Consequences and mechanisms of leadership in pigeon flocks

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Abstract

This thesis investigates how collective decisions in bird flocks arise from simple rules, the factors that give some birds more influence over a flock's direction, and how travelling as a flock affects spatial learning. I used GPS loggers to track pigeons homing alone and in flocks, and applied mathematical modelling to explore the mechanisms underlying group decisions. Across several experiments, the key results were as follows:

Flying home with a more experienced individual not only gave a pigeon an immediate advantage in terms of taking a more direct route, but the followers also learned homing routes just as accurately as pigeons flying alone. This shows that using social cues did not interfere with learning about the landscape during a series of paired flights.

Pigeons that were faster during solo homing flights also tended to fly at the front of flocks, where they had more influence over the direction taken. Analysis of momentary interactions during paired flights and simulations of pair trajectories support the conclusion that speed increases the likelihood of leading.

A pigeon's solo homing efficiency before flock flights did not correlate with leadership in flocks of ten, but leaders did have more efficient solo tracks when tested after a series of flock flights. A possible explanation is that leaders attended more to the landscape and therefore learned faster.

Flocks took straighter routes than pigeons flying alone, as would be expected if they effectively pooled information. In addition, pigeons responded more strongly to the direction of several neighbours, during flock flights, than to a single neighbour during paired flights. This behaviour makes sense adaptively because social information will be more reliable when following several conspecifics compared to one.

Through a combination of high-resolution tracking and mathematical modelling, this thesis sheds light on the mechanisms of flocking and its navigational consequences.

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Author contributions

The work in this thesis is primarily my own. The following people contributed to one or more data chapters:

Dora Biro offered ideas and feedback that contributed to the development of all chapters.

Tim Guilford contributed ideas and feedback regarding Chapters 2, 3, and 6.

Andrea Flack participated in the data collection for Chapter 2 and offered feedback on the manuscript.

Robin Freeman contributed ideas for the data analysis and manuscript preparation in Chapter 2.

For Chapter 4, Zsuzsa Akos helped design the experiment, participated in collecting the data, and gave feedback on the manuscript.

Andrea Perna contributed to the data analysis and manuscript preparation in Chapter 3, including writing the simulation code, although I carried out most of the analysis, prepared the figures, and wrote most of the manuscript. He also contributed ideas for Chapter 5.

David Sumpter contributed to the analysis framework and manuscript preparation for Chapter 3.

Richard Mann contributed ideas for how to analyse the data in Chapter 5.

As an appendix, I include a jointly authored paper in which I had a major role in designing the project, collecting the data, and writing the paper. The full list of author contributions were as follows: Máté Nagy, Tamás Vicsek, Dora Biro, and I designed the research; Máté Nagy, Isabella Roberts-Mariani, and I performed the research; Máté Nagy, Gábor Vásárhelyi, and I analysed the data; Máté Nagy, Gábor Vásárhelyi, Dora Biro, and I wrote the paper; and Gábor Vásárhelyi designed the GPS device and computer-vision software framework.

Chapter 1: General Introduction

1.1 Importance of understanding collective behaviour

Across many species, individuals benefit from their groups' collective capabilities. For example, group living allows cellular slime-moulds to become more mobile (Inouye & Takeuchi 1979), helps schooling fish avoid predators (Krause & Ruxton 2002; Ward *et al.* 2011), and enables ant colonies to select the best nest site or food source (Sasaki *et al.* 2013; Sumpter & Beekman 2003). From simulations, we know that collectively intelligent decisions can arise rapidly from simple local interactions, without any individual having a global perspective (Couzin *et al.* 2005).

I have collected data on group decision-making and collective motion in bird flocks, to find out how they combine information to reach a group decision, how individuals respond to cues from each other's movement, and whether travelling as a group leads to straighter flight routes.

This work is motivated by the desire to understand the behaviour of bird flocks and other animal aggregations seen in nature, both in terms of how the collective behaviour is coordinated and its adaptive benefits. Understanding the functional and mechanistic properties of group decisions is relevant to broader questions in behavioural ecology, in the design and control self-organized systems, and in the study of biological complexity in general. I will now give some background on the subject areas that inform this thesis, focussing first on group decision-making and then on the study system of pigeon homing.

1.2 Background on group decision-making

1.2.1 *Group living and social information*

Travelling as a group allows animals on the move to maintain the more general benefits of group living, for example dilution of predation risk, collective vigilance, cooperative defence, cooperative hunting, or maintaining the potential for cooperative breeding. Reduced predation risk is probably the most relevant to pigeons (Krause & Ruxton 2002; Rutz 2012; Wood & Ackland 2007). In addition, travelling as a group provides opportunities to orient more accurately, for example by pooling the estimates from many individuals, by following the better-informed members of the group, and/or by emergent sensing of environmental cues (Berdahl *et al.* 2013; Simons 2004; Wallraff 1996). The informational properties of animal groups are important for understanding the full benefits of group living, and might also explain the sizes of groups formed in different contexts. For example, many bird species form larger flocks for migration than typically occur at other times of year, and the longer the migration distance, the larger the flocks tend to be (Beauchamp 2011).

Because cohesion is often beneficial in itself, we cannot expect animal groups to always maximize collective intelligence. For example, accurate collective decisions depend on each individual collecting information independently (King *et al.* 2012; Krause *et al.* 2010). However, reducing attention to the group (or leaving it altogether) to seek independent information might increase predation risk, in which case copying the choices of others may be a safer strategy. In eusocial insects, we do see scouts leaving the relative safety of the group to find new nest sites (e.g. Pratt *et al.* 2002; Seeley & Buhrman 1999). In less cooperative species, this risky information-gathering role would be under negative frequency-dependent selection, as in a producer/scrounger game (Caraco & Giraldeau 1991).

1.2.2 *Consensus decision-making*

In order to reap the benefits of travelling as a group, animals must coordinate their behaviour despite conflicting information or conflicting interests. As when choosing a common timing or activity, staying together requires forming a consensus. In two useful reviews, Conradt and her colleagues suggest features of group decision-making that can be compared across species and contexts (Conradt & List 2009; Conradt & Roper 2005).

First, group decisions can be compared in terms of the degree of decision sharing. At one end of the spectrum, one individual decides and others abide by that decision (unshared), whereas in an equally shared decision all group members have equal influence over the outcome. This distinction is purely in terms of how the group decision reflects the conflicting information or preferences within the group, rather than the mechanism for resolving those conflicts.

Second, group decisions can be compared in terms of mechanism. Individual preferences could be processed in a centralized way, as in most human voting systems. In contrast, the mechanism could be self-organized, in that it does not require global communication or control but occurs through local interactions. Self-organizing mechanisms are more likely to explain decisions in large aggregations of animals, because (i) they are robust to perturbation and (iii) they are more parsimonious in that they do not require such complex communication (Couzin & Krause 2003).

Self-organization is not the same as being 'leaderless'. I generally use the term 'leadership' to describe unequal influence, rather than a specific control mechanism. If a decision is not equally shared, then those with more influence over the group outcome are leaders and those with less influence are followers. In models of self-organizing swarms, some individuals can still have greater weight in deciding where the group goes (Bode *et al.* 2012; Conradt *et al.* 2009; Couzin *et al.* 2005). With self-organizing leadership, there is no need to decide on a leader and no need for any member of the group to know who is leading.

1.2.3 *Self-propelled particle models*

One of the main ways of investigating the individual-level rules at work in collective behaviour has been to implement postulated rules in models and observe the resulting group-level phenomena. Self-propelled particle (SPP) models have been particularly widely used, especially for investigating flock-like collective motion.

Individuals are modelled as particles moving in one, two, or three dimensions, which update their velocities according to the behaviour of local neighbours.

For example, in the Vicsek model each particle aligns with the mean direction of the neighbours within a certain radius (Vicsek *et al.* 1995). In a slightly more complex version, there are three concentric zones defined by radii: an inner zone of repulsion from neighbours' centre of mass, a middle alignment zone as in the Vicsek model, and an outer zone of attraction to neighbours' centre of mass (Couzin *et al.* 2002; Reynolds 1987). Which rules to use and how to limit them in space is a topic of ongoing research and debate (Strömbom 2011; Yates *et al.* 2010). Rather than acting within a distance-based zone, attraction or alignment could be weighted by a continuous function of distance (Cucker & Smale 2007) or limited to a particular number of neighbours (Bode *et al.* 2011a).

Particularly relevant to this thesis are models that give particles preferred directions in addition to social responses, in order to simulate group decision-making. The group trajectory indicates how effectively information propagates through the group and how conflicting preferences are resolved. Using simulated groups of 10 to 200 particles, Couzin *et al.* (2005) showed that a small fraction of individuals could effectively lead an entire group in their preferred direction. If there were two subgroups with conflicting directional preferences, the outcome depended on the magnitude of the conflict (angular difference in preferred directions) and the relative sizes of the subgroups. For small conflicts, the group pooled information and chose a compromise direction, effectively combining the two preferences. For larger conflicts, the group chose the preference of the larger subgroup.

In addition to numeric majority, Conradt *et al.* (2009) found that subtle differences in how animals weigh cohesion and personal information bias leadership. In biological terms, this means we expect leadership by individuals that benefit less from being in the group or that have a greater motivation to reach a destination. Data in agreement with these predictions has been accumulating from a number of species. For example shoals of three-spined sticklebacks follow the numerically larger subgroup, tested by influencing group movements with replica fish (Ward *et al.* 2008). In Plains zebras, lactating females with higher water requirements lead harems (Fischhoff *et al.* 2007). Couzin *et al.* (2011) found that shoals of golden shiners were spontaneously biased toward a yellow target over a blue target in reinforcement learning. In mixed shoals of blue-trained and yellow-trained fish, the yellow-trained fish dominated the decision even if they were slightly outnumbered.

The examples above compare group outcomes to model predictions. With technology for tracking behaviour in groups, we can also infer interaction rules directly from data. This approach has been applied to fish shoals (Herbert-Read *et al.* 2011; Katz *et al.* 2011) and surface-swimming ducks (Lukeman *et al.* 2010). Comparing models to data at both the group level and the individual level helps to get around the problem that many different interaction rules can produce the same collective behaviour (Lopez *et al.* 2012; Mann *et al.* 2013).

SPP models are not the only approach to modelling group decisions. If the decision can be simplified to a pair of animals, a binary choice, or a sequential decision, then other types model may be more appropriate, for example systems of differential equations (e.g. Amé *et al.* 2006; Arganda *et al.* 2012; Biro *et al.* 2006b; Sumpter & Beekman 2003; Ward *et al.* 2008). I have focussed on SPP models here because they are appropriate for a wide range of collective navigation scenarios, and they pose a number of predictions and assumptions to test against data on bird flocks.

1.3 Homing pigeons as a study system

For many migratory birds, flocking is potentially a way of combining navigational information and learning from others, but the importance of social information in navigation is not well understood. Homing pigeons (*Columba livia*) are unique as a study system in that they enable kilometre-scale field experiments on group decision-making, tracked with high resolution. They have long served as a model for studying avian navigation. Because they are domestic animals, we have control over flock composition and individual experience. Furthermore, because of their size, homing behaviour, and tolerance of being handled, they are relatively easy to track repeatedly with GPS loggers. The various types of loggers used here weighed approximately 16g, compared to pigeon body mass of 390-570 g (based on the subjects in Nagy *et al.* 2013). In this overview of pigeon homing, I will focus on local area navigation and route recapitulation and describe how they can be used to study group decisions.

1.3.1 *Navigation and orientation*

Pigeons can find their way home after being displaced tens or even hundreds of kilometres. Because of their use for delivering messages, in pigeon racing, and in scientific research, pigeons' navigational abilities are particularly well known, but they are not unique. In the wild, several species of birds and mammals have been recorded returning home over long distances after being displaced, including white-chinned petrels (725 km, Benhamou *et al.* 2003), Cory's shearwaters (800 km, Gagliardo *et al.* 2013), Egyptian fruit bats (44 km, Tsoar *et al.* 2011), northern elephant seals (100 km, Oliver *et al.* 1998), and African elephants (160 km, Pinter-Wollman 2009). All of these are naturally long-range foragers or migrants.

According to Kramer's map-and-compass model, homing from unfamiliar areas involves the use of "map" cues to find position and "compass" cues to estimate the direction home (Wiltschko & Wiltschko 2009). The sun, when visible, is the primary source of compass information for pigeons, as demonstrated by the fact that clock-shifted pigeons leave the release site in a predictably rotated direction, whether the site is familiar or unfamiliar (Füller *et al.* 1983). Experiments manipulating the magnetic field in the lab, or attaching magnets to pigeons when homing, show that magnetoreception also provides compass information, especially when the sun is not visible (reviewed in Wiltschko & Wiltschko 2009). The source of map information is a topic of ongoing debate, but there is strong evidence that olfactory cues, magnetic intensity, and magnetic inclination can provide cues about location (Mora & Bingman 2013; Wallraff 1996; Wiltschko & Wiltschko 2009).

Over familiar areas, pigeons have the opportunity to use visual landmarks in addition to the mechanisms above. Although frosted lens experiments demonstrate that visual landmark guidance is not necessary for homing (reviewed in Wiltschko & Wiltschko 2009), viewing the landscape before being released does reduce homing time at familiar release sites (Braithwaite & Guilford 1991). With GPS tracking, evidence has accumulated that pigeons homing from familiar sites use landmarks not just to recognize the release site (Biro *et al.* 2002), but throughout the homeward route. Over repeated solo homing flights from the same site, pigeons learn idiosyncratic routes, which are not disrupted by magnets attached to the head or by changes in wind direction (Biro *et al.* 2006a; Meade *et al.* 2005). A pigeon displaced from its route by up to 1500m tends to re-join its route before flying home (Biro *et al.* 2004).

The most likely explanation for route recapitulation is that pigeons learn a series of landmarks. Analysis of repeated flights suggests that pigeons use linear features such as roads, railways, or rivers (Lau *et al.* 2006; Lipp *et al.* 2004), as well as point features such as buildings. The latter would explain “pinch points” where routes are recapitulated with particularly high fidelity. Mann *et al.* (2011) devised a Gaussian-process method for objectively identifying the most probable landmark locations from pigeon tracks.

This route-learning phenomenon has proved to be highly repeatable from many different release sites around Oxford. For release sites 5 to 15 km from home, pigeons are usually recapitulating routes after 10 to 20 solo homing flights. Route recapitulation is characterized by high route similarity within subjects compared to the similarity between subjects flying from the same release site. For example, the mean distance from the points on one route to the nearest points on the same pigeon’s previous route are typically 80-250m. In contrast, the mean distance from a pigeon’s route to the routes of other pigeons is typically in the range of 300-600m, depending on the subjects and the release site, although sometimes several pigeons will independently converge on very similar routes.

Using landmarks over familiar terrain does not mean that pigeons entirely stop using other navigational cues. Experiments putting visual and sun compass information into conflict found that pigeons’ routes were partially deflected in the direction predicted from the clock shift treatment, even within sight of the loft (Armstrong *et al.* 2013; Biro *et al.* 2007). Using sun-compass information in the familiar area could explain an earlier finding that pigeons displaced from their preferred routes tended to re-join "downstream", closer to the loft (Biro *et al.* 2004).

Recapitulation of individually distinctive routes is probably widespread among animals that make repeated journeys between the same points. It has been documented in the migration of several bird species (Dias *et al.* 2013; Guilford *et al.* 2011; Vardanis *et al.* 2011) and in the foraging routes of Australian desert ants (Wehner *et al.* 1996). Constraints of topography or weather cannot account for the individually distinctive routes in any of these cases. As more species are tracked in higher resolution, there will almost certainly be more examples of route recapitulation in the wild.

While there are still many open questions about the mechanisms of route recapitulation, for the purpose of this thesis the two most important features of pigeons' local area navigation are the following. First, during the first few releases from an unfamiliar site, there is a rapid reduction in the length of homing path, even if the site is close enough to home (4-7km) that the pigeons could conceivably have viewed it from a distance on previous flights. Chapters 2 and 4 involve this early stage when rapid learning was expected, and provide more evidence that routes become straighter through learning, even for short-distance flights. Second, once a pigeon is recapitulating a learned route, its recent solo homing tracks indicate the route it prefers to take (Biro *et al.* 2004), and correspond to the part of the landscape that the pigeon knows best. In Chapter 3, I quantify the route response in terms of turning behaviour during solo flights of experienced birds recapitulating their preferred routes. Distance-dependent attraction toward the preferred (recapitulated) route forms the basis of the group decision experiments in Chapters 3 and 6.

1.3.2 *Homing in flocks*

The flocking behaviour of pigeons raises the question of how navigating in groups differs from solo navigation, and whether flying as a flock reduces navigational error (Simons 2004; Wallraff 1978). Several studies used vanishing bearings to measure whether pigeons had lower navigational error in flocks than when released singly, with mixed results, reviewed by Simons (2004). From GPS tracking, there is more decisive evidence that flock flight results in straighter routes (Dell'Ariccia *et al.* 2008; Flack *et al.* 2013b).

To study group decisions, it is helpful to know the preferences of each member of the group, which is possible using the route recapitulation phenomenon described above. Another advantage of using pigeons with previous experience from the same release site is that they are less likely to split up when released as a flock, which is useful if the goal is to study group decisions. Pigeons completely naïve to a release site split off 50-95% of the time when released in pairs (Banks & Guilford 2000; Guilford & Chappell 1996; Pettit *et al.* 2013a).

Biro *et al.* (2006b) released pairs from familiar release sites where each bird already had an established route (20 solo flights each). The pairs resolved their conflicting route preferences by either taking a compromise route between the two preferences (for small conflicts) or by one bird following the other down its route (for large conflicts). Furthermore, the pairwise leader-follower relationships formed a transitive hierarchy among the subjects, suggesting that individual differences consistently give some birds more influence, rather than leadership being random.

Several follow-up papers investigated what factors contribute to leadership. Through further analysis of the dataset from Biro *et al.* (2006b), Freeman *et al.* (2011) found that leadership correlated with having higher route-fidelity on solo flights, in other words recapitulating the route with lower variance. If high fidelity corresponds to stronger attraction toward landmarks, then from models of group decision-making we would expect the birds with high route-fidelity to have more influence in the group decision (Conradt *et al.* 2009; Mann *et al.* 2010; Sumpter *et al.* 2008). In a second study, Flack *et al.* (2012) tested route choice of mixed-experience pairs, and found that the bird with more experience led the route choice, provided that there was a large enough difference in experience (3 flights vs. 15 flights).

In addition to the experiments on pairs, Nagy *et al.* (2010) found consistent patterns of leadership in flocks of approximately 10 pigeons, using a different method (directional correlation delay) inspired by statistical physics. This method finds the time delay (usually on the order of 0.5s) between two GPS tracks that maximizes their directional correlation. The pairwise delay times formed a hierarchy through the flock, which means the birds can be ranked according to their typical time delay. The method works for flights circling the loft as well as homing flights, and Nagy *et al.* found that birds' rankings were similar in both situations. Because the time delays are so small, this method requires tracks with high temporal resolution. I used variations of this method in Chapters 3 and 4.

Flack *et al.* (2013a) tested whether giving selected pigeons additional solo training flights changed their positions in the leadership hierarchies. Despite the fact that the trained birds became more efficient than their flockmates and had higher route fidelity, there was no significant directional effect on leadership. Therefore the factors uncovered by earlier studies of pair route choice, experience and route fidelity (Flack *et al.* 2012; Freeman *et al.* 2011), do not explain all of the variance in leadership observed in pigeon flocks. There are likely to be additional aspects of individual differences contributing to the leadership hierarchies discovered by Nagy *et al.* (2010).

1.4 Unifying questions

Given what is known about group decision-making and pigeon homing, there are several unanswered questions on the mechanisms of flock coordination and their consequences for group movements. Each question relates to more than one chapter of this thesis.

1.4.1 *How effectively do flocks pool information?*

By comparing solo and flock homing flights, Dell'Ariccia *et al.* (2008) showed that pigeon flocks fulfil a basic description of collective intelligence, in that pigeons took more direct routes in flocks than when flying alone. However, we do not know the mechanism by which the improvement occurs. Straighter paths or shorter homing times do not necessarily imply information pooling. The improvement could have been due to higher homing motivation when flying as a flock, or the flock following whichever bird knew the most direct route, or even a switch from landmark to compass-based orientation. Given that the mechanism is not well understood and that the results of Dell'Ariccia *et al.* (2008) were from just one flock, I repeat the comparison between flocks and solo flights (Chapters 4 and 6).

Another way of phrasing this question is to ask to what degree one bird can dominate the flock's decision, which might depend on the size of flock (Chapter 6), the asymmetry in experience (Chapter 2; Flack *et al.* 2012), or the degree of conflict between route preferences (Chapter 6; Biro *et al.* 2006b). I aim to provide additional insight into how effective bird flocks are at pooling information, the extent of navigational benefits from flocking, and where we should expect to find collective intelligence in avian social navigation.

1.4.2 *How do birds respond to each other within the flock?*

Related to investigating the homing routes of flocks, I have also taken advantage of the high-resolution GPS data to study the momentary flocking responses between pigeons. With high-resolution tracking data, we have the opportunity to directly measure correlations between a bird's motion and the positions and orientations of its neighbours. In Chapter 3 I focus on responses to the relative position and velocity of one neighbour when pigeons fly in pairs, and then in Chapter 5 I use these pairwise interactions as a basis for analysing behaviour within larger flocks.

Interaction rules are important to understand, because leadership, compromise, and group cohesion depend on how each member of the group balances personal information and social cues (Conradt *et al.* 2009). The interaction rules provide a mechanistic explanation of leadership, as I show in Chapter 3. At the same time, the adaptive consequences of individual-level strategies can only be understood in the context of the collective motion and group decisions they produce.

1.4.3 *What individual differences result in consistent leadership?*

Given the consistent leader/follower differences in pigeon flocks (Biro *et al.* 2006b; Flack *et al.* 2013a, 2012; Nagy *et al.* 2010), another question is what gives some birds greater influence within the flock. My approach is to look for behaviour in other contexts that correlates with leadership. I compare leadership to solo speed over the ground (Chapters 3 & 4), solo homing efficiency (Chapter 4), and social dominance when feeding (appendix A). This narrows the search for causal factors to explore with simulations (Chapter 3) or with future experimental manipulations.

Identifying factors that correlate with leadership will bring us closer to understanding (i) the mechanisms of leadership, in terms of interaction rules, and (ii) whether leadership enhances flock decision-making. Following the most knowledgeable individuals is expected to improve accuracy, whereas following a random individual will generally reduce accuracy compared to sharing the decision more equally (King *et al.* 2012). Large differences in experience affect leadership in pairs of pigeons (Flack *et al.* 2012), but this does not explain all leader-follower differences. In addition, it is still unclear how much influence any one leader has over the flock's choice of route as flock size increases beyond two birds.

1.4.4 *How does collective navigation affect spatial learning?*

The questions above mainly address group decision-making and flocking behaviour during a single homing flight. Over repeated homing flights, the group's choice of route will affect what cues are available for spatial learning. Collective decisions could become 'consolidated' in the learned behaviours of individual members of the group. On the other hand, collective navigation offers the opportunity to scrounge information by following others, as an alternative to learning a route. In Chapter 2 I test how effectively pigeons learn while following conspecifics by releasing birds with less local experience alongside more experienced individuals on repeated homing flights.

This question comes up again in Chapter 4, in which I release pigeons singly before and after flying as a flock of ten, and compare the improvement in homing efficiency to a bird's degree of leadership. If leaders learn faster than followers because they attend more to the landscape, learning will reinforce the pattern of leadership within the flock, and we should also expect leaders to gain navigational efficiency more rapidly. How well birds learn during collective navigation is a complex question because of the possible feedback between learning and leadership, but finding answers to this question is important for understanding whether migratory routes can be socially transmitted.

1.5 Structure of thesis

The thesis is organized as five self-contained manuscripts with a general discussion. The data collected for Chapters 2 and 4 are from distinct experiments and do not overlap with the other chapters. Chapters 5 and 6 tackle different questions within the same data. The data in Chapter 3 overlaps partially with the data in Chapters 5 and 6. Any supplementary information for a data chapter is included at the end of the chapter. As an appendix, I include a co-authored paper in to which I made a large contribution (see declaration of author contributions).

Chapter 2 examines the effects of collective navigation on route learning. Many bird species migrate in mixed-age flocks, but it is not known how accurately migration routes can be socially transmitted. I found that a pigeon was able to learn a homing route while following a more experienced flockmate. Furthermore, rather than there being a one-way transfer of information during the paired flights, the more experienced bird also shifted its route, such that routes became more efficient over repeated paired flights. This suggests an interaction between social learning and information pooling.

Chapter 3 combines data with a simulation to investigate how pairs of pigeons respond to each other in flight while choosing a navigational route. My approach was to infer interaction rules from a large volume of tracking data, implement the rules in a simulation, and test the simulation's predictions about group-level behaviour. I found that the particular interaction rules of pigeons stabilize a side-by-side configuration, promoting bidirectional information transfer and making pairs less likely to split up. My results also show how individual differences in speed spontaneously give rise to leader-follower roles, which could explain earlier findings of stable leadership in pigeon flocks (Nagy *et al.* 2010).

In Chapter 4 I quantify leadership in flocks of ten pigeons, using directional correlation delay, and test whether it is consistent across release sites. The pigeons homed alone before and after homing in flocks, and I compare solo homing flight characteristics to leadership in the group. As in Chapter 2, I found that solo speed was positively correlated with leadership. Leadership did not correlate with preceding homing efficiency, but birds with more of a leadership role did have higher efficiency when tested afterwards. Consistent individual differences in speed probably plays a role in the robustness of leadership hierarchies that have been measured here and elsewhere in flocks of this size.

In Chapter 5, I test how the pairwise interaction rules from Chapter 3 extend to larger flocks. In the study of interaction rules for collective motion, a question of widespread interest is how each individual combines information from the conspecifics around it. I collected data on flocks of two to five birds and tested how conformity to the direction of the other birds varies with flock size. Averaging pairwise responses does not explain the full response in larger groups. Using a model of group decision-making based on Bayesian estimation (Arganda *et al.* 2012; Perez-Escudero & de Polavieja 2011), I show that the observed responses can be explained by the higher reliability of social information in larger flocks.

In Chapter 6, I analyse how groups of different sizes resolve conflicting route preferences. I used a similar experimental design to the study of leadership and compromise in pairs of pigeons by Biro *et al.* (2006b), but scaled up to flocks of two to five pigeons. Pigeons took significantly shorter routes in flocks, but the size of flock did not affect homing efficiency. These results provide additional insight into the degree of compromise in the routes of larger flocks.

Appendix A compares leadership and social dominance. A previous study found hierarchical patterns of leader-follower relationships in pigeon flocks (Nagy *et al.* 2010), which were sometimes interpreted as an airborne ‘pecking order’. We compared aerial leadership hierarchies with social dominance. We found that leadership was independent of the pigeons’ pecking order on the ground, despite both types of interaction network having a transitive hierarchical structure. This context-dependent reorganization of interactions potentially means that social dominance does not constrain the flow of information during collective navigation. As part of this collaborative project with biological physicists, I helped develop algorithms for extracting dominance relationships from video-tracking data, which is a method with wide potential applicability in the study of animal social structure.

Chapter 7 contains a general discussion of the findings from the other chapters. It summarizes the progress on each of the unifying questions above, proposes topics for future research, and offers my own perspectives on homing behaviour and group decision-making gained through my research. The bibliography on p. 145 lists the references cited in Chapters 1 to 7. Any supplementary figures are included after each chapter.

Chapter 2: Not just passengers: Pigeons, *Columba livia,* can learn homing routes while flying with a more experienced conspecific

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Abstract

For animals that travel in groups, the directional choices of conspecifics are potentially a rich source of information for spatial learning. In this study, we investigate how the opportunity to follow a locally experienced demonstrator affects route learning by pigeons over repeated homing flights. This test of social influences on navigation takes advantage of the individually distinctive routes that pigeons establish when trained alone. We found that pigeons learn routes just as effectively while flying with a partner as control pigeons do while flying alone. However, rather than learning the exact route of the demonstrator, the paired routes shifted over repeated flights, which suggests that the birds with less local experience also took an active role in the navigational task. The efficiency of the original routes was a key factor in how far they shifted, with less efficient routes undergoing the greatest changes. In this context, inefficient routes are unlikely to be maintained through repeated rounds of social transmission, and instead more efficient routes are achieved because of the interaction between social learning and information pooling.

2.1 Introduction

When a group of animals travels together, its collective choice of route will affect what cues are available for spatial learning. Such group decisions can combine information from many group members (information pooling) or result from the group following certain individuals (Biro *et al.* 2006b; Conradt & Roper 2005; Couzin *et al.* 2005). Several theoretical and empirical studies have demonstrated that individuals with more information will spontaneously emerge as leaders (Couzin *et al.* 2005; Flack *et al.* 2012). If the followers are simultaneously learning routes, it raises the possibility of these routes being perpetuated through social transmission

(Laland & Williams 1998). Alternatively, followers may scrounge information without learning the routes themselves (Burt de Perera & Guilford 1999). In addition, if several animals have their own information, learning during information pooling is likely to result in convergence on a more efficient route (Simons 2004; Wallraff 1978). These various outcomes illustrate the potentially complex interactions between social learning and group decision-making in the context of collective animal navigation.

Social learning of migration routes is potentially widespread among bird species that migrate in multi-age flocks, and it could explain why long distance migrants tend to form larger flocks (Beauchamp 2011). There is evidence that migration routes are socially transmitted in storks, geese, and cranes (Ellis *et al.* 2003; Schüz 1950). The most likely mechanism is local enhancement (Hoppitt & Laland 2008), whereby attraction to conspecifics brings an animal into contact with particular stimuli that it learns to use for its own orientation. Laboratory experiments have demonstrated that foraging routes can be socially transmitted in fish (Laland & Williams 1998, 1997; Reebs 2000). In these studies, populations maintain particular routes even after the trained individuals (demonstrators) have been removed.

However, following a conspecific to a reward does not always result in effective learning. If the demonstrator is a reliable indicator of the reward, following can overshadow learning the task itself. Because of this overshadowing effect, the opportunity to scrounge food uncovered by a demonstrator can inhibit social learning (Beauchamp & Kacelnik 1991; Giraldeau & Lefebvre 1987). In a spatial context, this is known as the “passenger/driver effect”. Burt de Perera and Guilford (1999) found that accurate demonstration of the location of a food reward interferes with spatial learning by pigeons in the laboratory. However, there are numerous counter-examples from a range of species that learn from conspecifics despite scrounging (Caldwell & Whiten 2003; Fritz & Kotrschal 1999; Thornton & Malapert 2009a), making it difficult to generalize the contexts and conditions where social learning will occur.

Furthermore, it is not clear how these mechanisms facilitating and inhibiting social learning affect spatial learning in a field setting, where the route choices of demonstrators are not physically constrained. Subjects in field experiments can discover new routes to rewards that were not part of the demonstrator's pre-trained repertoire (Thornton & Malapert 2009a, 2009b). Although it is difficult to conduct controlled experiments on natural migration, two studies suggest that routes can be socially transmitted in the wild. One is an experiment on the daily routes taken by reef fish (Helfman & Schultz 1984). French grunts transplanted to new sites rapidly learned the routes of the resident fish schools, but only if the transplanted fish were allowed to interact with the residents. In another field experiment, cross-fostered white storks in their first year followed the migration direction of their foster population, as long as they departed the breeding area at the same time (Schüz 1950). Although this demonstrates a social influence on migration direction, the sparse data from sightings and ringing recoveries do not indicate how much spatial detail of the migration route was socially transmitted. It is also not known how well the fostered storks learned the migration direction, as data on migrations in subsequent years are lacking.

Homing pigeons, *Columba livia,* offer the opportunity to study social learning of travel routes in a field setting. They naturally fly in flocks, they cope well with handling, and they can be made to fly home from the same location repeatedly over a short period of time, in contrast to wild bird migration. During the past decade, several studies using GPS loggers have revealed that over repeated homing flights from the same site, pigeons develop individually distinctive routes, which are most likely based on visual landmarks (e.g. Meade *et al.* 2005). Furthermore, a pigeon with relatively little local experience can reach home by following a pigeon with an established route (Flack *et al.* 2012). Here, we make use of this robust route-recapitulation phenomenon to examine the transmission of route information in a classic observer-demonstrator paradigm. We test whether repeated flights with a more experienced pigeon (one that has been allowed to build up greater local familiarity with a route over 18 consecutive pre-training flights) affect route learning in a less experienced partner, both in terms of the ability to learn a route and the location of the route learned.

In a previous study of social transmission during pigeon homing, Banks and Guilford (2000) released pairs of pigeons in which one or both birds were naïve to the release site. Naïve pigeons with experienced partners reached home faster than those with naïve partners, but the improvement was not maintained when the pigeons were subsequently released singly. This scrounging-induced overshadowing – a large-scale version of Burt de Perera & Guilford's (1999) passenger/driver effect – supports the conclusion that following a conspecific does not always result in learning. However, single-flight interactions are not ideal for studying the transmission of information because pairs often split up if one or both pigeons had never been released from that particular site before (Banks & Guilford 2000; Guilford & Chappell 1996). Our experiment improves on the design of Banks & Guilford (2000) by releasing each observer-demonstrator pair multiple times, thereby providing the observer with additional opportunities to learn from their knowledgeable partner's performance.

Our study investigates two questions about social learning in the context of pigeon homing. First, we test whether the observers learn a route while following a locally experienced demonstrator over repeated homing flights. We compare the solo performance of observers, which were each released with a demonstrator throughout their training, to controls, which were given the same number of training flights but alone. Since we know that route efficiency and fidelity reliably increase with the number of solo flights from a particular site (Meade *et al.* 2005), if following a demonstrator impairs spatial learning due to overshadowing, we expect observers tested alone to take less efficient routes than controls and to recapitulate routes less closely. The second question, made possible by GPS tracking, is whether the solo routes of observers are more similar to that of their own demonstrator than other demonstrators. This will indicate whether the partner-following and route-learning processes have high enough spatial fidelity – and interact sufficiently – to maintain routes through social transmission.

2.2 Methods

2.2.1 *Subjects and Experimental Procedure*

We used 44 homing pigeons between 2 and 7 years of age and of both sexes, housed at the Oxford University Field Station, Wytham, UK. They had been bred at Wytham or transferred from local breeders during their first year. Most had been involved in experiments in previous years, involving up to 50 homing flights (mean 18.3) from up to three different sites within 11 km of the loft. In the two months before the experiment, all subjects received basic training, which consisted of at least one flock release and three solo releases from four locations 2 to 3 km from the loft, in approximately the four cardinal directions. We alternated locations to minimize learned directional bias.

We replicated the sequence of experimental releases at two sites: Site 1 was near South Leigh (home direction 74.0°, distance 7.05 km), and Site 2 was near Elsfield, a similar distance from the loft in the opposite direction (home direction 259.1°, distance 7.73 km). The two release sites were at least 3 km away from any sites where these pigeons had been released in previous experiments. We randomly allocated subjects into four groups of 10: demonstrators, observers, Site 1 controls, and Site 2 controls. At Site 2, we re-used the demonstrators and observers from Site 1 with their roles reversed, so that demonstrators from Site 1 became observers at Site 2 and *vice versa*. We kept the same demonstrator-observer pairings at both sites, so that the randomly occurring differences in experience, age, and sex at Site 1 were exactly reversed at Site 2. This provided a more systematic way to control for these factors than if we had randomly re-paired the demonstrators and observers. Four additional subjects were added to the Site 2 groups to replace demonstrators or observers who failed to return during training from Site 1, or whose Velcro strip (see below) became too loose to attach a GPS tracker. In total, seven demonstrator-observer pairs and ten controls completed the experiment at Site 1, plus ten demonstrator-observer pairs and nine controls at Site 2.

We completed the full sequence of experimental releases at Site 1 before switching to Site 2. The sequence at each site lasted 4 to 5 weeks, with up to four releases per bird per day and a minimum of 1 h rest period between releases. Pigeons were transported to the release sites in aluminium boxes inside a car with the windows open to allow access to atmospheric odours. Transportation time was approximately 20 min to Site 1 and 17 min to Site 2. We released birds during daylight hours in dry weather with wind less than 7 m s^{-1}.

The sequence of releases at each site consisted of three phases: demonstrator pre-training, paired/control training, and solo tests. Demonstrator pre-training (administered only to birds designated as demonstrators) consisted of 18 solo flights to allow each demonstrator to establish an idiosyncratic homing route and to create an asymmetry in local homing experience between demonstrators and observers. For the paired/control phase, we randomly paired each demonstrator with an observer, and released each pair 12 times. In parallel, control subjects received the same number of training flights as observers, but alone rather than in pairs. The release order each day alternated between controls and pairs, so that the treatment groups experienced the same weather conditions, time of day, and trial spacing. We chose 12 releases for the paired/control training phase, as this number of releases allowed controls to begin to develop landmark-based routes, while also allowing us to move past the initial phase of paired training during which observer pigeons frequently split from their demonstrators. Finally, the solo tests consisted of releasing every bird singly three times to test route memory retention and solo homing performance. At both sites, solo flights began the day immediately following the final paired flight and were completed within 2-4 days, depending on weather conditions.

2.2.2 *Data Logging and Analysis*

We tracked all flights using 1Hz micro-GPS data loggers (iGotU, Mobile Action Technology). The loggers weighed 20g and were attached to pigeons via a strip of Velcro glued to trimmed feathers on the back. When the pigeons returned to the loft, we removed the loggers and downloaded the data to a computer using

@trip PC software (Mobile Action Technology). We analysed tracks in Matlab (MathWorks, release 2010b). We converted positional data from degrees to metres using a Universal Transverse Mercator grid. In order to focus on the choice of homing route, we only used the segment of track from when a pigeon first passed outside a 200m radius of the release site to when it first entered a 200m radius of the loft, thereby excluding birds' initial circling of the release site immediately after take-off and their circling of the loft immediately prior to landing. We superimposed tracks onto Ordnance Survey maps using Fugawi software (Northport Systems Inc.). The GPS track data are available through the Dryad repository (doi:10.5061/dryad.53f4b).

To reduce the number of comparisons between tracks, we first calculated mean routes from each set of a pigeon's three consecutive GPS tracks, using the method of Freeman *et al.* (2011). Over 100 iterations, this method finds a mean path of 500 points that minimizes the distance to nearest neighbouring points on the original GPS tracks, while ensuring the distance between consecutive points on the mean path is more than 5m. There were two mean routes that we calculated using only two GPS tracks because the third track was lost due to GPS device failure.

We tested whether observers' routes from the solo test were significantly similar to their demonstrators' routes immediately before paired training, using a randomization test. We also used a randomization test to check for within-individual consistency among demonstrators, by comparing their ultimate and penultimate mean routes from pre-training. With additional randomization tests, we compared observer routes during paired training to demonstrator routes immediately before paired training, to test whether observers had been following demonstrators. In all cases, we quantified the similarity between two mean routes by finding the distance from each point on one route to the nearest neighbouring point on the other, applied reciprocally and averaged over the length of the routes.

Each randomization test compared real pairings to randomized pairings. Real pairings were either two routes from the same bird or one each from an observer-demonstrator pair. We aimed to test whether route similarity within these real pairings was significantly higher than in randomized pairings (i.e., whether the routes observed were more similar than those we would have expected at random). There were 17 pairs of routes in each test: seven from Site 1 and ten from Site 2. We quantified within-pair similarity using the median inter-route distance (M_{obs}). Then we randomly re-paired the routes, with the restriction that pairings had to be between routes from the same site. We calculated the median inter-route distance for each randomization (M_i^*), and used 10000 randomized pairings to build up a test distribution of this statistic. For a two-tailed significance test, the *p*-value was the proportion of M^* values that fell farther from the mean than M_{obs}.

To compare route learning of observers and controls, we calculated two metrics describing their homing routes during the solo test phase. First, we quantified homing route efficiency using distance from beeline, i.e., the distance from each point on the bird's GPS track to the nearest point on a straight-line path composed of 1000 points, averaged for all points on the track. Second, we quantified route fidelity as the mean variance between each bird's three solo test tracks. To find the mean variance, we calculated the variance at each point along the mean route using the distances to the nearest points on the three GPS tracks, and then averaged the variances from the 500 points comprising the mean route (see Freeman *et al.* 2011). We normalized both metrics using a log-transformation, and compared the observer and control treatments using a two-way ANOVA that also took into account any effect of release site (R version 3.1-102, R Core Team 2011). We used the same test to analyse the effect of treatment on distance to beeline at the beginning and end of the paired training phase. We also calculated the distance from beeline and the variance of the original demonstrator routes (mean of tracks 16-18), and then tested the effects of these route properties on how well the routes were subsequently transmitted to observers, again using a linear model in R that took into account any effect of release site.

2.3 Results

2.3.1 *Demonstrator pre-training*

Homing efficiency of demonstrators improved significantly over the course of the pre-training flights, with a 16 - 80% decrease in path length between the first and eighteenth flight (mean 58.9%, see ESM fig. 1). Distance to the beeline decreased in all but one of the demonstrators (mean decrease of 1230m, Wilcoxon sign rank test $p < 0.001$). At the end of pre-training, demonstrators were also significantly closer to the beeline than were the controls on their first solo flight (two-way ANOVA, $F_{1,33} = 25.8$, $p < 0.001$ for treatment effect, $F_{1,33} = 0.98$, $p = 0.330$ for site effect; figure 2a). Therefore it is meaningful to refer to the demonstrators as having greater local familiarity than observers and controls at this stage in the experiment, especially given that repeated solo training improved homing efficiency.

