwise time delays between birds' movement changes has revealed hierarchical leader-follower relationships in flocks of up to 30 pigeons [4, 23, 24]. This type of leadership is consistent over time and independent of social dominance [23], but previous studies have not resolved whether it arises from differences in navigational ability, or from some other factor such as flight speed or social indifference [1, 17].

In the current study, we first test whether a pigeon's degree of leadership correlates with its solo homing efficiency (calculated as the ratio between distance flown and the beeline distance from release to home). We know that in pairs with a large contrast in local experience, the bird with more experience, and therefore a more efficient route, effectively leads the less-experienced pigeon [6]. It is not known whether efficiency structures leadership in larger flocks, or in cases where differences in experience are less pronounced. Nagy *et al.* [4] suggest a positive correlation between solo homing efficiency and leadership, but their analysis – comparing only seven pigeons – lacked the statistical power to adequately test this hypothesis. In a more recent study, giving selected pigeons in a flock additional homing training did not significantly alter leadership relations, despite the fact that the trained birds' homing efficiencies had improved [24]. Next, we compare leadership to solo speed, because a recent study revealed that faster pigeons assume frontal positions within pairs and have more influence over the direction of the pair [17]. Finally, we examine the impact that leading vs. following has on birds' navigational learning whilst flying in flocks: we predict that attending differentially to landscape cues and to flockmates will affect how readily birds memorize routes. In sum, we aim to understand how individual differences structure flocks and affect information transfer, and whether leading and following have different effects on the learning of orientation cues.

We compared leadership during flock homing flights to pigeons' speeds and homing efficiencies when they flew alone before and after the flock flights. We tracked four flocks of ten pigeons using 10Hz miniature GPS loggers, and repeated the experiment from three release sites. This design allowed us to test whether the leadership hierarchy reorganized when birds learned new information at a new site, or if it remained consistent even when the flock faced a novel navigational task. At each site we released the pigeons singly at first, followed by a series of four flock flights. We quantified leadership in the flocks using the sub-second time delays between birds adopting a new direction (see Supplemental Experimental Procedures and figure S1) [4]. We tested whether leadership was predictable from solo homing efficiency, solo speed, or both.

After the flock flights, we released each pigeon singly a second time, to test whether a bird's improvement in solo efficiency was related to leadership.

Leadership compared to solo homing behavior

Leader/follower behavior showed significant consistency across the three sites ($r = 0.35$, table 1). It was also consistent across the four flock flights within each site ($r = 0.25$ to 0.30). Given this consistency, we averaged the leadership metric $\bar{\tau}_i^*$ across sites to obtain a mean measure of leadership for each bird.

We compared leadership to solo efficiency and speed using three linear mixed models (LMMs) with *group* as a random factor affecting slopes and intercepts. The first model predicted flock leadership from characteristics of solo flight 1 (the solo flight preceding the flock flights). Pigeons that had been faster by themselves tended to lead flock flights, but there was no relationship with previous homing efficiency (figure 2A-B). Speed and efficiency of solo flight 1 were positively correlated (figure S2A). Although it seems counterintuitive that only one of these variables predicted leadership, we show in figure S2B that leadership was predicted by the residual solo speed that was not associated with the straightness of the route.

The second model predicted the efficiency of solo flight 2 (that following the flock flights), which was generally higher than in solo flight 1 (39 out of 40 points in Figure 2C are above the line $y = x$). After taking into account their homing efficiencies from solo flight 1, leaders had more efficient solo routes than followers after the flock flights (figure 2C,E). The third model predicted the speed of solo flight 2. Ground speeds in this second solo flight were unaffected by leadership, after taking into account the speed from solo flight 1 (figure 2D,F).

Leadership and position in the flock

We also found that leaders tended to fly at the front of the flock (Pearson correlation of mean $\bar{\tau}_i^*$ *vs.* $\bar{d}_i$, $r = 0.76$, $p < 0.001$, $N = 40$, tested using 10^4 randomizations in which $\bar{d}_i$ values were shuffled within groups). Like leadership, the mean front-back position in the flock ($\bar{d}_i$) was positively associated with solo speed and was predictive of a bird's solo homing efficiency after the flock flights (figure S3).

