Collective attention in navigating homing pigeons: Group-size effect and individual differences

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Abstract (300 word limit)

One prominent feature of collective attention is the so-called ‘group size effect’. Often documented in studies of vigilance by animals foraging gregariously, this effect describes how individual group members are able to reduce their attention to environmental cues (e.g. predators) as group size increases, since the group can pool information from multiple individuals. Despite extensive literature in one context (foraging-vigilance), it remains unclear whether this effect can be observed in other contexts where animals face different informational demands (e.g. navigation). Using a custom-made sensor combining head-mounted IMU (Inertial Measurement Unit) and back-mounted GPS, we examined head movement, a proxy for visual scanning behaviour, in homing pigeons flying alone, in pairs, and in flocks (~10 individuals). Individual birds’ head movements decreased sharply as a function of group size: the degree of head turning per unit time dropped by 35% when the same birds switched from solo to paired flights, and decreased by a further 39% when they switched from paired to flock flights. Homing efficiency (or route straightness) did not decrease in parallel with decreasing head movement, but continued to increase over repeated flights. We also found systematic individual differences during flock homing flights, where birds positioned more frontally and more centrally in the flock made larger head movements. Moreover, leaders were positioned more frontally and tended to show larger head movements than followers. Decreased head movement by peripheral birds suggested increased attention to the rest of flock rather than increased individual vigilance (contra ‘the edge effect’). Overall, our results suggest that individual birds reduced their visual scanning during navigation likely because of the need to attend closely to fellow flock members to maintain flock cohesion. While reduced per-capita visual scanning may reduce the amount of environmental information available to individual birds, it is likely compensated by the flock’s collective attention.

Keywords: Bird navigation, Global Positioning System, Head movement, Inertial Measurement Unit, Vision

Introduction

Individuals living in groups benefit from sharing information in multiple contexts, including collectively detecting predators, searching for food, or navigating to a common destination (Clark & Mangel, 1986; Krause & Ruxton, 2002; Sumpter, Buhl, Biro, & Couzin, 2008). Visual cues are often critical not only in detecting the relevant stimuli in the environment, but also in efficiently transferring information between individuals within a group (Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015; Strandburg-Peshkin et al., 2013). The visual attention of a group is thus a collective phenomenon, in the sense that local interaction among individuals determines its form and individuals benefit from grouping by relying on others' sensory information.

One key characteristic of this collective attention is the 'group size effect', which is often documented in studies of vigilance when animals forage as a group. Previous studies, conducted primarily with birds and mammals (Elgar, 1989; Roberts, 1996), have found that individuals in larger groups decrease the time they spend being vigilant (pausing to feed and lifting their head up to scan the environment) and instead increase the time they spend on foraging (lowering the head to search for and consume food on the ground). A common interpretation of this pattern is that individuals can afford to be less attentive to non-food environmental cues in a group, as having more individuals watching out for potential danger (collective detection, or 'many eyes') allows each individual to spend more time on other activities, such as foraging (Pulliam, 1973). Other factors, such as increased competition for food, dilution of predation risk, and predator confusion, might also be involved, although the group size effect can be observed even when these factors are experimentally controlled for (Lima & Zollner, 1996; Lima, Zollner, & Bednekoff, 1999).

However, controversy remains, even after decades of research, as to what factors are critical (Beauchamp & Ruxton, 2008; Bednekoff & Lima, 1998; Cresswell, 1994; Delm, 1990; Elgar, 1989; Roberts, 1996), which renders the interpretation of the group size effect particularly complex.