After 18 solo pre-training flights, demonstrators were stably recapitulating homing routes (red routes in figure 1 and ESM fig. 1). To test whether the demonstrator routes were individually distinctive, we compared the mean route from pre-training flights 13-15 to the mean route from flights 16-18. Distance between these consecutive mean routes was 107 ± 80m at Site 1 and 276 ± 362m

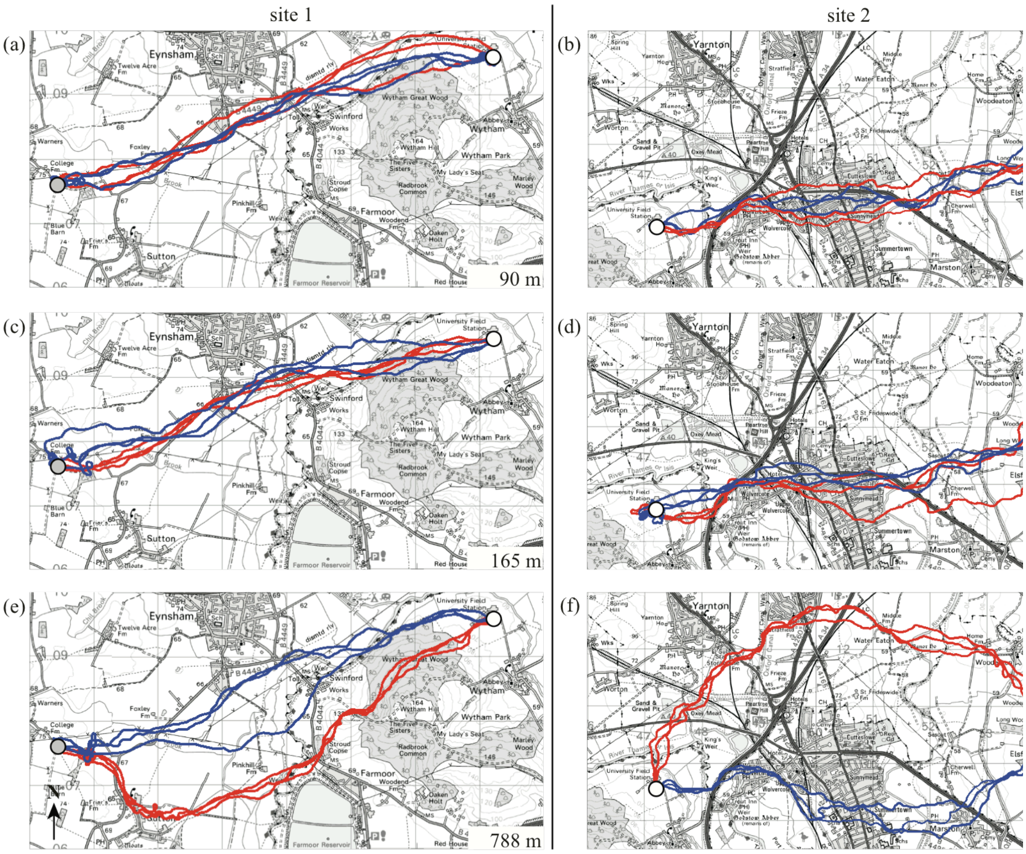

Figure 1. Comparison of routes flown by demonstrator pigeons and their respective observers. Each panel shows three consecutive GPS tracks of a demonstrator (red) flying alone before paired training and its observer (blue) flying alone after paired training. Grey circles indicate release site location; white circles indicate home. The value below each map is the mean distance between demonstrator and observer routes. To display the range of outcomes from each site, we show the pairs with the minimum (a, b), median (c, d), and maximum (e, f) distances. Grid: 1km. Maps Crown copyright Ordnance Survey. All rights reserved.

at Site 2, whereas the distance between the routes of different demonstrators in pre-training flights 16-18 was 553m ± 411m at Site 1 and 654m ± 547m at Site 2. A randomization test confirmed that demonstrators flew closer to their own previous route than to the previous route of a randomly selected demonstrator ($p = 0.040$).

2.3.2 *Paired releases*

Each demonstrator-observer pair was released 12 times, and they homed together on a mean of 8.65 ± 1.87 releases. We classified a pair as having split if they became separated by more than 150m at any point on the homeward flight. During the first paired release, all but one of the 17 observers split from their demonstrators, but over the course of the remaining paired releases the observer-demonstrator pairs split less often. If splitting was due to unfamiliarity with the partner or with the experimental procedure, rather than unfamiliarity with the site, one would expect less splitting at Site 2 than at Site 1. However, splitting did not vary significantly between the sites (mean flights with split: 3 ± 1.8 at Site 1, 3.8 ± 2.7 at Site 2, Wilcoxon rank sum test $p = 0.58$). The mean observer routes from paired flights 4-6, 7-9, and 10-12 were all significantly similar to their demonstrators' pre-training routes (randomization tests: $p = 0.022$, $p = 0.003$, $p = 0.044$), indicating that observers were generally following demonstrators close to the pre-trained routes.

However, not all demonstrators maintained their pre-trained routes when flying with observers. On the whole, demonstrators' homing routes shifted significantly closer to the beeline, away from their previously established routes (2). While most demonstrator routes shifted by less than 200m, a few demonstrators at each site adopted completely new homing routes that were much more direct than before paired training (figure 2c). Demonstrator routes that were initially farther from the beeline shifted more during the paired training phase ($F_{1,14} = 28.21$, $p < 0.001$, from a linear model with release site as a fixed factor). The indirect demonstrator routes in figures 1e and 1f are among those that subsequently shifted by large amounts during paired training.

2.3.3 *Route learning by observers*

To assess the impact of paired training on observers, we compared the homing routes of observers and controls. Control pigeons showed a significant

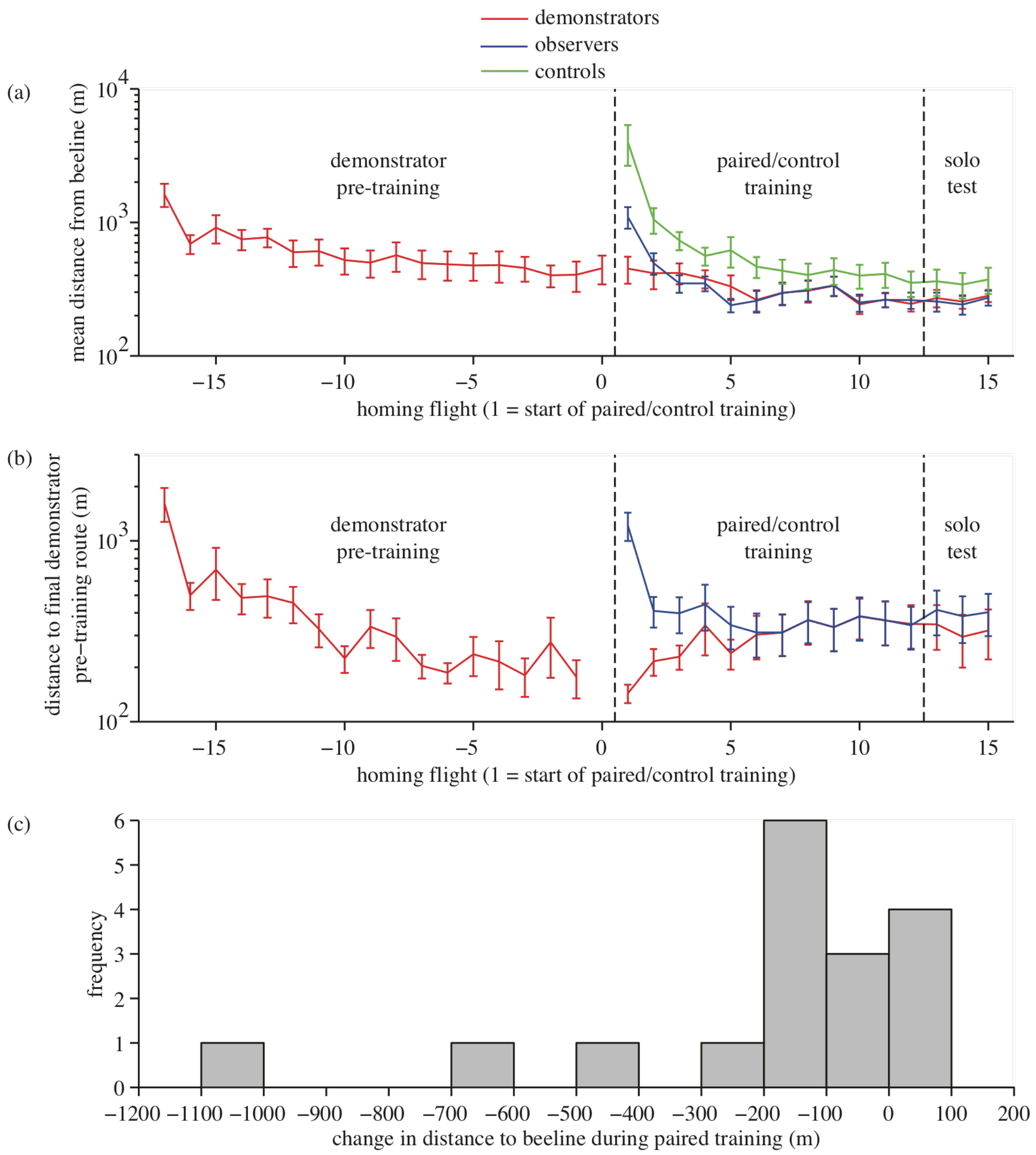

Figure 2. Development of homing routes in demonstrator and observer birds. (a) Mean distance from homing routes to the beeline, by treatment group, pooled across both sites. Bars show SEM. (b) Distance to the final solo demonstrator track recorded immediately before paired training. (c) Histogram showing shift in demonstrator routes during paired training (mean distance during solo test – mean distance during paired flights 10-12). Median is significantly below zero, indicating routes got closer to beeline (Wilcoxon signed rank test, *p* = 0.006, *N* = 17).

improvement in homing efficiency over their first 12 solo flights. Eighteen out of nineteen reduced both their path length (mean reduction of 68.4%, Wilcoxon sign rank p < 0.001) and their mean distance to the beeline (mean reduction of 5527 m,

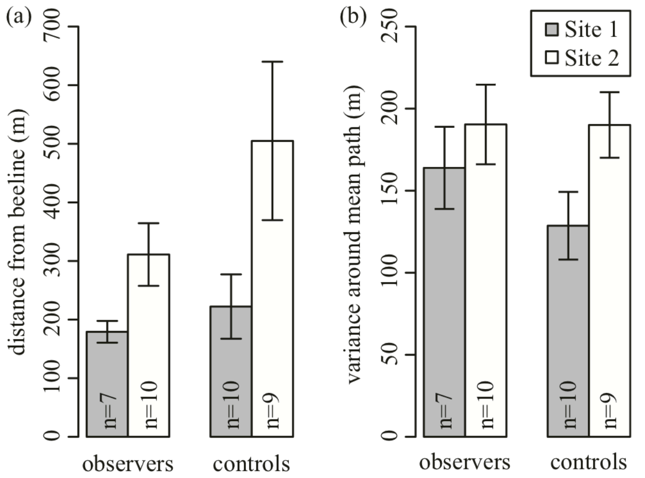

Figure 3: Homing route characteristics of observers and controls, during the solo test phase (three solo flights per bird). (a) Mean distance of solo routes from beeline. (b) Mean spatial variance of solo routes about their mean route. Bars show mean ± SE.

Wilcoxon sign rank $p < 0.001$; ESM fig. 1). The observers, each released with a demonstrator, were initially closer to the beeline than controls (figure 2a. two-way ANOVA comparing observer and control distance to beeline in flights 1 to 3, $F_{1,33} = 18.40$, $p < 0.001$ for treatment effect, $F_{1,33} = 4.75$, $p = 0.036$ for site effect). However, by the end of the training the average distance from the beeline did not depend on whether the pigeons flew singly or in pairs (flights 10 to 12: $F_{1,33} = 0.58$, $p = 0.453$ for treatment effect, $F_{1,33} = 10.89$, $p = 0.002$ for site effect).

Afterwards, when the observers flew alone in the solo tests, their distance from the beeline was not significantly different from that of controls (figure 3a, $F_{1,33} = 0.31$, $p = 0.581$ for treatment effect, $F_{1,33} = 9.99$, $p = 0.003$ for site effect). In addition, there was no significant difference between observers and controls in their degree of route recapitulation during solo tests, measured as the mean spatial variance of the three homing routes about their mean route (figure 3b, $F_{1,33} = 1.22$, $p = 0.277$ for treatment effect, $F_{1,33} = 5.34$, $p = 0.027$ for site effect). This indicates that paired training over 12 consecutive releases did not affect route learning compared to what birds achieve individually, at least in terms of the directness and fidelity of routes. Homing routes from Site 1 tended to be more direct and more accurately recapitulated than those from Site 2. The effect of site did not depend on treatment (interaction terms added to above ANOVA models: $F_{1,33} = 0.41$, $p = 0.527$ in distance-from-beeline model; $F_{1,33} = 0.97$, $p = 0.333$ in route-variance model).

2.3.4 *Transmission of route information*

The mean distance from observer solo routes to their demonstrators' pre-paired route was 312 ± 262 m at Site 1 and 370 ± 553 m at Site 2. Large standard deviations and positive skew at both sites indicate that a minority of observers learned very different routes from their demonstrators. The observer routes that closely match the original routes of their demonstrators tend to be near the beeline (figure 1 a-d), where it is difficult to detect information transmission because of the low diversity among demonstrator routes, and where the routes are likely to be similar even if they were learned independently. Separate randomization tests for each site found significant demonstrator-observer route similarity at Site 2 ($p = 0.014$) but not at Site 1 ($p = 0.330$), indicating that there was some transmission of route information but that the effect was not consistent. A combined randomization test showed that over all, the observer routes were not significantly closer to their own demonstrators' routes than to randomly chosen demonstrator routes from the same release site ($p = 0.250$).

We used a linear mixed-effects model to test which features of the pre-training and post-training routes predicted high observer-demonstrator route similarity. Given that indirect demonstrator routes shifted farther during paired training, it is not surprising that the farther from the beeline the original demonstrator route, the less similar it was to the final observer route (figure 4, linear model, $F_{1,12} =$

43.71, $p < 0.001$). There was no significant effect from the demonstrator's route variance during pre-training ($F_{1,12} = 2.02$, $p = 0.181$) or the number of flights on which the pair split ($F_{1,12} = 0.56$, $p = 0.468$).

2.4 Discussion

Our study used GPS tracking to examine how flying with a more locally experienced partner affects both a pigeon's ability to learn a homing route and the shape of the route it learns. Following a conspecific did not overshadow route learning, but neither did it facilitate learning – observers learned routes that were just as efficient and just as accurately recapitulated as those of controls flying alone. Given that observers did learn routes, one might expect their routes to be similar to the initial routes of their respective demonstrators. However, there was no consistent pattern of social transmission (figure 1), largely because demonstrators shifted their routes over the course of repeated flights with observers. This suggests that observers were not only able to learn landmark-based routes, but that as they learned they may have taken an increasingly active role in the pair's navigation.

Our finding that observers learned just as well as controls contrasts with previous lab-based studies of pigeons, in which the opportunity to scrounge a food reward from a knowledgeable conspecific inhibited the learning of a food-extraction technique (Giraldeau & Lefebvre 1987) or food location (Burt de Perera & Guilford 1999). There are several factors that could account for the difference in results. In Burt de Perera & Guilford's study (1999), the small spatial scale meant that the demonstrator and the reinforcer (food) were closely paired in time and space compared to our study. Another – likely very important – difference was the use of repeated training, which gave observers in our study additional opportunities and time to learn routes. Our results do not rule out an overshadowing or passenger/driver effect in the earlier stages of route learning, as found by Banks and Guilford (2000). Their study also used a more difficult navigational task than ours, with the longer homing distance and lower experience of subjects at the start of the experiment perhaps contributing to the overshadowing effect they found.

The development of homing routes over repeated solo releases by our demonstrator pigeons was fully expected given previous studies (Biro *et al.* 2006a; Meade *et al.* 2005). Despite the relatively short homing distance and the subjects' previous experience, we were able to use this route-learning phenomenon to create a significant asymmetry in local route familiarity between demonstrators, with established routes, and observers or controls. Routes from the solo test phase were straighter and more accurately recapitulated at Site 1 than at Site 2. This site effect was equally strong in observers and controls, even though controls had experience with only one site. While it is possible that the observers at Site 2 had difficulty learning new routes because of their prior experience at Site 1, a more likely explanation is that geographically related factors underpin these differences in flight paths. The greater difficulty of the homing task from Site 2 may explain why we detected social transmission at Site 2 but not Site 1: (1) a more difficult homing task increases the likelihood that observers will use social information (Flack *et al.* 2012), and (2) higher diversity among demonstrator routes makes social learning easier to detect. An alternative explanation is that the observer-demonstrator pairs were already familiar with each other, and with the experimental procedure, from their use at Site 1. However, if familiarity with the partner facilitated social information use, we might expect pairs to split less often at Site 2, which was not the case.

The shift in demonstrator routes during the paired training phase was unexpected, and it interfered with the accurate social transmission of routes to observers. Although some of the shift can be attributed to gradual improvement with additional homing experience, in some cases demonstrators shifted their routes by hundreds of metres. This behaviour is surprising because it breaks with the asymptotic increase in efficiency normally seen over repeated homing flights, during which pigeons flying alone continue to recapitulate relatively indirect routes even after as many as 24 releases (Meade *et al.* 2005). A future study could test whether flying with the observers was responsible for the improvement in our demonstrators' routes, using an additional control group that flew home singly the same number of times as demonstrators. If adding observers leads to straighter routes, then repeated rounds of learning will converge on a more efficient solution rather than faithfully perpetuating inefficiencies, similar to the "hill climbing" property of social learning in nine-spined sticklebacks (Kendal *et al.* 2009). This does not require any sophisticated selective copying strategy, but could emerge from the interaction between learning and following in both demonstrators and observers.

If the paired routes combined information from both birds, then the pairs' increase in homing efficiency is less surprising (Dell'Ariccia *et al.* 2008; Simons 2004). Although observers were not as proficient as demonstrators at the start of paired training, they did have their own navigational information from sources such as olfaction, a sun compass, and geomagnetism (Wallraff 1996; Wiltschko *et al.* 1981), as well as landmarks seen, perhaps less locally, during previous experiments and during early flights when they split from their demonstrators. With this information, the observer may be able to influence the trajectory of the pair and therefore shape the content of the local enhancement process, rather than just passively follow. The observer's probability of leading would have increased as it gained more local experience over repeated homing flights (Flack *et al.* 2012).

Where alternative routes to a reward are easy for individuals to discover on their own, arbitrary traditions are not likely to be maintained, as Thornton and Malapert (2009b) found in meerkats. In guppies, social transmission of a circuitous route to food is less persistent than social transmission of a short route (Laland & Williams 1998). These studies, along with ours, demonstrate that animals can avoid social learning's potential cost in perpetuating relatively inefficient behaviour.

This is the first field experiment on birds to investigate whether the distinctive shape of a route can be transmitted from one individual to another, a type of social learning that is potentially widespread among species that migrate or forage in groups. For pigeons, following a more experienced individual and learning a landmark-based route are not mutually exclusive strategies, but can happen in parallel. However, rather than resulting in the accurate social transmission of homing routes, the demonstrators' original routes shifted over repeated interactions, possibly due to input from the less locally experienced pigeon. Our results support an interaction between information pooling and social learning. Although learning-while-following offers a mechanism for the maintenance of socially transmitted migratory routes, such a tradition will not persist if newcomers have inherent navigational abilities that allow them to discover new routes and influence the path of the flock.

Ethics Statement

The protocols outlined in this paper were approved by the Ethical Review Committee of Oxford University's Department of Zoology.

Acknowledgements

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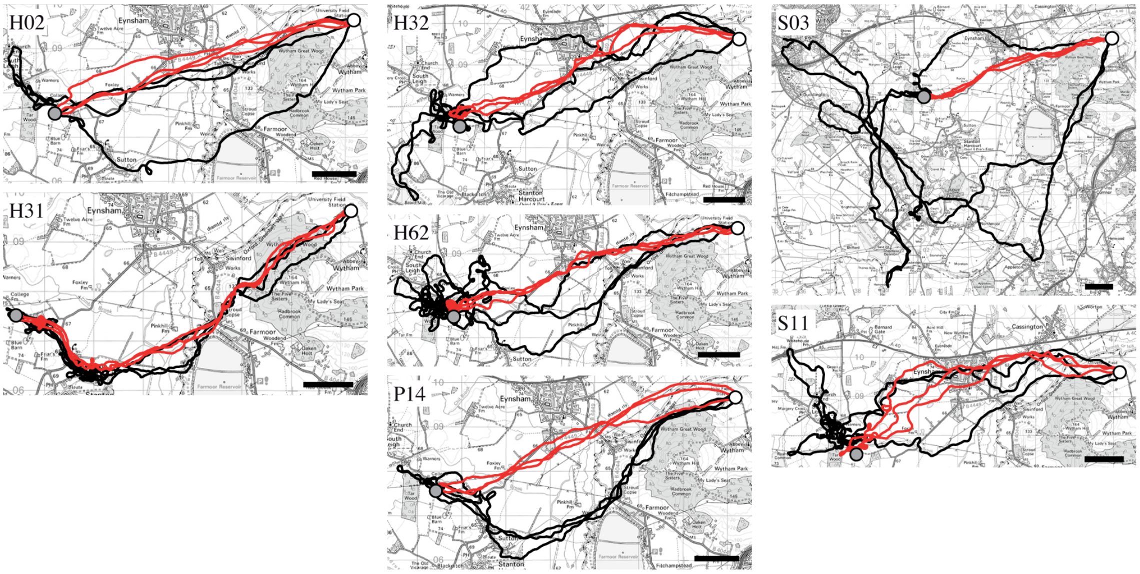
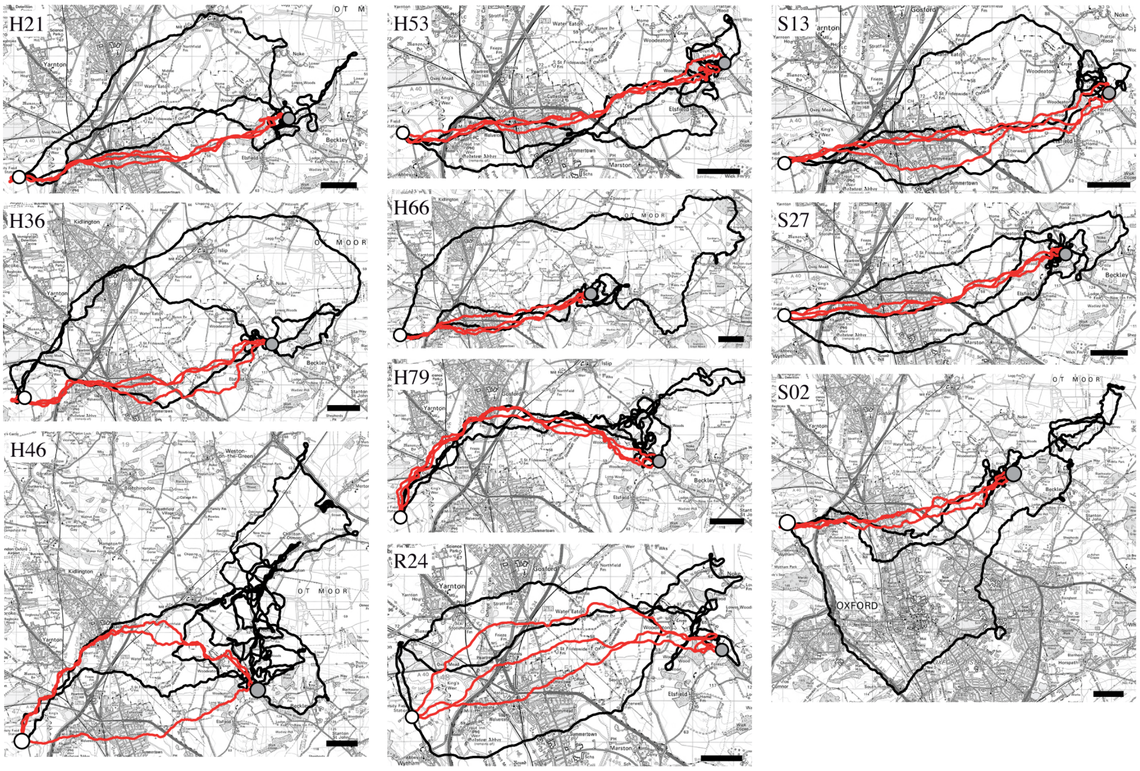
Supplementary Material - Figure S1

GPS tracks of homing pigeons showing learning of stereotyped routes. Each panel shows a pigeon's first three (black) and final three (red) GPS tracks from a sequence of solo homing flights. The final three tracks are from flights 16-18 for demonstrators, and flights 13-15 for controls. Tracks S27-16, P87-13, and H44-01 were lost due to GPS failure, and in these cases the next/previous available track is shown instead. Grey circle shows release site location; white circle shows home loft. Scale bar: 1 km. Maps Crown copyright Ordnance Survey. All rights reserved.

demonstrators: site 1



demonstrators: site 2



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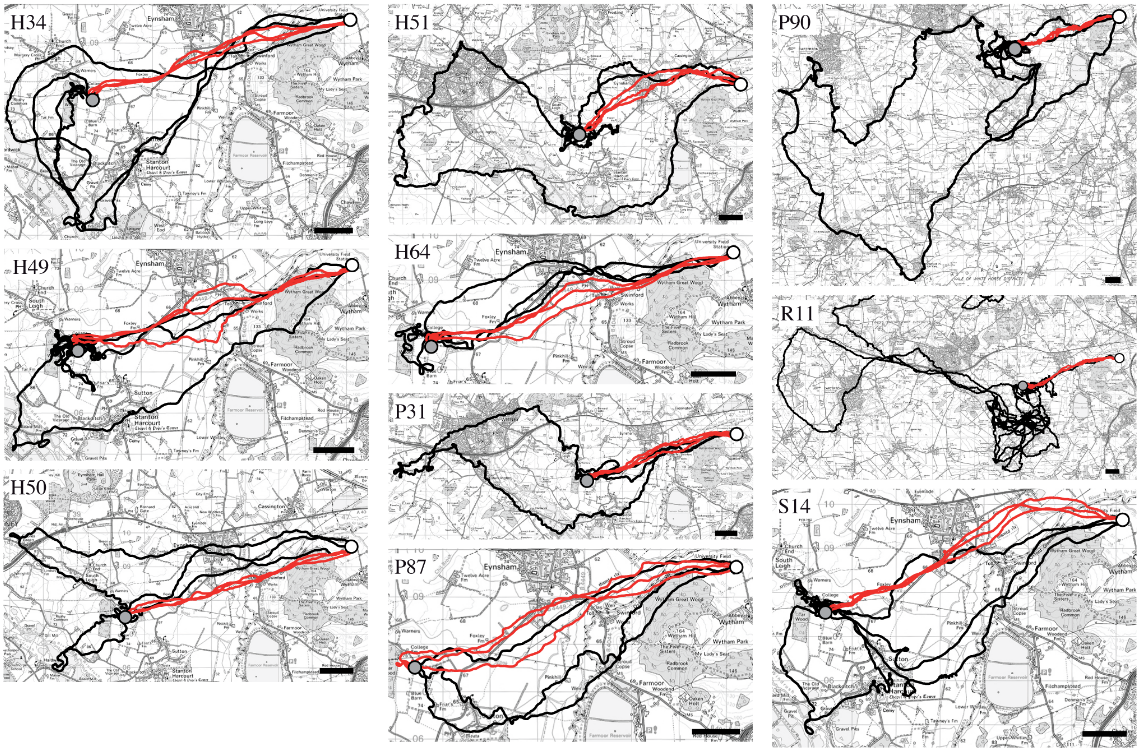

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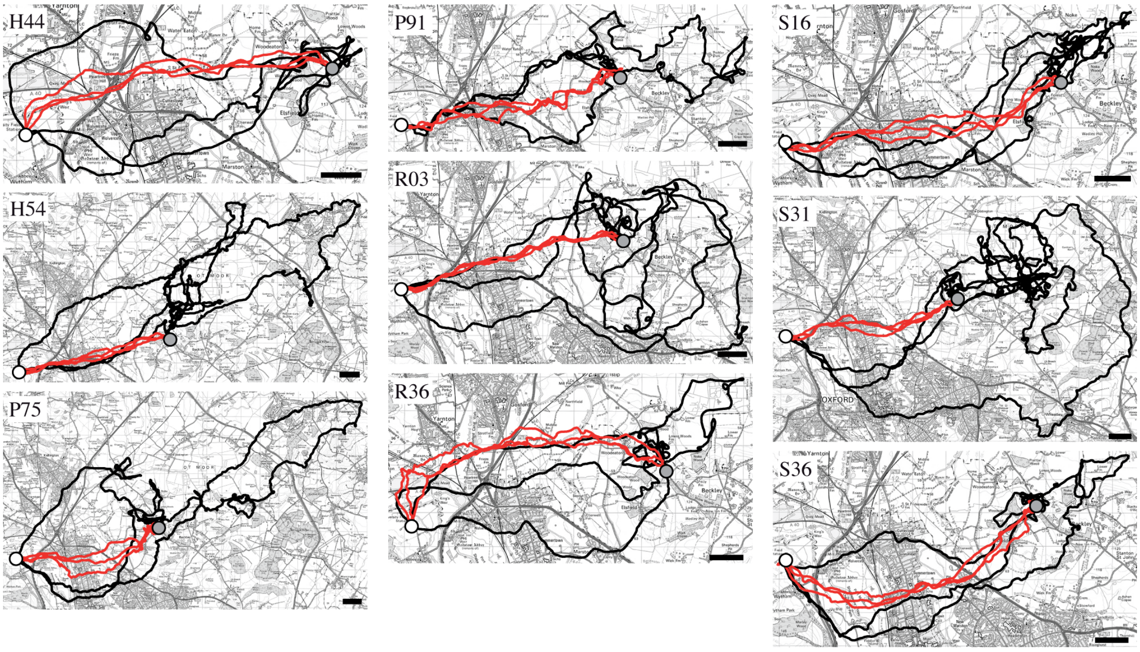

Chapter 3: Interaction rules underlying group decisions in homing pigeons

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Abstract

Travelling in groups gives animals opportunities to share route information by following cues from each other's movement. The outcome of group navigation will depend on how individuals respond to each other within a flock, school, swarm, or

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herd. Despite the abundance of modelling studies, only recently have researchers developed techniques to determine the interaction rules among real animals. Here we use high-resolution GPS (global positioning system) tracking to study these interactions in pairs of pigeons flying home from a familiar site. Momentary changes in velocity indicate alignment with the neighbour's direction, as well as attraction or avoidance depending on distance. Responses were stronger when the neighbour was in front. From the flocking behaviour, we develop a model to predict features of group navigation. Specifically, we show that the interactions between pigeons stabilize a side-by-side configuration, promoting bidirectional information transfer and reducing the risk of separation. However, if one bird gets in front it will lead directional choices. Our model further predicts, and observations confirm, that a faster bird (as measured from solo flights) will fly slightly in front and thus dominate the choice of homing route. Our results explain how group decisions emerge from individual differences in homing flight behaviour.

Keywords: collective animal behaviour; leadership; bird flocks; collective decision making; self-propelled particles

3.1 Introduction

Bird flocking is an intriguing and spectacular collective phenomenon. Some bird species, such as starlings, can form large groups that move together in a coordinated way, with changes of direction propagating quickly through the entire flock (Procaccini *et al.* 2011). Many species flock together during migration and remain cohesive over long distances. In order to stay together in a coordinated flock, individual birds need to respond appropriately to their neighbours' positions and directions of movement. Modelling studies have investigated flocking interactions through a class of models known as self-propelled particle (SPP) models (Conradt *et al.* 2009; Couzin *et al.* 2005, 2002; Hemelrijk & Hildenbrandt 2012; Strömbom 2011; Vicsek *et al.* 1995). These models, largely inspired by statistical physics, simulate individuals as particles that interact locally with their neighbours. Usually, a simple set of interaction rules is sufficient to reproduce realistic collective patterns (Couzin *et al.* 2002; Hemelrijk & Hildenbrandt 2012), including cohesive flocks in which information propagates through the entire group (Couzin *et al.* 2005).

From a functional perspective, animals moving in groups benefit in several different ways from staying together and moving cohesively. These include an increased ability to detect and avoid predators (Krause & Ruxton 2002) or to reach a target destination (Couzin *et al.* 2005; Simons 2004). However, in order to stay with the others, individuals have to balance their own preferences against the benefit of staying in a group, for instance when negotiating a common direction of movement or a common activity (Conradt & Roper 2005). There is an extensive biological literature on how such consensus decisions are achieved. The focus has been either on the mechanisms involved in reaching consensus (including non-linear, quorum-sensing type responses (Sumpter & Pratt 2009)), or on individual differences that affect an animal's weight in a group decision (Fischhoff *et al.* 2007; Flack *et al.* 2012; Freeman *et al.* 2011; King & Sueur 2011). Although many features of collective decision-making do not require heterogeneity in individual behaviour, consistent individual differences in leadership have been found in a range of species, including pigeons (Biro *et al.* 2006b; Nagy *et al.* 2010), mosquitofish (Burns *et al.* 2012), zebras (Fischhoff *et al.* 2007), and several species of primates (King & Sueur 2011).

By leadership, we mean that some individuals have more influence over a group decision, inferred from the fact that the group's choice reflects those individuals' information or preferences. This definition of leadership does not imply any particular mechanism. Importantly, a group decision can display leadership without the group members actively choosing a leader. Simulations by Conradt *et al.* (2009) demonstrate several types of heterogeneity that cause self-organized leadership, without the need for global communication or individual recognition. These fall into the categories of 'leading by need' (stronger attraction to a target stimulus) and 'leading by social indifference' (weaker response to conspecifics). The two categories are based on contrasting functional priorities of the individual: the importance allocated to reaching the target vs. the importance of remaining with the rest of the group.

We cannot understand group decision-making without understanding the underlying interactions among individuals. The interaction rules that a particular species has evolved will reflect a trade-off between various features of collective behaviour, such as group cohesion, the speed and accuracy of group decisions, and an individual's ability to seek cover from predators within the 'selfish herd' (Hamilton 1971; Ioannou *et al.* 2012; Krause & Ruxton 2002). Because of these competing selection pressures, it is not clear that interaction rules will always optimize collective information processing. Nonetheless, making mechanistic links between measured interaction rules and group outcomes will help us discover the functional significance of the interaction rules, for example whether they optimize tracking a gradient (Berdahl *et al.* 2013) or avoiding predation (Ioannou *et al.* 2012). If we can explain the positioning of individuals within the group in terms of their interactions, then we may also be able to make a link between interaction rules and information processing at the group-level. To illustrate this, let us consider a group of only two individuals. Assuming there is a blind visual angle, information transfer will be unidirectional if they travel one behind the other, whereas moving side by side they can see each other, which enables bidirectional information transfer.

Homing pigeons provide an excellent system for testing how movement interactions determine group decisions. They can be tracked with high spatial and temporal accuracy under field conditions, and their route-learning behaviour can be used to set up group decision-making experiments over a scale of kilometres (Biro *et al.* 2006b). When a pigeon is released far from its home loft, it heads back home, relying on a variety of different sensory cues (Wallraff 2005). If a pigeon is released many times from the same site, it usually learns a stereotyped route back to the loft, with varying degrees of similarity among the routes of different birds (as in Meade *et al.* 2005). This creates a conflict of information when a pair of pigeons flies home together. Biro *et al.* (2006b) found that pairs take a compromise route if their previous solo routes are close together, but above a critical distance one bird leads the other. Further studies found that navigational certainty and experience with the local landscape give a pigeon more influence over a pair's choice of homing route (Flack *et al.* 2012; Freeman *et al.* 2011). Tracking experiments also confirm that flocking allows pigeons to pool information (Biro *et al.* 2006b) and achieve more efficient routes (Dell'Ariccia *et al.* 2008), as predicted from theoretical studies. However, there is still no empirical data on how flock decisions emerge from birds' momentary responses to each other and to the environment.

In this study, we measure flocking responses from movement data on 80 co-navigating pairs of homing pigeons, recorded with high-resolution GPS (Global Positioning System) loggers. We compare each pair's track to the pigeons' previous solo tracks from the same release point, to determine whose navigational information the pair followed. With the aid of a model informed by the collective motion data, we investigate how leadership emerges from individual differences in flight behaviour, measured during the solo flights. We then compare pigeon collective behaviour to that of other species and to the assumptions of previous modelling studies.

3.2 Methods

3.2.1 *Data collection*

We recorded GPS tracks from 23 homing pigeons bred and housed at Oxford University Field Station, Wytham, Oxford, UK. The pigeons were between one and two years old and all had the same level of homing experience, having been previously released from sites 6-8km to the north and east of the home loft and from shorter-distance sites to familiarize them with the area within 3km of home. All flights in this study were from a site 10.4 km SSW of the home loft (bearing to loft: 26°). We tracked homing flight using GPS data loggers set to record 5 fixes/s (QStarz BT-Q1300ST, 15g), attached to pigeons via Velcro strips glued to trimmed feathers on their backs. Each pigeon made up to two homing flights per day, with at least 2h to rest between flights.

First, we released each pigeon singly 21 times to allow it to learn a landmark-based route (Biro *et al.* 2004; Meade *et al.* 2005). We recorded GPS tracks of the last five solo flights. To summarize the difference between any two routes, we found the distance to the nearest point on the target track from every point along the focal track, and then took the mean of these distances. For flights 19 to 21, a bird's distance to its own previous solo route was $160 \pm 86m$ (mean ± s.d.), compared to $648 \pm 459m$ to other birds' previous routes, indicating route recapitulation as in previous studies (Biro *et al.* 2006b, 2004; Meade *et al.* 2005). We then released pigeons in pairs (figure 1), by placing two birds in a carrying crate and opening a door in the side of the crate. Between paired flights, we released each bird singly again to test whether it retained its established solo route. If the mean nearest-neighbour distance from the previous solo route was more than 275m (the 90th percentile from flights 19 to 21), we gave a pigeon additional solo flights

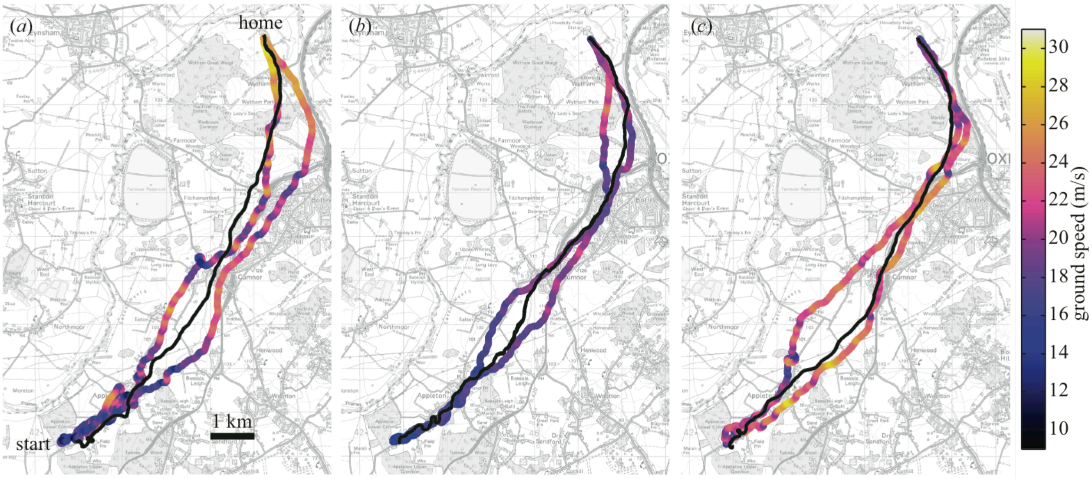

Figure 1: **Tracks of pairs of homing pigeons and their previous solo routes.** In each panel, black lines show a pair's GPS tracks and shaded lines show the two birds' previous solo tracks, illustrating the conflicts that arise due to differing route preferences. Ground speed is plotted along the solo tracks, smoothed using a 4s moving average. Maps Crown copyright Ordnance Survey. All rights reserved.

until its route achieved this criterion of similarity. No pigeon flew with the same partner more than once. Where possible, we chose pairings with a large distance between solo routes because these cases are more informative about group decision-making. Nonetheless, across the pairs there was a wide range of distances between solo routes, from 69 to 1573m (measured as mean of point-by-point nearest-neighbour distances). We removed a pigeon from the experiment if its Velcro strip began to detach from the feathers. In total we recorded 85 paired flights over the course of seven weeks, with 1 to 12 paired flights per pigeon. We excluded from the analysis five pairs in which the mean distance between birds was more than 200m. A previous study estimated 200m as pigeons' perceptual range for flocking (Biro *et al.* 2006b), so these five pairs that split would have been out of range for a large proportion of the homeward track.

We tested the error in GPS measurements of relative position and direction by fixing two trackers to a pole, 1m apart, and carrying the pole on a bicycle back and forth along a straight track (approx. 500m) with a clear view of the sky. We repeated the procedure with the pole either perpendicular or parallel to the direction of travel. At each time step, we calculated the difference (φ) between the trackers' measured directions of travel. The spatial error responsible for φ $(\text{distance travelled} \times \sin\varphi)$ was normally distributed with a standard deviation of 0.054m. The total error in measuring relative position was somewhat larger (median 1.69m, 95th percentile 4.33m). The total error is consistent over a timescale of minutes and therefore has little effect on direction measurements. This validates the claim in previous studies that velocities measured from GPS have less error than positions (Nagy *et al.* 2010).

3.2.2 *Data analysis*

We converted latitude and longitude to metres using a Universal Transverse Mercator projection and excluded points before takeoff or after landing. At every time step on the paired tracks, we calculated each bird's direction of travel in the horizontal plane ($\alpha_i(t)$), which we used to calculate its turning rate, $(\alpha_i(t + \Delta t) - \alpha_i(t))/\Delta t$, and the difference in direction between the two birds ($\varphi = \alpha_j(t) - \alpha_i(t)$). We also calculated the angle (θ) and distance (r) to the neighbour (figure 2), such that $\theta = 0$ when the neighbour was directly in front in the direction of flight, $\theta > 0$ when the neighbour was on the right, and $\theta < 0$ when the neighbour was on the left. Turn rate and φ were also signed negative for anti-clockwise and positive for clockwise. We analysed flocking responses in the combined data from all paired flights.