Homing efficiency within and between sites

To analyze changes in efficiency across flights, we used the mean efficiency from each group of 10 because the pigeons' efficiencies during the flock flights were not independent. We fit an LMM with *group* and *site* as random factors and *flight* as a fixed factor with six categories (see figure 1A legend and table 2). We compared efficiency among these six categories using Tukey post-hoc tests in the *multcomp* R package [25].

The pigeons took straighter routes in flocks than when flying singly. The mean efficiency of a group of 10 increased sharply between solo flight 1 and flock flight 1, and then dropped from flock flight 4 to solo flight 2 (table 2). Release site also had a significant effect on homing efficiency: in both efficiency models in table 2, adding site effects lowered AIC and significantly improved the model according to a likelihood ratio test. Rather than there being continuous improvement over the course of the experiment, the highest homing efficiency was at site 2 (figure 1).

Homing efficiency improved with experience at a release site: between the two solo flights, efficiency increased from 0.55 ± 0.21 to 0.74 ± 0.13 (mean ± SD), which represents a mean reduction in distance flown of 23% (figure 1A, table 2). As well as being inefficient compared to later flights, the initial solo flights from each site had highly variable path length, ranging from 1.1 to 10.3 times the straight-line distance (figure 1A). Comparing the three sites, very little of this variability was attributable to consistent differences between birds (15%, table 1). In contrast, the efficiency of solo flight 2 did show significant within-bird consistency across sites, as did solo ground speed (table 1).

Speed compared to mass

To explore how the solo speed differences might have arisen, we compared solo speed and body mass. Mass had been measured as part of a different experiment and was available for 29 out of 40 subjects (mean = 480 ± 66 g; range 370-600 g). The birds with harnesses (group K) rather than Velcro attachments (groups B, L, M) flew significantly slower (effect of harness ± SE = -2.24 ± 0.50 m/s, $p = 0.0001$ in ANOVA predicting mean solo speed, figure S4). Among the 21 birds with mass data in groups B, L and M, there was a positive correlation between speed and body mass (Pearson's $r = 0.511$, $p = 0.018$), as we would expect from flight mechanics [26].

General discussion

Our results demonstrate a hitherto undocumented *consequence* of group movements: leaders learn more effectively than followers during collective travel. Pigeons with more influence during flock flights took straighter routes when they later flew home alone, even though they had not necessarily started with the most efficient routes from each site. Furthermore, a pigeon's degree of leadership correlated with the speed rather than the straightness of its preceding solo flight. We therefore demonstrate that both leadership and learning during collective movements can be predicted from inherent, consistent individual differences (in this case, speed).

The speed/leadership correlation agrees with earlier data from pairs [17]. Faster individuals sorted to the front of the flock, as predicted by simulations [27]. Because pigeons attend more to flockmates in front than behind [17], the birds in front will have more influence over direction changes – a pattern also found in fish shoals [28]. In order to stay with the group, the slower pigeons have to give up a degree of navigational control and follow their faster conspecifics. This mechanism does not mean all leadership is due to speed differences. Large differences in experience have also been found to influence flock leadership [6]. Nonetheless, individual differences in speed provide a plausible explanation for several observed features of leadership in pigeon flocks: (i) it is stable over time [4, 24]; (ii) it is similar during homing flights to when circling the home loft [4]; and (iii) it is unaffected by moderate differences in local experience [24]. To further understand flock leadership, we need to know how different factors interact to make a pigeon faster. Besides the effects of morphological factors such as body mass, which we found evidence of here, a previous study on this species found that speed increased with homing motivation [29].

At each new release site, the pigeons started with relatively inefficient routes and improved over repeated flights, a pattern that has also been found at further homing distances in previous studies [6, 30]. The improved efficiency was not transferrable to the next site, probably because the pigeons had learned site-specific homeward compass bearings or local visual cues [31]. The pigeons also flew straighter routes in flocks than when alone. This advantage of flocking does not imply knowledge-based leadership. Instead, it could arise from the birds pooling information [21]. We found no evidence that flocks followed the pigeons that were initially the best navigators. Alongside the navigational benefits, it is important to keep in mind that cluster formation flight, as characteristic of pigeon flocks, has energetic costs [32], added to by the fact that some birds must have changed their speeds to stay together with the flock.