Despite extensive literature on collective attention in the foraging-vigilance context, it remains unclear whether the group size effect can be observed in other behavioural contexts where sharing information with others is again beneficial, but in different ways. This lack of knowledge hampers an understanding of both the function and mechanism of collective attention across behavioural domains. In this study, therefore, we aimed to examine whether the group size effect can be observed in the context of collective problem-solving, specifically visually guided navigation performed in groups. During collective navigation, individuals benefit from grouping because groups tend to find more accurate or more efficient routes than individuals, via local interactions among group members (Berdahl et al., 2018). Multiple distinct mechanisms are likely involved in this process, such as ‘many wrongs’ (where groups average out individual errors to arrive at an accurate mean directional estimate) (Simons, 2004), leadership (where a subset of knowledgeable individuals lead others) (Nagy, Ákos, Biro, & Vicsek, 2010), collective sensing (where individuals in a group sense a gradient of environmental cues that is beyond each individual’s perceptual range) (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013), and, over repeated trips, social and collective learning (where individuals learn better routes by following, or making decisions together with, others) (Biro, Sasaki, & Portugal, 2016; Jesmer et al., 2018; Mueller, O’Hara, Converse, Urbanek, & Fagan, 2013; Pettit, Flack, Freeman, Guilford, & Biro, 2012). Due to these advantages of collective navigation, it may be hypothesized that individual animals in a larger group allocate more attention to social-visual cues (i.e. nearby conspecifics) instead of environmental-visual cues (i.e. visual landmarks) when making moment-to-moment movement decisions. To examine this hypothesis, we utilized a system that we developed to track both the flight trajectories (by miniature GPS) and the head movements (by Inertial Measurement Units; IMU) of homing pigeons, *Columba livia* (Kano, Walker, Sasaki, & Biro, 2018).

A few previous studies have examined the visual strategy of free-flying homing pigeons navigating both individually and as a flock, but none of them have focused on the group size effect systematically (i.e. by comparing several different flock sizes). Vyssotski et al. (2009) combined the use of GPS and EEG (electroencephalography) devices and examined how attentional EEG signals changed during pigeons' homing flights. They found that EEG signals of a certain frequency range (12-60 Hz) activated particularly strongly when birds were flying over prominent visual landmarks (e.g. roads and isolated architectural structures), but not when they were flying over open ocean where few identifiable landmarks were present, suggesting that EEG of this range was related to pigeons' increased attention to visual landmarks. Moreover, the activation of 12-60 Hz EEG signals was significantly weaker when birds flew over the same prominent visual landmarks with conspecifics (~6 individuals) and also for the whole duration of the flights compared when flying alone, suggesting that they attended less to visual landmarks in flocks than when travelling solo.

Kano et al. (2018) used a head-mounted IMU to compare the head movements of homing pigeons flying alone and as a pair. Head movement is a good proxy for visual scanning behaviour in pigeons because these birds (along with many other avian species) shift their gaze mainly via head movements, and the role of eye movement is limited (approx. 2-3 degrees during walking) (Haque & Dickman, 2005; Wohlschläger, Jäger, & Delius, 1993). In an analysis similar to that of Vyssotski et al. (2009), birds changed the pattern of their head movement when flying alone over prominent visual landmarks (e.g. roads and railways). Such head movement change was characterized by a decrease in both the frequency of head-saccades (indicating how often birds update their view) and the amplitude of each head-saccade (indicating how widely birds scan the environment), as well as their combined values (i.e. the degree of head movement per unit time; head turning rate). Moreover, it was found that during the initial four flights from a new release location, over which birds rapidly improved their homing efficiency (i.e. the straightness of their flight path between the release site and home), head movements tended to increase, before plateauing in later flights. This suggests that birds increased their visual scanning as they developed reliance on visual landmarks (possibly over other sources of navigational information, such as the sun compass, and olfactory and magnetic cues) (Walcott, 1996). Critically, when birds were flying as a pair, their head movements were smaller compared to when flying alone, and did not decrease when flying over prominent landmarks unlike in the solo flights. Further, pair-flying pigeons showed reduced head movement when they flew side-by-side (compared to when they flew in front of or behind the partner) – a flight formation which likely maximizes bidirectional information transfer via birds' lateral vision (Pettit, Perna, Biro, & Sumpter, 2013). These results suggest that head movement is related to visual scanning of landmarks in homing pigeons, and a decrease in their head movement indicates inhibition of such visual scanning, possibly driven by sustained attention instead to particular targets, such as prominent visual landmarks and flock partners.