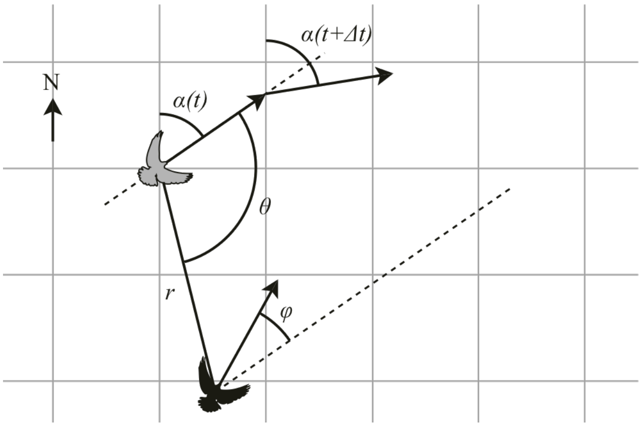

Figure 2: **Interaction variables calculated from the pigeon tracks and from the simulation.** For the focal individual (grey), we calculated the distance (r) and angle (θ) to its neighbour (black), as well as the difference in flight direction (φ). We estimated the instantaneous direction of travel ($\alpha(t)$) from the vector to the next GPS fix. The angles θ and φ were measured relative to $\alpha(t)$. $(\alpha(t + \Delta t) - \alpha(t))/\Delta t$ gave the focal bird's turn rate. We calculated all variables in the horizontal plane, because the horizontal dimension contains most of the variation between homing routes and is therefore more relevant to route choice.

As a metric of momentary leadership in pairs, we found the time delay (τ^*) at which the neighbour's flight direction was maximally correlated to that of the focal bird (Herbert-Read *et al.* 2011; Nagy *et al.* 2010). For this purpose, we calculated the correlation between the focal bird's direction at time t and the neighbour's direction at time $t + \tau$, where $-10s < \tau < 10s$, using the dot product of unit-length velocity vectors ($\mathbf{v}$).

$$C_{ij}(t+\tau) = \mathbf{v}_i(t) \cdot \mathbf{v}_j(t+\tau) \qquad (1)$$

To test how directional correlation delay varies with the neighbour's position, we divided the data into bins based on r and θ. For each value of τ, we averaged $C_{ij}(t+\tau)$ across all points in the bin, and then found the time delay τ^* than maximized directional correlation. Note that $C_{ij}(t) = \cos\varphi$, so τ^* is the time delay that minimizes the birds' absolute difference in direction $|\varphi|$. If τ^* is positive, the neighbour tends to follow the flight direction adopted by the focal bird, and *vice versa* if τ^* is negative.

As a second method of analysing leadership, we analysed the position of the paired routes relative to the preferred solo routes of the two birds. We calculated the distance, d_i from a bird's position during a paired flight to the nearest point on its previous solo route. Δd_i is negative when pigeon i approaches its solo route. For a pair of birds flying together (i and j), $\Delta d_i < \Delta d_j$ indicates that their movement is more towards i's route, and in this circumstance we estimate that i had more influence over route choice, provided that the solo routes were diverging ($\Delta d_i + \Delta d_j > 0$). We excluded portions of track where the solo routes were converging, for example when nearing home, which might cause a pair to move toward j's route even when following i's route and regardless of j's influence. If the pair split it is meaningless to classify either as a leader or follower, so we restricted the analysis to times when the pigeons remained within 200m of each other (perceptual range of flocking estimated by Biro *et al.* (Biro *et al.* 2006b)).

To investigate individual differences that might predict a bird's position and influence in a pair, we analysed speed and route fidelity in the five solo tracks preceding each paired flight. First, we discarded portions of the solo tracks within 200m of the release point or the home loft. We calculated instantaneous ground speed along the remaining portion of the track. We quantified route fidelity using the method of Freeman *et al.* (2011), which iteratively finds a mean path of 1000 points that minimizes the distance (d_i) to the nearest neighbouring points on the five original GPS tracks. At each point on the mean path, the spatial variance is

$$\frac{\sum_{i=1}^{N} {d_i}^2}{N-1} \tag{2}$$

where $N = 5$ in this case. High variance indicates low route fidelity.

Having calculated speed and variance, we compared these solo-flight variables to behaviour in a pair (front-back positioning, influence over route choice). To make the comparison using solo-flight variables from a nearby part of the landscape, we started with a point on the paired track, found the nearest point on each of the pigeon's five preceding solo tracks, and used the mean speed from those five points. Similarly, we used the variance from the nearest point on the mean path. We tested the significance of relationships between solo and pair flight variables using a randomisation test, in which we randomly assigned a set of solo tracks to each pair track and then repeated the analysis. The sets of solo tracks each consisted of five consecutive tracks from the same bird, randomly chosen without replacement from the 160 sets preceding paired flights. We obtained a two-tailed p-value by comparing the regression slope (β) from the real dataset to the distribution of β from 10^3 randomisations.

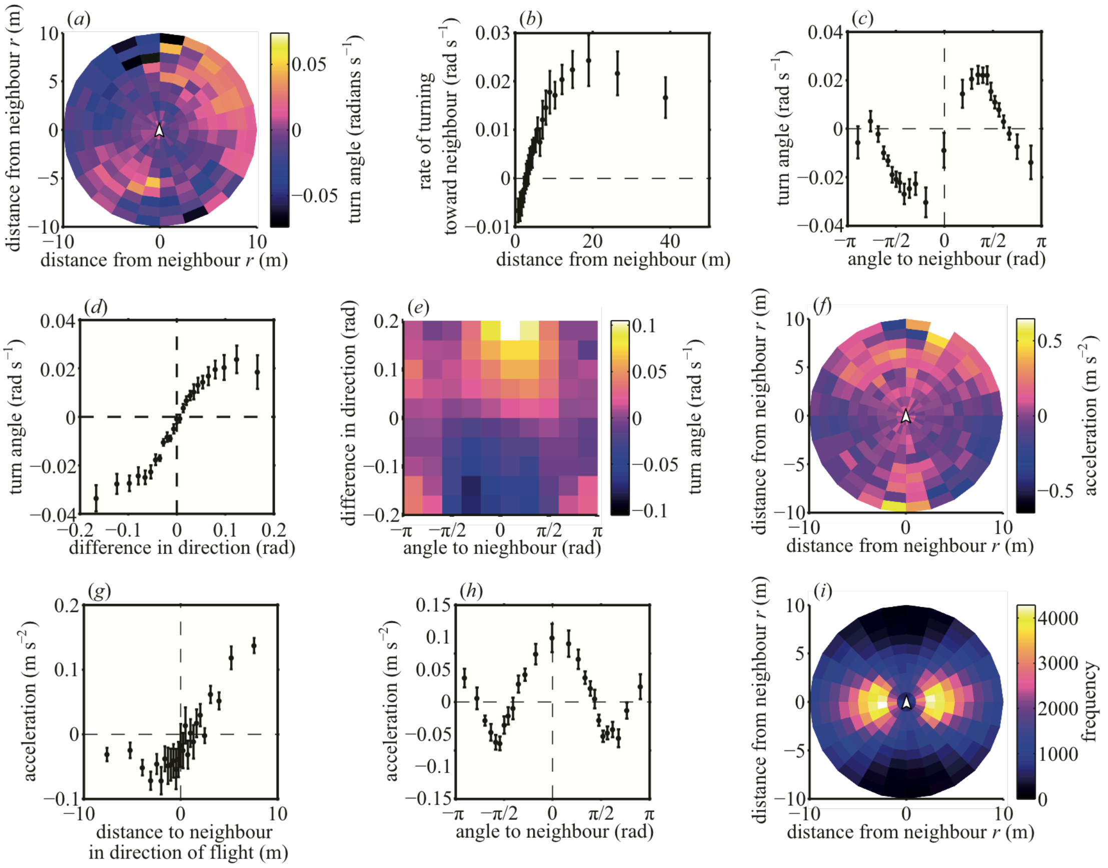

Figure 3: **'Rules' of flocking interaction.** (*a*) Average turning rate of the focal bird vs. the relative position of the neighbour. (In these plots, the focal bird is at the origin, facing up). As shown in *i*, some bins contain very few occurrences of the neighbour and are therefore more likely to assume extreme values. (*b*) Distance r to the neighbour vs. average rate of turning. (*c*) Angle θ to the neighbour vs. turning rate. Positive values of θ indicate that the neighbour is on the right side; positive values of the turning angle indicate a right turn. Only neighbours at distance $r > 3m$ were considered in the average. (*d*) Alignment response of the focal bird vs. difference of orientation to the neighbour φ. (*e*) Alignment response of the focal bird vs. angle to the neighbour θ and difference in orientation φ. (*f*) Average change of speed of the focal bird vs. the relative position of the neighbour. (*g*) Average change of speed vs. the projected front-back distance to the neighbour, $rcos\theta$. Positive or negative x-axis values indicate that the neighbour was respectively in front or behind the focal bird. (*h*) Average change of speed vs. angle θ to the neighbour. (*i*) Frequency of counts of the neighbour being in each particular bin of r and θ. Note that the bins are not of equal area. Error bars in *b, c, d, g,* and *h* show the standard deviations of bin-means from 500 bootstrap replicates, created by randomly sampling the 23 birds, with replacement.

3.3 Results

3.3.1 *Response to partner*

From the GPS tracks of paired flights, we calculated the distance (r), angular direction (θ), and relative orientation (φ) of the partner, and compared these to the focal bird's changes in speed and direction (see Methods 3.2.2 and figure 2). A pigeon tended to turn towards its neighbour when $r > 3m$ and away from its neighbour when $r < 3m$ (figure 3*a,b*). Turning was strongest when the neighbour was directly left or right of the focal bird (figure 3*c*). A pigeon's turn rate was positively correlated with φ (figure 3*d*), indicating alignment with the partner's direction. Rather than being mediated by attraction, this alignment response is in addition to the effect of the neighbour's position (figure 3*e*). Therefore the highest magnitudes of mean turn rate occurred when φ and θ had the same sign, in other words when the partner was on the left going left or on the right going right.

Changes in speed also mediate flocking. When the neighbour was more than 2m in front in the direction of travel, a pigeon tended to speed up, but otherwise tended to slow down (figure 3*f,g*). The acceleration, attraction, and alignment responses were forward biased, being absent or reversed in most of the range $|\theta| > \frac{3}{5}\pi$ (figure 3*a,c,e,f,g*). This forward bias is also prevalent in the fact that the rate of acceleration toward a neighbour in front is higher than the rate of deceleration toward a neighbour behind (figure 3*g*). Speeding attraction peaked when the neighbour was directly in front ($\theta = 0$), and turning attraction peaked near $\theta = \pm\frac{\pi}{3}$ (figure 3*c,h*). An immediate result of these various flocking responses was that pairs most frequently flew side by side (i.e. $\theta = \pm\frac{\pi}{2}$), approximately 3m apart (figure 3*i*). The pairs were also highly aligned in their flight directions, with median absolute difference in orientation of $|\varphi| = 0.053$ rad. Bootstrap standard errors (figure 3*b,c,d,g,h*) indicate that these responses are observed robustly across subjects.

3.3.2 *Response to established route*

In addition to the flocking interaction, we found that each bird was also attracted towards its preferred route. In some cases the pigeons flew down the established route of one of the birds, and in other cases they took compromise routes (figure 1). We calculated the percentage of time that the partner and the nearest point on the previous route were on opposite sides of the focal bird, combining data from both birds to give one data point per paired flight. These values had a mean (± s.d.) of $62.9 \pm 9.8\%$ and were significantly higher than the 50% occurrence expected by chance ($t_{79} = 11.8,\ p < 0.01$, 99% CI of 60.0 to 65.8%), which indicates that the pigeons' established routes affected their left-right positioning within the pair. It is further evidence that the birds flying in pairs continued to respond to landmarks along their previous solo routes. The partner and the preferred route are still on the same side a large portion of the time, which is expected given that the pairs did not always fly in between the two preferred routes, and portions of the paired flights have very little conflict of information (figure 1).

We quantified route attraction during solo flights, when there was no confounding influence of conspecifics. The intensity of turning in the direction of the previous solo route was maximized when the bird was ~ 212m from the nearest point on its previous route (figure S1). This shape of route response is probably because pigeons tolerate small perturbations within a route corridor but are increasingly motivated to return to the route after larger perturbations (Biro *et al.* 2004), counteracted by reduced visibility of landmarks over hundreds of metres. To avoid introducing extra parameters, we made the simplifying assumption that a pigeon is attracted to the nearest point on its preferred route, when in fact a pigeon displaced from its preferred route is more likely attracted to a point downstream, i.e. closer to home (Biro *et al.* 2004). Our approximation realistically captures the behaviour of a pigeon flying roughly parallel to its preferred route, first because attraction either to the nearest point or to a downstream point will generally require turning in the same direction, and second because repeatedly making small turns towards the nearest point will result in the bird re-joining downstream.

3.3.3 *Simulation model*

To test our understanding of how the birds interact with each other and their environment, we developed a self-propelled particle model based on the interaction rules inferred from figure 3. Our model builds on those by, for example, Vicsek *et al.* (1995) and Strömbom (2011) in which direction changes are mediated by the positions and directions of neighbours. In the model we now propose, we also incorporate the speed changes observed in the pigeons, rather than assuming constant speed. The model allowed us to test the sufficiency of the inferred rules for reproducing patterns of paired movement - both local flocking geometry as well as the decision-making properties of the pair when they had conflicting route information. Furthermore, we could use the model to test the effects of individual differences on the decision outcome, even if these individual characteristics were not directly manipulated in the experiment.

In the model, each bird turns in response to the neighbour's orientation and position and alters its speed to draw level with a neighbour in front or behind. Simulated birds only respond to a neighbour within a visual angle of $|\theta| < \frac{3}{5}\pi$. We define each simulated bird i in terms of its position $(x_i(t), y_i(t))$, direction $\alpha_i(t)$, and speed $s_i(t+1)$. Each bird has its own preferred route, which it will fly towards in the absence of a partner. To simulate a conflict of information, the two preferred routes are assumed to be straight lines that originate at the release point and continually diverge with an angle of $0.245\,rad$ (figure 4). On each time step Δt (corresponding to 0.2 s of real time) bird i changes its direction according to the sum of four separate response angles, i.e.

$$\alpha_i(t+1) = \alpha_i(t) + P_i(t) + O_i(t) + A_i(t) + E_i(t) \tag{3}$$

Each of these angles are small and represent the various forces acting on the bird. Below we provide details about the form of each of these components.

The preferred route response is given by

$$P_i(t) = \begin{cases} \lambda d_i(t) e^{-\frac{d_i(t)}{d_0}} & \text{if the established route is to the right of } i \\ -\lambda d_i(t) e^{-\frac{d_i(t)}{d_0}} & \text{if the established route is to the left of } i \end{cases} \tag{4}$$

where $d_i(t)$ is the distance to the closest point in the preferred route at time t and d_0 is the distance from the preferred route at which the attraction reaches its maximum. The parameter λ controls the amplitude of turning in the direction of the preferred route. The attraction response function in equation (4) had previously

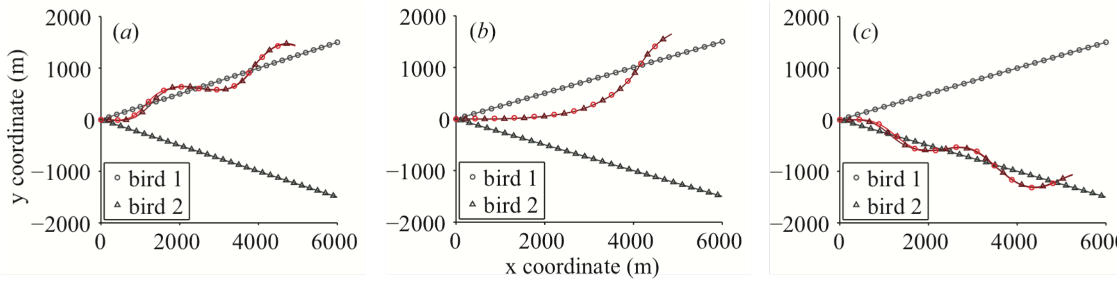

Figure 4: **Typical trajectories in separate runs of the simulation of two birds with different preferred speed.** Diverging straight lines: preferred routes; curved lines: paired flights. The preferred speed of bird 1 is $s_1^* = 20.66 m/s$, which is equivalent to the average speed in the experiments. The preferred speed of bird 2 is 19.72 m/s in (*a*), 20.62 m/s in (*b*) and 21.52 m/s in (*c*). The faster bird can effectively lead the pair towards its preferred route.

been proposed by Biro *et al.* (2006b), but not fitted to empirical data. We found a good correspondence between this function and data (figure S1), with fitted parameters $d_0 = 212m$ and $\lambda = 3.53\times10^{-4}\,rad/s$.

Alignment with the neighbour's direction of movement is given by

$$O_i(t) = a\tanh(\varphi_{\mathrm{i}}(t)a_{sl}), \tag{5}$$

where $\varphi_i(t) = \alpha_j(t) - \alpha_i(t)$ is the relative orientation of the neighbour at time t (figure 2). We use a sigmoidal function (here expressed by the hyperbolic tangent function tanh) to mediate the relation between φ and the turning angle, as suggested by the data in figure 3*d*. The slope of the sigmoid is controlled by the parameter $a_{sl} = 14.15$ and $a = 2.79\times10^{-2}\,rad$ is the asymptotic magnitude of the alignment term. Both the value of a_{sl} and a are obtained by fitting equation (5) to the empirical data of pigeons flying in pairs.

Attraction and repulsion to the neighbour are expressed as

$$A_i(t) = c\sin(\theta_i(t))\tanh\big((r_i(t) - r_0)r_{sl}\big). \tag{6}$$

Here, the angle $\theta_i(t) = \mathrm{atan2}\big(x_j(t) - x_i(t), y_j(t) - y_i(t)\big) - \alpha_i(t)$ gives the direction of the neighbour relative to the position and flight direction of the focal bird (figure 2). Since the focal individual turns away from very close neighbours and towards more distant neighbours (figure 3*b*), we use a sigmoidal function of distance to modulate the transition between repulsion and attraction. Specifically, $\tanh\big((r_i(t) - r_0)r_{sl}\big)$ is positive when the distance to the neighbour $r_i(t)$ is larger than the repulsion radius $r_0 = 2.92$ (the neighbour is in the attraction zone) and negative when $r_i(t) < r_0$ (repulsion at close range). The parameter $r_{sl} = 0.4$ determines how steep the transition is between attraction and repulsion, and $c = 2.63\times10^{-2}\,rad/s$ gives the magnitude of the attraction/repulsion response. Finally, the error term $E_i(t)$ is a normally distributed random variable with mean 0 and standard deviation σ_1.

After updating direction according to equation (3), the bird will move with speed

$$s_i(t+1) = Is_i(t) + (1-I)s_i^* + g\cos\theta_i(t) + e_i(t) \qquad (7)$$

where s_i^* is the preferred speed in the absence of interactions. Bird 1's preferred speed was set to the mean experimental value of $20.62 m/s$ and and bird 2's preferred speed was randomly chosen from the range $[19.62\ 21.62] m/s$. The parameter $I = 0.9944$ is a measure of inertia, $g = 2.08 \times 10^{-2}\ m/s$ is the strength of response to the position of the neighbour and $e_i(t)$ is a Gaussian distributed noise with mean 0 and standard deviation σ_2. This equation expresses the fact that birds speed up when their partner is in front and slow down when the partner is behind but, in the absence of interaction, they progressively revert to adopt their preferred cruise speed s^*.

The forms of equations ((4) - (7)) are summarized in figures S1 and S2. All parameter values were fitted from the empirical data, with the exception of the errors $\sigma_1 = 2.24 \times 10^{-2}\ rad/s$ and $\sigma_2 = 6.7 \times 10^{-3}\ m/s$ and the slope of the transition from repulsion to attraction r_{sl} (fitted value 0.166), which is related to variability in the repulsion radius. These differences are justified by the observation that a fraction of the measured variability was due to GPS noise and did not reflect real variability in the position and movement of the pigeons.

These simple rules reproduce qualitatively many of the observed features of interactions between real birds. In the simulations, as in the data, birds typically flew side by side (figure 5*i*). Some less intuitive aspects of the empirically observed interactions also appeared in the simulation output. In both the simulations and the empirical data, the focal bird turned away from its neighbour when the neighbour entered the blind angle (figure 5*a,c,e*, figure 3*a,c,e*). The simulation demonstrates that this behaviour can arise without any explicit avoidance response to a neighbour behind, and instead it is due to the higher relative influence of the preferred route once the neighbour enters the blind angle. In the empirical data, the focal bird also presented an acceleration response when the neighbour was directly behind (figure 3*f,h*), whereas there was no such acceleration in the simulation (figure 5*f,h*). This acceleration response might arise if real birds accelerate in response to the preferred route, something we did not implement in the simulation.

The other plots in figure 5 are qualitatively similar to the corresponding plots in figure 3. Most differences between the two figures stem from the fact that in the simulation the birds are always in a conflicting situation. For this reason, simulated birds are observed to turn away from neighbours positioned behind them with greater intensity than real birds. This higher level of conflict in the previous routes also decreases the total signal in figure 5*b*. Furthermore, the intensity of the responses observed from the simulation did not match the data exactly (e.g. figure 5*a,f* vs. figure 3*a,f*). Response intensity in the simulations could be manipulated by increasing or decreasing the noise parameter, but the sign of the response typically remained stable. For readers interested in testing combinations of parameters different from those reported in the figures, we make available a commented version of the Matlab simulation code as Electronic Supplementary Material.

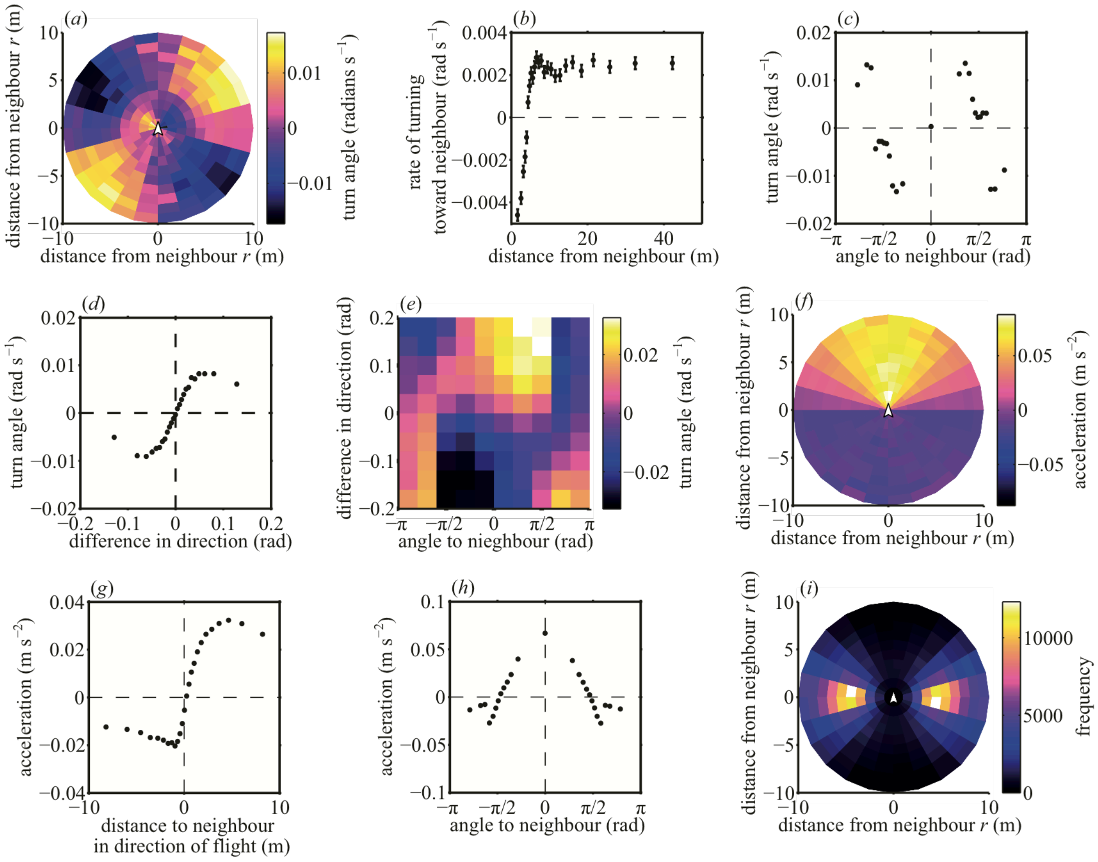

Figure 5: **'Rules' of flocking interaction apparent in the simulation output.** (*a*) Average turning rate of the focal bird vs. the relative position of the neighbour. (In these plots, the focal bird is at the origin, facing up). (*b*) Distance r to the neighbour vs. turning rate. (*c*) Angle θ to the neighbour vs. turning rate. Positive values of θ indicate that the neighbour is on the right side; positive values of the turning rate indicate a right turn. Only neighbours at distance $r > 3m$ were considered in the average. (*d*) Alignment response of the focal bird vs. difference of orientation to the neighbour φ. (*e*) Alignment response of the focal bird vs. angle to the neighbour θ and difference in orientation φ. (*f*) Average change of speed of the focal bird vs. relative position of the neighbour. (*g*) Average change of speed vs. distance to the neighbour projected onto the direction of travel, $r\cos\theta$. Positive or negative x-axis values indicate that the neighbour was respectively in front or behind the focal bird. (*h*) Average change of speed vs. angle θ to the neighbour. (*i*) Frequency of counts of the neighbour's occurrence in each particular bin of r and θ. Note that the bins are not of equal area. Error bars in *b, c, d, g,* and *h* (often smaller than symbol size) show standard errors based on the number of points in each bin.

3.3.4 *Leadership*

In the model, we assume that each bird has its own preferred speed of flight, with one bird slightly faster than the other. The two simulated birds converged on a common speed, but the bird with faster preferred speed was more frequently positioned in front (figure 6*a*). The model further predicts that, because alignment and attraction are forward biased (i.e. limited visual angle), the bird in front will have a disproportionate influence over directional decisions by the pair. We quantified leader-follower asymmetry using two metrics that reflect different scales of decision-making. On a small spatial and temporal scale, we quantified influence over momentary changes of direction using directional correlation delay (Nagy *et al.* 2010). In the simulations, the bird in front tended to initiate turns and was followed by its neighbour behind (figure 6*b*). On a more global scale, we tested which bird dominated the pair's choice of route. The simulated bird with the faster preferred speed consistently led the slower bird towards its preferred route, provided that the simulation included a blind angle (figure 6*c*, figure 4). In simulations without a blind angle, getting in front did not give a bird more influence, either measured using directional correlation delay (figure 6*d*) or from the global route decision (figure 6*c*).

These predictions are confirmed in the data. Because solo speed varies along the route (figure 1), we compared pair behaviour to nearby portions of solo track (see Methods 3.2.2). Out of the two birds in a pair, the bird with a faster local solo speed tended to be in front during paired flights (figure 6*e*, $p = 0.004$ from randomisation test). The bird in front also had a positive directional correlation delay time, indicating that it tended to lead momentary changes in direction (figure 6*f*). To establish which bird had more influence over route choice, we determined which solo route the pair moved toward, and which they moved away from, during the portions of track where the solo routes diverged (see Methods 3.2.2). The bird in front was significantly more likely to be successful in leading the pair towards its preferred route (slope from logistic regression of $r\cos\theta$ vs. route leadership, $\beta = -0.016$, mean ± s.d. of randomized $\beta = -3.2\times10^{-4} \pm 3.2\times10^{-3}$, $p < 0.001$). Local solo speed was positively correlated with route leadership, but not significantly (slope from logistic regression of difference in solo speed vs. leadership, $\beta = 0.039$, mean ± s.d. of randomized $\beta = 0.052 \pm 0.014$, $p = 0.34$). There was no significant effect of the variance among the five preceding solo routes (slope from logistic regression of variance $^{-2}$ vs. leadership: real $\beta = -8.9\times10^{-5}$, mean ± s.d. of randomized $\beta = 1.3\times10^{-4} \pm 2.9\times10^{-4}$, $p = 0.46$).

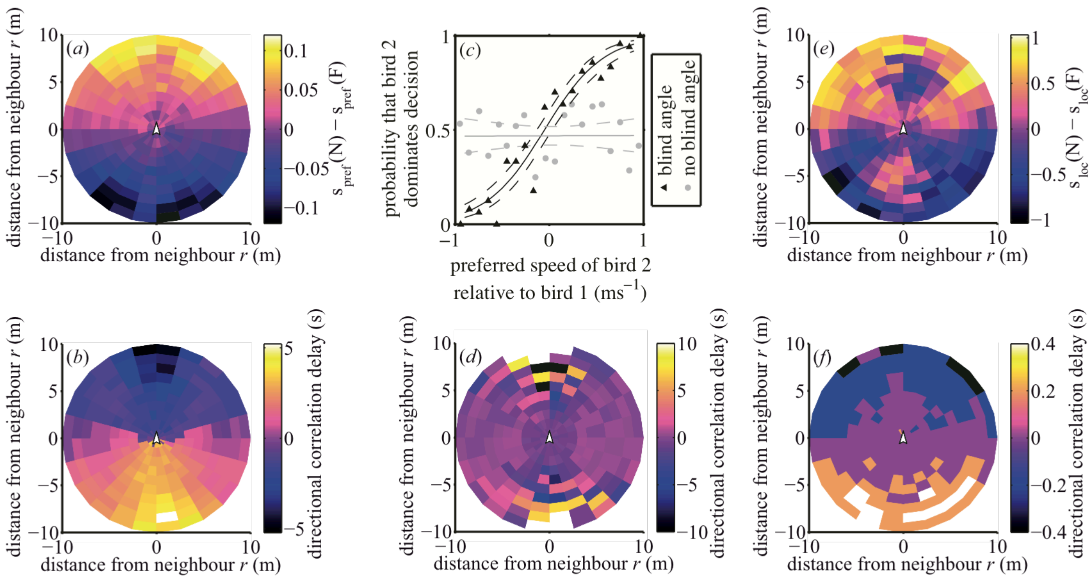

Figure 6: **Properties of pigeon movement visualized from the simulation (*a-d*) and the data (*e-f*).** (*a*) Difference between the preferred speed of a simulated bird and the preferred speed of the neighbour vs. the relative position of the neighbour, for simulations with a blind angle. Birds with faster preferred speed tend to position in front during the simulated paired flights. (*b*) Directional correlation delay vs. neighbour's relative position, for simulations with a blind angle. The bird in front usually changes direction first and the bird behind follows. (*c*) Route choice in simulations vs. the difference in preferred speed. A bird 'dominated' the route choice if the pair ended the simulation closer to that bird's preferred route. Symbols show proportion of simulations that bird 2 dominated, for each of 20 equally spaced bins. Fit lines show logistic regression (±95% C.I.) for simulations with a blind angle (black line, slope ± s.e. 3.21 ± 0.30, $N = 401$, $p < 0.001$) vs. no blind angle (grey line, slope ± s.e. 0.0062 ± 0.17, $N = 401$, $p = 0.97$). The faster bird is significantly more likely to dominate the decision, but only if there is a blind angle. (*d*) Directional correlation delay vs. the neighbour's relative position, for simulations without a blind angle. Leadership does not depend on position. (*e*) Difference between the 'local solo speed' of the focal bird (the average speed during nearby points on solo tracks, in m/s) and that of the neighbour, as a function of the relative position of the neighbour. Faster birds tended to position in front during the paired flights (slope from linear regression of difference in solo speed vs. $r\cos\theta$: real $\beta = -0.025$, mean ± s.d. of randomized $\beta = -5.4\times10^{-4} \pm 8.8\times10^{-3}$, $p = 0.004$). (*f*) Directional correlation delay times from empirical data vs. the neighbour's relative position. In *b*, *d*, and *f*, negative delay indicates that the focal bird adopts a particular direction after its partner, whereas positive delay indicates that the focal bird adopts a direction before its partner.

3.4 Discussion

With high resolution GPS tracking of co-navigating homing pigeons, we have characterized the momentary responses that form the basis of flocking behaviour. Our simulations based on these 'rules' of interaction are able to reproduce several key phenomena in the empirical data. Furthermore, we used a combination of data and simulation to investigate how individual differences affect the outcome of group decisions when there is a conflict of information between birds.

The attraction, alignment, and avoidance responses we observed support the assumptions of many SPP models (Couzin *et al.* 2005; Hemelrijk & Hildenbrandt 2012; Vicsek *et al.* 1995). The attraction response was sustained over a distance of at least 40m (figure 3*b*), which suggests that attraction does not have a short-range metric limit that would restrict interactions within large pigeon flocks. Instead, there might be a topological limit to interactions, as data on starling flocks suggest (Ballerini *et al.* 2008), which could be investigated in larger pigeon flocks. At very long range, there is likely to be a metric limit at which pigeons cannot easily see each other and therefore stop interacting (previously estimated at 200m (Biro *et al.* 2006b)). In addition, our data indicate an effective 'blind angle' for neighbours located behind. The blind angle should not necessarily be understood as a region in which visual or sensory perception is impossible, but simply that pigeons do not normally respond to conspecifics within this region.

In contrast to pairs of shoaling fish (Herbert-Read *et al.* 2011; Katz *et al.* 2011), pigeons displayed strong and explicit alignment behaviour. In other respects, the interaction rules of pigeons are broadly similar to those found in fish shoals as well as surface-swimming ducks (Lukeman *et al.* 2010). Our observation of a distance-dependent transition from avoidance to attraction is similar to findings of

Kattas *et al.* (2012), who also parameterized a model using data on pigeon flocks. However, Kattas *et al.* estimated the transition at a much larger radius ($\sim 20\mathrm{m}$) because they fit a response to the average position of multiple neighbours, regardless of distance, in flights when some pigeons had separated hundreds of metres from the rest of the flock. The contrasting results demonstrate the difficulty of inferring pairwise behaviour from data on larger groups, because collective behaviour underdetermines the pairwise interactions, i.e. many different models can produce similar collective behaviour (Lopez *et al.* 2012).

The pigeons most frequently flew side by side (figure 3*i*). This configuration has also been observed within large flocks of starlings, where each bird's nearest neighbour is most frequently positioned at $\theta = \pm\frac{\pi}{2}$ in the horizontal plane (Ballerini *et al.* 2008). Pigeons and starlings contrast with several fish species, which tend to have the nearest neighbour in the school directly in front or behind (Herbert-Read *et al.* 2011; Katz *et al.* 2011). We can explain the pigeons' spatial configuration mechanistically from the interaction rules we observed. Because repulsion is mediated by turning (figure 3*b*) and not by changes in speed (figure 3*g*), flying side by side is the only stable configuration in which neither bird adjusts its position with respect to the other (Hemelrijk & Hildenbrandt 2012). Fish, on the other hand, tend to avoid each other by changing speed, leading to an oblong school shape with fish travelling one behind the other (Hemelrijk *et al.* 2010; Herbert-Read *et al.* 2011). These differences in how pigeons and fish maintain distance from each other may be due to the biophysics of their locomotion. For a bird in flight, slowing down would reduce lift, so making small turns may be a more aerodynamic and energetically efficient way for a bird to maintain its position relative to its neighbours (Hemelrijk & Hildenbrandt 2012). Whereas flocking is energetically costly to pigeons (Usherwood *et al.* 2011), there are other bird species that benefit aerodynamically from flocking. It would therefore make an interesting comparison to measure the rules of motion that give rise to aerodynamically efficient, V-shaped flocks, such as those of geese or pelicans (Weimerskirch *et al.* 2001).

In addition to mechanistic reasons for a side-by-side configuration, there are several possible functional explanations. When flying side by side, neither pigeon is in the blind angle of the other, which will help maintain flock cohesion and the associated anti-predator benefits (Krause & Ruxton 2002). A bidirectional transfer of information between pigeons may also have navigational benefits. If birds attend to each other mutually, leadership remains dynamic in that it can shift according to which bird has the best local information. Such information-based leadership has already been demonstrated in SPP models (Couzin *et al.* 2005) and supported by experiments on homing pigeons (Flack *et al.* 2012). Our study goes further in discovering interaction rules that make information-based leadership more robust. The type of flocking interaction we found will destabilize a front-back configuration, making leadership less sensitive to initial conditions and allowing compromise routes that average individual preferences (Biro *et al.* 2006b; Dell'Ariccia *et al.* 2008). Our findings suggest a mechanism for the reciprocal relationships that Xu *et al.* (2012) found in pigeon flocks, but also demonstrate that compromise and leadership are not necessarily distinct strategies at the individual level. They can both arise from a single set of rules sensitive to the neighbour's position.

The flocking responses we have characterized provide a mechanism by which individual differences affect leadership through changing the spatial configuration of a flock. This is a topic that has previously been explored with SPP models (Conradt *et al.* 2009), but with little empirical data for comparison. In our study, leadership correlated with having a faster ground speed during solo flights. Our simulation shows that a speed difference alone is sufficient to cause one bird to lead. We found that a bird in front was more likely to have a positive directional correlation delay (figure 6*f*), a trend that was previously measured in larger pigeon flocks (Nagy *et al.* 2010), and which can now be explained in terms of interaction rules. Based on this remarkably simple mechanism, a gradient of individual differences through the population would be sufficient to produce the hierarchical leadership patterns seen in larger flocks (Nagy *et al.* 2010). However, that is not to say that speed is the sole cause of leadership in our study. High ground speed implies low tortuosity. These flight characteristics might correlate with homing motivation or navigational certainty. Previous studies of pigeons have implicated the latter as an important factor in leadership (Flack *et al.* 2012; Freeman *et al.* 2011). These other factors could either act on leadership directly, in the sense of ‘leading by need’, or they could act via increasing one bird’s speed. In either case the principle is similar: one bird accelerates in a particular direction and ‘pulls’ the other bird with it.

Our results and model provide a data-driven, mechanistic explanation of flocking and group decision-making. Rather than formulating an abstract model with as few parameters as possible, we fit our model to pigeon behaviour. In doing so we reveal important differences between the rules of motion in pigeon flocks vs. fish schools. The flocking responses in pigeons give rise to two opposing tendencies. Turning-based avoidance stabilizes a side-by-side configuration, which is optimal for information pooling and allows dynamic, fluctuating leadership. This is the opposite of what was found in, for example, mosquitofish, where collision avoidance was mediated mainly by speed changes, and the fish preferentially assumed a configuration of one behind the other (Herbert-Read *et al.* 2011). In addition to allowing a bidirectional transfer of information, flocking interactions in pigeons create a system that is sensitive to individual differences. If these differences are stable over time then one individual can maintain a forward position and have more influence over the group's direction. We therefore demonstrate how leadership emerges from simple, anonymous differences in the population. The next question in group navigation is to scale up the observations to more than two interacting birds.

Acknowledgments

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Data accessibility

GPS track data is available from the Dryad Digital Repository: doi:10.5061/dryad.3k31s.

Ethics statement

The protocols in this study were approved by the Ethical Review Committee of Oxford University's Department of Zoology.

Supplementary figures

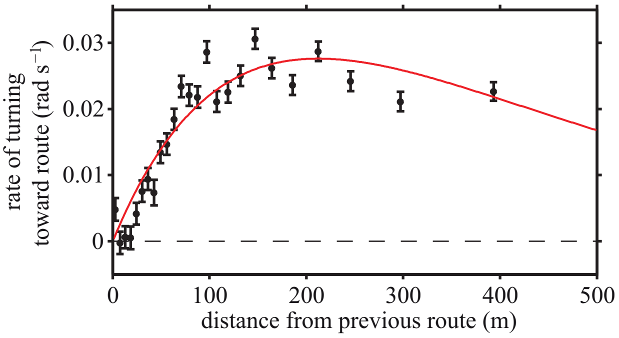

Figure S1: **Response to the established route.** Distance from the nearest point on the established route vs. the rate of turning towards the established route. Turning rates are measured during the 160 solo flights immediately preceding the paired flights, and for each pigeon we used its previous solo flight as the location of its established route. The circles show mean turn rates in 25 quantiles of distance, with error bars showing standard error. The red line shows a nonlinear function, fitted to all data points, in order to parameterize the route response used in the simulation (see Equation (4)).

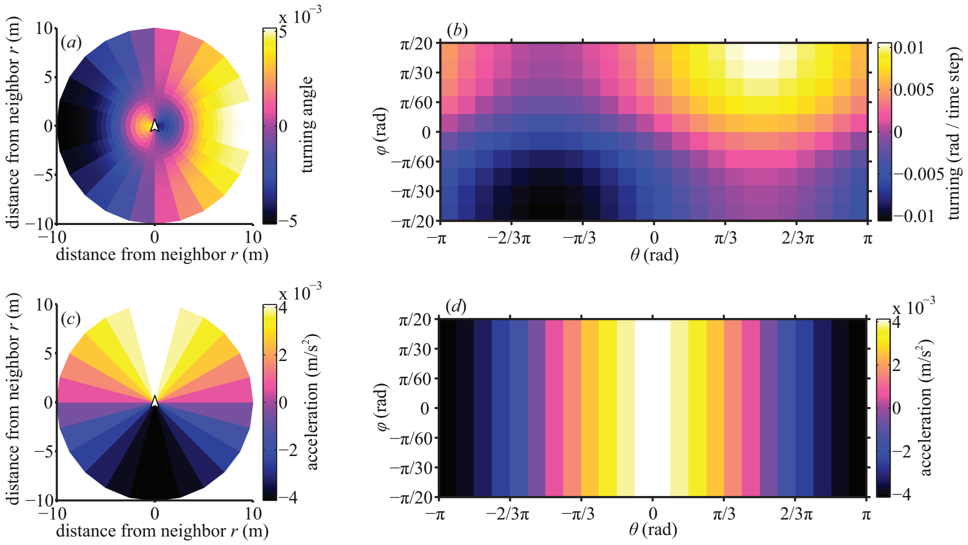

Figure S2: **Rules of interaction implemented in the simulation. (a)** Implemented turning rate of the focal bird vs. distance (r) and angle (θ) of the neighbour; (neighbour orientation $\varphi = 0$). **(b)** Implemented turning rate of the focal bird vs. angle to the neighbour θ and difference in orientation φ (neighbour distance $r = 10m$). **(c)** Implemented acceleration of the focal bird vs. distance (r) and angle (θ) of the neighbour; (current speed of the focal bird is equal to the preferred speed $s(t) = s^*$; neighbour orientation $\varphi = 0$). **(d)** Implemented acceleration of the focal bird vs. angle to the neighbour θ and difference in orientation φ (current speed of the focal bird is equal to the preferred speed $s(t) = s^*$; neighbour distance $r = 10m$).