Across the three sites, some birds consistently learned straighter routes than others. More effective learning correlated positively with leadership. There are several possible explanations for this finding. The first is that the tendency to lead or follow affected learning. Followers might have learned more slowly because they attended to conspecifics rather than environmental cues, or perhaps because keeping up with the flock was very energetically demanding (see [33] for a review of exercise effects on human cognition). Previous work found that following a single conspecific, *vs.* flying alone, made no difference to the efficiency of a pigeon's learned route [34]. However, that study gave followers more learning opportunities, with 12 homing flights compared to four here. Also, following a large group might inhibit learning more than following a single individual. Not only are there more flockmates to keep track of, but also a larger group is theoretically a more reliable source of information, reducing the incentive to learn navigational cues.

A second possibility is that faster fliers also learn faster, which in turn gives them more influence within flocks, because from the beginning of the flock flights they are more certain about the direction home. However, previous studies found that knowledge only affected leadership in flocks with much larger differences in experience, for example when one pigeon had been on at least 8 more homing flights than another [6, 24]. A third possibility is that some other factor, such as homing motivation, influences speed, leadership, and spatial learning. Previous studies found that motivation towards resources promotes leadership in fish shoals and zebra herds [3, 7]. Pigeons would be expected to learn faster if they confer a higher value to getting home [35].

These three explanations are not mutually exclusive. Further research could identify the causal relationship between leadership, speed, and the rate of learning, for example by testing whether the correlation between speed and learning also holds for isolated homing pigeons or whether it is specific to flock flights. Another approach would be to manipulate speed by changing the weight or drag on particular birds in the flock. Future work will also need to address how much influence a single leader has over the flock's choice of route and whether leadership hierarchies enhance or reduce the flock's collective navigational ability.

Our results suggest that the robust hierarchical leadership patterns previously observed in pigeon flocks [4, 23, 24, 36] arise from an anonymous, self-organizing mechanism related to individual differences in flight speed. Leaders learned more effectively during flock flights, and a likely explanation is that faster birds flying at the front of the flock have no choice but to learn navigational cues, whereas the slower followers are able to rely on social information. The enhanced learning by leaders would be expected to reinforce a particular direction of information transfer through the flock. Flocks did end up following the pigeons that best knew the way home, but the initial leader/follower asymmetry arose from speed differences rather than knowledge. Only after finding themselves at the front of the flock did leaders become more efficient at homing. By studying the relationship between leadership and solo navigation, we are beginning to understand how leadership patterns are stabilized and what the consequences are for individuals of being a leader or follower. Leadership does not imply social complexity, but it may have complex effects by giving rise to different levels of knowledge within the group.

Experimental Procedures

Experiment

The subjects were 40 homing pigeons, two to eight years old, of both sexes. They had been bred at the University Field Station, Wytham, UK, or transferred there in their first year. They were divided into four groups of 10 (labeled B, K, L, M). We replicated the same sequence of homing flights at three release sites, finishing all flights from one site before moving to the next (figure 1A) and keeping the same flock composition across sites. The sites approximated an equilateral triangle centered on the home loft (figure 1B-D): site 1 at Filchampstead (4.20 km, 206.5° from loft), site 2 at Cutteslowe Park (4.11 km, 86.4° from loft), and site 3 at Burleigh Wood (5.03 km, 329.0° from loft). All of the pigeons had experience homing singly and in flocks from sites 3-7 km from the loft. Although the previous homing experience was from different sites (at least 1.8 km from the sites used here), this experiment was still very much a test of orientation within the birds' familiar area.

At each site, the procedure was to release each bird singly for its first homing flight, followed by four releases in flocks of 10, followed by a second solo flight (figure 1). This sequence took 5 to 9 days to complete at each site for all four groups. Each pigeon made a maximum of two flights per day. We took pigeons to the release sites in aluminum boxes in a car with windows open for access to airborne odors. For each round of solo releases, the ten pigeons in a group were released within a 3-hour period to minimize differences in weather conditions. Release order was random with 10-20 min between consecutive birds. The sun was visible during all releases, with wind speed less than 8 ms^{-1}. Because the strength of tailwind varied across different releases of the same pigeon, we restricted our analysis of ground speed to between-subject rather than within-subject variation.