Taylor et al. (2019) combined the use of a head-mounted IMU and back-mounted GPS and accelerometer to examine how homing pigeons adjusted the frequency of their flapping when they were flying alone or as a pair, as well as how such changes were related to head movements and the energetic cost of flights. Pair-flying birds showed increased wingbeat frequency (consistent with Usherwood, Stavrou, Lowe, Roskilly, & Wilson, 2011) while also increasing their homing efficiency compared to solo-flying birds. These two changes likely offset one another: the increased energetic cost of faster flapping was counterbalanced by the enhanced navigational performance in pairs. It was also found that the increased wingbeat frequencies of pair-flying birds significantly attenuated vertical oscillatory head displacement, suggesting that faster flapping was related to the stabilization of birds' gaze, and improved visibility of the flight partner (with reduced motion blur). Therefore, consistent with Kano et al. (2018), these results suggested that, when flying as a pair, pigeons inhibit their head movement to enhance their ability to attend to flock partners (even at the expense of increased kinematic cost).

These previous studies are consistent with the hypothesis that flock-flying pigeons become more attentive to nearby partners while at the same time becoming less attentive to distant visual landmarks during navigation. However, at least two key questions remain to be answered. First, given that previous studies have only compared two conditions each – solo versus pair or solo versus flock – how exactly patterns of attention change as a function of flock size is unknown. Second, it remains unclear whether and how individuals differ from one another in their patterns of attention within a large flock. This question has been addressed in the literature on foraging-vigilance, which suggests that individuals positioned more peripherally in a group show increased visual scanning because they are likely more susceptible to predation (i.e. 'the edge effect') (Beauchamp & Ruxton, 2008; Elgar, 1989; Hirsch, 2007; Krause & Ruxton, 2002). No previous work has addressed this question in the context of collective navigation, but we can make a prediction distinct from the pattern just described. Specifically, it is well established that in flocks of homing pigeons a subset of birds (leaders) have proportionally greater influence on directional decisions than others (followers) (Nagy et al., 2010; Pettit, Akos, Vicsek, & Biro, 2015; Pettit et al., 2013). These leaders presumably devote more attention to scanning for visual landmarks to make navigational decisions than do followers, while followers inhibit their head movement to a greater extent than leaders to better track nearby flock members. As such, we would expect leaders to show increased head movement compared to followers. Finally, both simulations and empirical studies have shown that the best strategy for a predator to attack a moving group is a pursuit of peripheral or isolated individuals (Demšar & Lebar Bajec, 2014; Ioannou, Guttal, & Couzin, 2012; Nishimura, 2002). Therefore, it is expected that, if peripherally-positioned individuals are more vigilant for predator attacks than centrally-positioned individuals within a flock, the former would show increased visual scanning compared to the latter. Notably, some authors have argued that this edge effect could partly or entirely account for the group size effect, since the proportion of peripheral individuals decreases as a function of group size (Inglis & Lazarus, 1981).

In sum, in this study we aim to 1) determine whether birds flying in a flock (~10 individuals) decrease head scanning compared to those flying as a smaller flock (i.e. pair) or alone, and 2) quantify how individuals differ from one another in their head movements according to the physical position they occupy within a large flock (~10 individuals) and according to the degree to which they act as leaders or followers, measured as the extent to which they copy others' moment-to-moment directional changes (directional correlation delay analysis; Nagy et al., 2010).

Methods

Subjects

The subjects were 22 homing pigeons (*Columba livia*; age, 4.1 ± 2.5 years; weight, 443 ± 25 g; mean ± s.d.) bred and housed at the Oxford University Field Station at Wytham, UK (51°46′ 58.34″N, 1°19′02.40″W). The same birds had participated in a previous study (Kano et al., 2018) and the experiments reported here commenced the day after testing for that study concluded.

Ethical notes

Pigeons were housed in two neighbouring lofts (sized 6.1w×2.2d×2.1h m each, with 3.0w×1.3d×2.2h m aviaries attached). They had free access to the outside except on experimental days, and were provided with food, water and grit *ad libitum*. The study protocols were approved by the Local Ethical Review Committee of the University of Oxford's Department of Zoology (no. APA/1/5/ZOO/NASPA/Biro/PigeonsHeadmountedsensors). All birds were habituated to wearing the custom-made mask and backpack prior to this study following the protocols approved by the Committee (see Appendix for details).