Chapter 4: Faster pigeons lead flocks: comparison between solo homing behaviour and collective motion

Benj Pettit, Zsuzsa Akos, Tamas Vicsek, Dora Biro

Abstract

A key question in collective behaviour is how individual differences structure animal groups, affect the flow of information, and give some group members greater weight in decisions (Bode *et al.* 2011b; Burns *et al.* 2012; Conradt *et al.* 2009; Fischhoff *et al.* 2007; Flack *et al.* 2012; Nagy *et al.* 2010; Nakayama *et al.* 2012; Rands *et al.* 2003). Depending on what factors contribute to leadership, it could either improve decision accuracy or interfere with swarm intelligence (King *et al.* 2012; Krause *et al.* 2010). We need to identify how leadership arises from individual differences in order to understand its functional significance. In four flocks of ten pigeons, we compared pigeons' relative influence over flock direction to their solo

flight characteristics. We repeated the experiment from three homing sites, and found individual consistency in leadership across sites. Leadership was predicted by previous solo speed, but not by how straight solo routes had been. After the flock homing flights, leaders had learned more efficient homing routes than the followers, perhaps because they attended more to the landscape or were more motivated to get home. Our results point to a simple explanation for previously observed leadership hierarchies, arising from birds' typical speeds, which may in turn be due to motivation.

4.1 Introduction

Combining information from many individuals will often improve the accuracy of collective decisions (Krause *et al.* 2010; Simons 2004). As humans, we usually rely on centralized systems for aggregating votes, guesses, or bids. Information can also be aggregated using distributed, self-organized mechanisms, as demonstrated by ant colonies, honeybee swarms, and fish schools (Miller *et al.* 2013; Pratt *et al.* 2002; Seeley & Buhrman 1999). Information-pooling mechanisms are especially well understood from simulations, which demonstrate, for example, the effective averaging of time preferences (Conradt & Roper 2003) or directional preferences (Couzin *et al.* 2005) through local interactions. However, arithmetically-perfect averaging relies on each animal having the same influence, and simulations have also uncovered a wide range of factors that give some individuals greater weight in group decisions, including motivation (Conradt *et al.* 2009; Rands *et al.* 2003), social indifference (Conradt *et al.* 2009), spatial position within the group (Bode *et al.* 2012; Pettit *et al.* 2013b, Chapter 3), and position in the underlying affiliation network (Bode *et al.* 2011b; Sueur *et al.* 2012).

Real animal groups are never as homogeneous as is possible in models, and furthermore research on behavioural syndromes/personality shows that many individual differences persist over time (Sih *et al.* 2004), so any effects on leadership would not average to zero over repeated collective movements. Indeed, several empirical studies of group movements have found that some individuals consistently have greater influence over group decisions, which we will call ‘leadership’ (Burns *et al.* 2012; Nagy *et al.* 2010; Šárová *et al.* 2010). These observations raise questions concerning which characteristics give an animal more or less influence, what the mechanisms are by which leadership operates, how much influence leaders actually have, and how leadership affects individual fitness. If leading or following affect learning, energy expenditure, predation risk, collective intelligence, or the overall benefits of group membership, then there will be feedbacks on individual behaviour over evolutionary and/or behavioural timescales (Johnstone & Manica 2011).

Navigation and orientation are contexts in which we might expect collective intelligence in the wild, whether for long distance migration or daily foraging trips (Simons 2004). A wide range of bird species potentially gain informational benefits by travelling in flocks, either by pooling information from a large number of individuals (Beauchamp 2011; Simons 2004) or by following the most experienced group members (Flack *et al.* 2012; Mueller *et al.* 2013). Homing pigeons allow us to study how individual differences structure moving animal groups and affect information transfer in a field setting. They naturally prefer to fly in flocks, they can be tracked with GPS in high resolution, and their individual navigation and spatial learning have been extensively studied. Analysis of pairwise time delays has revealed hierarchical leader-follower relationships in flocks of up to 30 pigeons (Flack *et al.* 2013a; Nagy *et al.* 2013, 2010). This type of leadership is consistent over time but independent of social dominance (Nagy *et al.* 2013). One expectation from theory is that leadership will be based on knowledge, in other words flocks will follow whichever individuals best know the way (Couzin *et al.* 2005; Guttal & Couzin 2010). Knowledge-based leadership is relevant to understanding migratory behaviour of many species, for example it would explain why the straightness of whooping crane migration routes correlates with the age of the oldest flock member (Mueller *et al.* 2013).

In the current study, we test whether a pigeon's degree of leadership correlates with its solo homing efficiency. 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 (Flack *et al.* 2012), but it is not known whether efficiency structures leadership in larger flocks, or in cases where differences in experience are less pronounced. Nagy *et al.* (2010) found a positive correlation between solo homing efficiency and leadership, but their study lacked the statistical power to adequately test this hypothesis because it only compared seven pigeons. In a more recent study, giving selected pigeons in a flock additional homing experience did not significantly alter leadership relations, despite the fact that their homing efficiencies had improved (Flack *et al.* 2013a).

Whether or not leadership is based on knowledge, a bird's influence will also depend on its spatial position in the flock. Because flocking responses are forward biased, a faster bird that gets in front will have more influence (Pettit *et al.* 2013b, Chapter 3). Therefore consistent differences in flight speed could also give rise to stable leadership relations. This mechanism has support from a study of co-navigating pairs (Pettit *et al.* 2013b, Chapter 3), and it might also explain the hierarchies observed in larger groups.

We compare leadership, efficiency, and speed in flocks of ten homing pigeons, using four replicate flocks, each tested at three release sites. This design allows us to test whether the leadership hierarchy reorganizes when birds learn new information at a new site. At each site we released the pigeons singly at first, and then over the course of four flock homing flights we quantified leadership using the sub-second time delays between birds adopting a new direction (Nagy *et al.* 2010). We test whether leadership is 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 or speed was related to leadership. The results will bring us closer to understanding how individual differences structure flocks and affect information transfer in a field setting, and whether leaders and followers differ in how well they learn orientation cues.

4.2 Methods

4.2.1 *Experiment*

This study involved 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 (labelled 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 centred 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 previous experience was from different release sites to those used here (minimum distance 1.8 km between sites), this experiment was still very much a test of orientation within the familiar area.

The procedure at each site 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). We took pigeons to the release sites in aluminium boxes in a car with windows open for access to airborne odours. The sun was visible during all releases. For each round of solo releases, the ten pigeons in a group were released on the same day and in a random order.

We tracked all homing flights using custom made GPS devices with a log rate of 10Hz (Flack *et al.* 2013a; see Nagy *et al.* 2013). 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 analysed 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 (Nagy *et al.* 2013, 2010).

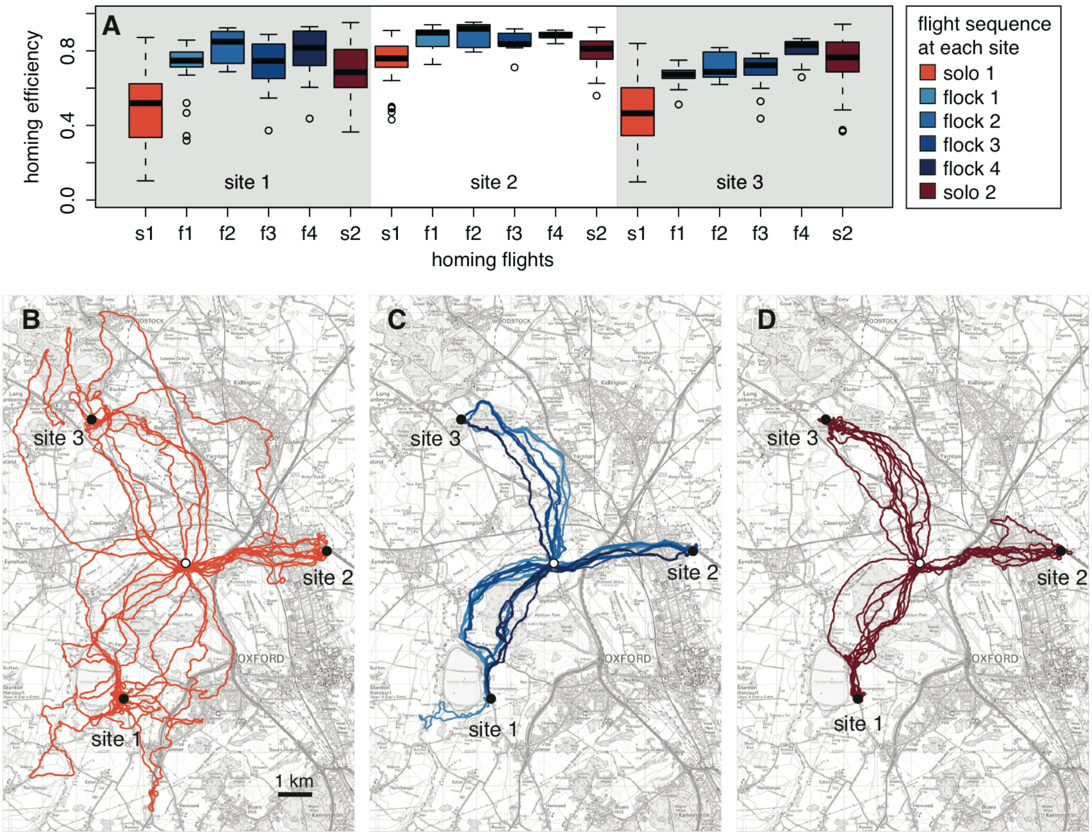

Figure 1. GPS tracks and homing efficiency for solo and flock flights. (A) Homing efficiency of all pigeons across their 18 flights, in time order. Box plots are coloured according to the flight sequence within each site. Points are shown as outliers if they are below the lower quartile by at least 1.5 times the interquartile range. **(B-D)** GPS tracks from one of the four subject groups, with the same colour 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. Maps Crown copyright Ordnance Survey. All rights reserved.

4.2.2 *Analysis*

We converted latitude and longitude to flat-earth coordinates using Universal Transverse Mercator projection. We estimated the ground speed using the distance between successive GPS fixes. To filter out portions of track when the pigeons had landed, we kept points where the speed was continuously above 2 ms^{-1} either for

10s before the point or for 10s after the point. We defined homing efficiency as the straight-line distance between start and finish, divided by the distance travelled (Biro *et al.* 2006; Dell'Ariccia *et al.* 2009, 2008). To focus on the homeward portion of the flight and exclude circling at the start and on arrival, homing efficiency was calculated using the portion of the track more than 100m from the release site and the loft. We summarized a track's ground speed using the median from this portion of the track.

We calculated leadership rank during flock flights using a directional correlation delay method based on Nagy *et al.* (2010), which has also been applied to starling flocks and fish schools (Herbert-Read *et al.* 2011; Katz *et al.* 2011). We first smoothed the tracks using a Gaussian filter with $\sigma = 0.2$ s and a window of $t \pm 3\sigma$, in order to capture changes in direction that persisted over multiple measurements and were less likely to be GPS noise. For each pair of birds (i, j), we found their directional correlation as a function of the time delay between velocity measurements, $C_{ij}(\tau) = \boldsymbol{v_i}(t) \cdot \boldsymbol{v_j}(t + \tau)$, where $\boldsymbol{v_i}$ and $\boldsymbol{v_j}$ are unit vectors in the birds' directions of travel. The value of tau, ${\tau_{ij}}^*$, that maximizes $C_{ij}(\tau)$ over all t indicates the typical delay between birds i and j adopting the same flight direction (figure S1). If ${\tau_{ij}}^* > 0$, i tends to turn first, followed by j, and *vice versa* if ${\tau_{ij}}^* < 0$. We only included time steps when i and j were within 50m of each other. If a bird split from the rest of the flock such that there was less than 60 s of data for calculating ${\tau_{ij}}^*$, we removed that GPS track from further analysis (8 cases).

To summarize a bird's leadership within a flock, we created a combined correlation function, $C_i(\tau)$, which was the average of pairwise $C_{ij}(\tau)$ functions across all other birds j, weighted according to the number of time steps used to calculate $C_{ij}(\tau)$ (black lines in figure S1). The time delay that maximizes this combined function, $\bar{\tau}_i{}^*$, is less susceptible to outliers than simply taking the mean of $\tau_{ij}{}^*$ values. In order to more accurately estimate $\bar{\tau}_i{}^*$, given the relatively coarse time sampling, we fit a quadratic function to $C_{ij}(\tau)$. To summarize each bird's leadership for a site, we took the mean of the $\bar{\tau}_i{}^*$ values from the four flights, weighted by the number of time steps used to calculate each $\bar{\tau}_i{}^*$. 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.* (2010).

Our general statistical approach was to fit linear mixed models (LMMs) using the *lme4* package in R (Bates *et al.* 2013; R Core Team 2011). 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 (Nakagawa & Schielzeth 2010), 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 *site* as a random effect (or *flight*, if examining consistency of leadership within a site, 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 $r_{\text{rand}} < r$.

4.3 Results

4.3.1 *Leadership*

We quantified leadership as the time delay that maximized a bird's directional correlation with the rest of the flock (figure S1). We found moderate but significant individual consistency in leader/follower behaviour across the three sites ($r = 0.35$) and across the four flock flights within each site ($r = 0.25$ to 0.30, table 1). Given this consistency, we averaged $\bar{\tau}_i^*$ across sites to get a mean measure of leadership for each bird.

We compared leadership to solo efficiency and speed using three LMMs with *group* as a random factor affecting slopes and intercepts. The first model compared

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). After calculating r, we tested effects of age and breeding status by adding these additional factors to the same LMMs. *significance at $\alpha = 0.00625$ (Bonferroni-adjusted threshold for 8 separate models).

response	**random effects**	r		**age effect**		**breeding effect**	
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	-0.13	0.023	-0.03	0.883
solo 1 efficiency	bird, site	0.15	0.124	-0.01	0.569	0.01	0.832
solo 2 efficiency	bird, site	0.43*	$< 10^{-4}$	-0.02	0.030	0.04	0.175
solo 1 speed	bird, site	0.67*	$< 10^{-4}$	-0.43*	0.002	0.26	0.615
solo 2 speed	bird, site	0.46*	$< 10^{-4}$	-0.33*	0.002	0.53	0.182

flock leadership to the preceding solo flight. The pigeons that had been faster on their own tended to lead flock flights, but there was no relationship with previous homing efficiency (figure 2A-B). The second model predicted the efficiency of solo flight 2 (after flock flights) from leadership and initial solo efficiency. Leadership was associated with having more efficient homing routes on subsequent solo flights from the same site (figure 2C,E). In other words, leaders did not necessarily start with efficient homing routes, but improved more than followers. The third model predicted the speed of solo flight 2. After accounting for initial solo speed, ground speed in the second solo flight was unaffected by leadership (figure 2D,F).

Leaders tended to fly more toward 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 speed and was predictive of a bird's solo homing efficiency after the flock flights (figure S2).

4.3.2 *Homing efficiency*

To analyse changes in efficiency across flights, we used the mean efficiency from within each group of 10 because their efficiencies were not independent when they flew in flocks. We then 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 between flight-categories using Tukey post-hoc tests in the *multcomp* R package (Hothorn *et al.* 2008).

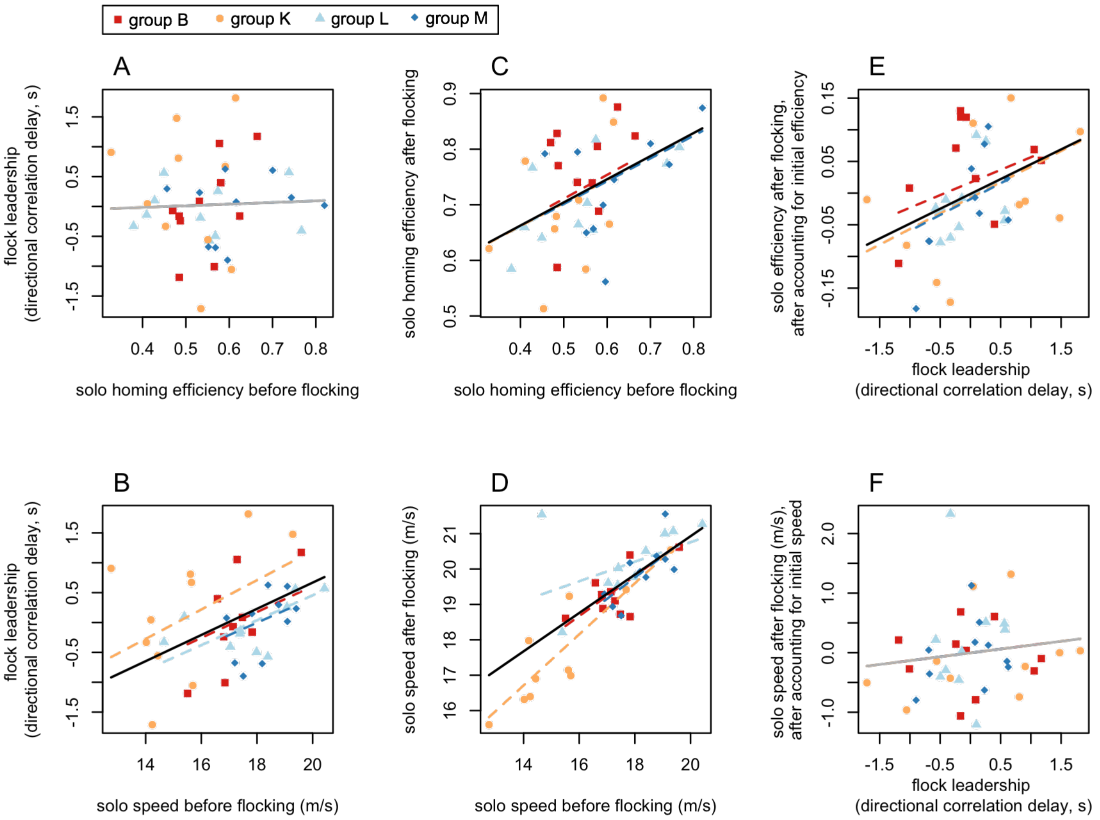

Figure 2. Flock leadership compared to solo homing efficiency and speed. Plots show the mean value for each bird, with different symbols for the four replicate groups. Fit lines are from an LMM with group as a random factor. The estimated regression for the fixed effect is shown in black, or grey if non-significant, as judged from 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. **(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 efficiency after flock flights, compared to solo efficiency 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.

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 ± s.d.), which represents a mean reduction in distance flown of 23% (figure 1A, table 2). In addition to being relatively inefficient, the initial solo routes 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 (table 1). Solo ground speed also had significant within-bird consistency across sites, in both the first solo flight and the second solo flight from each site.

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). Across the four flock flights, there was a slight but non-significant increase in homing efficiency (LMM with *group* and *site* as random factors: flight order effect 0.016, 95% high probability density interval of [-0.001,0.034], *p*MCMC = 0.0618 from a significance

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**	
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

test using 10^4 Markov Chain Monte Carlo samples (Baayen 2011; Bates *et al.* 2013)). There were also significant site-level effects on homing efficiency: in the model of flock efficiency above and in both efficiency models in table 2, including site effects lowered AIC and significantly improved the model according to a likelihood ratio test. The highest homing efficiency was at site 2 (figure 1), which suggests site-specific effects rather than a continuous improvement over the course of the experiment.

4.3.3 *Effects of age and breeding status*

To give a clearer understanding of the underlying individual differences affecting the flight variables above, we tested for effects of age and breeding status. Age (rounded to the nearest year) ranged from 2 to 8 years. Younger pigeons were significantly faster during solo flights (table 1). We classified pigeons as breeding if they had eggs or chicks at any point in the experiment (22 out of 40 subjects). Speed, leadership, and efficiency did not differ between breeders and non-breeders (table 1).

4.4 Discussion

Our results demonstrate how leader/follower relationships in flocks of pigeons relate to individual differences in homing flight characteristics, as measured when the birds flew alone. Faster pigeons tended to have greater influence over a flock's changes of direction. Leaders, in turn, had more efficient routes than followers when tested on their own after flocking, even if they had not started with the most efficient routes from that release site.

The speed/leadership correlation agrees with earlier data on pairs and is what we would expect from simulations based on observed flocking interactions

(Pettit *et al.* 2013b, Chapter 3). Because pigeons attend more to conspecifics in front than behind, faster birds that consistently get in front will have more influence. This mechanism does not mean all leadership is due to speed differences. Other factors, for example large differences in experience (Conradt *et al.* 2009; Couzin *et al.* 2005; Flack *et al.* 2012), could still influence flock leadership. Nonetheless, consistent individual differences in speed provide a plausible explanation for the component of leadership that is stable over time (Flack *et al.* 2013a; Nagy *et al.* 2010), is similar on homing flights and when flying freely around the home loft (Nagy *et al.* 2010), and is unaffected by moderate differences in local experience (Flack *et al.* 2013a).

A role of speed in the organization of flocks raises the question of what makes a pigeon faster. Speed is likely to be influenced by morphological factors such as wing dimensions, body mass, and musculature (Tobalske *et al.* 2003), and our finding that younger pigeons were faster might be explained by their physical condition. There is also evidence that homing motivation increases speed without affecting the straightness of routes (Dell'Ariccia *et al.* 2009). Further research on the causes of speed variation will indicate, in turn, whether leadership hierarchies improve group decision-making.

Birds toward the front of a flock had more positive directional correlation delay values, as found previously in flocks of a similar size (Nagy *et al.* 2010). Occupying a front position is not necessarily equivalent to leadership, but there are a range of species in which the two do correlate, including several species of fish (Bumann & Krause 1993; Burns *et al.* 2012; Herbert-Read *et al.* 2011; Katz *et al.* 2011). In principle, the causal link between leadership and position could be in either direction. If there is forward bias in the sensory basis of the interaction rules, animals positioned toward the front will have more influence (Pettit *et al.* 2013b, Chapter 3). Equally, leaders will tend to sort to the front because they take more direct paths than followers (Couzin *et al.* 2002). Both of these mechanisms have support from models of collective motion. It is possible that both are at work within pigeon flocks, creating positive feedback between position and influence.

At each new site, pigeons started with relatively inefficient routes and improved with repeated flights, a pattern that has also been found at further homing distances in previous studies (Flack *et al.* 2012; Meade *et al.* 2005). Despite the short homing distances of 4 to 5 km, pigeons had considerable capacity to improve their routes through learning. The improved efficiency was not transferrable to the next site, probably because the pigeons learned site-specific homeward compass bearings or local visual cues (Wallraff 2005).

Across the three sites, birds were consistent in their homing efficiencies on flight 6 (the second solo flight), despite the variability during flight 1. In other words, the learning process of each pigeon plays out similarly at different sites. More effective learning correlated with leadership, and there are several possible explanations for this finding. The first is that followers learn more slowly than leaders because they attend more to conspecifics and less to environmental cues such as landmarks. Previous work investigated this potential effect using pairs of pigeons and found that following a conspecific, *vs.* flying alone, made no difference to the efficiency of learned routes (Pettit *et al.* 2013a, Chapter 2). However, that study gave followers 12 flights to learn an efficient route, compared to only four in this experiment. Also, following a large group might have a different effect on learning than following a single individual.

A second possibility is that some pigeons consistently learn quickly, so that early on in the series of flock flights they become more certain about which direction to take, which then gives them more influence. However, previous studies only found effects of experience on leadership in flocks with much larger differences in local experience, for example when one pigeon had been on at least 8 more homing flights than another (Flack *et al.* 2013a, 2012). A third possibility is that leadership and spatial learning are both affected by a third factor. For example, if some pigeons have higher homing motivation, that might be an underlying cause of speed, leadership, and rate of learning, since their motivational states confer higher value to getting home (Dickinson & Balleine 1994). These three explanations are not mutually exclusive.

Our results provide further evidence of robust hierarchical patterns of leadership in pigeon flocks (Biro *et al.* 2006b; Flack *et al.* 2013a; Nagy *et al.* 2013, 2010), but also raise the possibility that these hierarchies arise from a simple anonymous, self-organising mechanism related to individual differences in typical flight speed (Pettit *et al.* 2013b, Chapter 3). Although a flock's homing efficiency would probably benefit from following the straightest homer, there are clearer mechanisms by which speed and motivation give a bird greater influence (Conradt *et al.* 2009; Pettit *et al.* 2013b, Chapter 3). Motivation towards resources has been previously identified as a factor affecting leadership in fish shoals and zebra herds (Fischhoff *et al.* 2007; Nakayama *et al.* 2012), as well as in self-propelled particle models (Conradt *et al.* 2009).

Even though we found no evidence that flocks followed the best navigator, pigeons still flew straighter routes in flocks than when alone. This improvement does not imply knowledge-based leadership, because it could arise from information pooling (Simons 2004). We are only beginning to understand the causes and consequences of persistent tendencies to lead or follow. Stable leader/follower roles, initially due to speed and motivation, might affect spatial learning and further reinforce a particular flow of information through the flock. There are still open questions concerning how much influence a single leader has over the flock's choice of route and whether leadership hierarchies enhance or reduce the collective navigational ability of a flock.

Supplementary Figures

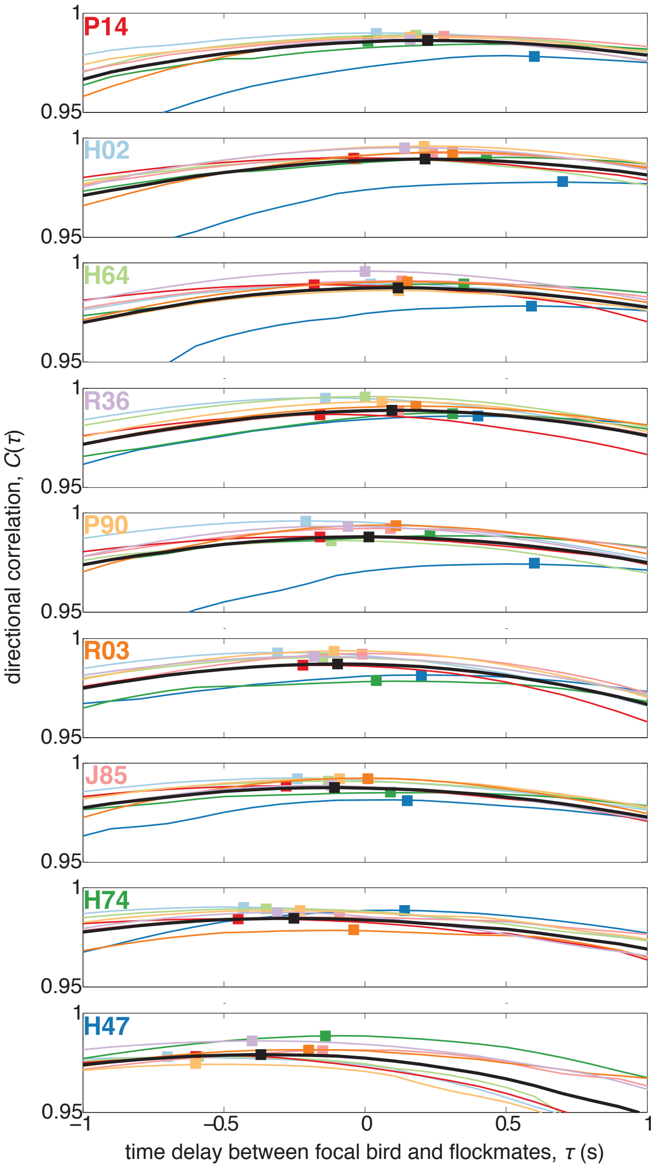

Figure S1. Leadership analysis. Each panel shows a focal bird's directional correlation with the rest of the flock as a function of time delay, τ, for one flock homing flight. The birds are ordered from leading (top) to following (bottom). Each bird is shown in a different colour, indicated by the label in its own panel. Coloured lines show $C_{ij}(\tau)$, the correlation with flockmate j. Black lines show $C_i(\tau)$, the duration-weighted average of the coloured lines. Using quadratic interpolation we found the time delay, τ^*, that maximized correlation. The values of τ_{ij}^* (coloured squares) quantify pairwise leader/follower behaviour; $\bar{\tau}_i^*$ (black squares) quantify overall leadership with respect to the rest of the flock. Data shown correspond to site 1, flight 1 in figure 1C. For this flight we only analysed leadership for nine birds, because the tenth split from the rest of the flock within 30 s of being released.

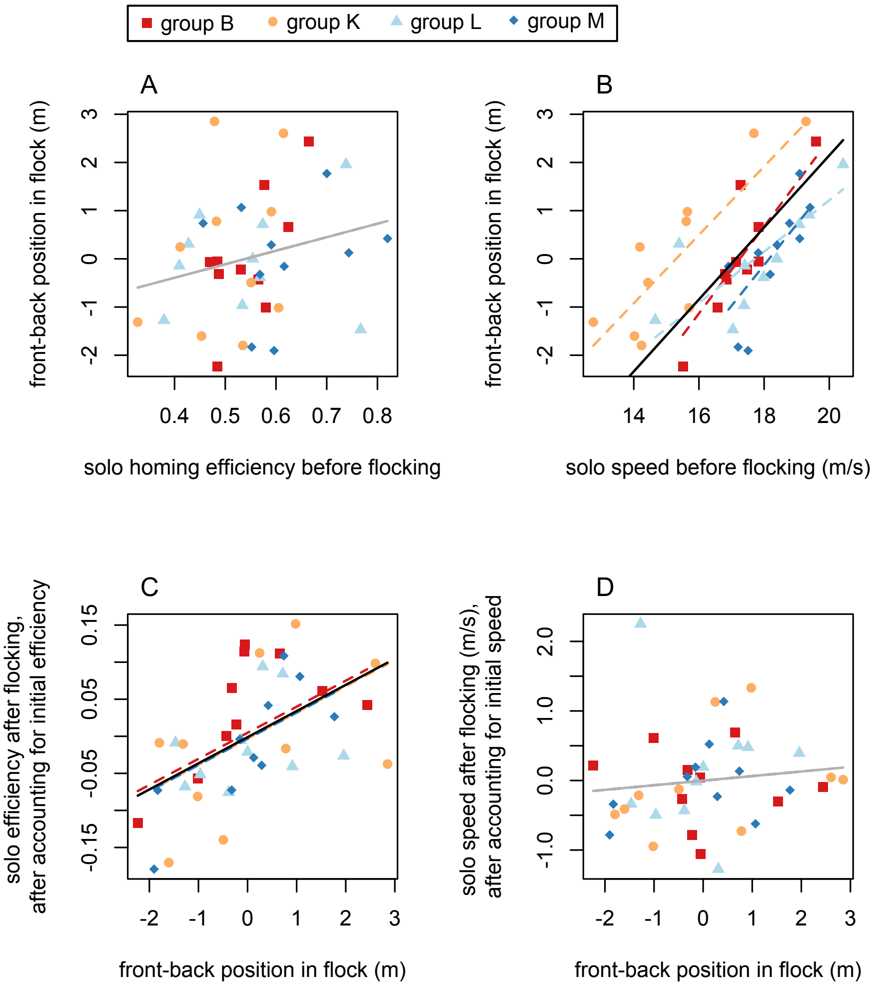

Figure S2. Front-back position in flock compared to solo homing efficiency and speed. Plots show the mean value for each bird, with different symbols for the four replicate groups. Fit lines are from an LMM with group as a random factor. The estimated regression for the fixed effect is shown in black, or grey if non-significant, as judged from likelihood ratio test comparing models with or without that fixed effect ($\alpha = 0.05$). Dashed coloured lines show random effects of group on slope and intercept. **(A-B)** Position in flock ($\bar{d_i}$) is predicted by a bird's previous solo speed but not by previous homing efficiency (slope ± SE for speed effect in minimum adequate model: 0.70 ± 0.11). **(C)** The residuals from figure 2C plotted against position in flock, showing the additional effect of position on subsequent homing efficiency. $\bar{d_i}$ slope ± SE = 0.038 ± 0.009; *p* = 0.004. **(D)** The residuals from figure 2D plotted against flock position in flock. $\bar{d_i}$ slope ± SE = 0.14 ± 0.14; *p* = 0.39.

Chapter 5: Bayesian estimation rule captures how flocking responses scale with group size

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Abstract

Models of collective motion have been successful at reproducing many features of flocking, schooling, and swarming behaviour seen in nature. However, because different interaction rules in models can produce similar collective outcomes, finding out how animals in swarms actually behave requires detailed data on tracked individuals. With new GPS data on flocks of two to five birds, we tested how pigeons combine information from multiple neighbours. We found that averaging the expected pairwise responses underestimates responses within larger flocks. Instead, the observed flocking behaviour is what we would expect if a pigeon

responds in proportion to its certainty about which direction is ‘good’, which increases with the number of flockmates going in one direction. A model based on Bayesian estimation accurately captures a pigeon’s increasing strength of alignment as the number of flockmates increases. This type of model has already proved versatile in explaining collective behaviour of ants and fish. We show how collective motion can be explained as a series of left/right decisions that make use of others’ behaviour to estimate the best direction.

5.1 Introduction

How much to copy the choices of others is a crucial factor in collective decisions, defining the line between swarm intelligence and cascades of misinformation (Giraldeau *et al.* 2002; Pratt *et al.* 2002). At an individual level, the optimal strategy for following others involves a trade-off between the benefits of group cohesion and of acting on personal information. Adopting the same behaviour as conspecifics (e.g. feeding at the same time, travelling in the same direction) has several advantages, which either arise directly from cohesion (e.g. dilution of predation risk (Ioannou *et al.* 2012; Krause & Ruxton 2002)) or from the fact that others have useful information about the environment (e.g. predation risk, food quality, navigational cues (Flack *et al.* 2012; Valone & Templeton 2002; Ward *et al.* 2011)). On the other hand, conforming too strongly causes one’s own interests and information to be absent from the group decision (Conradt *et al.* 2009; Giraldeau *et al.* 2002). Even where group members’ interests are aligned, as in house-hunting swarms of ants and honeybees (Pratt *et al.* 2002; Seeley & Buhrman 1999), individual decisions strike a balance between following social information and independent exploration of the environment. In the social insect case this reduces positive feedback on whichever nest site is first discovered.

Experiments in group decision-making and social facilitation have demonstrated that responses often increase with the number of conspecifics adopting a particular behaviour (Arganda *et al.* 2012; Gautrais *et al.* 2007; Milgram *et al.* 1969; Pratt *et al.* 2002; Ward *et al.* 2008). In some cases the experimenter can manipulate the subjects' social environment, for example with 'stimulus shoals' of fish (e.g. Arganda *et al.* 2012), with robots (Faria *et al.* 2010; Halloy *et al.* 2007), or with secret collaborators in human crowd experiments (Milgram *et al.* 1969). Even without manipulation, if members of a group decide sequentially between discrete options, individual behaviour can be interpreted based on the numbers that have already chosen each option (Gautrais *et al.* 2007; Miller *et al.* 2013). With this level of detail on individual behaviour and the social environment, it is possible to fit models that explain the group outcomes in terms of individual decisions. For example, a recent model based on Bayesian estimation and probability matching has proved versatile for explaining individual decisions within groups of zebrafish, three-spined sticklebacks, and Argentine ants (Arganda *et al.* 2012; Perez-Escudero & de Polavieja 2011).

Compared to sequential choices, the collective motion of free-moving animals is a much more complex scenario, where many simultaneous interactions can make it difficult to tell what social cues each animal is using. One approach has been to find interaction rules that reproduce group-level behaviour when implemented as self-propelled particle simulations (Couzin *et al.* 2002; Reynolds 1987; Vicsek *et al.* 1995). Group-level behaviours studied in this way include group cohesion, phase transitions (Buhl *et al.* 2006), rotating mills (Bazazi *et al.* 2012; Couzin *et al.* 2002; Strömbom 2011; Tunstrøm *et al.* 2013), lane formation (Moussaïd *et al.* 2012), and propagating waves (Procaccini *et al.* 2011). A typical set of interaction rules are attraction, alignment, and repulsion, each applied to a local subset of the flock, for example within distance-based zones (Couzin *et al.* 2002; Vicsek *et al.* 1995). Even if these are not necessarily the real rules animals use, they provide hypotheses to test against the high-resolution tracking data now available on a variety of species.

A more directly data-driven approach is to infer interactions from the motion of tracked individuals (Herbert-Read *et al.* 2011; Katz *et al.* 2011; Lukeman *et al.* 2010; Mann *et al.* 2013; Pettit *et al.* 2013b, Chapter 3). Inferring the response to a single neighbour is relatively straightforward, but raises the question of how to extrapolate the expected response from one neighbour to several (Herbert-Read *et al.* 2011; Katz *et al.* 2011; Pettit *et al.* 2013b, Chapter 3). We studied how pairwise interaction rules between pigeons scale to multiple neighbours by collecting high-resolution GPS data on 85 flock flights, each of two to five birds. We tested how the strength of flocking response changed as flock size increased. Keeping flocks small allowed more replicates for each size of flock. Based on our previous work on pairs of pigeons (Pettit *et al.* 2013b, Chapter 3), we can calculate the expected response to each neighbour and then ask what function of these pairwise responses best describes the observed momentary turning behaviour.

The first approach we tested was to average the predicted pairwise responses, making the assumption that in these small flocks, all flockmates were visible except in the rear blind angle. This approach to multi-neighbour interaction is often used in SPP models, for example attraction to neighbours' centre of mass (Couzin *et al.* 2002; Reynolds 1987; Strömbom 2011) or alignment with the mean orientation of neighbours (Couzin *et al.* 2002; Cucker & Smale 2007; Vicsek *et al.* 1995). However, there is already evidence from golden shiners (*Notemigonus* *crysoleucas*) that averaging is insufficient to explain the response to two neighbours (Katz *et al.* 2011). Therefore we also compare the data to a model based on Bayesian estimation and probability matching (Arganda *et al.* 2012; Perez-Escudero & de Polavieja 2011). We show how thinking of flocking behaviour as a series of decisions based on uncertain information captures how interactions change with group size.

5.2 Methods

5.2.1 *Data collection*

We recorded 5Hz GPS tracks of pigeons flying home in small flocks of two to five birds. The training, release, and GPS tracking procedures were the same as in Pettit *et al.* (2013b, Chapter 3). In total there were 33 pairs, 20 threes, 18 fours, and 14 fives. We used 51 birds in total, aged 1 to 2 years, bred and housed at the University Field Station, Wytham, UK. Most birds flew in multiple trials with different flock sizes (1 to 9 trials per bird, median 4). To maximize independence among the trials, we avoided flying the same two birds together in more than one trial. There were four cases of the same two birds flying together a second time (one pair, three flocks of three, less than 5% of the data).

The flights were from two homing sites, roughly the same distance from the home loft in opposite directions. In 2011 we used a release site near Appleton (10.4 km, home bearing $26°$), with 24 subjects, flying as 11 pairs, 6 threes, 6 fours, and 4 fives. In 2012 we used a release site near Kirtlington (10.6km, home bearing $194°$), with a new set of 27 subjects, flying as 22 pairs, 14 threes, 12 fours, and 10 fives. Each pigeon had at least 21 solo pre-training flights, from the same release site as the flock flights, to familiarize it with the homing task (as in Pettit *et al.* 2013b, Chapter 3). The pigeons had additional solo flights between the flock flights. We systematically arranged the order of releases so that flock size was not confounded by time or experience. Part of the dataset we analyzed here (the paired flights from Appleton) also formed part of an earlier study (Pettit *et al.* 2013b, Chapter 3). For this analysis, we only included the pairs from Appleton from the earlier study that were systematically interspersed in time with flights of larger flocks.

5.2.2 *Data processing*

We converted latitude and longitude to a flat-earth model using Universal Transverse Mercator projection. We excluded points before take-off and after landing based on speed (see Chapter 4) and also excluded points within 200m of home, where the tracked pigeons were most likely to have encountered other pigeons not in the experiment. To focus on cohesive flocking behaviour and ensure that the trials were accurately classified by flock size, we defined a flock as having split if any two birds were more than 200m apart. If the split occurred during the second half of the flight (14 trials), we kept the first portion up until the flock first split. If the split occurred during the first half of the flight, we either discarded the entire flight (three trials) or, if only one bird split off at the release site, we reclassified the rest of the birds' tracks as a smaller flock (three trials). The numbers of trials by flock size (above) reflect the final trial counts used in the analysis, after discarding/reclassifying split flocks.

The flocking behaviour variables were calculated in the same way as in Pettit *et al.* (2013b, Chapter 3). First, we calculated each bird's momentary direction of travel from one time step to the next. For turn rate, we used the change in bearing between successive time steps. Taking each bird in turn as the focal bird, we calculated the angular position θ_j, distance r_j, and relative direction of flight φ_j, for every flockmate j at every time step. The turn rate and the angles θ_j and φ_j were signed positive for right (clockwise) or negative for anticlockwise (left) relative to the focal bird's direction of flight. We calculated the average flight direction of the flockmates ($\bar{\varphi}$) using the circular mean (Fisher 1993).

5.2.3 *Model fitting*

For models with turn rate as a response variable (equations 5, 6, and 9) we fitted parameters by iterative least squares estimation (*nlinfit* in Matlab), using all turn rates regardless of magnitude. For models where the response variable was the probability of turning right, P_R (equations 8 and 10), the fitting procedure was slightly more complicated. We restricted the dataset to large turns with low autocorrelation, with the rationale the measured momentary turn rate may be the execution of previous decisions or it may be too small to justify inferring a left/right decision. These are effectively sources of noise that would push P_R closer to 0.5 and reduce model accuracy, rather than biasing the results. Nonetheless, by applying the following two filters we avoided making the assumption that a pigeon made new decisions at the same rate we measured its behaviour (5 times per second in this case).