We tracked all homing flights using custom made GPS devices with a log rate of 10Hz [23, 24]. Loggers weighed 13 g (2.2-3.5% of pigeon mass). Each logger was affixed to a pigeon's back using either an elastic harness (for birds in group K) or a Velcro strip glued to trimmed feathers (groups B, L, M). We randomly allocated loggers to pigeons before every flight. Three tracks from flock flights were lost due to device failure. Three birds went missing over the course of the experiment, one from group L at site 2 and two from group K at site 3. In these cases of missing data, we analyzed the remaining flocking data from the other birds in the group, because previous studies show that a particular bird's presence or absence does not substantially change the leadership network among the other birds [4, 23]. The experimental protocols were approved by the Ethical Review Committee of Oxford University's Department of Zoology.

Analysis

We measured each bird's leadership as the directional correlation delay with the rest of the flock, $\bar{\tau}_i{}^*$, a method based on Nagy *et al*. [4] that has also been applied to fish schools [28, 37]. For comparison to $\bar{\tau}_i{}^*$, we also calculated each bird's front-back position within the flock, $\bar{d}_i$, using the same method as Nagy *et al.* [4]. See Supplemental Experimental procedures for details on the calculation of leadership, speed, and homing efficiency from GPS tracks.

Our general statistical approach was to fit linear mixed models (LMMs) using the *lme4* package in R [38, 39]. Unless otherwise noted, we tested significance using a likelihood ratio test comparing the full model to a model without the effect in question. We checked the assumptions of Gaussian error and homogeneous variance by visual inspection of plotted residuals. To test individual consistency in leadership, speed, and homing efficiency, we calculated intra-class correlation coefficients from LMMs [40], using the formula $r = \sigma^2_{\text{bird}}/(\sigma^2_{\text{bird}} + \sigma^2_{\epsilon})$. The coefficient r is the proportion of variance due to bird, within a model that also included either *site* or *flight* (within site) as a random effect (see table 1). For solo-track variables, we tested the significance of r using a likelihood ratio test to compare models with and without *bird* as a random effect. For leadership, we tested the significance of r by randomizing the ten $\bar{\tau}_i{}^*$ values within each group and re-calculating the coefficient (r_{rand}) for each randomization. Within-group randomization accounts for the fact that $\bar{\tau}_i{}^*$ values from the same group cannot vary independently of each other. The *p*-value was the proportion of 10^4 randomizations with $r_{\text{rand}} < r$.

Author contributions

All authors designed the study, B.P. and Z.A. conducted the experiments, B.P. analysed the data, and all authors contributed to writing the manuscript.

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Figure legends

Figure 1. GPS tracks and homing efficiency for solo and flock flights. (A) Homing efficiency of all pigeons across their 18 flights, in time order. Box plots are colored according to the flight sequence within each site. Points are shown as outliers if they are below the lower quartile by at least 1.5 times the interquartile range. **(B-D)** GPS tracks from one of the four subject groups, with the same color coding as panel A. From each site, each pigeon had an initial solo flight (B) followed by four flock flights (C) and then a second solo flight (D). The sequence was repeated using four separate groups; the group shown (group L) had a mean efficiency closest to the overall mean. Contains OS data © Crown copyright (2015)

Figure 2. Flock leadership compared to solo homing efficiency and speed. Plots show the mean value for each bird, with different symbols for the four replicate groups. Fit lines are from an LMM with group as a random factor. The estimated regression for the fixed effect is shown in black, or grey if non-significant, as judged from a likelihood ratio test (LRT) against a model without that fixed effect ($\alpha = 0.05$). Dashed coloured lines show random effects of group on slope and intercept. Dotted black lines in C and D are the diagonals $y = x$. **(A-B)** Flock leadership plotted against previous solo efficiency (A) and speed (B). Speed effect in minimum adequate model: slope = 0.19, SE = 0.06. **(C)** Solo efficiency after flock flights, compared to solo efficiency before (slope = 0.40, SE = 0.12). **(D)** Solo speed after flock flights, compared to solo speed before (slope = 0.53, SE = 0.12). **(E)** The residuals from C plotted against flock leadership to show the additional effect of flock leadership on subsequent homing efficiency. LRT against model without leadership: $p = 0.014$, leadership slope = 0.055, SE = 0.017. **(F)** The residuals from D plotted against flock leadership. LRT against model without leadership: $p = 0.37$, leadership slope = 0.20, SE = 0.17. See figures S1-S4 for additional explanation and analysis of the variables shown here.