Apparatus

A custom-made logger recorded each pigeon's head movement with a head-mounted nine-axis IMU at 60 Hz (Inertial Measurement Unit; a combination of gyroscope, accelerometer, and magnetometer; BNO055 Absolute Orientation Sensor, Adafruit) and flight trajectory (latitude and longitude) with a back-mounted GPS at 10 Hz (Global Positioning System; -165 dBm sensitivity GPS, 66 channels, positional accuracy < 3m, velocity accuracy < 0.1 m/s; Adafruit Ultimate GPS, Adafruit, New York, NY, USA). The IMU sensor (1g) was glued to a custom-built mask (3.8 g) made to fit each bird's unique head shape. The IMU sensor was fitted to the bird's head so that the roll and pitch axes of the IMU sensor became roughly parallel to the sagittal and coronal planes of the head, respectively, and the yaw axis diagonal to these roll and pitch axes as well as the eye-ear line (Figure A1). The body unit (20.7 g) consisted of GPS, microcomputer (Adafruit Feather) and a micro-SD card (32 GB; SanDisk, Milpitas, CA, USA), stored in a customized backpack (3 g). The total weight of the devices worn was 28.5 g, which corresponded to 6.4 ± 0.9 % of the subjects' body weight. All birds were habituated to wearing the custom-made mask and backpack as described in our previous study (Kano et al., 2018). Briefly, habituation to the mask lasted a minimum of 7 days (with each daily session lasting a maximum of 4 h) inside or around the birds' home loft. The criterion for a bird passing habituation was that the bird did not remove its mask on two consecutive days out of a total of 7 days. No bird was dropped from the experiment on the basis of this criterion.

Experimental Procedures

This study includes both published (Kano et al., 2018) and new datasets (flock flights), collected using the same subjects. Here, we describe the new dataset in relation to the previous dataset, and reanalyse the previous dataset with parameters described in this article. In both previous and new datasets, all birds flew from the same release site, 3.82 km north of the home loft (51°49′ 02.85″N, 1°18′50.05″W, bearing to the loft was 185.1 deg.) once per day on days when the sun's disc was visible. In the previous dataset, all birds flew for a total of eight days as solo (*solo-1*), then for a total of nine days as a *pair*, and finally for a total of two more days as solo (*solo-2*). The solo-2 flights were conducted to check that any key difference observed between the pair and flock flights were not caused by continued route learning over repeated flights. The new dataset consists of data from additional flight sessions. First, we randomly assigned these 22 birds to either of two *flocks* (comprising 9-11 birds) each day and released each flock once per day over a total of 11 days. Second, after these flock flights were completed, we released the birds individually over the course of two more days (*solo-3*) for the same reason as that described above. In the previous dataset, due to logger malfunction we lost 4 and 6 individual flights respectively in the initial solo-1 and paired flight sessions. In the new dataset, two birds were dropped from the experiment from the 2nd and 4th day of the flock-flight phase due to injury in the case of one (completing only 1 flock flight), and consecutive failures to return home without landing along the way in the case of the other (completing 3 flock flights); these birds did not continue with the subsequent flock and solo-3 flights. Also, we excluded data where the focal bird did not fly in coordination with its partner during a paired flight or with more than 7 partners (i.e. in a flock larger than 8 birds) for longer than 1 minute during a flock flight (see below for the definition of coordination). Eight and 7 individual flights were excluded from the paired- and flock-flight sessions, respectively (4.0 and 2.9 % of the total samples, and these excluded data consisted of flights from 8 and 4 birds). Accordingly, our dataset included a total of 172, 178, 44, 217, and 40 individual flights respectively in the solo-1, pair, solo-2, flock, and solo-3 flight sessions (see also Table 1 for the data summary).

Finally, we also recorded head movements in pigeons during non-homing flights. Birds were fitted with the same equipment as described above, and were allowed to freely fly around their home loft while forming flocks of various sizes spontaneously. We then examined how their head movements changed as a function of group size in this, non-navigational, flocking context. We summarize the most relevant results in the main text below and report full details in Appendix.