First, we set a lower threshold for turns by visual inspection of the frequency distribution of turn magnitude (figure S1). We chose the threshold of ±0.15 rad/s as the smallest that maintains an approximately straight line on the log-log plot. Within the remaining 36% of the data above this threshold, we then removed any turn angles that had the same sign (left or right) as the previous turn angle, so that out of a sequence of right turns (or left turns), we only used the first turn to fit the model (7.4% of the total dataset). There are other ways of extracting decision points from trajectories (e.g. Byrne *et al.* 2009; Mann *et al.* 2013), but these two filters were a simple way to reduce noise and autocorrelation.

After applying the two filters above, we found parameters that maximized the log likelihood function,

$$\ln\mathcal{L} = \sum_{x\in R} \ln(P_R(x)) + \sum_{x\in L} \ln(1 - P_R(x)), \tag{1}$$

where each data point x has an observation of the focal bird turning left (L, negative turn rate) or right (R, positive turn rate). For likelihood maximisation, we used unconstrained nonlinear optimisation (*fminunc* in Matlab), checked against a coarse-grained exhaustive search across a wide range of allowable parameter values. We compared models using the Bayesian information criterion (BIC), which penalizes log likelihood by the number of parameters estimated from the data. The probability that the data favour a more complex model (H_1) over a nested model with fewer parameters (H_0) is $p_{\mathrm{BIC}} = \exp\left(\frac{\Delta\mathrm{BIC}}{2}\right)$, where $\Delta\mathrm{BIC} = \mathrm{BIC}(H_1) - \mathrm{BIC}(H_0)$ (Masson 2011). In practice, either $\Delta\mathrm{BIC} < -30$ ($p_{\mathrm{BIC}} < 10^{-6}$, very strong evidence for H_1), or $\Delta\mathrm{BIC} > 0$ ($p_{\mathrm{BIC}} > 1$, favouring H_0). There were no borderline cases, so we always preferred models with lower BIC and do not show values of p_{BIC}.

5.3 Results

5.3.1 *Response intensity with varying numbers of neighbours*

A pigeon's total response to the flock was greater in larger flocks than in pairs (figure 1). Based on earlier work on pairs (Pettit *et al.* 2013b, Chapter 3), the turning response to one neighbour can be expressed as

$$\mathrm{turn} = A + C, \tag{2}$$

where A is alignment with the neighbour's direction of flight (φ),

$$A = \begin{cases} \beta_1 \tanh(\varphi \beta_2), & \text{if} |\theta| \leq \pi - \frac{b}{2}, \\ 0, & \text{otherwise} \end{cases} \tag{3}$$

and C is attraction or repulsion depending on distance (r) and angular position (θ),

$$C = \begin{cases} \beta_3 \sin(\theta) \tanh\big((r - \beta_4)\beta_5\big), & \text{if} |\theta| \leq \pi - \frac{b}{2}. \\ 0, & \text{otherwise} \end{cases} \tag{4}$$

The functional forms of A and C are transformations of the sigmoidal $\tanh$ function, chosen based on plots of turning behaviour against φ, θ, and r (see Pettit *et al.* 2013b, Chapter 3).

Both A and C are conditional on the neighbour not falling into the rear blind angle, which we set to $b = \frac{3}{5}\pi$ (see Pettit *et al.* 2013b, Chapter 3). We fitted the other five parameters using the data on paired flights ($\beta_1 = 0.0367,\ \beta_2 = 8.70,\ \beta_3 = 0.0222,\ \beta_4 = 2.92,\ \beta_5 = 0.421$). As a naïve way of predicting behaviour in larger flocks, we averaged the pairwise predictions across all neighbours,

$$\text{turn} = \frac{1}{n} \sum_{j=1}^{n} \left(A_j + C_j\right). \tag{5}$$

Because the predicted turn angles are very small (within the range ± 0.053 rad, approximately $\pm 3.0°$), their mean can be approximated by the arithmetic mean rather than the circular mean.

The measured responses in flocks of 3, 4, and 5 were significantly stronger than predicted from equation (5), as indicated by the fact that the slope of observed *vs.* expected turn rate was greater than 1 (figure 1A, ANOVA of the regression slopes fitted to each trial, with categorical flock size effect: $F_{3,81} = 8.6,\ p < 10^{-4}$). Rather than the slopes increasing linearly with flock size, as would be predicted from the sum of pairwise responses, each additional neighbour had less effect on the total turn rate. The responses in flocks of 3 to 5 of very similar magnitudes.

In the alignment component of the flocking response, we found the same pattern of steeper slopes in larger flocks (figure 1B & C). Although alignment is not a complete description of flocking behaviour, we chose to focus on alignment to simplify model comparison, and also because the GPS measurements of velocity are more accurate than the measurements of position (Nagy *et al.* 2010; Pettit *et al.* 2013b, Chapter 3). Many self-propelled particle models include alignment with the mean velocity of neighbours (Couzin *et al.* 2002; Cucker & Smale 2007; Reynolds 1987; Vicsek *et al.* 1995), as represented in figure 2A. Assuming that it takes the same form as pairwise alignment in equation (3), the response to the neighbours' mean flight direction ($\bar{\varphi}$) is

$$\text{turn} = c\tanh(m\,\bar{\varphi}). \tag{6}$$

This alignment model is considerably simpler than equation (5). It only has two free parameters as opposed to five, and it ignores the blind angle. We estimated c and m by fitting equation (6) to the data on pairs (see figure 1B).

The increase in alignment response with the number of neighbours is most clearly illustrated by cases when the focal bird's bearing was either the most clockwise or the most anticlockwise compared to the mean bearing of the flock, *i.e.* when all φ_j had the same sign. In these situations, the larger the flock, the more rapidly the focal bird adopted its neighbours' direction (figure 1C). The actual turn rate was greater than the averaging-based response in equation (6), but less than the sum of predicted pairwise responses,

$$\text{turn} = c\sum_{j=1}^{n}\tanh(m\,\varphi_j). \tag{7}$$

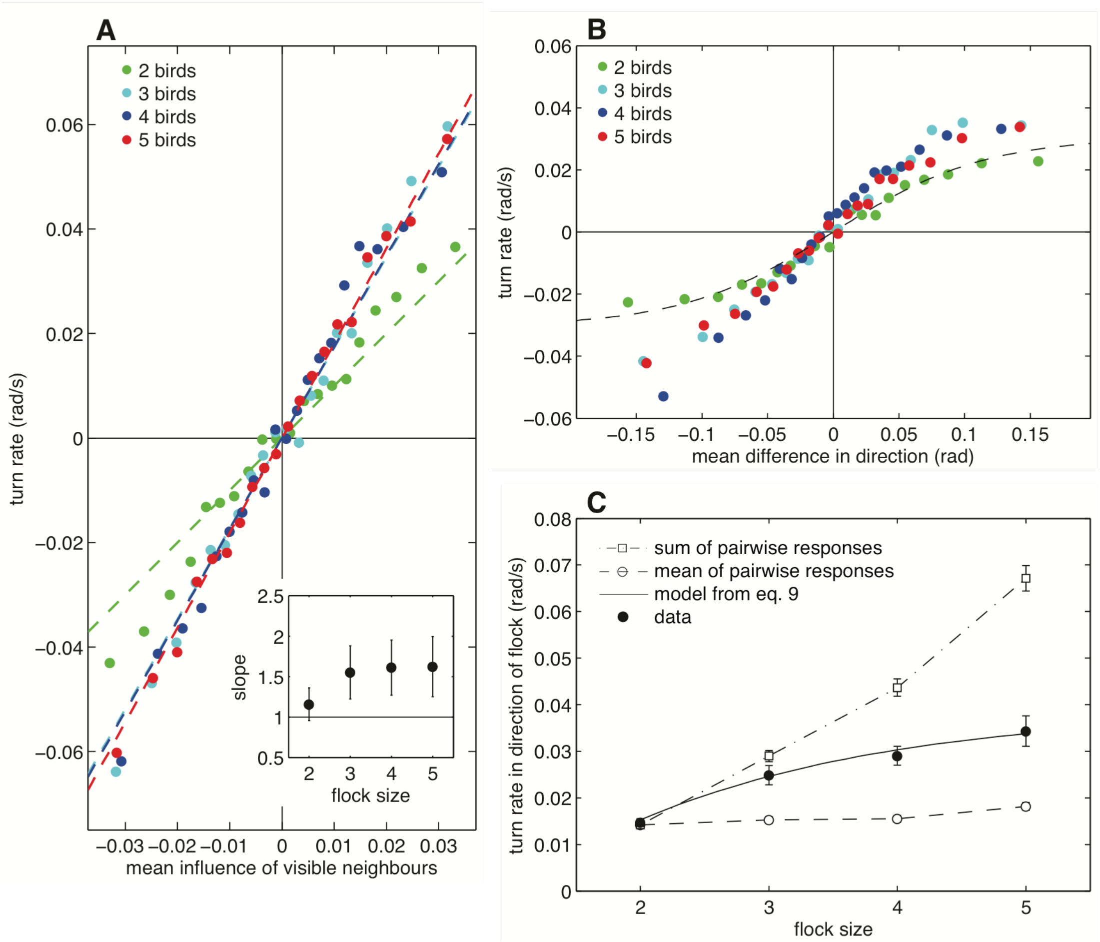

Figure 1: Scaling pairwise responses to multiple neighbours. (A) Observed turn rate plotted against the turn rate predicted by averaging pairwise predictions across all flockmates. The pairwise prediction (equation 2) is parameterized using data on pairs. Points, coloured by flock size, show means from 20 quantiles, with a regression line fitted to all data from each size of flock. Inset shows means and 95% confidence intervals for the regression slopes estimated within each trial. **(B)** Turn rate of the focal bird vs. the relative orientation of the rest of the flock. Points show the means from 20 quantiles from each size of flock. The dashed line shows equation (6) fitted to the data from pairs (green). In **A** and **B**, the x-axes span 95% of the data. **(C)** Rate of turning toward the flock's direction of flight, for cases when flockmates' velocities were all rotated in the same direction (all left or all right) compared to the focal bird. Additional lines with circles and squares show predictions based on the mean (equation 6) and sum (equation 7) of pairwise alignment responses, respectively. Solid line shows the model in equation (9) for comparison. Turn rates from the data are re-centred on zero (actual mean -0.004 rad/s).

5.3.2 *Left/right decision model*

For choices between discrete options in the presence of social information, Perez-Escudero, Arganda, and de Polavieja (2012; 2011), proposed a common modelling framework based on Bayesian estimation and probability matching. Their model predicts an increasing response with the number of conspecifics choosing a particular option, which is what we found found in flocking behaviour (figure 1C). For two choices, L (left) and R (right), their model for the probability of choosing R is

$$P_R = \left(1 + \frac{1 + as^{-(n_R - k\, n_L)}}{1 + as^{-(n_L - k\, n_R)}}\right)^{-1}, \tag{8}$$

where n_R and n_L are the numbers of conspecifics that have already chosen R and L. The parameter a scales the response to personal information, s scales the response to conspecific behaviour (given personal information), and k controls the inhibitory effect of conspecifics going left on the probability that right is a good option (and *vice versa*). Setting $k = 1$ or $k = 0$ create simplified cases of the model with fewer parameters to estimate from the data.

Implementing this model on the pigeon flocking data required classifying neighbours as ‘left’ or ‘right’ (figure 2). To create an alignment model for comparison to equation (6), we defined n_L as the number of flockmates oriented left of the focal bird (negative φ) and n_R as the number of flockmates oriented right (positive φ). To include effects of attraction, repulsion, and the blind angle, it would be possible to base n_R and n_L on the predicted leftward/rightward influence of each neighbour, as calculated in equations (2)-(4). In addition to defining n_L and n_R, a second consideration in fitting equation (8) to the data is that pigeons might not make new decisions at the same rate we measured their behaviour (5 times per second).

Therefore we fitted the model to a subset of the data containing relatively large turns with low autocorrelation (see Methods).

The maximum-likelihood estimates of the parameters in equation (8) were $a = 4.01$, $s = 3.92$, and $k = 0.02$. We found the $k = 0$ case to be most parsimonious ($\mathrm{BIC} = 60639$, 2 parameters: $a = 4.44$, $s = 3.88$), compared to the $k = 1$ case ($\mathrm{BIC} = 61543$, 2 parameters), or the full model with $0 < k < 1$ ($\mathrm{BIC} = 60649$, 3 parameters). In the $k = 0$ regime of the model, observing a conspecific going right increases the likelihood that ‘right’ is a good option but does not reduce the likelihood that ‘left’ is a good option (Arganda *et al.* 2012). This model is a good fit to the turning probabilities in the data (figure 3A & B). It captures two key features of the observed behaviour. First, the total range of P_R increased with flock size, which is similar to our observation in figure 1 regarding mean turn rates. Second, in larger flocks the orientation of any one flockmate had less effect on the behaviour of the focal bird, i.e the gradient $\frac{\Delta P_R}{\Delta n_R}$ decreased with flock size. This

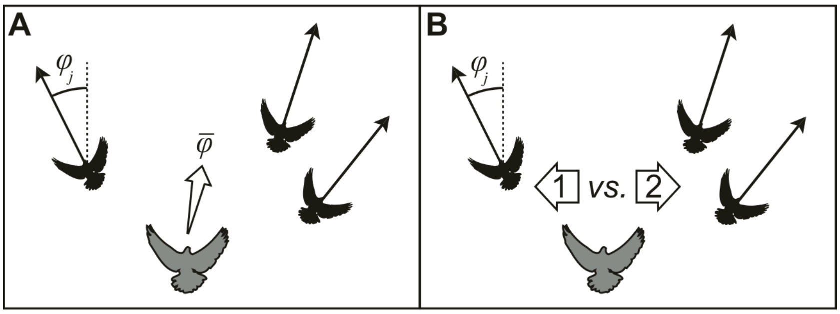

Figure 2: Diagrams contrasting two models of flocking behaviour. (A) Response to the mean flight direction of flockmates, $\bar{\varphi}$, as in equation (6). **(B)** Response to numbers of individuals oriented left and right, as in equations (8) and (9). In both panels, black arrows represent the flight directions φ_j of each flockmate. The focal bird (grey) decides which direction to turn based on the information represented by the white arrows. Although we focus on the alignment aspect of flocking (equations 6-12, figures 3 & 4), the full influence of each flockmate also depends on its position (Pettit *et al.* 2013, Chapter 3), as in equations (2)-(5).

second feature is what we would expect if pigeons responded to the average behaviour of their flockmates, as in equations (5) and (6).

For a more direct comparison to the turn rate data in figure 1, we created a modified version of the model from Arganda *et al.* (2012), with turn rate as a response variable rather than P_R. For this purpose, we used a logit transformation of equation (8), with $k = 0$,

$$turn = \ln\left(\frac{1 + a's'^{-n_L}}{1 + a's'^{-n_R}}\right). \tag{9}$$

In other words, we hypothesized that turn rates would follow the functional form of $\ln(P_R/P_L)$, where positive turn rates correspond to right turns. Fitting equation (9) to the full set of turn angles, we estimated $a' = 0.0399$ and $s' = 1.65$ (figure 3C). Note that these parameters do not have the same biological meaning as a and s in equation (8). Unlike the model based on averaging in equation (6), the model in equation (9) correctly predicts the increasing response magnitude as flock size increases (figure 3C). This difference between the models is most clearly seen when the flockmates are oriented either all left $(n_R = 0)$ or all right $(n_L = 0)$ compared to the focal bird (figure 1C).

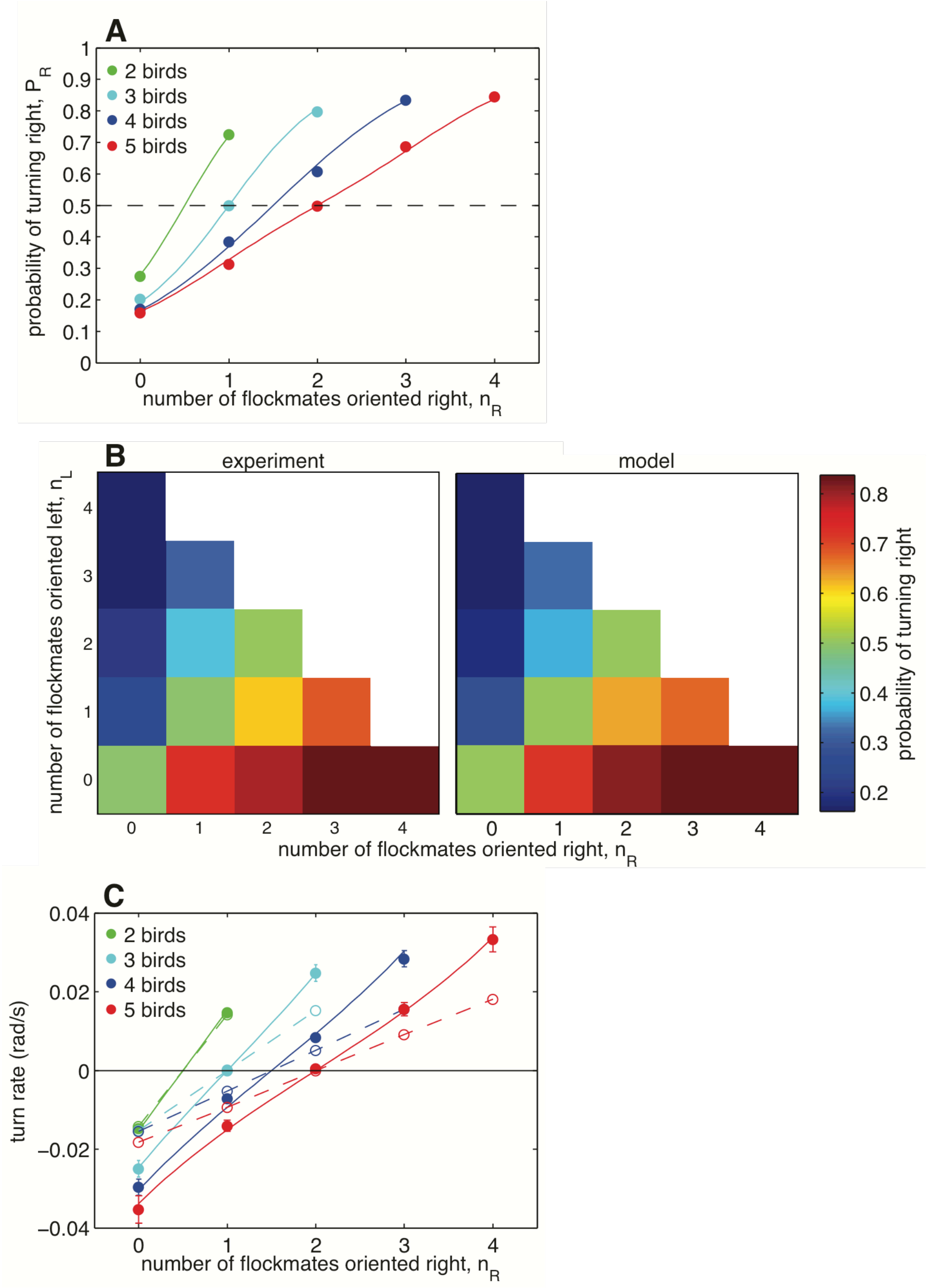

Figure 3: Flocking responses compared to Bayesian estimation model. Focal bird's response compared to the numbers of flockmates oriented left and right. In **A** & **B**, response is measured as the proportion of mean turns after removing small turns and autocorrelation (see Methods). In **C**, response is measured as mean turn rate. Filled circles in **A** and **C** show the mean and standard error of the values from each trial, re-centred on $P_R = 0.5$ or turn $= 0$. Error bars are sometimes smaller than marker size. Solid lines show the fitted models from equation (8) (with $k = 0$) and equation (9), respectively. In C, open circles connected by dashed lines show the responses predicted from the mean direction of flockmates (equation 6).

5.3.3 *Alignment rule with uncertainty*

The theoretical basis of the Bayesian estimation model in equation (8) is that the more conspecifics adopt a particular behaviour, the more likely that it is a good option (Arganda *et al.* 2012; Perez-Escudero & de Polavieja 2011). For estimating a continuous variable, a related concept is that a larger sample of observations narrows the error distribution of the mean. We therefore created a model of alignment as a function of $\bar{\varphi}$ that takes into account the reduced uncertainty in larger flocks. In common with equation (8) we model alignment as a left/right decision based on probability matching, in which the degree of certainty in estimation affects the predicted response.

In this model, a pigeon has a probability d of updating its direction in response to the flock. Each time it updates its direction, the pigeon estimates the relative flight direction of the rest of the flock $\bar{\varphi}$ and turns in the direction of its estimate. This estimate has Gaussian error with standard deviation σ/n^b, where n is the number of neighbours and b is a positive parameter fitted from the data. Dividing by n^b accounts for the fact that the mean direction might be estimated with greater certainty the larger the flock. The probability of turning right is given by

$$P_R = \frac{1-d}{2} + d\,\Phi\left(\frac{\bar{\varphi}n^b}{\sigma}\right). \tag{10}$$

Φ is the cumulative distribution function of the normal distribution, which creates a sigmoidal response to $\bar{\varphi}$, like equation (6) (figure 4A). By fitting equation (10) to the data from all sizes of flock, we obtained parameter values $d = 0.72$, $\sigma = 0.059$ rad, and $b = 0.22$. Including n^b improves the fit to the data ($BIC = 58924$, compared to $BIC = 58955$ for an alternative model with $b = 0$), which confirms that the more neighbours, the steeper the alignment response (figure 4).

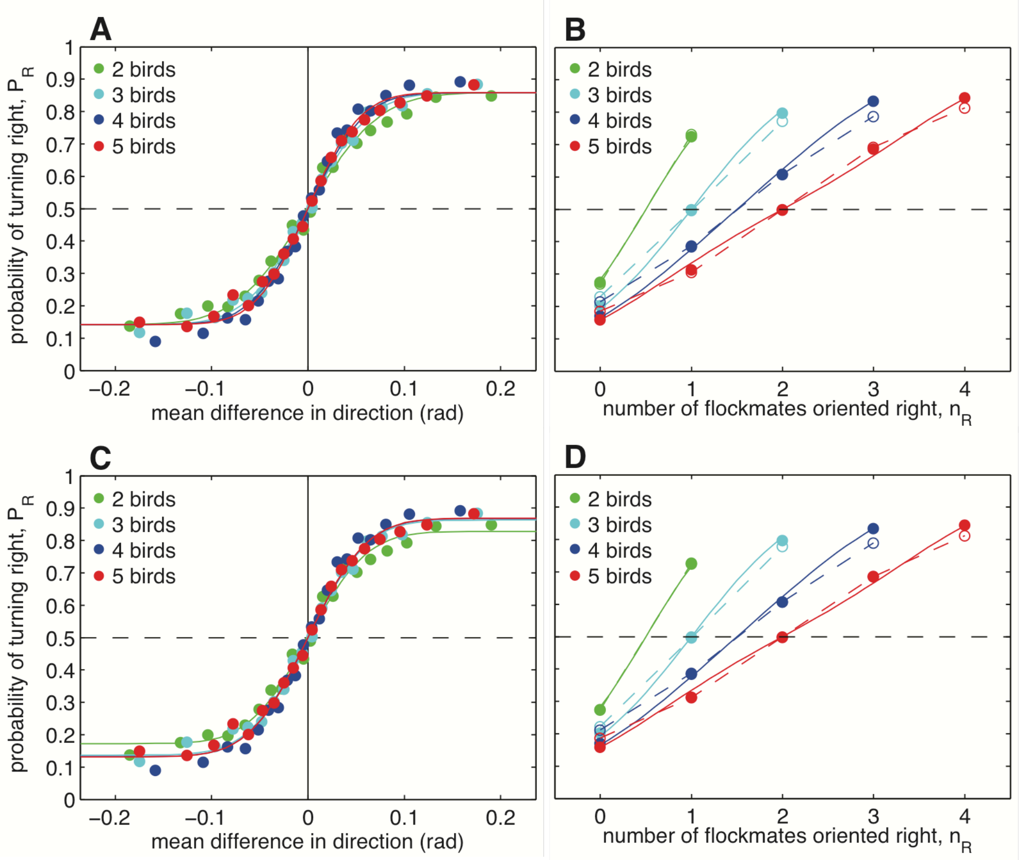

Figure 4: Model predictions of alignment modulated by flock size. (A) Response to the mean relative direction of the rest of the flock ($\bar{\varphi}$). Data from the experiment are summarized by the means from 20 quantiles from each size of flock (coloured circles). Coloured lines show the fitted model from equation (10). **(B)** Response to the numbers of flockmates on the left and right, as in figure 3. Open circles connected by dashed lines show the fitted model from equation (10). Solid lines show the fitted model from equation (8), as in figure 3. **(C-D)** Same data as A-B, but with the fitted model from equation (12) instead of equation (10). In all panels, P_R-values from the experiment (filled circles) are re-centred on 0.5.

An alternative way of expressing the effect of n on the alignment response is for birds in larger flocks to have a higher probability d of responding to the flock at each time step. The Bayesian estimation model by Arganda *et al.* (2012) gives us an expectation of how d should increase with n. We can form the likelihood ratio,

$$\frac{P(X|B_n)}{P(X|B_1)} = \frac{1+s^{-1}}{1+s^{-n}} \tag{11}$$

$P(X|B_n)$ is the probability that direction x is a good option, given the observation (B_n) that n conspecifics are flying in direction x. This likelihood ratio describes the fact that x is more likely to be a good option if several conspecifics have chosen x compared to if just one conspecific has chosen x (provided $s > 1$). For scaling the magnitude of the flocking response, it has the required property of increasing with n and approaching an asymptote in large flocks.

Substituting d in equation (10) for an expression proportional to equation (11) gives

$$P_R = \frac{1-D}{2} + D\,\Phi\left(\frac{\bar{\varphi}}{\sigma}\right) \tag{12}$$

$$\text{where } D = d\left(\frac{1+s^{-1}}{1+s^{-n}}\right).$$

Each time a pigeon makes a turning decision it has a probability D of choosing to align with the flock's mean direction, where D increases asymptotically with flock size. Whereas equation (10) increases the slope of the alignment function with flock size, equation (12) increases the asymptote (figure 4C), which resulted in a better fit to the data ($BIC = 58916$) than equation (10). The fitted parameter values were $\sigma = 0.048$ rad, $d = 0.65$, $s = 7.9$. Using $\frac{\sigma}{n^b}$ instead of σ in equation (12) increases BIC (58922, 4 free parameters). In other words, if we allow the asymptotes to change with n, as in equation (12), there is not strong evidence for an additional effect of n on the slope.

5.4 Discussion

Alignment to the mean direction of neighbours (equation 6) has already been included in many collective motion models (Couzin *et al.* 2002; Vicsek *et al.* 1995). Our contribution here is to describe the relationship between the response to one neighbour (straightforward to measure experimentally) and responses in larger groups. We found that the strength of flocking response was modulated by the number of flockmates. By applying the model of Arganda *et al.* (2012) to the behaviour of pigeons in flight, we show that collective motion can be described as a series of decisions based on Bayesian estimation and probability matching. Regardless of whether we quantified a pigeon's flocking response as a turning rate or a turning probability, the response increased asymptotically with the number of neighbours (figure 3).

The model by Arganda *et al.* (2012) gives a biological explanation for why we would expect this shape of increase for an animal that estimates the quality of a particular direction based on social information. Given the observation β that one conspecific is moving in direction x, there is still some probability that x is 'bad', which can be represented as $P(\neg X|\beta)$. This probability decreases as more conspecifics adopt direction x. If the n conspecifics made their decisions independently, then $P(\neg X|\beta)^n$ is the probability that x is bad. Even if the conspecifics did not decide independently of each other, a larger group going in direction x will still indicate higher quality most of the time (Perez-Escudero & de Polavieja 2011).

In equations (10) and (12), we show how the reduced uncertainty in larger flocks can be implemented within an alignment rule. Compared to equation (8) (from Arganda *et al.* 2012), these models have the advantage that they are sensitive to the magnitude of the flockmates' mean direction, $|\bar{\varphi}|$. Equation (8) could also be made sensitive to $|\bar{\varphi}|$ by weighting n_R and n_L by the magnitudes of the positive and negative φ_j values, respectively. For example, if there is Gaussian error in estimating whether each neighbour is on the left or the right, n_R will not be an integer but a sum of n probabilities,

$$n_R = \sum_{j=1}^{n} \Phi\left(\frac{\varphi_j}{\sigma}\right). \tag{13}$$

Beyond the models examined here, there are other types of interaction rule that could also explain the observed asymptotic increase in flocking response with flock size. For example, response to neighbours might decline with topological distance, meaning the second-nearest neighbour has less influence than the nearest neighbour, and so forth. Herbert-Read *et al.* (2011) made this assumption when fitting functions to multi-neighbour interactions in mosquitofish. For starling flocks, Ballerini *et al.* (2008) also proposed a topological interaction rule as an explanation for the fact that neighbours' relative positions came closer to a uniform distribution with increasing topological distance.

In terms of cognition and sensory systems, there are several reasons we might expect each additional neighbour to have less influence, for example if an animal can only keep track of a limited number of neighbours (Ballerini *et al.* 2008) or if near neighbours obscure farther neighbours from view (Strandburg-Peshkin *et al.* 2013). The Bayesian estimation model from Perez-Escudero, Arganda, & de Polavieja (2012; 2011) gives a functional explanation for the decreasing influence of additional neighbours. If observing additional conspecifics (within a large flock or shoal) would have a negligible effect on an individual's estimation of a 'good' direction, then it may not be worth evolving additional cognitive or sensory capabilities to expand the topological interaction range.

If an averaging-based response is calibrated correctly for the particular group size, it produces approximately the same response to n_L and n_R as the Bayesian estimation rule (figure 4B,D). This is because in highly aligned groups, such as pigeons, the average direction of neighbours ($\bar{\varphi}$) will generally be correlated with $n_R - n_L$. The biological implication is that in some contexts, heuristics based on averaging will recover the optimisation benefits of the Bayesian estimation model. Obviously averaging will only work for decisions that are effectively between a continuous range of options (Conradt 2008). As a practical consideration for research in collective motion, our results show why it is important to compare a range of group sizes, as we did here. Within one group size many models can explain the same behaviour, and they will not necessarily extrapolate to other sizes of group.

We have described the mean behaviour within flocks, but all birds do not necessarily follow the same general rule throughout a flight. Analyzing individual variation in interaction rules would be an interesting future direction for this model-fitting approach, especially given the persistent leader/follower differences found in pigeon flocks (Biro *et al.* 2006b; Flack *et al.* 2013a; Nagy *et al.* 2010). Individual differences could be investigated by fitting different parameter values for each bird. A pigeon with a consistently higher value of a (individual certainty) or lower value of s (social indifference) would be expected to have more influence over the flock's direction (Conradt *et al.* 2009; Zafeiris & Vicsek 2013). A flock might momentarily follow one bird, so analyzing shorter timescales is probably necessary for understanding a flock's particular choice of route.

Another question for future work is how well the models here explain interactions in larger flocks. For large aggregations of animals, there is often the assumption that interactions are limited in metric or topological space, justified in terms of individual cognitive or sensory capabilities (Ballerini *et al.* 2008; Couzin *et al.* 2002). By applying the model from equation (8) to collective motion, we provide an additional reason to expect pairwise interaction strength to effectively tail off with additional neighbours. As Arganda *et al.* (2012) pointed out, this model has large areas of variable-space where 'counting' extra conspecifics has a negligible effect on individual behaviour. Our interpretation of flocking behaviour as a series of decisions based on estimation and probability matching not only explains key features of the pigeon data, but also shows how interaction rules in collective motion can incorporate the degree of individual uncertainty, which depends on the social environment.

Supplementary figure

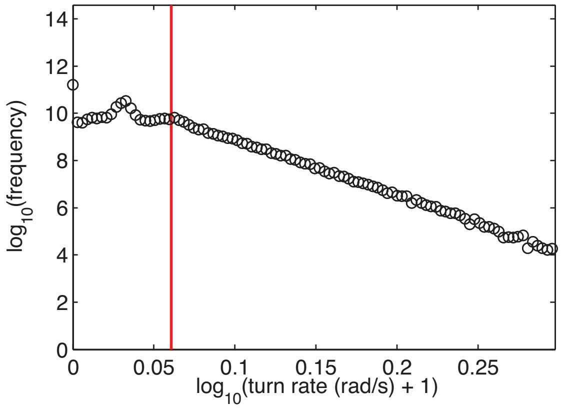

Figure S1: Threshold for turns used to fit decision models. Log-log frequency distribution of the absolute value of turn rate. The plot is a detail of the lower end of the distribution, with frequencies plotted for 100 bins. We set the threshold approximately where the log-log distribution deviates from a straight line (red line, turn rate of ±0.15 rad/s). When fitting models of left/right decisions (equations 8, 10, 12), we only used turns greater than this threshold (see Methods). Irregularities in the distribution near zero are caused partly by the spatial resolution of position measurements (10^{-6} degrees, approx. 10 cm).

Chapter 6: Route choice in collective navigation

Benjamin Pettit, Tim Guilford, Dora Biro

Abstract

Travelling as a flock is expected to aid orientation toward a common destination if the group follows the average estimate of its members. Previous work on pigeon flocks showed that some birds consistently had more of a leadership role, but it is not known how leadership affects homing routes in flock sizes larger than two. We tracked pigeons homing in 85 flocks ranging from two to five birds. Each pigeon had previously learned its own preferred route over repeated solo flights, which created conflicting preferences within the flock. We quantified the degree of conflict using the standard deviation of the preceding solo tracks about their mean. For a given level of conflict, larger flocks were closer to the mean path, in other

words their choices more closely resemble compromise. In addition, flock routes were generally biased toward the majority preference. To investigate the mechanisms that could explain the flock routes, we presented similar informational conflicts to a self-propelled particle model of group decision-making. We controlled the skew of leadership among the simulated birds by varying the degree to which they followed their route preferences. Simulations with strong differences in leadership do not come as close to the average preference as we see in the empirical data. Our data and model show that pooling information is not always possible in collective navigation, but depends on leader/follower differences, the spatial scale of the conflict, and the size of group.

6.1 Introduction

Travelling as a group presents the opportunity to pool information but also the challenge of how to resolve conflicting preferences (Conradt & Roper 2005). Pooling information is likely to be beneficial when all group members have a common goal, as in the case of a flock of birds flying toward a common destination (Simons 2004; Wallraff 1978). Using the average estimate across all members of the group will often result in more accurate decisions, provided that the individual errors are uncorrelated and unbiased (Krause *et al.* 2010). The larger the group, the more accurate the mean is likely to be, but also the higher the variance among the individual estimates. This diversity might make it more difficult for larger groups to reach a compromise in practice.

Pigeon homing provides a way to test how bird flocks resolve conflicting preferences and reach group decisions. Pigeons tend to take straighter routes in flocks than when alone (Biro *et al.* 2006b; Dell'Ariccia *et al.* 2008; Flack *et al.* 2012; Chapter 4). To test whether pigeon flocks effectively pool information, we can create flocks in which we know each bird's preferred route. Over repeated solo homing flights from the same site, pigeons learn individually distinctive routes (e.g. Meade *et al.* 2005), which I refer to here as 'preferences'. Flying in a flock puts these preferences into conflict. We can estimate the degree of conflict from the distance between the birds' previous solo routes. Biro *et al.* (2006b) found that pairs took a compromise route if the conflict was small, but for larger conflicts (more than ~600m between route preferences) either one bird followed the other down its route or the pair split up. Flack *et al.* (2013b) tested the same situation in flocks of four, in which two birds had one preference and the other two had a different preference, because they had learned routes as pairs. Unexpectedly, compromise was more stable in the fours than in the pairs tracked by Biro *et al.*, in that some of the fours took compromise routes close to the mean preference of the flock, even when there was a large distance (600-1500m) between preferred routes. However, the effect of flock size on the degree of compromise has yet to be studied among the same set of subjects flying from the same site.

Here, we have analysed the GPS tracks of flocks of two to five pigeons in terms of their distance from the mean preference, which we calculated from their previous solo routes. Each bird had learned its own preferred route over the course of at least 21 solo training flights. We tested how the degree of conflict (variance among preferred routes) and the size of flock affected the flocks' deviations from the mean preference. In the flocks with odd numbers of birds, we also tested the relative influence of minority vs. majority subgroups.

Although we quantified the degree of 'averaging' in the flock routes, averaging coordinates in space is not an accurate description of the mechanism behind a flock's route. Instead, the route must come about through each bird following its own navigational information while staying with its flockmates. To better capture this process, we made an agent-based model of route choice based on these two forces – social attraction and attraction to a personal preference. Similar models have already shown that self-organized flocking behaviour can be effective at pooling information, provided the conflicts are small enough (Biro *et al.* 2006b; Couzin *et al.* 2005).

Within our model, we could give some birds greater leadership ability by varying the relative strength of route attraction compared to social attraction (Conradt *et al.* 2009; Freeman *et al.* 2011; Sumpter *et al.* 2008). This modification to the model is particularly relevant given that in many species, including pigeons, some individuals consistently have more influence over the group's direction (Biro *et al.* 2006b; Burns *et al.* 2012; King & Sueur 2011; King *et al.* 2009; Nagy *et al.* 2013). In pigeons, some of variance in leadership is due to local experience and correlates with the fidelity of route recapitulation (Flack *et al.* 2012; Freeman *et al.* 2011), but experience does not explain all differences in leadership (Flack *et al.* 2013a). Some of the variation in leadership is instead related to speed (Pettit *et al.* 2013b; Chapters 3 & 4). Our goal here is to investigate how leadership affects flock decisions, rather than what causes leadership. At one extreme, the entire flock could follow one bird, and at the other extreme the decision could be shared equally (Conradt & Roper 2005). By comparing these scenarios in the model to the experiment, we present possible mechanisms behind flock homing routes.

6.2 Methods

6.2.1 *Data collection*

We released pigeons in flocks of two to five birds from two sites approximately 10.5 km from home in opposite directions. There were 51 pigeons in total. Each pigeon made flights from one of the two release sites. The flock data were the same as in Chapter 5. See Chapter 3 (Pettit *et al.* 2013b) for details of the release procedure and GPS data logging. See Chapter 5 for details of the subjects and release sites.

Before flying in flocks, each pigeon had at least 21 solo flights from the same release site to allow it to learn a distinctive homing route (Biro *et al.* 2006b; Meade *et al.* 2005). Tracking the last five flights confirmed that successive homing tracks from the same bird were near each other (mean distance 161m, quartiles 90m, 139m, 180m) compared to successive tracks from different birds released from the same site (mean distance 661m, quartiles 297m, 532m, 923m). For this purpose, we calculated distances between tracks by finding the nearest point on the previous track at each point along the current track, and then taking the mean of these nearest-neighbour distances along the entire track. Most pigeons flew in several flock homing trials with different flock sizes and different flockmates (see Chapter 5). Between flock flights, we released the birds singly again to check that they were still recapitulating their previous solo routes, as described by Pettit *et al.* (2013b, Chapter 3).

Most of the flocks homed together, as in figure 1. We defined a flock as having split if any two birds were more than 200m apart. Out of 88 flocks released, 20 split. Most of these (14 out of 20) split during the second half of the flight, and we still analysed the part of the flock track up until they split. In three flock releases, one bird split off at the release site, and we reclassified the birds that homed together as a smaller flock: one release of five birds became a flock of four, and two releases of three became pairs. In the three remaining cases of splitting, we discarded the tracks from the analysis altogether (one pair, one flock of three, and one flock of four). After reclassifying or discarding some of the trials when flocks split, there were 33 paired flights, 20 flocks of three, 18 flocks of four, and 14 flocks of five.

Positions were logged five times per second and converted to metres using a Universal Transverse Mercator projection. To focus on the homeward portion of track rather than when pigeons were circling the release site or loft, we excluded portions of the track before a bird first left a radius of 500m around the release site and after it first entered a radius of 500m around the home loft.

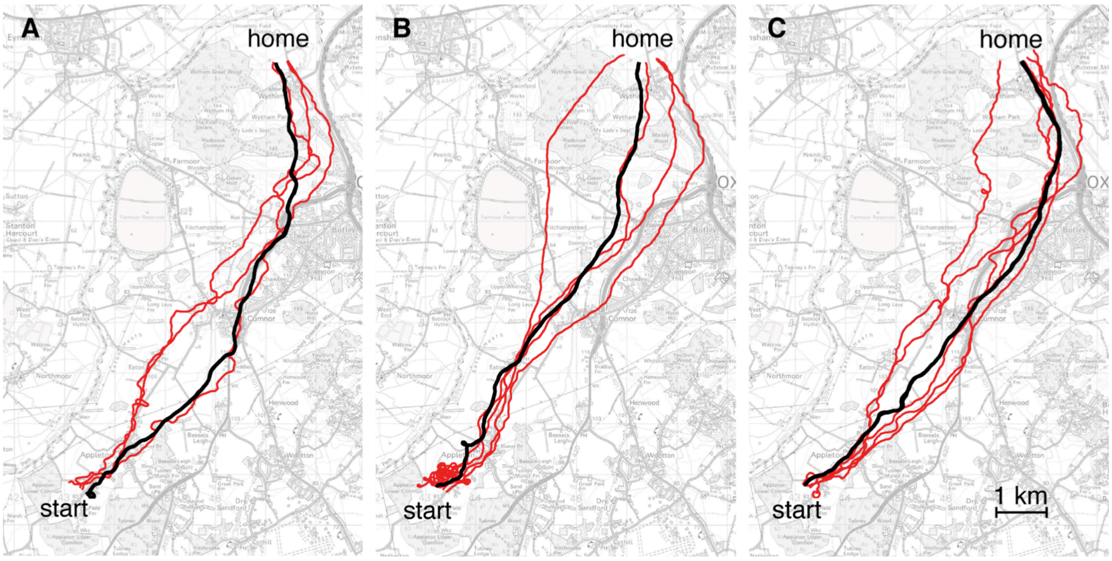

Figure 1: Examples of GPS tracks. Each panel shows the flock homing tracks (black) compared to the solo tracks (red) of the same birds immediately before the flock flight. Flock sizes: (**A**) three, (**B**) four, and (**C**) five, all from Appleton. Tracks have been trimmed using a 500m radius around the start and home. Maps Crown copyright Ordnance Survey. All rights reserved.