Tables

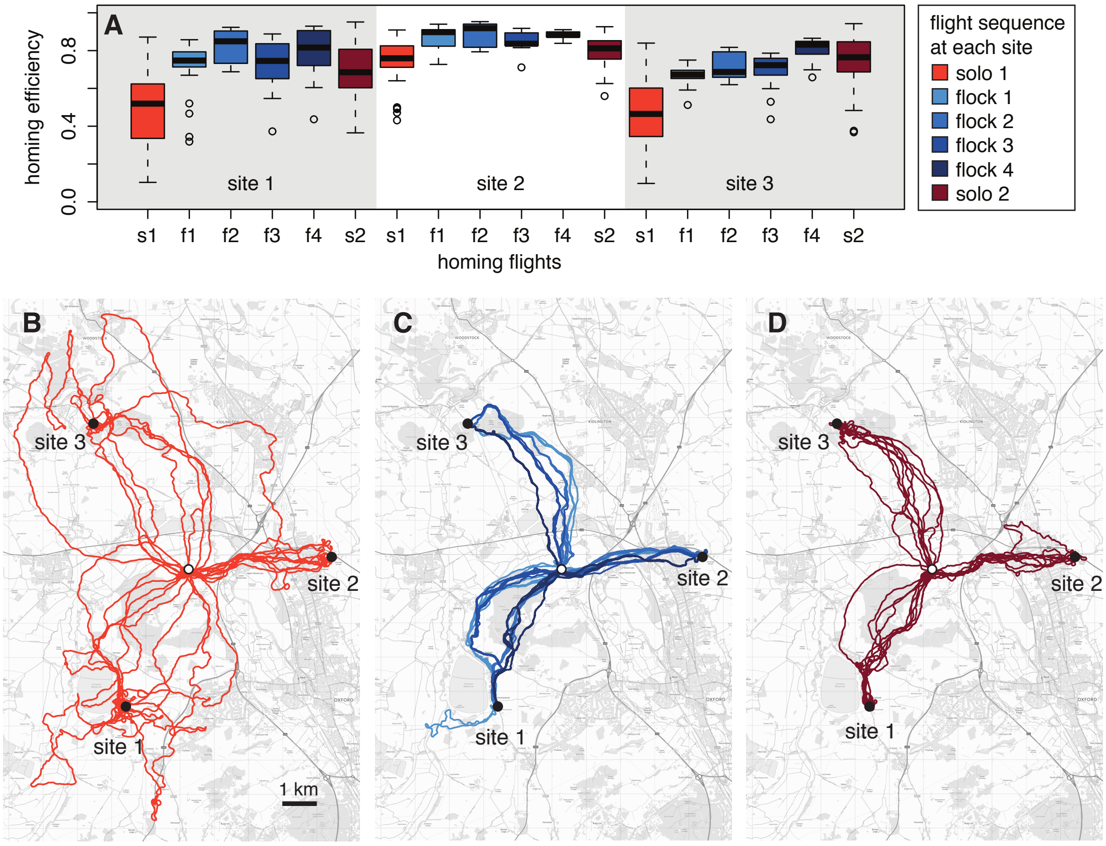
Table 1. Individual consistency of leadership and of solo track characteristics. r is the intra-class correlation coefficient from an LMM with the crossed random effects shown. For leadership there are four values of r: three for consistency of leadership among flights within a site (rows 1-3) and one for consistency of leadership across sites (row 4). *significance at $\alpha = 0.00625$ (Bonferroni-adjusted threshold for 8 separate models).

Response	**random effects**	***r***	***p***
leadership ($\bar{\tau}_i{}^*$) at site 1	*bird, flight*	0.28*	0.0016
leadership ($\bar{\tau}_i{}^*$) at site 2	*bird, flight*	0.30*	0.0002
leadership ($\bar{\tau}_i{}^*$) at site 3	*bird, flight*	0.25*	0.0009
leadership (mean from each site)	*bird, site*	0.35*	0.0033
solo 1 efficiency	*bird, site*	0.15	0.124
solo 2 efficiency	*bird, site*	0.43*	$<10^{-4}$
solo 1 speed	*bird, site*	0.67*	$<10^{-4}$
solo 2 speed	*bird, site*	0.46*	$<10^{-4}$

Table 2. Changes in homing efficiency between flights, using the mean efficiency of each group on each flight. Significance tested using Tukey post-hoc tests on an LMM with group and site as random factors and flight as a categorical variable. ***$p < 0.001$, *$p < 0.05$.