Data analysis

Head movement was recorded as the rotational movements along yaw, roll and pitch. Birds' head movements were characterized as a series of saccadic movements (Figure 1). A head-saccade was defined if the combined angular speed (defined as $\sqrt{y^2 + r^2 + p^2}$, where y, r, and p are respectively yaw, roll and pitch angular speed) exceeded 60 deg/sec, and the duration of this data segment was longer than 50 ms. These parameters were chosen to eliminate recording noise as well as a population of short/small saccades which likely function to stabilize the head rather than to shift gaze (Figure S1 in Kano et al., 2018). From the head-saccade data, three dependent variables can be derived: *saccade frequency* (saccades/sec) – the mean number of saccades per second; *saccade amplitude* (deg/saccade) – the angular distance travelled by the head in each saccade; and *head turning rate* (deg/sec) – the combined angular distance travelled by the head per second (i.e. speed) calculated by including only saccadic periods (i.e. saccade amplitude × frequency). Saccade frequency and amplitude indicate related but distinct aspects of head movement, analogously to human eye movement (Henderson & Hollingworth, 1999); the former indicates how long a bird attended to one location over another, whereas the latter indicates how large an area the bird scanned. We primarily focused on head turning rate to examine the effect of various independent variables on head movement, but also analysed saccade frequency and amplitude to further examine which aspects of head movement were affected. Occasional head shakes (presumably due to the presence of the mask) were detected as the combined head angular velocity exceeding 800 deg/sec and were eliminated from the analysis.

The GPS data were averaged with a 200-ms moving window for noise reduction, and then interpolated to 60 Hz to be synchronized with the IMU data. Longitudes and latitudes were converted to meters (X and Y) using a Universal Transverse Mercator projection. *Ground speed* and *flight turning rate* (or tortuosity) were defined as momentary changes in coordinates (km/h) and flight direction (deg/sec), respectively. Only time points in which the focal bird flew faster than 20 km/h were included in the analyses in order to exclude any stops along the route. Moreover, to exclude periods during which birds were in the process of taking off or landing, only time points in which the focal bird was further than 100 m from the release site or the loft were included in the analyses. After excluding these time points, birds flew for 6.1 ± 2.3, 5.3 ± 0.7, 4.5 ± 0.9, 4.4 ± 0.5, and 4.3 ± 0.6 minutes (mean ± s.d.) in the solo-1, pair, solo-2, flock, and solo-3 flights, respectively (also see Table 1 for the data summary). *Homing efficiency* was defined as the beeline distance between the release site and the loft divided by the length of the path flown; to calculate this variable, the flight in which the focal bird was not within 100 m of the home loft when the first bird reached that boundary was (additionally) removed from this analysis in the pair (6 individual flights removed) and flock flights (34 individual flights removed).

Coordination with a given partner in the paired and flock flights was defined as the focal bird flying (> 20 km/h ground speed) cohesively (within a 50-m distance) with the partner bird in the paired flights and with more than 7 partners (i.e. a flock larger than 8 birds) in the flock flights. Only time points in which the focal bird flew in coordination with the partner in the paired flights and with more than 7 partners in the flock flights were included in the analyses. This yielded 17.1 ± 26.4 and 17.2 ± 24.1 %, mean ± s.d., of time points excluded in analyses of paired and flock flights, respectively (also see Table 1 for the data summary).

Leader-follower dynamics in flocks were quantified using directional correlation delay analysis, following methods established in previous studies (Flack, Ákos, Nagy, Vicsek, & Biro, 2013; Nagy et al., 2010; Pettit et al., 2013). Specifically, we calculated the time delay at which the flight direction of a given partner was maximally correlated to that of a focal bird, repeated this pairwise calculation for all possible partners in a flock, and then calculated the mean of these values to indicate overall influence of the focal bird. We then determined the leadership rank of the focal bird according to the mean delay scores of all birds in the flock (where a larger positive value indicated a higher rank). Spatial position in a flock (in each flight) was examined as three variables: *distance from the flock centre* – the mean distance (per individual flight) from the averaged XY of all flock members in a given flight (m); and *front-back position* and *left-right position* (m) – the mean distance (per individual flight) from the flock centre projected onto the average flight direction of all flock members in a given flight (where a larger positive value indicated more frontward / more rightward).