6.2.2 *Homing efficiency analysis*

We used two metrics to compare straightness of solo and flock homing tracks. We calculated homing efficiency as the straight-line distance divided by the sum of point-to-point distances along the track, as in earlier work (e.g. Chapter 4; Biro *et al.* 2006b; Dell'Ariccia *et al.* 2008). We calculated distance to beeline by finding the distance from each point on the track to the nearest point on a straight-line path of 1000 points from release to home, and then taking the mean of these distances for all points on the track. Efficiency is likely to improve from flight to flight (Meade *et al.* 2005), so we compared flock flights to the solo flights after as well as before. For each bird, we calculated the mean homing efficiency of the solo flights before and after, and then subtracted the value from the flock flight. We averaged these changes in efficiency across the birds that flew in the same flock, in order to treat each flock trial as one independent data point. We used the same procedure to compare distance to the beeline in flock and solo flights.

6.2.3 *Proximity to mean path*

We estimated the mean route preference of the birds in a flock by averaging their solo tracks from immediately before the flock release, using the iterative method from Freeman *et al.* (2011). This method finds a path of 1000 equally-spaced points between start at home, with each point positioned at the mean of the nearest neighbouring points on the original tracks. At each point x on the mean path, we calculated the distance $d_{i,x}$ to the nearest point on each of the N solo tracks used to calculate the mean path. These can be used to calculate a standard deviation at each point on the mean path by taking the square root of the mean squared distance,

$$\sigma_x = \sqrt{\frac{\sum_{i=1}^{N} d_{i,x}^2}{N}}.$$

At each point on the mean path, we also found the distances to the nearest points on each of the flock tracks, and took the mean to give a single value y_x for that point x on the mean path. To investige how σ_x and y_x vary with flock size, we calculated summary statistics for each trial as follows. We summarized the solo deviation from the mean path by taking the square root of the mean of all $d_{i,x}^2$. Similarly, we summarized the flock's deviation from the mean path using the square root of the mean of all y_x^2.

We tested whether N had a significant effect on the slope of σ_x against y_x, using linear regression with an intercept of zero, $y' = \theta_1 \sigma_x{}' + \theta_2 (N * \sigma_x{}')$, with the coefficients θ fitted using all data points x across all trials. We used the transformations $y' = \sqrt{y+1}$ and $\sigma_x{}' = \sqrt{\sigma_x + 1}$ so that the residuals approximated a normal distribution. Because of pseudo-replication within trials, we estimated parameter confidence intervals by fitting the model to 1000 bootstrap samples of trials. Each bootstrap sample had the same number of trials for each flock size, resampled with replacement from the full set of trials. The 95% confidence interval is between the 2.5 and 97.5 percentiles of the bootstrap parameter estimates.

In flocks with an odd number of birds, we classified the flock's deviation from each point on the mean path as being either toward the majority of preferences or toward the minority. We calculated the proportion of deviation toward the majority within each flock flight by dividing the sum of squared distances on majority's side by the sum of all squared distances (d_x^2), excluding any rare points where a solo route exactly coincided with the mean and caused a tie.

6.2.4 *Simulated route choice*

Our simulation of collective route choice is based on the differential equation model for pairs of pigeons in Biro *et al.* (2006b). Each bird has a one-dimensional spatial position ($y_{i,t}$), which it updates over time (t) as a function of social attraction, route attraction, and noise,

$$y_{i,t+1} = y_{i,t} + A_{i,t} + B_{i,t} + \nu\epsilon\,.$$

$A_{i,t}$ is a social attraction term,

$$A_{i,t} = \alpha \sum_{j=1}^{N} (y_{j,t} - y_{i,t}) \exp\left(-\left(\frac{y_{j,t} - y_{i,t}}{r_a \sqrt{2}} \right)^2 \right),$$

where the parameter α scales the over all strength of social attraction and r_a is the distance at which the bird is maximally attracted to conspecifics. $B_{i,t}$ is a route attraction term,

$$B_{i,t} = \beta\big(d_{i,t} - y_{i,t}\big) \exp\left(-\frac{|d_{i,t} - y_{i,t}|}{r_b} \right).$$

where $d_{i,t}$ is the preferred position of bird i at time t, which represents its preferred route. The parameter β controls the strength of route attraction, and r_b is the distance at which the bird is maximally attracted toward its route. Each update also has normally distributed noise ϵ with standard deviation ν.

The preferences ($d_{i,t}$) in each run of the simulation were based on the set of solo tracks that preceded a flock flight in the experiment. We used the values of $d_{i,x}$, signed negative if they were on the left hand side of the mean path (with respect to a homeward direction) or positive if they were on the right. The simulation updated once for every position along the mean path. We initialized the simulation at the release site, with $d_{i,0} = 0$ and $y_{i,0} = 0$ for all simulated birds. We set $r_a = 80\mathrm{m}$ (as in Biro *et al.* 2006b) and $\nu = 15\mathrm{m}$. We tested values of r_b between 100 and

600 to simulate different levels of conflict. As shown in an earlier analytical version of the model (Biro *et al.* 2006b), r_b controls the critical distance between two preferences at which a compromise route becomes unstable. Within each simulation we kept r_b the same for all individuals.

Birds with higher ratios of $\frac{\beta}{\alpha}$ are more likely to influence the flock's decision (Biro *et al.* 2006b; Conradt *et al.* 2009; Sumpter *et al.* 2008). Many birds with low α are likely to split up, so to simulate heterogeneity in leadership, we gave birds different values of the route-attraction coefficient β_i, between 0 and 1, while keeping α relatively high ($\alpha = 15$). Another reason to vary β rather than α is that experience and route fidelity have been previously identified as factors that affect leadership during pigeon homing (Flack *et al.* 2012; Freeman *et al.* 2011). Before each run of the simulation, we randomly ranked the birds 1 to N and set

$$\beta_i = \frac{\text{rank}_i^k}{\sum_{j=1}^{N} j^k}$$

where k controls the skew of route attraction within the group. If $k = 0$ all simulated birds are equally attracted to their routes with $\beta_i = \frac{1}{N}$, and there is no bias toward one bird leading. If $k \to \infty$, one randomly chosen bird will have $\beta_i \approx 1$ and the rest will have $\beta_i \approx 0$, so only one bird's route preference will affect the flock's decision.

6.3 Results

6.3.1 *Homing efficiency*

Pigeons' homing routes in flocks were significantly shorter in length and closer to the beeline than the solo flights immediately before and after (figure 2). The mean increase in homing efficiency (0.031) corresponded to a reduction in path length of 457m, which was 4.1% of the mean path length of a solo track. The mean reduction in the distance to the beeline (43m) was 6.4% of the mean distance to the beeline from solo tracks. Neither metric changed significantly as flock size increased from 2 to 5 (efficiency: regression slope = 0.0032, $F_{1,83} = 0.29$, $p = 0.59$; distance to beeline: regression slope = -13, $F_{1,83} = 0.64$, $p = 0.43$).

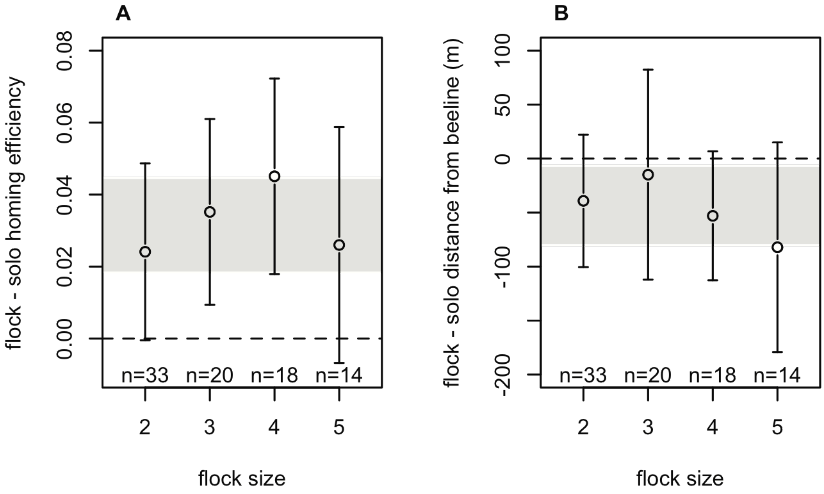

Figure 2: Change in homing efficiency when flying as a flock. (A) Change in homing efficiency, calculated as the straight line distance divided by the path length. Mean 0.031 m, t84 = 4.8, p < 0.001. (B) Change in distance to beeline. Mean -43 m, t84 = -2.4, p < 0.021. In both panels, points show mean and 95% CI by flock size, and shaded area shows 95% CI of over all mean. Each flock is one independent data point, calculated as the mean change in the efficiency metric.

6.3.2 *Proximity to mean path*

As shown in figure 3B, the dispersion of the preceding solo tracks around the mean path increased with flock size. Despite the increasing dispersion of the solo tracks, the distance of the flock tracks from the mean preference did not change significantly with flock size (figure 3C). For all sizes of flock, the flocks were closer to the mean route than were the solo tracks, and this difference increased significantly with flock size (figure 3D).

We used linear regression to test how the flock's distance from the mean preference at each point on the journey varied depending on the dispersion of solo tracks (σ_x) and the size of flock (N). In larger flocks, σ_x had a weaker effect (figure 3E), as indicated by a significant interaction term (σ_x coefficient: 0.846, bootstrap 95% CI: [0.722, 0.969]; $\sigma_x * N$ coefficient: -0.051, bootstrap 95% CI: [-0.085, -0.016], assuming intercept of zero). In other words, for a given spatial variance of route preferences, larger flocks were closer to the mean preference.

In the flocks with an odd number of birds (three or five), flock routes were biased toward the side of the mean solo path with the majority of preferences. For each of the 34 odd-sized flocks, we calculated the proportion of deviation that was toward the majority's side. The median of these 34 values was 0.785 (interquartile range [0.515, 0.948], $p = 0.0052$ in a one-sample Wilcoxon signed-rank test against the null hypothesis that the median was 0.5).

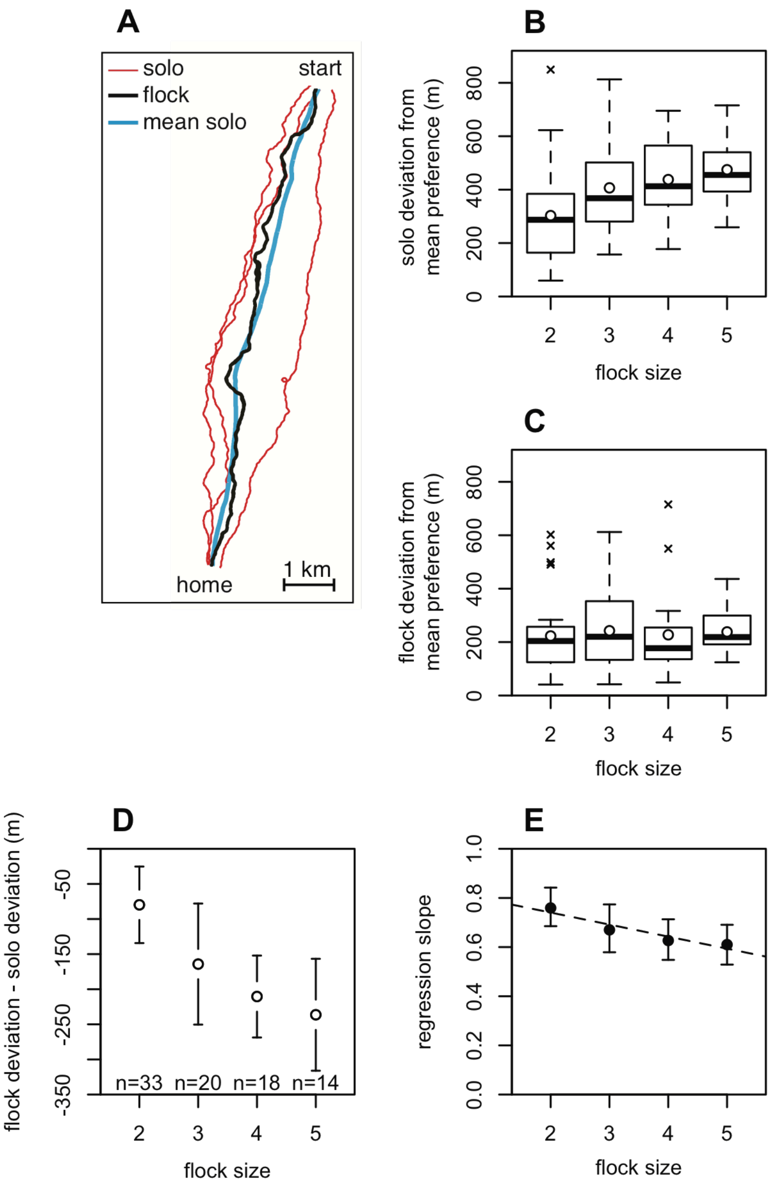

Figure 3. Flock and solo flights compared to the mean preference. (**A**) Example of mean-preference path (blue) calculated from the preceding solo tracks (red) of the three birds in a flock homing flight (black). (**B**) Deviation of solo tracks from mean preference. Each data point is from one trial, calculated by taking the square root of the mean squared distance, in other words it is a type of standard deviation of solo tracks around their mean (see Methods). Regression of log deviation against flock size: slope = 0.219, $F_{1,83} = 17.8$, $p < 0.001$. (**C**) Deviation of flock tracks from mean preference. Regression of log deviation against flock size: slope = 0.0348, $F_{1,83} = 0.4$, $p = 0.54$. Box plots in (B) and (C) show median and quartiles, with the mean shown as a white circle. Crosses indicate points that were above the upper quartile by more than 1.5×interquartile range. (**D**) Difference between flock deviations in (C) and solo deviations in (B) (means ± 95% CI). Regression against flock size, with flock size centred on 2: slope = -56.5, intercept (i.e. difference for flock size of 2) = -89.6, $p < 0.001$ for both slope and intercept, $F_{1,83} = 13.9$. (**E**) Slopes from linear regression of flock deviation against solo deviation, with bootstrap 95% confidence intervals (see Methods). Line shows fitted linear effect of flock size on slope, *i.e.* the interaction between flock size and solo deviation in predicting flock deviation.

6.3.3 *Simulated route choice*

To further investigate mechanisms that could result in the flocks' observed deviations from the mean preference, we ran simulated flock decisions using a 1-dimensional self-propelled particle model, with a set of individual preferences based on the solo tracks preceding a flock flight in the experiment (figure 4A,B). We varied the skew of leadership by giving the simulated birds different route-attraction parameters (see Methods). Large k (more heterogeneous route attraction) increased the distance of the flock from its mean preference (figure 4C). This effect was more pronounced in larger groups where there was generally higher variance among solo tracks (figure 3B). When route attraction was homogeneous within the flock (small k) or acted at long distances (large r_b), the simulated flocks came closer to the mean preference. An earlier study estimated r_b at 230m (figure S1 in Pettit *et al.* 2013b, Chapter 3). Simulation results with $r_b = 200$ or $r_b = 300$ come close to the observed magnitude of flock deviations only if the simulated flocks are relatively homogeneous in terms of route attraction (i.e. low value of k, black contours in figure 4C).

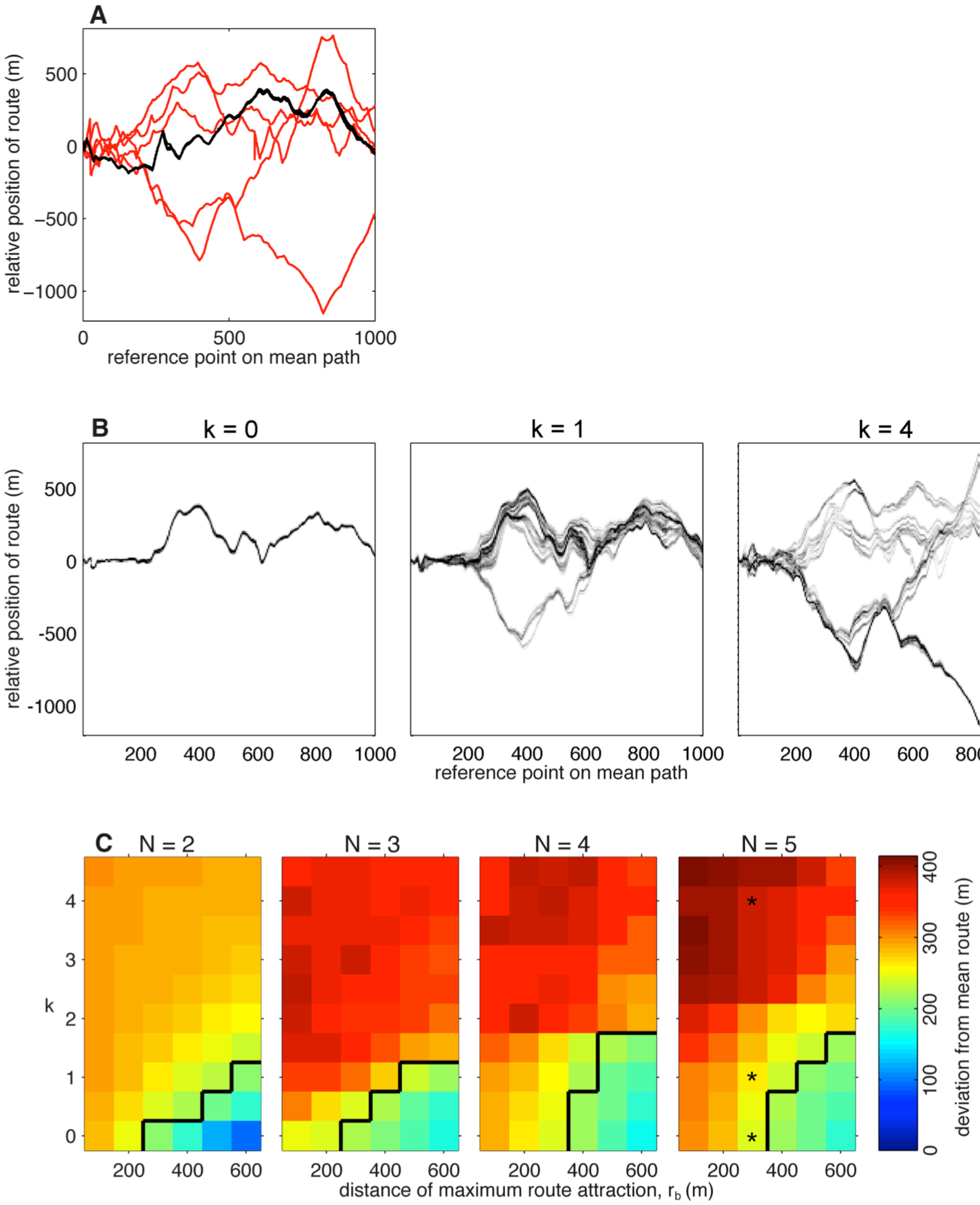

Figure 4. Simulation of collective route choice. (**A**) Example of flock route (black) and preceding solo routes (red) expressed as distances left (negative) or right (positive) from the mean-preference path. Original tracks from the same flock of five are in figure 1C. (**B**) Simulations of the flock in (A) for three values of k, which controls the heterogeneity of route attraction among birds. $r_b = 300$ throughout. Route preferences are taken from the solo route data (red lines in A). Shading shows the relative occurrence of each left/right position (y-value) from 25 runs of the simulation. (**C**) Deviation from the mean preference in simulations with different parameterizations, which correspond to larger asymmetry in route attraction and therefore leadership (k, y-axis) and increasingly long-range attraction to preferences (r_b, x-axis). Colour indicates mean result from N^2 runs of the simulation for each set of solo tracks. The simulation results above or to the left of the black contour line are higher than the mean value from the empirical data for that size of flock, whereas simulation results below or to the right of the black line are less than the empirical value (see figure 3C for the empirical values). Asterisks mark the three parameterizations used in (B).

6.4 Discussion

We used a comparatively large dataset on flock homing routes to investigate how groups of different sizes combine information and choose a route. Flock flights were shorter and closer to the beeline than the same birds' solo flights, a result that agrees with earlier work (Chapter 4; Dell'Ariccia *et al.* 2008; Flack *et al.* 2013b). However, it is surprising that efficiency did not increase with flock size. Larger flocks had a larger sample of estimates for finding an accurate direction, so in theory we would expect them to take straighter routes if they effectively pooled information (Simons 2004). One possibility is that groups of two to five are too small to detect an effect of flock size. When Ward *et al.* (2011) tested predator detection in shoals of 2 to 16 mosquitofish, larger shoals were significantly more accurate in general, but there was actually no difference between shoals of 2 and 4.

Even if a flock effectively pools information, its route will not approach a straight line if landscape features bias the pigeons' route preferences to one side or the other. "Site bias" is well known from the vanishing bearings of homing pigeons (Wiltschko & Wiltschko 2009). To take the example of the Appleton release site in figure 1, most routes lie east of a straight line. For this site, the bias might be because different pigeons independently chose to follow a major road east of the straight line (Lau *et al.* 2006; Lipp *et al.* 2004), and/or because they avoided flying over a wooded hill southwest of home.

For a given variance in solo routes, larger flocks flew closer to the mean preference of the group. One explanation is that decisions in larger flocks were less easily dominated by one bird, and the flock routes were some form of compromise. Another possibility is that leadership was biased toward whichever birds preferred routes closer to the mean preference of the flock. If any bird could lead, regardless of the relative position of its preferred route, then we would expect the flocks' deviations from the mean preference to increase with flock size, as in the model with large k. The results of Flack *et al.* (2013b) on flocks of four support the interpretation that compromise is more likely in larger flocks.

Compared to the mean preference, the flock routes were significantly biased toward the side with the majority of preferences. In other words, deviations from the mean path are not just noise but tend to amplify the majority preference. Despite this general bias, we also observed unexpected cases of flocks following a minority preference (e.g. the flock of three in figure 1A).

From previous work, we expect some pigeons to consistently have greater influence over the flock routes, across trials (Chapter 4; Biro *et al.* 2006b; Nagy *et al.* 2013, 2010). Consistent leader-follower differences could be analysed within this dataset in the future. For example, we could test whether solo speed correlates with leadership, as we found in Chapters 3 & 4 (Pettit *et al.* 2013b). There are several possible techniques for quantifying individual influences over the flock's trajectory at different spatial and temporal scales. At a small scale, we could use directional correlation delay (Nagy *et al.* 2010; Pettit *et al.* 2013b, Chapter 3). At a large scale, we could model the entire flock route as a weighted average of individual preferences and use linear regression to compute the likely weights. These techniques can help quantify the degree to which one bird can influence the flock's route, depending on flock size.

Theoretical treatments of collective navigation have usually assumed it to be a problem in continuous (or circular) space (Krause *et al.* 2010; Simons 2004; Wallraff 1978). As with guessing the weight of an ox or the number of beans in a jar, large groups have an advantage, in theory, because their average estimate of the goal direction will be more accurate. However, for an actual flock of birds deciding on a route, there are several reasons they might not take the average. Besides leader/follower differences, conflicts are sometimes so large that compromise is not a viable option, and the decision in continuous space effectively becomes a decision between discrete options (Biro *et al.* 2006b). How the “many wrongs” hypothesis applies in nature depends on the mechanism of reaching a group decision and on the spatial distribution of estimates. Our results show that flock size affects how the flock resolves conflicting preferences and whether a compromise route is possible.

Chapter 7: General discussion and conclusions

This thesis has presented research on flocking behaviour in the context of local area navigation. Pigeon flocks are a tractable system for investigating collective behaviour in a field setting. I have examined how self-organized group decisions come about, what gives some birds more influence, and how equally decisions are shared among members of the group depending on the size of flock and asymmetry in experience. I will structure this discussion around the questions posed in the opening chapter. For each question, I will show how this thesis advances our understanding and raises questions for future work.

7.1 Unifying questions revisited

7.1.1 *How effectively do flocks pool information?*

Even though some birds do have more of a net effect on the direction of the flock, my findings suggest that the flow of information in pigeon flocks is rarely one-way, from a single leader to followers. Many of the results in this thesis could be explained in terms of flocks effectively pooling information. In Chapters 4 & 6, the flock routes were straighter than the solo routes of the same birds before and after flock flight. Even if the birds have different levels of local experience, the chosen route probably incorporates information from the less experienced bird as well, as I discuss in Chapter 2.

The interaction rules I identified in Chapter 3 also contribute to our understanding of information pooling in pigeon flocks. First of all, they confirm some of the assumptions of self-propelled particle models, which already demonstrated effective information pooling (Couzin *et al.* 2005). Secondly, the most stable configuration is for the pair to fly side by side where both birds can see each other. We still do not fully understand how the hierarchical patterns of leadership measured from directional correlation delay affect flock routes (Flack *et al.* 2013a; Nagy *et al.* 2010; Appendix; Chapter 4). Because these hierarchies only reflect the average leadership pattern over time, they are compatible with mutual responses, fluctuating leadership, and a degree of information pooling (Nagy *et al.* 2010; Xu *et al.* 2012).

7.1.2 *How do birds respond to each other within the flock?*

Chapters 3 and 5 show that pigeons’ momentary responses to flockmates have many overall similarities to the interaction rules posed in self-propelled particle models, and also show how to create more accurate, data-driven models of bird flocks. The interactions among pigeons are different to those among fish, which do not explicitly align to neighbours, at least in the species studied so far (Herbert-Read *et al.* 2011; Katz *et al.* 2011). A second difference from fish is that the interactions in pigeons result in a side-by-side configuration, rather than the nearest neighbour being in front or behind. In Chapter 5, I found that pigeons align more strongly to the direction of multiple flockmates than to a single flockmate. This is what we would expect if birds respond in proportion to their certainty about which direction is best

(Arganda *et al.* 2012; Perez-Escudero & de Polavieja 2011; Simons 2004). In the future it would be interesting to use models to investigate how flock size affects cohesiveness and decision-making given the multi-neighbour interaction rules in Chapter 5.

Group decisions depend not just on interactions between individuals, but also on each individual's response to asocial cues in the environment. To understand flock decisions in pigeon homing, we need better models of how pigeons respond to the landscape. Specifically, it would be useful to have an agent-based model of route recapitulation calibrated on pigeon behaviour. Agent-based models are already being used to explain landmark-based routes in ants (Baddeley *et al.* 2012). I made some progress in this direction by finding the distance from the previous solo route that maximized attraction during route recapitulation (Chapter 3, figure S1). However, I assumed that the 'target' of attraction was always the nearest point on the preferred route. Landmarks used for orientation are likely to be further towards home (Biro *et al.* 2004) and they are likely to be clustered in space (Mann *et al.* 2011). Furthermore, pilotage towards landmarks interacts with compass information (Biro *et al.* 2007). Fitting models to the momentary decisions of homing pigeons will help us understand solo homing routes as well as collective behaviour.

Another area for future research, even using this same dataset, is to study responses to the acceleration of flockmates and responses that integrate social cues over time (e.g. Mann *et al.* 2013). It might be that pigeons are more sensitive to sudden changes in the behaviour of flockmates, or that they can gauge a flockmate's directional certainty from the consistency of its velocity. These dynamic aspects of flocking interactions may affect how information propagates through flocks, which birds have more influence over flock decisions, and how often leadership changes over the course of a homing flight.

Future research on bird flocks should aim to express interaction rules in a way that is more closely based on visual perception (e.g. Moussaïd *et al.* 2011 for human crowds; Strandburg-Peshkin *et al.* 2013 for fish shoals). Rather than interaction rules depending on neighbours' positions and velocities in Cartesian space, each neighbour can have a size, shape, and velocity on the retina or within the field of view. Heuristics based on optic flow are important in insect flight control and have also been implemented in unmanned vehicles (Srinivasan 2011). Traditionally, the creators of SPP models have preferred "simple" rules in that they have a simple mathematical formulation (e.g. vector addition) and few parameters (reviewed by Vicsek & Zafeiris 2012; Yates *et al.* 2010). The abstraction gives these models a greater degree of universality, in other words they could describe many species, regardless of sensory systems or locomotion. However, a different definition of simplicity is a rule that is easy to implement based on the available sensory information. This type of interaction rule is likely to come closer to the control heuristics that animals actually use given their sensory systems.

7.1.3 *What individual differences result in consistent leadership?*

Major themes in this thesis are how differences between birds create persistent asymmetries in the way information passes through the flock, and what consequences these asymmetries have for group decisions. Previous work showed that large differences in local experience can determine which pigeon leads, but that experience does not explain all cases of leadership (Flack *et al.* 2013a, 2012). I found that faster pigeons tended to lead flocks (Chapters 3 & 4), and that it did not matter whether they were socially dominant on the ground (Appendix). The link between speed, position, and leadership makes sense intuitively and was predicted by self-propelled particle models (Conradt *et al.* 2009; Couzin *et al.* 2002).

Even though speed and leadership are correlated and we have a plausible mechanism, speed is not necessarily the direct cause of leadership. Speed and leadership might both depend on homing motivation (see Chapter 4 discussion). To understand leadership in pigeon flocks, we need to understand what causes the differences in ground speed. We might then be able to manipulate speed to test its effect on leadership directly. The wider body of work on homing pigeon flocks shows that several factors affect leadership. In statistical terms, the proportion of variance in leadership explained by each factor probably depends on what birds a flock contains and their experience in the local area.

What do these findings tell us about leadership more generally? My perspective is that we should not be surprised to find consistent leader-follower differences in moving animal groups. Leadership does not necessarily reflect evolutionarily derived complexity, but instead it is an inevitable result of a heterogeneous population. Hierarchical leadership networks, like social networks more generally, are prone to over-interpretation. It is possible that the networks we measure are the result of social relationships, in the human sense, involving individual recognition, but we should ask first whether there is an anonymous, self-organizing mechanism that can explain the observed pattern.

Sometimes the word “leadership” is taken to imply that followers choose who to follow or that leaders actively choose to lead (Burns *et al.* 2012; Jorge & Marques 2012). With self-organizing leadership, it should be possible for none of the group to know who has the most influence over the decision, including the leader itself. Mathematical models are helpful for showing exactly what we mean by self-organized leadership, and are less prone to misinterpretation than the words “lead” and “follow”. Self-organizing leadership may not be as exciting as discovering a “commander” within the group that all members have chosen to follow. However, it is important to understand precisely because it is subtler, and group members are not necessarily aware of its action, including in human groups. Furthermore, self-organizing leadership has the potential to be biologically widespread, because it is scalable to large groups and does not require individual recognition or complex communication (Couzin & Krause 2003).

7.1.4 *How does collective navigation affect spatial learning?*

I found that in pigeon homing, following another individual does not interfere with spatial learning (Chapter 2). Routes chosen collectively can therefore become consolidated in individual memory. The interaction between group decision-making and social learning was not the main focus of this thesis, but it is a fascinating area for future research. There were several intriguing findings in Chapters 2 and 4 that could be investigated with additional experiments. Firstly, the results in Chapter 2 raised the possibility that repeated rounds of social learning might have a “ratcheting” or “hill climbing” effect on route efficiency. Changes to group membership may disrupt the formation of stable, idiosyncratic routes and lead to convergence on a straighter path (Chapter 2, Pettit *et al.* 2013a), in contrast to stable groups learning routes together (Flack *et al.* 2013b). Secondly, In Chapter 4 I found that followers had lower homing efficiency than leaders when tested alone after homing in flocks. This might be because followers do not attend as much to the landscape or learn as quickly as leaders in these larger flocks. One way to test whether flock size and leadership interact to affect learning would be in an experiment similar to that in Chapter 2, but with varying numbers of demonstrators for each observer.

Since Chapter 2 was published, a study on whooping cranes found that flocks took straighter routes if they contained older, more experienced birds (Mueller *et al.* 2013). Although this was presented as evidence of social learning, whether these routes were actually socially transmitted depends on how effectively the younger cranes in the flock learned the route. The feedback between spatial learning and group decision-making is important for understanding the role of flocking in migration and for the more general question of how collective intelligence plays out over repeated journeys and repeated generations.

7.2 Adaptive benefits of flocking behaviour

This thesis has tended to focus on the accuracy of orientation, in terms of how short a path pigeons took to get home. However, because aggregation is beneficial in itself, we should not expect flocking behaviour to be optimized for accurate orientation. Staying together as a group may be so beneficial that it outweighs the cost of a certain degree of collective inaccuracy. We already know that experienced pigeons homing alone do not necessarily take straight-line paths. Pigeons recapitulating idiosyncratic routes appear to be minimising the variance in route length rather than minimising route length itself. Route recapitulation may be a way of minimising risk. These pigeons have sufficient fat reserves to cover much longer distances than 10-20 km, whereas attempting a short cut might increase the risk of getting lost. If reducing risk is a priority during flock homing flights as well, then staying with the rest of the flock may be more important to each bird than maximising navigational accuracy.

As a more general point for interpreting flocking/schooling/herding behaviour across species, optimal social information use does not always coincide with the optimal behaviour for avoiding predators. Interaction rules in collective navigation may therefore be under opposing selection pressures for orientation accuracy and for predator avoidance. Individual-level selection for navigational accuracy could lead to a mixture of social 'followers' and less-social 'leaders' existing in equilibrium, as in a producer-scrounger game (Caraco & Giraldeau 1991; Guttal & Couzin 2010; Johnstone & Manica 2011). Predation pressure, on the other hand, is more likely to have a stabilising influence on interaction rules because of predators targeting prey that stand out from the group, lag behind, or set out on their own (Ioannou *et al.* 2012; Rutz 2012; Wood & Ackland 2007). Neither selection pressure will necessarily maximize group efficiency.

7.3 Prediction and control of self-organizing systems

In addition to the functional perspective on flocking behaviour, the mechanisms behind group decision-making and collective motion are interesting in themselves. These mechanisms not only explain how patterns of collective motion arise in nature (Ballerini *et al.* 2008; Couzin *et al.* 2002) but also improve our ability to predict and control the behaviour of multi-agent systems. Previous applications have included designing interaction rules for robot flocks (Virágh *et al.* 2013), predicting the behaviour of gregarious pests such as marching locust bands (Buhl *et al.* 2006), preventing crowd disasters (Helbing *et al.* 2007), monitoring animal welfare (Febrer *et al.* 2006), and informing reintroductions of social migratory species (Ellis *et al.* 2003; Mueller *et al.* 2013).

Self-organized decision-making occurs in many human contexts as well. Here we have the opportunity to influence 'interaction rules', for example through the design of auctions, markets, committees, the built environment, and communication platforms. Self-organization and social influence are especially important to understand given the new opportunities to aggregate social information online, as well as the challenges posed by crowd disasters and herding behaviour among investors. Humans are particularly reliant on social information, and to a certain extent we have the opportunity to engineer our informational environment.

As a whole, my research demonstrates how flocks function as distributed decision-making systems. Simple, rapid responses allow birds to remain in the safety of the group and take advantage of the navigational information of their flockmates. Each individual is continually updating its learned information about the landscape, and the interaction rules allow leadership to shift dynamically according to who has the best local information. The approach in this thesis is to understand a particular system in detail, with more general principles in mind. If we understand the essential variables that affect the degree of collective intelligence across many species and contexts, then we will be in a better position to answer ecological questions as well as engineer multi-agent systems.

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Appendix: Context-dependent hierarchies in pigeons

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Abstract

Hierarchical organization is widespread in the societies of humans and other animals, both in social structure and in decision-making contexts. In the case of collective motion, the majority of case studies report that dominant individuals lead group movements, in agreement with the common conflation of the terms “dominance” and “leadership”. From a theoretical perspective, if social relationships influence interactions during collective motion then social structure could also affect leadership in large, swarm-like groups such as fish shoals and bird flocks. Here we use computer-vision based methods and miniature GPS tracking to study, respectively, social dominance and in-flight leader-follower relations in pigeons. In both types of behavior we find hierarchically structured networks of directed interactions. However, instead of being conflated, dominance and leadership hierarchies are completely independent of each other. Although dominance is an important aspect of variation among pigeons, correlated with aggression and access to food, our results imply that the stable leadership hierarchies in the air must be based on a different set of individual competences. In addition to confirming the existence of independent and context-specific hierarchies in pigeons, we succeed in setting out a robust, scalable method for the automated analysis of dominance relationships, and thus of social structure, applicable to many species. Our results, as well as our methods, will help to incorporate the broader context of animal social organization into the study of collective behavior.

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Introduction

For a group of humans or non-human animals, networks can be constructed from a number of different types of interaction and across a range of contexts, including association, aggression, courtship, and leadership (1–4). This raises the question whether interaction network structure is maintained across contexts, due to stable relationships or underlying individual differences, or whether network structure re-organizes in every new situation where the same individuals may have different competences. For example, does social dominance routinely endow individuals with leadership roles within the group? By leadership, we refer to an individual’s degree of influence over a group’s decision – in the case of collective travel this largely concerns the timing or direction of the group’s movements (5). Dominance signifies the consistent winning of agonistic interactions (6). Most studies of the relationship between leadership and social structure have focused on mammals, especially primates. In species with highly asymmetrical dominance relationships, such as gray wolves (7), mountain gorillas (8), and chacma baboons (9), there is a consistent trend for dominants to lead. This effect may be mediated by factors other than dominance, such as the central position of dominants in the association network (10) or their greater metabolic needs due to body size. Decision-making is more egalitarian in species where dominance relationships are weak or absent, such as Tonkean macaques (11).

However, the relationship between social structure and leadership is still unknown in some of the most rapid, large-scale, and impressive examples of collective motion – bird flocks and fish shoals. Initial simulations of these groups posed anonymous, homogeneous interaction rules (12, 13), but individual differences are now the focus of both theoretical and empirical investigations (3, 14–19). Elucidating how social structure and individual differences affect group decision-making across a range of taxonomic groups will put the study of collective behavior into a broader biological context. Addressing these questions requires improved tracking technology and computational methods for quantifying interactions in large groups of identified individuals. These high-throughput tools can thus open up new areas of research in social behavior (20, 21).

In this study, we develop automated methods for assessing social dominance, and use them to compare dominance and leadership in domestic pigeons (*Columba livia*). Agonistic encounters in pigeons are characterized by frequent reversals of aggression (22), requiring prolonged observation to determine which bird dominates within a dyad. We build on advances in high-throughput video tracking by using computer vision and custom-made algorithms to find interactions between marked individuals, as they feed indoors in groups of 10 or 30. We measure leadership hierarchies in the same groups of birds, by tracking free flights around the home lofts using custom made high-resolution GPS loggers. Applying two tracking technologies to the same animal groups allows us to test (i) the degree of hierarchical structure in both dominance and leader-follower interactions and (ii) whether dominance and leadership correlate.

Results

Social dominance. We analyzed videos of groups of 10 and 30 pigeons as they fed from a cup in the center of the camera’s field of view (Fig. 1A,B and Movies S1, S2). Each pigeon carried a unique three-color barcode on its back, which enabled computer vision based reconstruction of individual trajectories. The accuracy of the automated method was confirmed through detailed manual identification (see SI). We quantified dominance relationships from the video tracking data using two metrics: Feeding-Queuing (FQ) and Approach-Avoidance (AA). FQ is the pairwise asymmetry in access to food, taking into account the spatial positions of the birds relative to the food cup (Fig. 1A, Movie S1). AA, on the other hand, uses velocity and relative position to determine the degree to which pairs of birds tend to approach and avoid each other (Fig. 1B, Movie S2).

Having constructed interaction matrices for each group, we computed their transitivity and symmetry. The full interaction matrix describes a weighted directed network with two edges reciprocally connecting every pair of vertices (i.e. a complete directed graph). We decompose it into (i) a weighted undirected network, representing the amount of interference/aggression that is reciprocated by the other bird, which we call the ‘common part’, and (ii) a weighted directed network, now with only one edge at most connecting each pair of vertices, representing the asymmetry in those birds’ interactions, which we call the ‘dominant part’ (see SI, Fig. S1). Transitivity (T) is calculated from the dominant part. It ranges from 0.5 to 1, with a score of 1 for fully transitive hierarchies, i.e. networks containing no directed loops. Symmetry (S) is a measure of hierarchy flatness, ranging from 0 to 1, with a score of 1 if the two-way interaction is symmetrical within every pair. We calculate S as the total weight of the common part relative to the total weight of all interactions.

We found highly transitive dominance hierarchies in all three groups of 10 (designated groups A, B, and C), based on both the FQ [T_A=0.960, T_B=0.998, T_C=0.959; P<0.001 for all groups] and AA [T_A= 0.892 (P=0.021), T_B=0.896 (P=0.018), T_C=0.951 (P<0.001)] metrics (FQ shown in Fig. 2 A-C). These transitivity values are all significantly higher than would be expected from randomly-directed interactions (Fig. S2, see SI for details of the randomization). In addition to being highly transitive, the degree of symmetry in FQ matrices demonstrates that a normally subordinate bird frequently blocked the dominant from accessing food [S_A=0.660, S_B=0.402, S_C=0.614], in line with previous reports of frequent reversal events in pigeon social dominance (22). Despite these reversal events, we amassed enough data through automated video tracking to construct a hierarchy based on which bird in a pair dominated a greater proportion of the time. Due to the high level of transitivity, we could summarize dominance by calculating a score for each individual (23). We chose the Normalized David's Score (NormDS) (24) because its assumptions best matched our dataset, however, all calculated scores showed close agreement with each other (see SI).

To test whether the automated dominance metrics above correspond with more traditional measures of dominance, we manually identified pecking, fighting and chasing events on approximately half of the videos (10.4 h out of 22.2 h, see SI for details of scoring method). We use the term Pecking Order (PO) for dominance estimates based on these manually scored interactions, in order to distinguish them from those derived from the automated methods. For each method, we tested whether the NormDS values correlate with those from the other methods (Table 1), as well as testing for correlations between the pairwise interaction matrix values from different methods (Table S1). Both types of comparison produce very similar results. PO dominance correlates positively with FQ dominance, and has a weaker positive correlation with AA dominance. FQ dominance is also a good predictor of a pigeon's total time at feeder (TAF), a measure that is often used as a proxy for dominance or competitive ability in the absence of interaction data (6, 25). Finally, FQ dominance correlated positively with body mass, but not with age (Table 1).