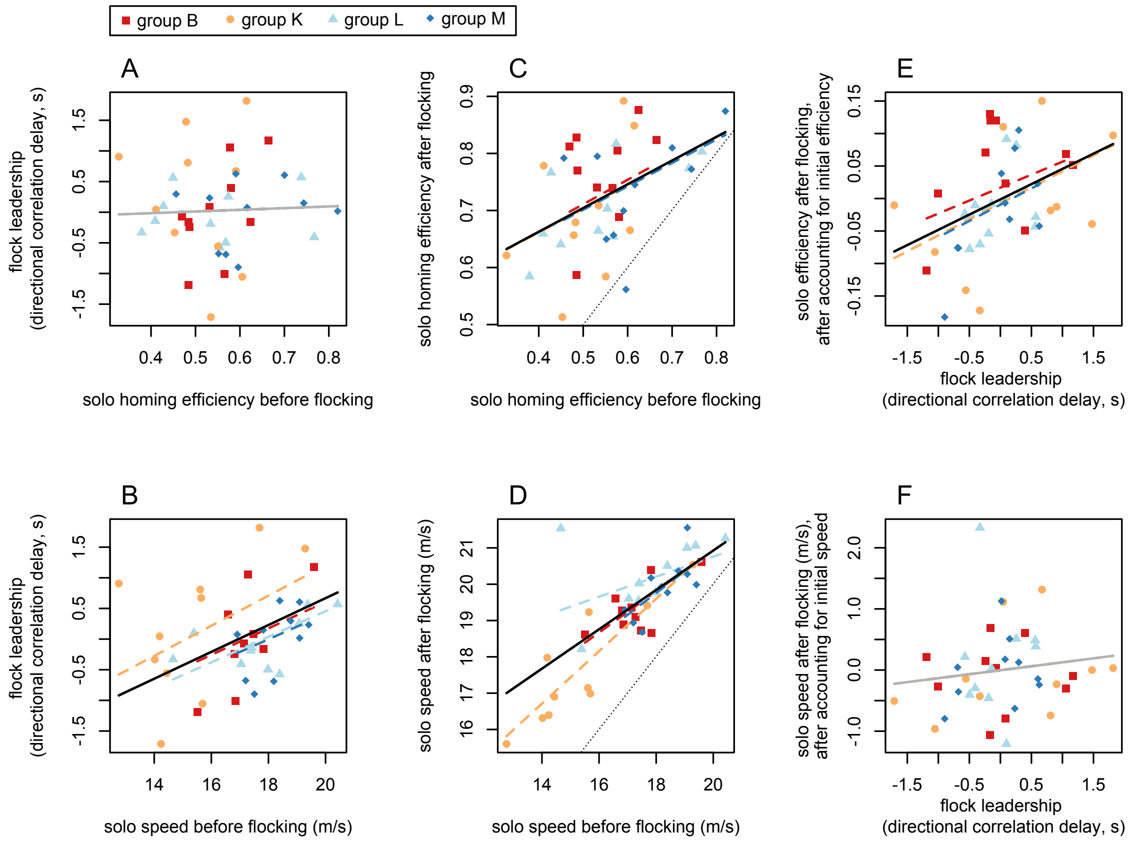
comparison	**mean change in efficiency**	***p***
flock 1 vs. solo 1	0.197***	< 0.001
flock 2 vs. flock 1	0.049	0.39
flock 3 vs. flock 2	-0.043	0.55
flock 4 vs. flock 3	0.061	0.17
solo 2 vs. flock 4	-0.086*	0.01
solo 2 vs. solo 1	0.178***	< 0.001

Figure 1



A
homing efficiency
0.0
0.4
0.8
site 1
site 2
site 3
s1
f1
f2
f3
f4
s2
homing flights
flight sequence at each site
solo 1
flock 1
flock 2
flock 3
flock 4
solo 2
B
C
D
site 1
site 2
site 3
1 km

Figure 2



group B
group K
group L
group M
A
B
C
D
E
F
flock leadership
(directional correlation delay, s)
solo homing efficiency before flocking
solo homing efficiency after flocking
solo efficiency after flocking,
after accounting for initial efficiency
solo speed before flocking (m/s)
solo speed after flocking (m/s)
solo speed after flocking (m/s),
after accounting for initial speed