As an additional test of the robustness of our dominance measurements and of the pigeons' social structure, we compared the three groups of 10 to the combined group of all 30 birds (group ABC). All of these groups were sub-samples from a freely interacting population of 100. For the FQ and manual measurements of dominance, the scores in the groups of 10 correlate positively with the scores in the group of 30 (Fig. 2, Table 1, final column). This suggests that the dominance relationships measured via the FQ method are robust to third party interference and are indicative of inherent behavioral variance in the population, with individual qualities that serve as predictors of dominance maintained across different group configurations. Compared to FQ, the AA score has a weaker positive correlation between groups of 10 and 30 (Table S1). This score considers any neighbor within 50 cm as a potential interactor, and is perhaps less scalable to high densities than the FQ score, which considers only the nearest feeding neighbor.

Leadership. We analyzed leader-follower relationships from high-resolution GPS tracks of flock flights. For each dyad in a flock, we quantified leadership as the mean time delay between the two birds' directional choices (τ, Fig. 1C) (3). These pairwise time delays constitute a weighted (i.e. non-binary) network based on data from multiple flights. In the rest of the manuscript we focus on the directed edges (non-zero time delays) as a proxy for leadership. It is also possible to form a non-directed network from those pairs where the measurable time delays are close to zero (26). This alternative analysis, containing both mutual and directed connections, produced very similar results to the weighted directed case (for details see the SI).

The directed networks from flock flight trajectories revealed transitive leadership hierarchies in all three groups of 10 and in the combined group of 30 [$T_A=1$, $T_B=0.989$, $T_C=1$, $T_{ABC}=0.986$, $P<0.001$ in all cases, see Fig. S3]. We thus confirm Nagy *et al.*'s (3) earlier finding of hierarchical leadership, and extend both the methods and results to larger flocks of 30. Individual leadership scores were consistent between the groups of 10 and 30 (Pearson $r=0.56$, $N=30$, $P=0.002$), indicating that a pigeon's propensity for leadership does not depend on group composition, but more likely arises from some individual attribute that changes little from flight to flight. Leadership correlated neither with body mass nor with age (Table 1). In agreement with Nagy *et al.* (3), we found that leaders tended to be positioned toward the front compared to the average direction of motion of the whole flock (groups of 10: $r=0.87$, $P<0.001$, $N=30$ (3×10); group ABC: $r=0.92$, $P<0.001$, $N=30$).

Comparison of hierarchies. We performed a thorough correlation analysis between the stable hierarchies emerging in the contexts of social dominance and leadership, both at the level of individual ranks and using the more detailed pairwise interaction matrices (Tables 1, S1, S2). We used Fisher's combined probability test to summarize the correlations for the three independent groups of 10 (Table 1, Fig. 3, Fig. S4). For all our measures of social dominance, correlations with flight leadership remained non-significant ($P>0.05$). Given the reliability of our measurements of individual scores in both contexts (see above for tests of robustness of each of our metrics), this lack of correlation is unlikely to be due to a failure to detect an existing relationship. Thus, crucially, we found that leadership was independent of social dominance, despite the robustness and transitivity of both the dominance and leadership hierarchies.

Discussion

Our results clearly demonstrate that multiple, context-dependent hierarchies can co-exist simultaneously in the same group of animals. The computer-vision based analysis of interactions among feeding pigeons revealed transitive social dominance hierarchies, significantly different from randomly-directed networks. When we compared social dominance to leader-follower relationships in the air, we found that the stable, hierarchical pattern of in-flight leadership does not build upon the stable, hierarchical social dominance structure evident in the same birds. Instead, in the case of pigeon flocks, the emergence of leadership and dominance hierarchies are each affected by different factors. By ignoring social dominance when in flight, flocks of pigeons potentially make better navigational decisions because leadership can emerge from relevant attributes such as local experience and route fidelity (27, 28). In despotically organized societies of mosquitofish and meerkats it has also been observed that the dominant individual is not necessarily the leader (18, 29), however in neither of these cases were dominance relationships quantified as multilevel networks.

The dissociation between dominance and leadership in pigeons suggests that pigeons have a different mechanism either of dominance or of leadership, when compared to species where dominants lead (e.g. grey wolves, chacma baboons) (7, 9, 30). In common with those species, dominance in pigeons is associated with aggression and large body size. Therefore it is likely that what makes pigeons different from, for example, baboons, is the way leadership emerges. An airborne flock deciding on a direction cannot interact aggressively in the same way as it can on the ground, which may isolate leadership from dominance to a greater extent than in purely terrestrial animals.

Dominance is not the only aspect of individual variability that may be relevant to compare to leadership. We expect that our study will motivate more research into how leadership relates to other individual differences, either measured from other contexts of interaction network (association, courtship, mate choice, etc.) or from biophysical parameters. We did not find a correlation between leadership and age, but all of our subjects were experienced adults, so this does not rule out a difference between adults and juveniles. Age-related leadership has been reported in African elephants (31) and in some migratory birds such as broad-winged hawks, where adults tend to fly in front of juveniles (32). In these wild migratory species, experience accumulates linearly with age, which is not necessarily the case in domestic pigeons.

In addition to our findings concerning dominance and leadership, our automated dominance analysis methods could be applied to other forms of tracking data (e.g. RFID tags, GPS loggers), even in species with prolonged, noisy contests (Table S3). The results of our automated methods were in close agreement with the more traditional method of manually scoring aggressive encounters, with the added benefit that the automated methods can monitor multiple pairwise interactions occurring in parallel within large groups. Our study demonstrates the benefit of applying different types of tracking technology to the same group of animals, to investigate the wider biological context of patterns in collective motion. We provide new tools for studying social complexity within the emerging field of high-throughput ethology (20), applicable across a wide range of group-living species from insects to mammals including humans. A broader taxonomic perspective, including our current results on pigeons, will aid in understanding how the structure of interaction networks changes across different behavioral contexts.

Materials and Methods

Subjects. We used 30 homing pigeons (*Columba livia*) from two neighboring lofts at the Oxford University Field Station. Birds were allocated to three groups of 10 (A, B and C) and also tested in a combined group of 30 (group ABC). Groups A and B contained individuals only from Lofts 1 and 2, respectively. Group C contained birds from both lofts. Feeding trials took place in the home loft (groups A and B) or alternated between the two lofts (groups C and ABC). Both feeding and flock flight experiments were interspersed over a period of two months. The procedures outlined in this article were approved by the Ethical Review Committee of Oxford University's Department of Zoology.

Feeding experiments. Groups of 10 or 30 pigeons were given access to a single food source (a small ceramic cup containing grain mix; Fig. 1A) inside the pigeon loft. Food was replenished every 12mins, and trials were terminated when 10mins passed with only one pigeon feeding. Each pigeon participated in no more than one trial per day. All trials were video recorded by a camera fixed to the ceiling (Panasonic DMC-FS10, 2.1x1.2 m^2 field of view, 1280x720 resolution, 30 fps). Eight, 6, 8, and 10 trials were conducted for groups A, B, C, and ABC, respectively, producing 21.4 h of video. Each pigeon carried a unique three-color barcode on its back, enabling computer vision based reconstruction of individual trajectories resulting in 10 million identified pigeon positions on the 2.4 million frames of video.

The recorded video sequences were analyzed off-line and verified against frame-by-frame manual identification (see SI for details).

Flock flights. GPS data were collected from free flights of flocks around the loft (7 flights each for groups A, B, C; 10 for group ABC). Maximum two flights were conducted per day. The GPS logger weighed 13g, was based on a commercially available embedded device (Gmsu1LP), logged time-stamped longitude, latitude and altitude data at 10 Hz, and was affixed to a pigeon's back with an elastic harness. Loggers were randomly allocated to pigeons before every flight. In other respects, the flight experimental procedure and data handling were identical to those in Nagy *et al.* (3). Of the 360 individual trajectories flown, 25 were partly or entirely missing due to device error. In total, GPS devices logged 90.5 h of flight time, representing >3,250,000 data points.

Automated dominance analysis. We used two methods: Feeding-Queuing (FQ) and Approach-Avoidance (AA), both of which are pairwise measures calculated for each pair of birds. FQ provided an estimate of the relative frequency with which bird *i* was in a position that excluded bird *j* from accessing food. We classified a bird as "feeding" if it was located within a radius of <20 cm from the cup, with the head pointing towards the cup's center (±30°). We classified a bird as "queuing" if it was in the vicinity of the food cup (<60 cm from the cup) but was not "feeding" according to our criteria (Fig. 1A, Movie S1). When bird *j* was queuing, we calculated the total time that bird *i* was its closest feeding neighbor, and divided this by the total time that *i* or *j* was classed as feeding or queuing. FQ relations were detected in a total of 4 million position pairs.

AA was defined for each pair of birds (*i*≠*j*) as the time-averaged dot product of *i*'s velocity ($v_i(t)$) and the direction from *i* to *j* ($d_{ij}(t) = \left(x_j(t) - x_i(t)\right)/\left|x_j(t) - x_i(t)\right|$): $AA_{ij} = \left\langle v_i(t) \cdot d_{ij}(t) \right\rangle_t$. We averaged AA_{ij} across all frames when *i* and *j* were within 50 cm of each other ($\left|d_{ij}(t)\right| \le d_{\max} = 50$cm) and *i* was moving at least 0.05 ms^{-1} ($\left|v_i(t)\right| \ge v_{\min} = 0.05$m/s). AA_{ij} is positive if *i* tends to approach *j* and negative if *i* tends to avoid *j* (Fig 1B, Movie S2).

To check both types of automated dominance analysis against human observation, we manually scored agonistic interactions in approximately half of the videos. We recorded pecking, wing slapping, chasing, and whether the attacked bird retreated or fought back (see SI). From these events, we compiled a third type of interaction matrix for each group, which we termed Pecking Order (PO), and then compared the three dominance analysis methods PO, FQ, and AA.

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Author Contributions

M.N., B.P., T.V. and D.B designed the experiments; B.P. and M.N. performed the experiments; G.V. designed the GPS device and the computer vision software framework; I. R-M. performed the manual scoring; M.N., G.V. and B.P. designed the analysis of data; G.V. and M.N. performed the data analysis and visualization; and B.P., M.N., G.V., and D.B. wrote the paper.

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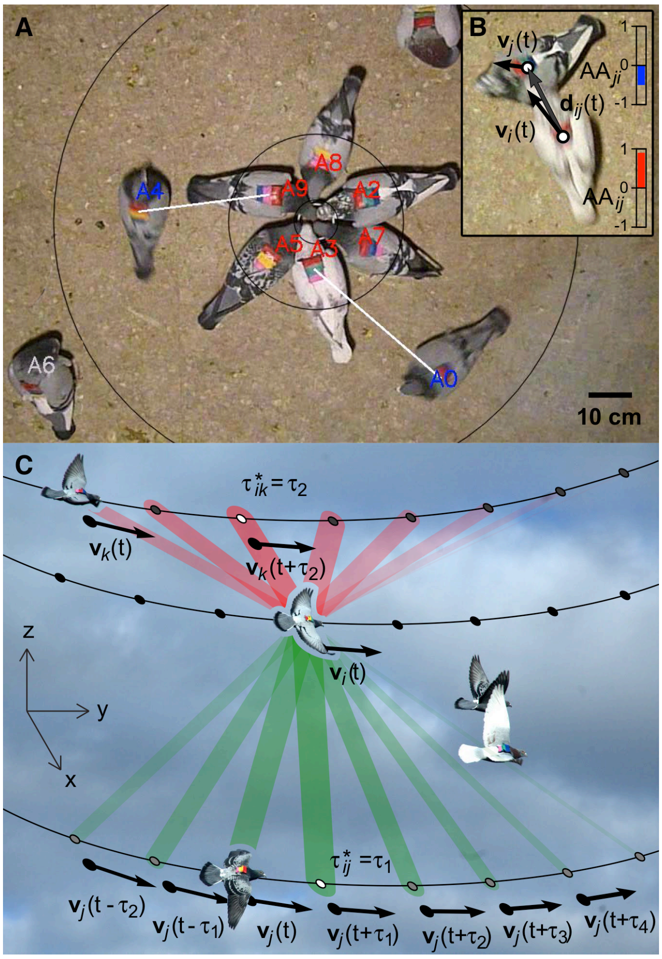

Fig. 1. Automated analysis of dominance and leader-follower relationships. (**A**) Frame from feeding experiment. Color of identified IDs indicates automated behavior categorization based on the concentric zones: red – feeding (5–20cm), blue – queuing (20–60cm), grey – outside zone of interest. White lines indicate FQ interactions between queuing birds and their respective closest feeding neighbors. (**B**) Illustration of Approach-Avoidance (AA) calculation. For birds *i* and *j* AA (shown by bars on the right) is the dot product of *i*'s velocity ($\mathbf{v}_i$) and the direction from *i* to *j* ($\mathbf{d}_{ij}$). $AA_{ij} \approx 1$: bird *i* is approaching; $AA_{ji} < 0$: bird *j* is avoiding. (**C**) Schematic illustration of leader-follower analysis, superimposed on a photo of subjects carrying GPS devices. For three birds (*i*, *j* and *k*) a segment of trajectories are shown, with arrows indicating their direction of motion, $\mathbf{v}_i(t)$ in the horizontal plane. For each pair ($i \neq j$), $\mathbf{v}_i(t) \cdot \mathbf{v}_j(t+\tau)$ is the dot product of the normalized velocity of bird *i* at time *t* and that of bird *j* at time $t+\tau$, indicated by the width of the colored edge. τ^* is the time delay with the maximal correlation (marked with white dot) with which birds *j* and *k* are following bird *i*.

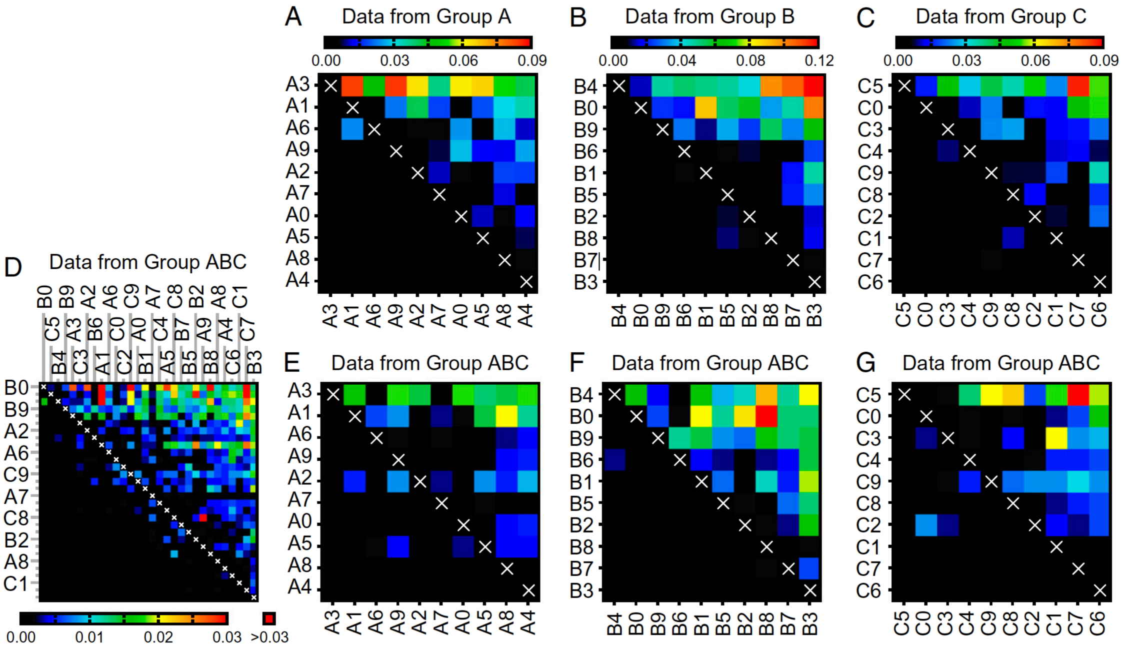

Fig. 2. Dominant part of the Feeding-Queuing (FQ) interactions, comparing the groups of 10 and the combined group of 30. The color-coding illustrates the strength of the dominant part of the FQ interaction matrix. In all panels, the more values above the diagonal, the higher the transitivity of the matrix. (**A-C**) Interactions measured in the groups of 10. Individuals are ordered according to their Normalized David's Scores (NormDS). (**D**) Interactions measured in the combined group of all 30 individuals. Individuals are ordered according to NormDS from the group of 30. (**E-G**) To visualize the stability of dominance (and our dominance metric) across independent measurements involving 10 and 30 individuals, we plotted on Panels E to G the same data as on Panel D but with individuals in the same order as in panels A-C (i.e. using NormDS calculated within groups of 10). The matrices for groups A (in A and E), B (in B and F), and C (in C and G) are highly similar, meaning that the dominance relationships in the groups of 10 were also detected in the group of 30. The corresponding interaction matrices for leadership are shown in Fig. S3.

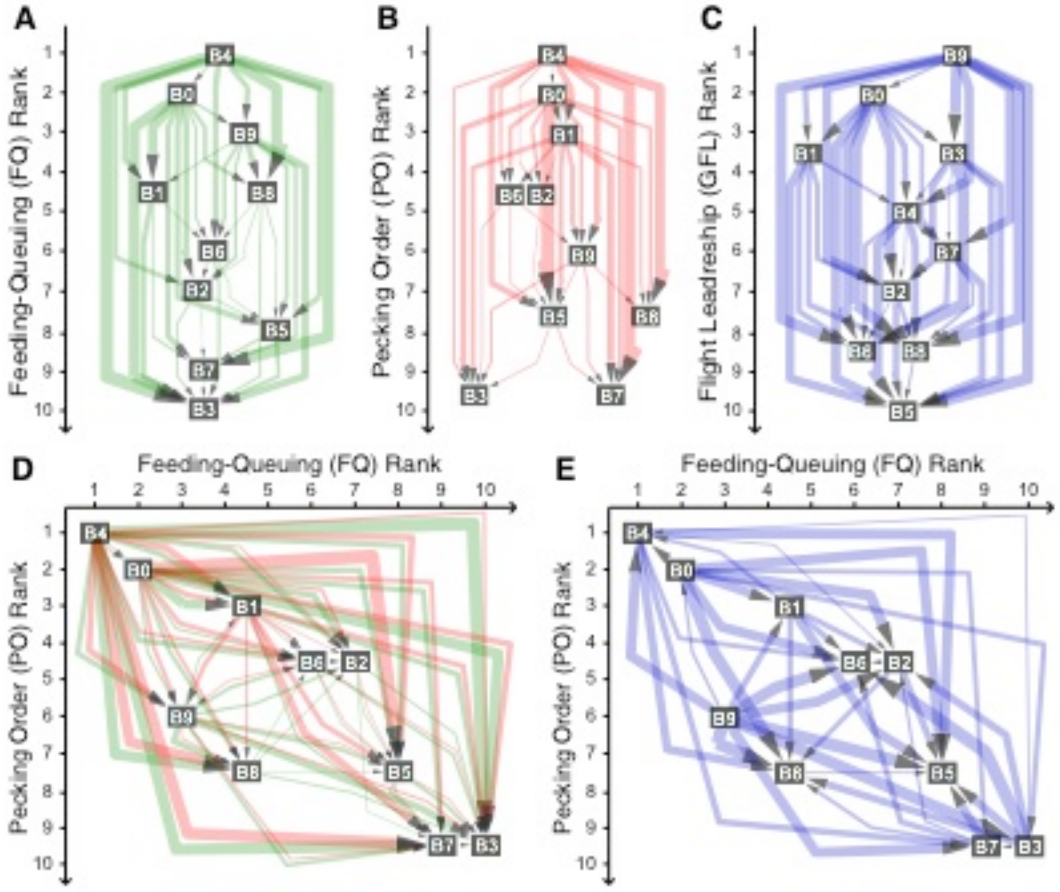

Fig. 3. Dominance and leadership networks. (**A)** Feeding-Queuing (FQ), (**B**) Pecking Order (PO), (**C**) Group Flight Leadership (GFL) networks for group B. Directed edges point from the dominant or leader to the subordinate or follower, with edge widths corresponding to interaction strength. Nodes are ordered vertically according to rank, with dominants/leaders at the top. (**D**) Comparison of FQ (green) and PO (red) networks (same edges as panels A and B). Horizontal position of nodes corresponds to FQ rank, vertical to PO rank. Nodes close to the diagonal and the similarity of green/red edges indicate high correlation between FQ and PO. (**E**) Flight leadership network superimposed on the layout created from dominance ranks FQ and PO (i.e., same node positions as panel D, same edges as panel C). The absence of correlation between the GFL and FQ/PO rankings is apparent from the random direction of the arrows. See Fig. S4 for the corresponding networks for groups A and C.

	Dominance			Other parameters			Leadership	
	AA	FQ	PO	TAF	Size	Age	GFL	10 vs. 30
Dominance								
AA	X	**<0.001**	**<0.001**	**0.044**	0.768	0.730^{-}	0.183	**0.025**
FQ	**<0.001**	x	**<0.001**	**<0.001**	**0.020**	0.649^{-}	0.104	**<0.001**
PO	**<0.001**	**<0.001**	x	**0.007**	0.421	0.866^{-}	0.411	**<0.001**
Other parameters								
TAF	**0.044**	**<0.001**	**0.007**	x	**0.002**	0.787^{-}	0.126	**<0.001**
Size	0.768	**0.020**	0.421	**0.002**	x	0.213^{-}	0.522^{-}	x
Age	0.730^{-}	0.649^{-}	0.866^{-}	0.787^{-}	0.213^{-}	x	0.298	x
Leadership								
GFL	0.183	0.104	0.411	0.126	0.522^{-}	0.298	x	**0.010**

Table 1. Correlation between Dominance, Leadership and Other Parameters. The table shows *P*-values of the meta-analysis of the Pearson correlations for the three groups of 10 (A, B, C), using Fisher's combined probability test (*29*). For each group, we calculated two-tailed Pearson correlations for the Normalized David's Scores (NormDS) from the antisymmetrized interaction matrices. The final column contains *P*-values for Pearson correlations between individual scores of the same 30 birds when measured in their respective groups of 10 and their scores in the group of 30 (*N*=30), using NormDS to score dominance and leadership. Cells that contain significant correlations (*P*<0.05) are in bold and strong significant correlations (*P*<0.01) are highlighted in grey. AA – Approach-Avoidance; FQ – Feeding-Queuing; PO – Pecking Order; TAF – Time at Feeder; GFL – Group Flight Leadership. See main text and Table S3 for descriptions of variables. See Table S1 for correlation coefficients and *P*-values of all groups, calculated using pairwise interaction values as well as NormDS.

Supporting Information

Supplementary Materials and Methods:

The computer vision algorithm and its validation. The recorded video sequences were analyzed off-line. The position and orientation of all visible colored barcodes were identified in each frame using a dedicated script based on OpenCV, an open-source computer vision library (1). Barcode colors were chosen to minimize interference from the natural coloring of the scene. The first part of the algorithm identified the position of the possible barcode bins using HSV (hue-saturation-value) color space filtering. This set of bins was analyzed further heuristically to obtain optimal matching with existing barcode definitions for all frames on a possible, smooth trajectory for each barcode. The recognized barcode IDs were added to the original videos for visual inspection of the accuracy and to aid the manual analysis of agonistic interactions.

We tested the accuracy of the automated video tracking against the detailed manual identification of all barcode positions and orientations in all frames of a 12-minute video segment, using custom-made software and many hours of manual work. The barcode detection was robust; only 13% remained undetected. For the detected IDs, the match between the automatic and manual recognitions with acceptable error in position (2 pixels = 3.3cm) and orientation (15 degrees) was 90%. The visual inspection of the other barcode-tagged videos showed acceptable performance as well, especially for the purpose of statistical analysis.

Pecking Order Interaction coding protocol. After the automated detection of IDs, we manually scored agonistic interactions, in order to test how our automated dominance analysis methods compared to human observations. For this purpose, we tagged the original video recordings with the identified IDs of birds and used a subtitle editing software to comment on all pairwise interactions with IDs involved, interaction time, duration and type (i.e. pecking, wing flapping, chasing, retreat, etc.). Again, automatic methods were used to quick-check the manual tagging and categorize interactions into most aggressive, non-aggressive or mutual types.

The format of the subtitles was the following:

x ID1 *s* ID2

where *x* denoted the interaction type (see the full list below), ID1 and ID2 denoted the color barcode on the backpacks of birds (3 letters, initials of the colors from head to tail),

s denoted the interaction type between the birds, i.e. directed (>) or mutual (–). In case of directed interactions, ID1 was dominant, ID2 was subordinate.

Identified interaction types:

p	pecking
w	wing slapping
pm/wm	pecking or wing slapping which is missed
c	chasing
o	obtrusion, pushing
s	scaring away or frightening
f	fighting, could be mutual or clearly one way
d	defense: the attacked one (second bird) tries to defend itself for example by waving its wings or expresses its distress any other way, but not trying to directly attack its attacker
2x	in a fight a clearly defined action (x could be w, p, o, etc.) initiated by the attacked bird (2nd in the interaction)
r	retreat: when the attacked one clearly retreats after the action (2nd bird)
g	give up the fight: when the attacker one moves away after the action (1st bird)
i	interesting other event
n	note: any type of comment.

Definition of transitivity and symmetry indices. In addition to defining simplified dominance scores for each individual, we treat the pairwise interactions as a matrix M, where M_{ij} is the number of interactions (e.g. PO, FQ, etc.) initiated by bird i towards bird j. We separate the full interaction matrix into common (C) and dominant (D) parts:

$M = C + D$, where

$$C_{ij} = \min(M_{ij}, M_{ji})$$
$$D_{ij} = \max(M_{ij} - M_{ji}, 0) = M_{ij} - C_{ij}$$

Note that this matrix separation is similar to but slightly different from the standard symmetric/anti-symmetric matrix decomposition. Instead of a symmetric part, which is the average of the pairwise interactions, we have a common part that represents the strength of two-way interactions. Similarly, instead of the anti-symmetric part, which can contain negative values that are incompatible with some methods, we have a dominant part containing the strength of outgoing interactions, above the level of two-way (common) interactions.

The symmetry index (S) is defined from the C and M matrices as follows:

$$S = \frac{\sum_{i,j,i\neq j} C_{ij}}{\sum_{i,j,i\neq j} M_{ij}}$$

S ranges from 0 to 1; high S values mean that the interactions are overwhelmingly mutual, small S represent a society where most of the pairwise interactions are dominant in one direction only.

The transitivity index (T) is defined from the D matrix as follows:

$$T = \frac{\sum_{i,j,j>i} D_{ij}}{\sum_{i,j,i\neq j} D_{ij}}$$

Note that *T* is basically the ratio of the total interactions in the upper triangle of *D* relative to all the interactions in *D* and thus it is dependent on the order of the rows and columns of the matrix. Therefore, before calculating *T*, we need to calculate a ranking among the individuals and order the rows accordingly. This is equivalent to the feedback-arc set problem in graph theory. The solution is straightforward if there are no loops and the hierarchy is linear/transitive, and it has multiple equivalent solutions if there are loops or independent subgroups. For a quick close-to-optimal solution, we used a heuristic ranking with the Eades method (2).

T ranges from 0.5 to 1. Higher values correspond to fewer loops in the hierarchy. However, further analysis of the *D* matrix itself might be needed to interpret *T* (cluster analysis, careful manual analysis of cases with many loops, etc.). To test the significance of *T* for a given matrix size, we formed a null distribution by calculating *T* from the Eades-ordered Dominant part (*D*) of 1 million random matrices (values in the range of 0-100). The *T* values from this randomization approximate a normal distribution (see Fig. S2) with the following fit parameters for matrix sizes 10 and 30 (corresponding to the group sizes in our experiment): adjusted R^2_{10}= 99.87%, μ_{10}=0.79203 ± $7.3*10^{-5}$, σ_{10}= 0.04908 ± $7.8*10^{-5}$, adjusted R^2_{30}= 99.91%, μ_{30}=0.68010 ± $2.2*10^{-5}$, σ_{30}= 0.01676 ± $2.2*10^{-5}$ (mean ± S.E.).

Network representation of interaction data and its layout. The network representations in the manuscript and the supplementary materials (Fig. 3, Fig. S4, inset in top right corner of Movie S3) were based on the following procedure: i) The dominant part (See section “Definition of transitivity and symmetry indices”) of the interaction matrices (FQ, AA, PO and GFL) was calculated. This is similar to the composition of an anti-symmetric matrix and using 0 as a lower limit cut-off. For the network visualization, the cut-off value was actually not 0 but ε, to reduce the effect of noise. In pairs where both individuals fight/dominate/lead the other in almost equal times ($M_{ij} \approx M_{ji}$, where *M* represents any of the interaction matrices), the anti-symmetric part will be around 0 and the directionality of the interaction will be exposed to a high relative error. To filter these elements, the standard deviation (SD) of the matrix was calculated and $\varepsilon = \mathrm{SD}(M)/10$ was used as a cut-off. In other words, no edge was drawn between birds *i* and *j* if $D_{ij} < \varepsilon$ and $D_{ji} < \varepsilon$. If there was no chain of directed edges from *i* to *j* (i.e. no $i \to k \to j$) , then *i* and *j* were drawn on the same level in the hierarchy.

As shown in the section “Definition of transitivity and symmetry indices” these matrices were highly transitive, containing no or very few directed loops (even with 0 as cut-off). To convert the networks with ε cut-off to completely transitive networks, the weakest links in the loops were removed until all the loops were eliminated. For the FQ networks 4 edges were removed for the three groups of 10 (A: 2 edges, B: 0 edges, C: 2 edges). For the PO networks 1 edge was removed from group A. For GFL networks 1 edge was removed from group B.

In the simultaneous visualization of the different dominance and leadership networks the strength of the interactions are shown by the width of the edges (Fig. 3, Fig. S4). For this purpose the networks were normalized by the maximal value (there were no large outliers). The average and standard deviation for the resulted normalized networks (A+B+C) were 0.23 ± 0.20 for FQ, 0.25 ± 0.20 for PO and 0.50 ± 0.22 for GFL.

We used a hierarchical network layout on Fig. 3A-C, Fig. S4. These networks were all directed and acyclic, i.e. composed of directed edges and containing no directed loops. We used the hierarchical network visualization of Cytoscape (3), which is in principal based on the Sugiyama method (4). It is a layered graph visualization method in which the vertices of a directed graph are drawn in horizontal rows or layers with the edges generally directed downwards. The nodes within each layer are permuted in an attempt to reduce the number of crossings among the edges connecting it to the previous layer. So the horizontal layout contains no information, just supports transparency. The vertical layout contains information about the rank of the nodes. Nodes were added on the same layer if their relative position could not be resolved as either directly or indirectly connected by a directed chain of edges. Our networks were quite densely connected, so in the majority of the cases the rules written above give an unequivocal position for each node. However, on the few cases when a node could be placed on several layers, the highest possible layer was used.

To compare two different networks, we used the two-dimensional hierarchical layout where the vertical positions of the nodes represent the hierarchical layers of one of the networks, while the horizontal position of the nodes represent the hierarchical layers of the other network. Edges are placed to maximize transparency.

Dominance indices. We calculated and compared several dominance indices of the literature on our data, including Kalinoski's Frequency of Success Index, Lindquist's dominance index, the Batchelder-Bershad-Simpson Scale Score, and de Vries' (Modified) (Normalized) David's Scores (5–7; 23 in main text). Since our interaction matrices were highly transitive, the choice of the dominance index was not crucial, i.e. the final rankings defined by the different dominance scores were extremely similar (e.g. for FQ interactions the Pearson-correlation between the four scores was over 0.99 for all groups). Therefore, we chose one, the Normalized David's Score (NormDS) (23 in main text), which was simple to calculate and could easily be generalized to matrices with non-integer elements. This was needed in the case of AA and GFL data and for matrices generated from individual scores (e.g. size difference, age difference). In all these cases the normalization factor was not the maximal interaction, as defined originally for matrices with integers, but the total scale of the matrix values:

$$NormDS_i = \frac{DS_i - \min_{ij}(w_{ij})}{\max_{ij}(w_{ij}) - \min_{ij}(w_{ij})}(n-1),$$

where w_{ij} is the interaction of bird *i* towards bird *j*, *n* is the number of birds in the given group, DS_i is the original David's score defined as

$$DS_i = w_i(1) + w_i(w_j) - l_i(1) - l_i(l_j), \quad w_i(x) = \sum_{j=1}^{n} x \frac{w_{ij}}{w_{ij} + w_{ji}}, \quad l_i(x) = \sum_{j=1}^{n} x\left(1 - \frac{w_{ij}}{w_{ij} + w_{ji}}\right)$$

Note that the NormDS scores were calculated from the raw interaction matrices without the Common – Dominant separation. For the matrices generated from individual scores, the NormDS values ranked the individuals in the same order as the original data, with a perfectly linear relation between the two.

Comparing the interaction matrices. For each group of 10 (A, B, C) and the group of 30, two-tailed Pearson correlation was used to compare interaction data from different contexts. Table S1 shows the correlation between NormDS values, as well as an alternative method using the pairwise interaction values (i.e. all matrix elements). For Pearson correlations on pairwise interaction values, we tested significance using the quadratic assignment method (see e.g. Hemelrijk (8)), a type of random permutation procedure. One matrix is permuted by shuffling the individuals into a new order and using this random order in both the rows and the columns. The other matrix is left unchanged. For each permutation, the Pearson correlation between the elements of the two matrices is calculated. The correlation coefficients from 20000 randomizations formed a null distribution, which we compared to the correlation coefficient between the elements of the two original interaction matrices. In case of positive (negative) correlation the *P*-value was given as two times the proportion of randomized matrices with a higher (lower) correlation value than the original case.

The comparison described above used the interaction matrix elements as values, which is equivalent to a weighted directed network representation. As an alternative method, we compared the interactions in a way that treats the separated directed (dominant) and undirected (common) parts of the interaction matrices together, within the same framework. Here, the weighted interaction matrices are converted into unweighted mixed graphs containing both directed and undirected connections. For each pair the interaction is characterized by a directed edge represented by 1 (or -1) if the interaction is mostly dominant (or subordinate); an undirected edge represented by 0 if the interaction is best described as mutual; or with no connection if there is no significant interaction between the individuals.

The transformation of the Dominant and Common parts into directed and undirected edges was as follows: we calculated the average of all values in each matrix and used the averages as lower thresholds. If the Dominant part of an interaction was above average, we defined it as a directed edge, else if the Common part was above average, we defined it as an undirected edge, otherwise there was no edge. For the four interaction types (FQ, AA, PO, and GFL), and for all groups, the mixed graphs described above are presented as adjacency matrices in Fig. S5.

Two network similarity measures were used to compare the mixed graphs: the Jaccard Index (9) and the Hamming distance (10). The Jaccard Index is defined as the size of the intersection (the number of pairs that have the same edge in both networks) divided by the size of the union of the sample sets (the number of pairs that have an edge in at least one of the networks):

$$JI(A,B) = \frac{|A \cap B|}{|A \cup B|}.$$

For identical networks *JI*=1, whereas values close to 0 indicate low similarity.

The Hamming distance is defined as the number of pairs for which the edges in the two networks are different. Low Hamming distance therefore indicates high similarity between networks. The Hamming distance can be weighted for a given pair, by a factor of 2, when both networks had directed edges, but in opposite directions. The weighted Hamming distance gave very similar results to the original Hamming distance, so only the results for the latter are shown.

To test the significance of the similarities, we used the same randomization technique described above. The results of the comparison are presented in Table S2. To test the sensitivity of the results to the chosen threshold for defining edge types, we ran the analysis with thresholds of 120% and 80% of the average. Compared to Table S2, the results from these alternative thresholds only changed the significance of the similarities in 1.4% and 5.6% of cases, respectively, indicating that the results are robust to the choice of threshold. Overall, the comparison using the mixed graph representation gives very similar results to the weighted interaction representation (Tables 1, S1, S2). This supports the finding that the hierarchies are different in the dominance and leadership contexts.

Determination of momentary leadership. Movie S3 shows the momentary leadership role, based on the directional correlation delay method with a moving time window. At each time step *t*, $Corr_{ij}(\tau,t)$ correlation values were calculated for an interval [*t* – 3 s; *t* + 3 s], where $Corr_{ij}(\tau,t) = \left\langle v_i(t') \cdot v_j(t'+\tau) \right\rangle_{t' \in [t-3s;t+3s]}$. For each time step *t,* the maximal value of the $Corr_{ij}(\tau,t)$ correlation function was determined as $\tau_{ij}^*(t)$. The average directional correlation time delay, $\tau_i^*(t)$ of bird *i* at time *t* was determined by the average $\tau_{ij}^*(t)$ for all *j* flock members, with the following two conditions: i) $Corr_{ij}(\tau_{ij}^*,t) > Corr_{\min} = 0.9$; ii) $v_j(t) > 5$ m/s (most probably flying). For further calculations, we only used time steps for which at least three flock members fulfilled the previous two requirements. For each time step *t,* the degree of momentary leadership was determined by ranking all birds according to their $\tau_{ij}^*(t)$ in decreasing order using fractional ranking. In Movie S3, we label the top six momentary leaders. For these six birds, the size of the dots on both the trajectory and the leadership network is negatively proportional to the momentary leadership rank.

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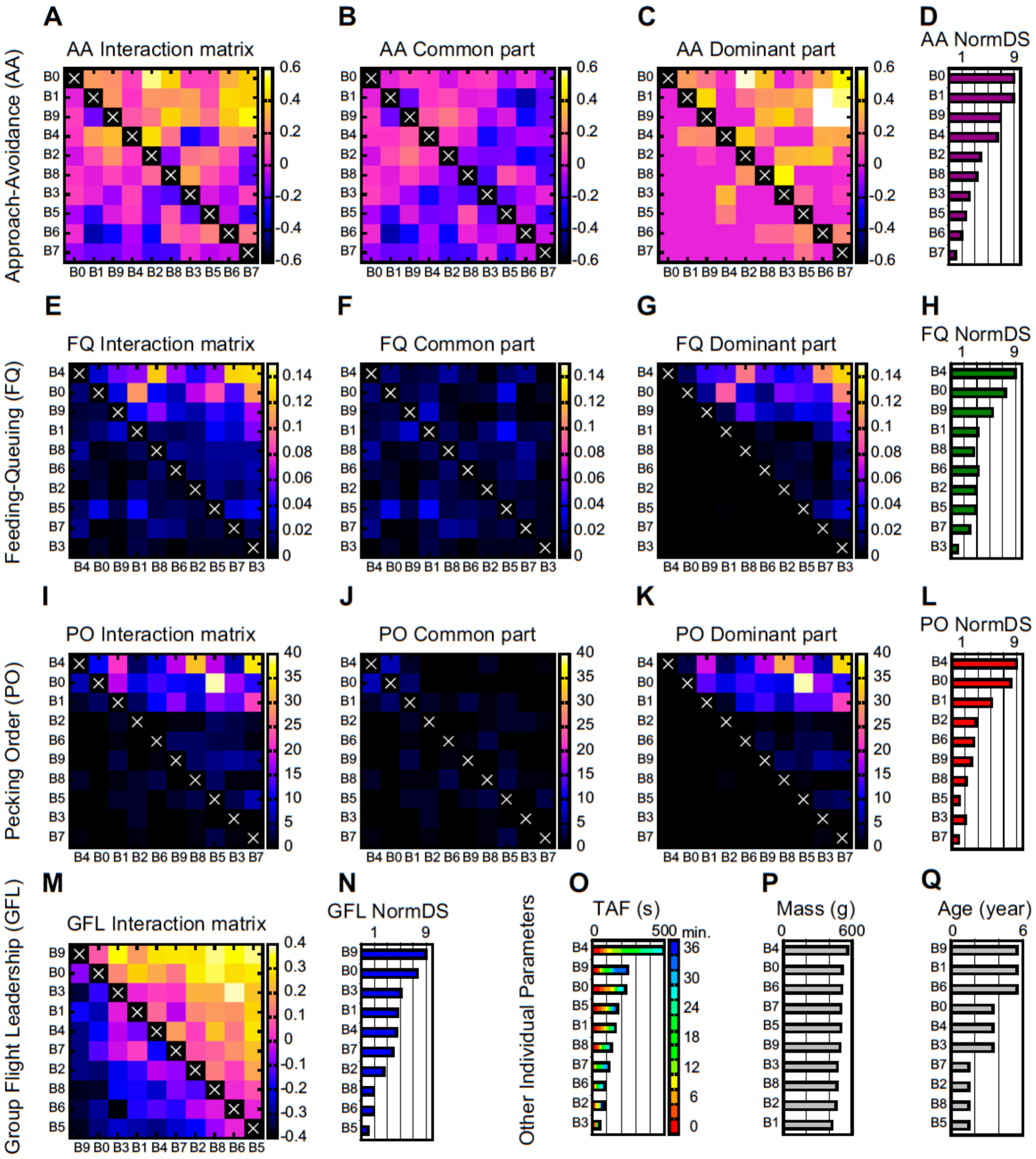
Fig. S1. Interaction matrices and Normalized David Scores (NormDS) of group B for Approach-Avoidance (AA; A-D), Feeding-Queuing (FQ; E-H), Pecking Order (PO; I-L) and Group Flight Leadership (GFL; M, N), as well as the individual parameters Time At Feeder (TAF; O), Body mass (P) and Age (Q). The interaction matrices (*M*; shown in A, E, I, M) contain all recorded interactions. They were decomposed into a common part (*C*; in B, F, J) as $C_{ij} = \min(M_{ij}, M_{ji})$ and dominant part (*D*; in C, G, K) as $D_{ij} = \max(M_{ij} - M_{ji}, 0)$. The Normalized David Scores (NormDS, shown in D, H, L, N) were calculated from the anti-symmetrized matrices (not shown). No decomposition was needed for GFL, because the interaction matrix is anti-symmetric by definition. The individuals were ranked separately for each variable, based on the interaction matrix. Therefore, the individuals are shown in the same order across the panels for a variable, but different variables can have different orders. The rankings are the same as used in Fig. 3 of the main manuscript. In panel o, the color coding shows how much time each bird spent on average at the feeder in each 3-minute segment of the feeding period. There was high correlation among all measured body size parameters (wingspan, breast perimeter, mass), so only mass is shown (P).


A
AA Interaction matrix
B
AA Common part
C
AA Dominant part
D
AA NormDS
Approach-Avoidance (AA)
B0 B1 B9 B4 B2 B8 B3 B5 B6 B7
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
1
9
E
FQ Interaction matrix
F
FQ Common part
G
FQ Dominant part
H
FQ NormDS
Feeding-Queuing (FQ)
B4 B0 B9 B1 B8 B6 B2 B5 B7 B3
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
I
PO Interaction matrix
J
PO Common part
K
PO Dominant part
L
PO NormDS
Pecking Order (PO)
B4 B0 B1 B2 B6 B9 B8 B5 B3 B7
40
35
30
25
20
15
10
5
0
M
GFL Interaction matrix
Group Flight Leadership (GFL)
B9 B0 B3 B1 B4 B7 B2 B8 B6 B5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
N
GFL NormDS
Other Individual Parameters
O
TAF (s)
0
500
min.
36
30
24
18
12
6
0
B4 B9 B0 B5 B1 B8 B7 B6 B2 B3
P
Mass (g)
0
600
B4 B0 B6 B7 B5 B9 B3 B8 B2 B1
Q
Age (year)
0
6
B9 B1 B6 B0 B4 B3 B7 B2 B8 B5

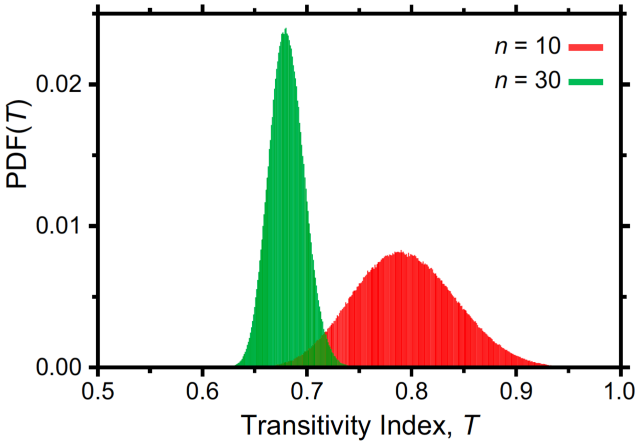


Fig. S2. Probability distribution functions of Transitivity Index based on 1 million random matrices of size 10 and 30. The transitivity is calculated on the Dominant part of the matrices after ordering their rows and columns with Eades-heuristics. The significance of a given T value of an arbitrary interaction matrix can be calculated based on the cumulative distribution function of a fitted normal distribution. Note that the significance of a given T value strongly depends on matrix size. Bin size on the horizontal axis is 0.001.

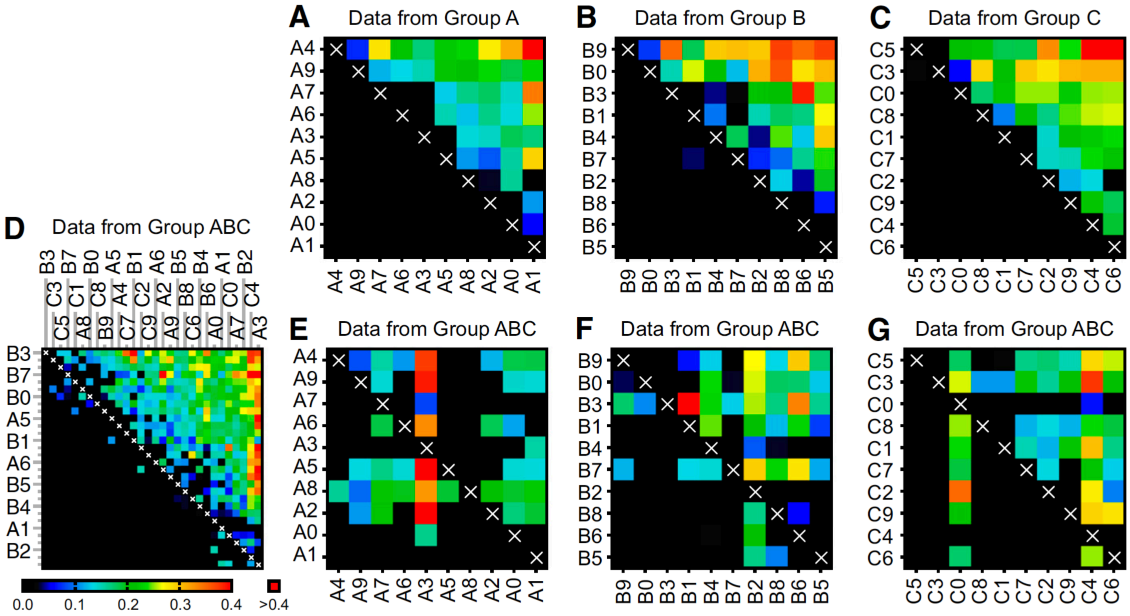


Fig. S3. Interaction matrices of group flight leadership, comparing the groups of 10 and the combined group of 30. Matrices are color-coded according to positive τ^* values (in seconds), i.e., the dominant part of the leader-follower interaction divided by 2. In all panels, the more values above the diagonal, the higher the transitivity of the matrix. (**A-C**) Interactions measured in the groups of 10. Individuals are ordered according to their Normalized David's Scores (NormDS). (**D**) Interactions measured in the combined group of all 30 individuals. Individuals are ordered according to NormDS from the group of 30. (**E-G**) To visualize the stability of leader-follower relationships across independent measurements involving 10 and 30 individuals, we plotted on Panels E to G the same data as on Panel D but with individuals in the same order as in panels A-C (i.e. using NormDS calculated within groups of 10). The matrices for groups A (in A and E), B (in B and F), and C (in C and G) indicate that most of the leader-follower relationships in the groups of 10 were also detected in the group of 30. The corresponding interaction matrices for FQ are shown in Fig. 2.

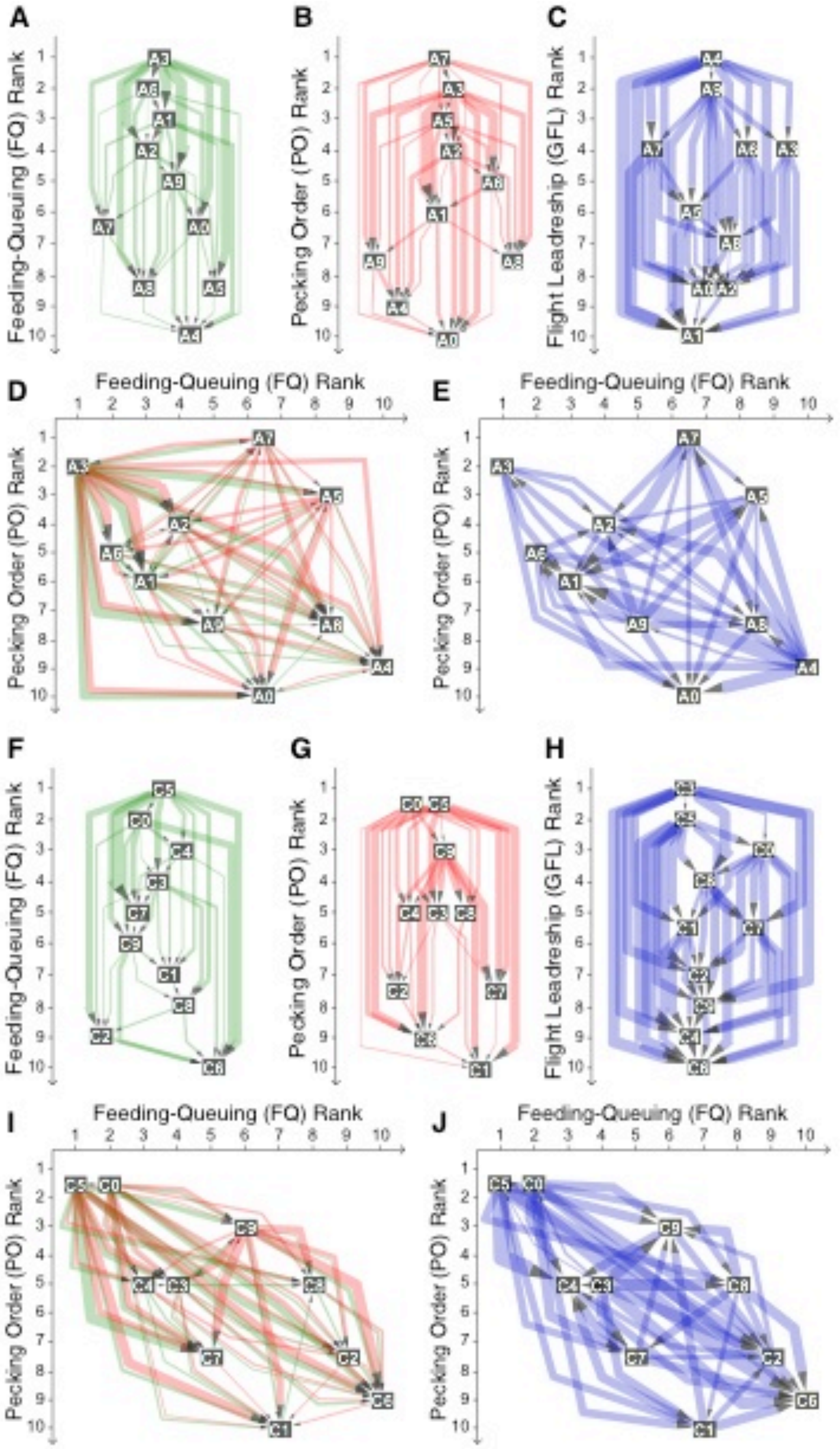


Fig. S4. Dominance and leadership networks for groups A and C. Data for groups A (**A-E**) and C (**F-J**) are presented here using the same types of plots as in Fig. 3 of the main manuscript. Fig. 3 shows the data for group B.

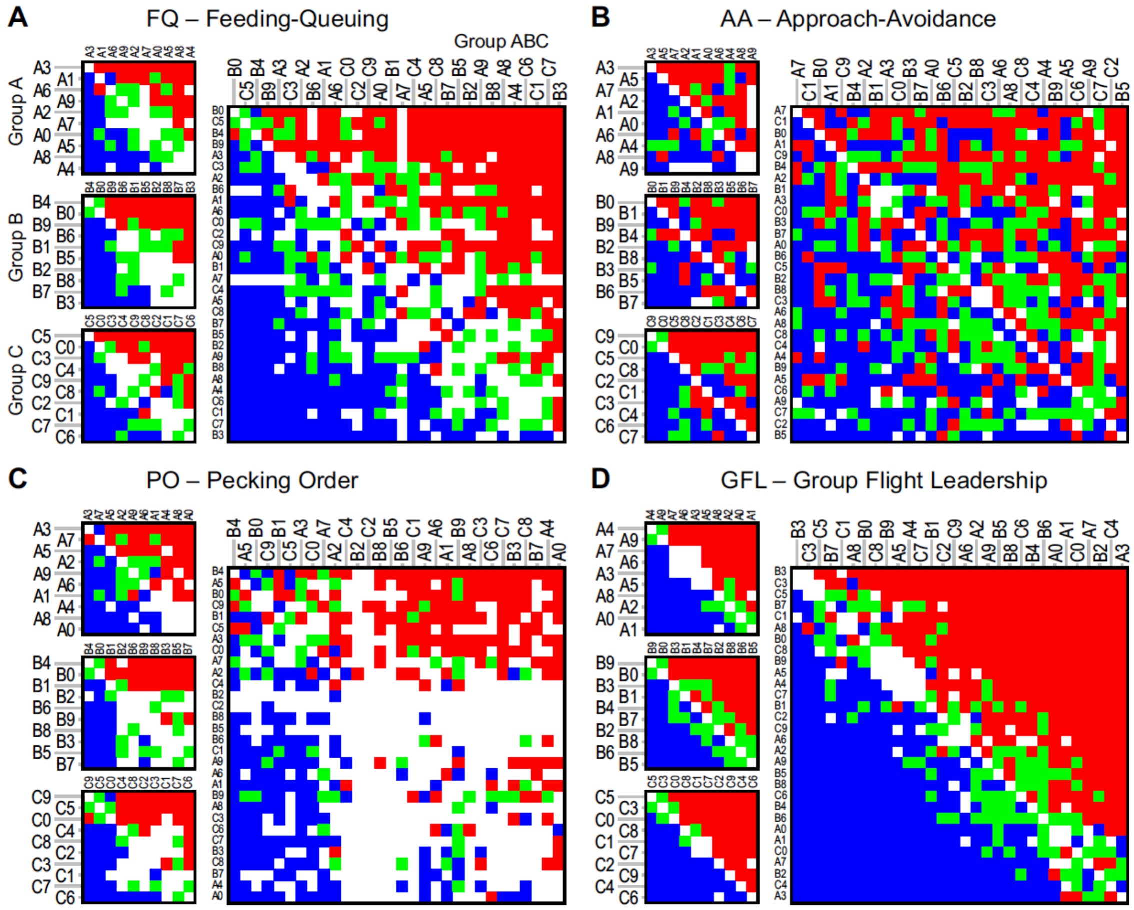
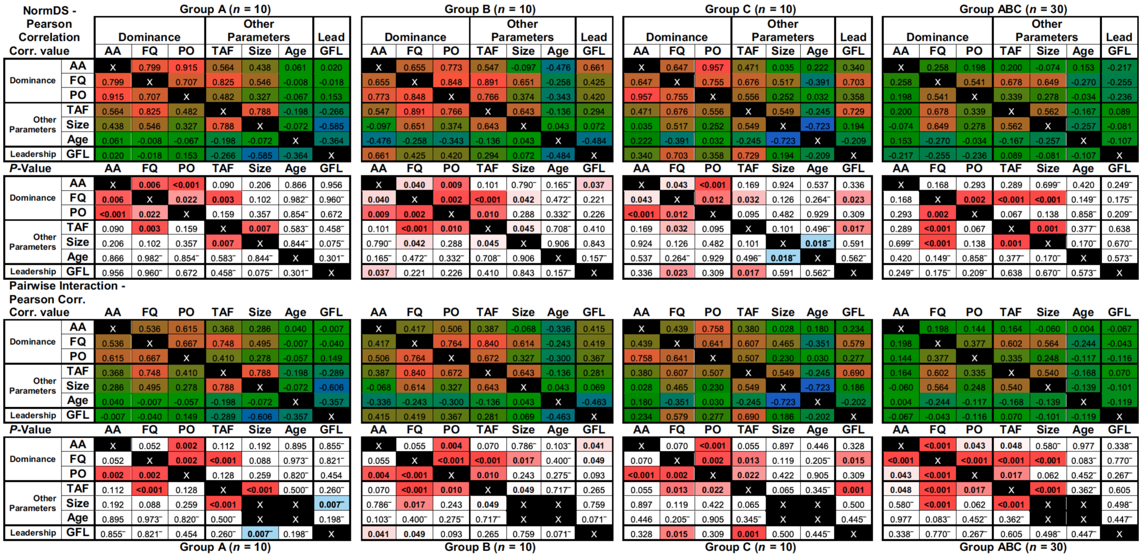


Fig. S5: Adjacency matrices of the mixed graph representation containing both undirected and directed edges for each interaction type (FQ on Panel A, AA on Panel B, PO on Panel C and GFL on Panel D). The 10x10 matrices on the left side of each panel show the data for the groups A, B and C (from top to bottom, respectively), and the 30x30 matrix contains data for the Group of 30. Color indicates the type of the edge: red - directed edge pointing from dominant/leader (in the row) to the subordinate/follower (in the column); blue - directed edge, reverse direction of a red edge; green - undirected edge for mutual interaction; white - no edge. In each matrix the individuals were ordered according to the NormDS scores of that interaction.

Table S1. Comparison of the dominance/leadership indices (top part) and the interaction matrices (bottom part) for groups A, B, C and ABC (from left to right). For more information please see section: Comparing the interaction matrices. Cells that contain significant correlations (*P*<0.05) are in bold. Color-coding of the *P*-values shows the significance of the correlation in red for positive correlations and in blue for negative correlations.



NormDS - Pearson Correlation Corr. value

Group A (*n* = 10)

		Dominance			Other Parameters			Lead
		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.799	0.915	0.564	0.438	0.061	0.020
	FQ	0.799	x	0.707	0.825	0.546	-0.008	-0.018
	PO	0.915	0.707	x	0.482	0.327	-0.067	0.153
Other Parameters	TAF	0.564	0.825	0.482	x	0.788	-0.198	-0.266
	Size	0.438	0.546	0.327	0.788	x	-0.072	-0.585
	Age	0.061	-0.008	-0.067	-0.198	-0.072	x	-0.364
Leadership	GFL	0.020	-0.018	0.153	-0.266	-0.585	-0.364	x

Group B (*n* = 10)

		Dominance			Other Parameters			Lead
		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.655	0.773	0.547	-0.097	-0.476	0.661
	FQ	0.655	x	0.848	0.891	0.651	-0.258	0.425
	PO	0.773	0.848	x	0.766	0.374	-0.343	0.420
Other Parameters	TAF	0.547	0.891	0.766	x	0.643	-0.136	0.294
	Size	-0.097	0.651	0.374	0.643	x	0.043	0.072
	Age	-0.476	-0.258	-0.343	-0.136	0.043	x	-0.484
Leadership	GFL	0.661	0.425	0.420	0.294	0.072	-0.484	x

Group C (*n* = 10)

		Dominance			Other Parameters			Lead
		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.647	0.957	0.471	0.035	0.222	0.340
	FQ	0.647	x	0.755	0.676	0.517	-0.391	0.703
	PO	0.957	0.755	x	0.556	0.252	0.032	0.358
Other Parameters	TAF	0.471	0.676	0.556	x	0.549	-0.245	0.729
	Size	0.035	0.517	0.252	0.549	x	-0.723	0.194
	Age	0.222	-0.391	0.032	-0.245	-0.723	x	-0.209
Leadership	GFL	0.340	0.703	0.358	0.729	0.194	-0.209	x

Group ABC (*n* = 30)

		Dominance			Other Parameters			Lead
		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.258	0.198	0.200	-0.074	0.153	-0.217
	FQ	0.258	x	0.541	0.678	0.649	-0.270	-0.255
	PO	0.198	0.541	x	0.339	0.278	-0.034	-0.236
Other Parameters	TAF	0.200	0.678	0.339	x	0.562	-0.167	0.089
	Size	-0.074	0.649	0.278	0.562	x	-0.257	-0.081
	Age	0.153	-0.270	-0.034	-0.167	-0.257	x	-0.107
Leadership	GFL	-0.217	-0.255	-0.236	0.089	-0.081	-0.107	x

***P*-Value**

Group A (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	**0.006**	**<0.001**	0.090	0.206	0.866	0.956
	FQ	**0.006**	x	**0.022**	**0.003**	0.102	0.982¯	0.960¯
	PO	**<0.001**	**0.022**	x	0.159	0.357	0.854¯	0.672
Other Parameters	TAF	0.090	**0.003**	0.159	x	**0.007**	0.583¯	0.458¯
	Size	0.206	0.102	0.357	**0.007**	x	0.844¯	0.075¯
	Age	0.866	0.982¯	0.854¯	0.583¯	0.844¯	x	0.301¯
Leadership	GFL	0.956	0.960¯	0.672	0.458¯	0.075¯	0.301¯	x

Group B (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	**0.040**	**0.009**	0.101	0.790¯	0.165¯	**0.037**
	FQ	**0.040**	x	**0.002**	**<0.001**	**0.042**	0.472¯	0.221
	PO	**0.009**	**0.002**	x	**0.010**	0.288	0.332¯	0.226
Other Parameters	TAF	0.101	**<0.001**	**0.010**	x	**0.045**	0.708¯	0.410
	Size	0.790¯	**0.042**	0.288	**0.045**	x	0.906	0.843
	Age	0.165¯	0.472¯	0.332¯	0.708¯	0.906	x	0.157¯
Leadership	GFL	**0.037**	0.221	0.226	0.410	0.843	0.157¯	x

Group C (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	**0.043**	**<0.001**	0.169	0.924	0.537	0.336
	FQ	**0.043**	x	**0.012**	**0.032**	0.126	0.264¯	**0.023**
	PO	**<0.001**	**0.012**	x	0.095	0.482	0.929	0.309
Other Parameters	TAF	0.169	**0.032**	0.095	x	0.101	0.496¯	**0.017**
	Size	0.924	0.126	0.482	0.101	x	**0.018¯**	0.591
	Age	0.537	0.264¯	0.929	0.496¯	**0.018¯**	x	0.562¯
Leadership	GFL	0.336	**0.023**	0.309	**0.017**	0.591	0.562¯	x

Group ABC (*n* = 30)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.168	0.293	0.289	0.699¯	0.420	0.249¯
	FQ	0.168	x	**0.002**	**<0.001**	**<0.001**	0.149¯	0.175¯
	PO	0.293	**0.002**	x	0.067	0.138	0.858¯	0.209¯
Other Parameters	TAF	0.289	**<0.001**	0.067	x	**0.001**	0.377¯	0.638
	Size	0.699¯	**<0.001**	0.138	**0.001**	x	0.170¯	0.670¯
	Age	0.420	0.149¯	0.858¯	0.377¯	0.170¯	x	0.573¯
Leadership	GFL	0.249¯	0.175¯	0.209¯	0.638	0.670¯	0.573¯	x

Pairwise Interaction - Pearson Corr. Corr. value

Group A (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.536	0.615	0.368	0.286	0.040	-0.007
	FQ	0.536	x	0.667	0.748	0.495	-0.007	-0.040
	PO	0.615	0.667	x	0.410	0.278	-0.057	0.149
Other Parameters	TAF	0.368	0.748	0.410	x	0.788	-0.198	-0.289
	Size	0.286	0.495	0.278	0.788	x	-0.072	-0.606
	Age	0.040	-0.007	-0.057	-0.198	-0.072	x	-0.357
Leadership	GFL	-0.007	-0.040	0.149	-0.289	-0.606	-0.357	x

Group B (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.417	0.506	0.387	-0.068	-0.336	0.415
	FQ	0.417	x	0.764	0.840	0.614	-0.243	0.419
	PO	0.506	0.764	x	0.672	0.327	-0.300	0.367
Other Parameters	TAF	0.387	0.840	0.672	x	0.643	-0.136	0.281
	Size	-0.068	0.614	0.327	0.643	x	0.043	0.069
	Age	-0.336	-0.243	-0.300	-0.136	0.043	x	-0.463
Leadership	GFL	0.415	0.419	0.367	0.281	0.069	-0.463	x

Group C (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.439	0.758	0.380	0.028	0.180	0.234
	FQ	0.439	x	0.641	0.607	0.465	-0.351	0.579
	PO	0.758	0.641	x	0.507	0.230	0.030	0.277
Other Parameters	TAF	0.380	0.607	0.507	x	0.549	-0.245	0.690
	Size	0.028	0.465	0.230	0.549	x	-0.723	0.186
	Age	0.180	-0.351	0.030	-0.245	-0.723	x	-0.202
Leadership	GFL	0.234	0.579	0.277	0.690	0.186	-0.202	x

Group ABC (*n* = 30)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.198	0.144	0.164	-0.060	0.004	-0.067
	FQ	0.198	x	0.377	0.602	0.564	-0.244	-0.043
	PO	0.144	0.377	x	0.335	0.248	-0.117	-0.116
Other Parameters	TAF	0.164	0.602	0.335	x	0.540	-0.168	0.070
	Size	-0.060	0.564	0.248	0.540	x	-0.139	-0.101
	Age	0.004	-0.244	-0.117	-0.168	-0.139	x	-0.119
Leadership	GFL	-0.067	-0.043	-0.116	0.070	-0.101	-0.119	x

***P*-Value**

Group A (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.052	**0.002**	0.112	0.192	0.895	0.855¯
	FQ	0.052	x	**0.002**	**<0.001**	0.088	0.973¯	0.821¯
	PO	**0.002**	**0.002**	x	0.128	0.259	0.820¯	0.454
Other Parameters	TAF	0.112	**<0.001**	0.128	x	**<0.001**	0.500¯	0.260¯
	Size	0.192	0.088	0.259	**<0.001**	x	x	**0.007¯**
	Age	0.895	0.973¯	0.820¯	0.500¯	x	x	0.198¯
Leadership	GFL	0.855¯	0.821¯	0.454	0.260¯	**0.007¯**	0.198¯	x

Group B (*n* = 10)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.055	**0.004**	0.070	0.786¯	0.103¯	**0.041**
	FQ	0.055	x	**<0.001**	**<0.001**	**0.017**	0.400¯	**0.049**
	PO	**0.004**	**<0.001**	x	**0.010**	0.243	0.275¯	0.093
Other Parameters	TAF	0.070	**<0.001**	**0.010**	x	**0.049**	0.717¯	0.265
	Size	0.786¯	**0.017**	0.243	**0.049**	x	x	0.759
	Age	0.103¯	0.400¯	0.275¯	0.717¯	x	x	0.071¯
Leadership	GFL	**0.041**	**0.049**	0.093	0.265	0.759	0.071¯	x

Group C (*n* = 10)

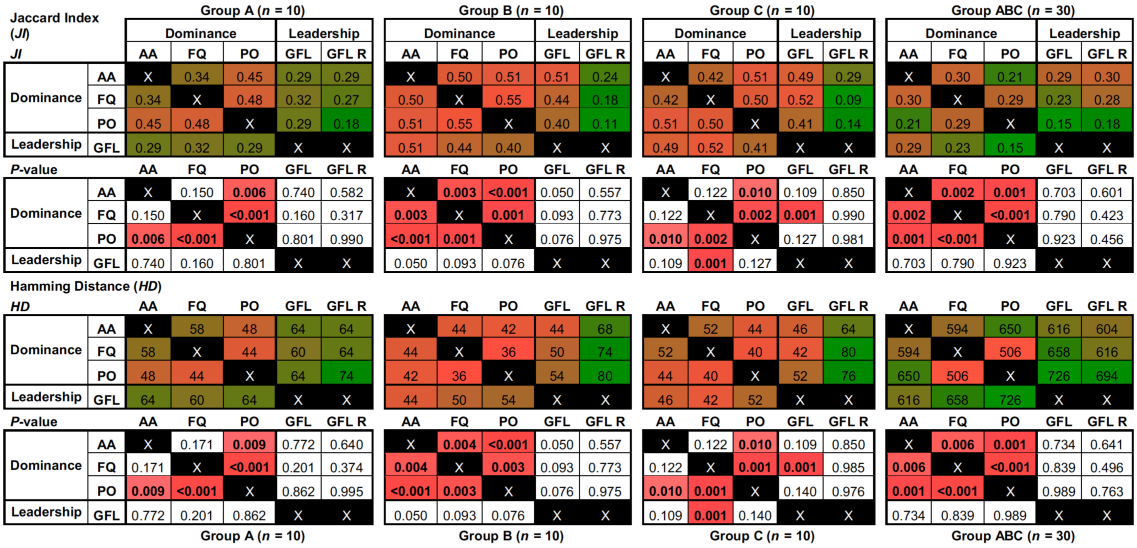
		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	0.070	**<0.001**	0.055	0.897	0.446	0.328
	FQ	0.070	x	**0.002**	**0.013**	0.119	0.205¯	**0.015**
	PO	**<0.001**	**0.002**	x	**0.022**	0.422	0.905	0.309
Other Parameters	TAF	0.055	**0.013**	**0.022**	x	0.065	0.345¯	**0.001**
	Size	0.897	0.119	0.422	0.065	x	x	0.500
	Age	0.446	0.205¯	0.905	0.345¯	x	x	0.445¯
Leadership	GFL	0.328	**0.015**	0.309	**0.001**	0.500	0.445¯	x

Group ABC (*n* = 30)

		AA	FQ	PO	TAF	Size	Age	GFL
Dominance	AA	x	**<0.001**	**0.043**	**0.048**	0.580¯	0.977	0.338¯
	FQ	**<0.001**	x	**<0.001**	**<0.001**	**<0.001**	0.083¯	0.770¯
	PO	**0.043**	**<0.001**	x	**0.017**	0.062	0.452¯	0.267¯
Other Parameters	TAF	**0.048**	**<0.001**	**0.017**	x	**<0.001**	0.362¯	0.605
	Size	0.580¯	**<0.001**	0.062	**<0.001**	x	x	0.498¯
	Age	0.977	0.083¯	0.452¯	0.362¯	x	x	0.447¯
Leadership	GFL	0.338¯	0.770¯	0.267¯	0.605	0.498¯	0.447¯	x

Note: ¯ shows a *P*-value where the correlation coefficient is negative. “x” indicates cells where correlations are not applicable.

Table S2. Comparison of the dominance/leadership networks using an unweighted (binary) mixed graph representation containing mutual and directed connections. Results from two network similarity measures are shown: the Jaccard Index (JI, top part) and Hamming distance (*HD*, bottom part) for groups A, B, C and ABC (from left to right). For details see section: Comparing the interaction matrices. *JI* and *HD* values are color-coded red for more similar networks, green for less similar networks. In the *P*-value tables, cells that contain significant correlations (*P*<0.05) are in bold, and color-coding shows the significance of the correlation. To check for possible anti-correlation between dominance and leadership, we also calculated the Jaccard Index and the Hamming distance with the directed GFL interactions reversed (GFL R column). No such anti-correlation was found. No such correlation was found.



Jaccard Index (*JI*)

		Group A (*n* = 10)					Group B (*n* = 10)					Group C (*n* = 10)					Group ABC (*n* = 30)				
		Dominance			Leadership		Dominance			Leadership		Dominance			Leadership		Dominance			Leadership	
JI		**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**
Dominance	**AA**	X	0.34	0.45	0.29	0.29	X	0.50	0.51	0.51	0.24	X	0.42	0.51	0.49	0.29	X	0.30	0.21	0.29	0.30
	FQ	0.34	X	0.48	0.32	0.27	0.50	X	0.55	0.44	0.18	0.42	X	0.50	0.52	0.09	0.30	X	0.29	0.23	0.28
	PO	0.45	0.48	X	0.29	0.18	0.51	0.55	X	0.40	0.11	0.51	0.50	X	0.41	0.14	0.21	0.29	X	0.15	0.18
Leadership	**GFL**	0.29	0.32	0.29	X	X	0.51	0.44	0.40	X	X	0.49	0.52	0.41	X	X	0.29	0.23	0.15	X	X

***P*-value**		**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**
Dominance	**AA**	X	0.150	**0.006**	0.740	0.582	X	**0.003**	**<0.001**	0.050	0.557	X	0.122	**0.010**	0.109	0.850	X	**0.002**	**0.001**	0.703	0.601
	FQ	0.150	X	**<0.001**	0.160	0.317	**0.003**	X	**0.001**	0.093	0.773	0.122	X	**0.002**	**0.001**	0.990	**0.002**	X	**<0.001**	0.790	0.423
	PO	**0.006**	**<0.001**	X	0.801	0.990	**<0.001**	**0.001**	X	0.076	0.975	**0.010**	**0.002**	X	0.127	0.981	**0.001**	**<0.001**	X	0.923	0.456
Leadership	**GFL**	0.740	0.160	0.801	X	X	0.050	0.093	0.076	X	X	0.109	**0.001**	0.127	X	X	0.703	0.790	0.923	X	X

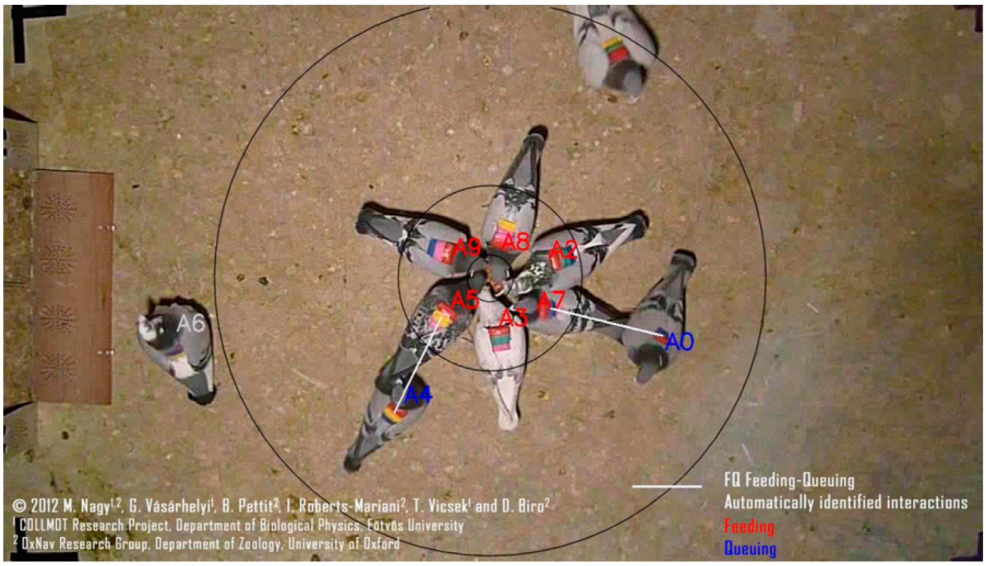
Hamming Distance (*HD*)

HD		**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**
Dominance	**AA**	X	58	48	64	64	X	44	42	44	68	X	52	44	46	64	X	594	650	616	604
	FQ	58	X	44	60	64	44	X	36	50	74	52	X	40	42	80	594	X	506	658	616
	PO	48	44	X	64	74	42	36	X	54	80	44	40	X	52	76	650	506	X	726	694
Leadership	**GFL**	64	60	64	X	X	44	50	54	X	X	46	42	52	X	X	616	658	726	X	X

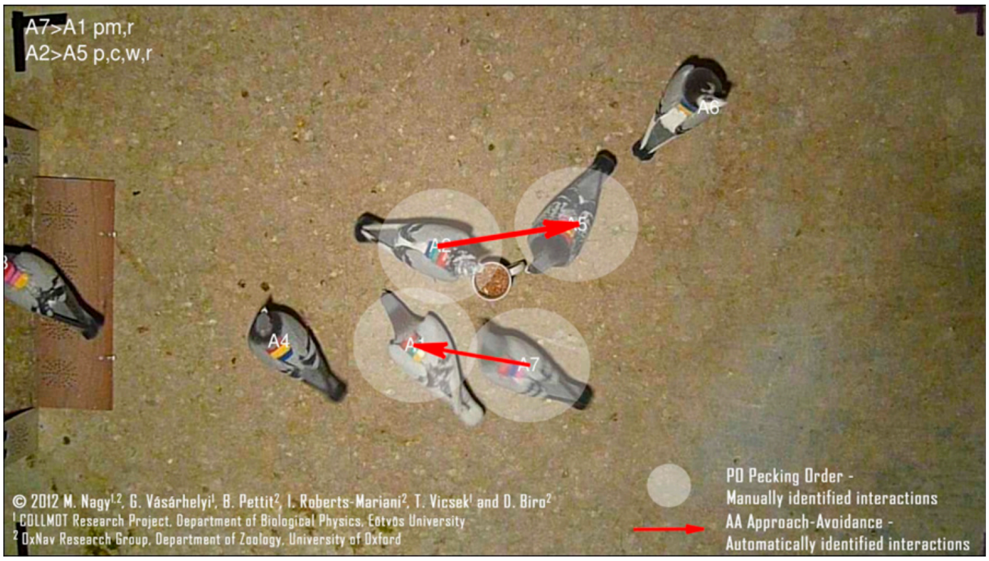
***P*-value**		**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**	**AA**	**FQ**	**PO**	**GFL**	**GFL R**
Dominance	**AA**	X	0.171	**0.009**	0.772	0.640	X	**0.004**	**<0.001**	0.050	0.557	X	0.122	**0.010**	0.109	0.850	X	**0.006**	**0.001**	0.734	0.641
	FQ	0.171	X	**<0.001**	0.201	0.374	**0.004**	X	**0.003**	0.093	0.773	0.122	X	**0.001**	**0.001**	0.985	**0.006**	X	**<0.001**	0.839	0.496
	PO	**0.009**	**<0.001**	X	0.862	0.995	**<0.001**	**0.003**	X	0.076	0.975	**0.010**	**0.001**	X	0.140	0.976	**0.001**	**<0.001**	X	0.989	0.763
Leadership	**GFL**	0.772	0.201	0.862	X	X	0.050	0.093	0.076	X	X	0.109	**0.001**	0.140	X	X	0.734	0.839	0.989	X	X
		Group A (*n* = 10)					Group B (*n* = 10)					Group C (*n* = 10)					Group ABC (*n* = 30)				

Table S3. Detailed information about all the automatic and manual methods used in our analysis. The last column describes the requirements of the methods and their applicability for analyzing data from other study systems.

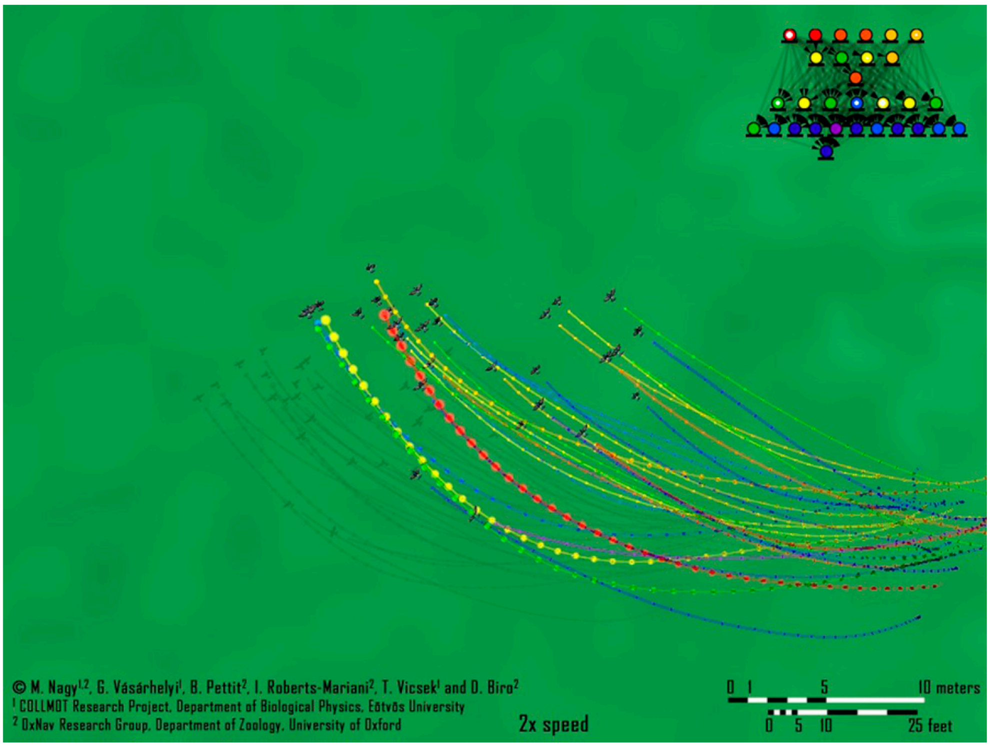
Type and abbreviation	Method	General description	Specific descriptions and comments	Applicability of method
Dominance				
AA	Approach-Avoidance	Automated scoring based on correlations between relative position and direction of motion	Autonomous identification of individual position on video recordings	Any global or local position data (e.g., GPS, motion tracker)
FQ	Feeding-Queuing	Automated scoring based on position to each other relative to the feeder		Proximity measurement from each other and from feeder, or any global or local position data (e.g., GPS, RFID, motion tracker, IR sensor, etc.)
PO	Pecking Order	Manual scoring of social interactions	Computer-aided manual identification of pecking, fighting and chasing actions (pecking, wing slapping, retreat events, etc.) on video recordings	
Other parameters				
TAF	Time-at-Feeder: Time spend with access to food	Automated scoring based on proximity to the feeder	Autonomous identification of individual position on video recordings	Proximity to feeder, or any global or local position data (e.g., GPS, motion tracker, IR sensor, ultrasonic sensor, laser proximity sensor, etc.)
Size	Body size measurements	Body mass (g) Breast size (cm) Wingspan (cm)	Biometric measurements taken several times over the experimental period	
Age	Age	Time since hatched (y)		
Leadership				
GFL	Group Flight Leadership	Directional correlation delay method on flight trajectory	Calculated from high-resolution GPS track logs	Any global or local position data (e.g., GPS, motion tracker)
	Front-Rear Position in Flock	Position (from front to rear) in flock relative to the direction of motion		Any global or local position data (e.g., GPS, motion tracker). Also could be calculated from directed proximity and distance)



Movie S1. Video of a feeding experiment of 10 pigeons (group A) including an overlay of Feeding-Queuing (FQ) interactions. The concentric circles indicate the outer boundaries of the Feeding and Queuing ranges. Feeding birds are marked with red IDs, Queuing with blue. White lines show FQ interactions.



Movie S2. Video of a feeding experiment of 10 pigeons (group A) including an overlay of Pecking Order (PO) and Approach-Avoidance (AA) interactions. White spotlights indicate manually identified PO interactions, coded in the top left corner (see Materials and Methods). Red arrows indicate AA interactions. For this purpose, AA_{ij} was averaged over a 0.5 s time window. An AA interaction is indicated with an arrow at time *t*, pointing from bird *i* (the approaching bird) towards bird *j* (the one that avoids the approach). To more clearly illustrate the most relevant interactions, we only display arrows where $AA_{ij}(t) \geq 0.8$, $AA_{ji}(t) \leq -0.5$, and $d_{ij} \leq 30$cm.



Movie S3. Animation showing 80 seconds of free flight by 30 pigeons, all equipped with GPS. Video speed is 2x real speed. Individuals are colored according to their rank in the hierarchy (top right), determined by pairwise directional correlation delay times for the whole flight. Colors near the red end of the spectrum indicate higher leadership on average. The top six momentary leaders (see Supplementary Materials and Methods) are indicated by larger dots on the trajectories and white dots on the hierarchy network. The white bars under nodes in the network show the amount of time individuals were among the top six birds.

Supplementary movies available at http://hal.elte.hu/pigeonhierarchies/videos.html