Statistical analyses were performed in R (ver. 3.6.0). We used Linear Mixed Models (LMM) with Gaussian error structure and identity link function (in the package 'lme4') when we analysed a continuous variable as a response. We checked the assumptions of normally distributed and homogenous residuals in diagnostic plots and found no issue in any of our analyses. We also inspected the Variance Inflation Factor (VIF; using the package 'car'), and found no collinearity issues in any of our analyses. To analyse an ordinal variable as a response (i.e. leadership rank), we used Cumulative Link Mixed Models (CLMM; in the package 'ordinal'). Random-effects structures were kept maximal in all models, except that we removed the correlation between random intercepts and slopes to maintain sufficient random-effects variation (Barr, Levy, Scheepers, & Tily, 2013). All covariates were standardized (with a mean of 0 and standard deviation of 1; using the 'scale' function) (Schielzeth, 2010). We tested significance using a likelihood-ratio comparing the full model with a model without the effect in question (using the 'drop1' function).

Results

Head movement and flock size

1) Comparison across the main flight sessions (solo-1, pair, and flock):

We tested whether birds changed their head movement across the main flight sessions (solo-1, pair, and flock). We included in the model the subject means of each head movement parameter (head turning rate, saccade frequency, or saccade amplitude) as the response variable, the flight session (solo-1, pair, and flock) as a fixed term and the subject ID as a random term. Birds sharply decreased head turning rate (degree/s) as flock size increased (Table 1 and Figure 2; $\chi^2_2 = 116.87$, $P < 10^{-4}$). This decrease in head turning rate was due to decreases in both saccade frequency (saccades/s; $\chi^2_2 = 85.16$, $P < 10^{-4}$) and amplitude (degree/saccade; $\chi^2_2 = 112.7$, $P < 10^{-4}$). See Table A1 for the details about the model structures and statistical results (formula, estimates, SE, and CI). Post-hoc pairwise comparisons revealed that pigeons flying as a pair exhibited smaller head turning rate: $\chi^2_1 = 48.08$, $P < 10^{-4}$), lower saccade frequency ($\chi^2_1 = 32.58$, $P < 10^{-4}$) and smaller saccade amplitude ($\chi^2_1 = 50.37$, $P < 10^{-4}$) than those flying as solo, and also that pigeons flying as a flock exhibited smaller head turning rate ($\chi^2_1 = 53.29$, $P < 10^{-4}$), lower saccade frequency ($\chi^2_1 = 47.61$, $P < 10^{-4}$), and smaller saccade amplitude ($\chi^2_1 = 44.43$, $P < 10^{-4}$) than those flying as a pair.

2) The effect of flight manoeuvres on head movement in relation to flock size effects

As our previous study (Kano et al., 2018) identified that birds' head movements are not only affected by visual scanning of landmarks but also by flight kinematics (birds turn their head when they change their flight directions), to dissociate these two effects, we next examined how head movement varied as a function of flock size and flight turning rate (degree/s) (Figure 3). We included the flight turning rate as an additional fixed factor into the above model (this factor and its interaction with the flock size). To do this, we classified the individual data into bins according to the flight turning rate (which varied between 0-30 degree/s), and recalculated the subject mean in each bin (the bin range was operationally defined as 5 degree/sec, i.e. 6 bins). These analyses revealed all significant, to varying degrees, interaction effects between flight turning rate and head movement parameters (head turning rate: $\chi^2_2 = 71.34$, $P < 10^{-4}$; saccade frequency: $\chi^2_2 = 75.67$, $P < 10^{-4}$; saccade amplitude: $\chi^2_2 = 54.52$, $P < 10^{-4}$; Figure 3, also see Table A1); to check that our definition of bin range did not affect these results, we performed the same analyses with a smaller range, 2.5 degree/sec, 12 bins, and confirmed the same pattern of results (head turning rate: $\chi^2_2 = 85.39$, $P < 10^{-4}$; saccade frequency: $\chi^2_2 = 89.46$, $P < 10^{-4}$; saccade amplitude: $\chi^2_2 = 61.18$, $P < 10^{-4}$). Specifically, when birds flew straight (with lower flight turning rate), their head turning rate decreased as flock size increased. However, when they turned steeply (with higher flight turning rate), this effect was more moderate, indicating that they needed to maintain head movement to a certain degree during steep turns. Notably, during such periods, birds maintained the saccade frequency while they decreased the amplitude of each saccade; namely, they made a number of small saccades. This was likely because birds needed to frequently update their visual field (to scan ahead or to the side) but at the same time minimize the area that their visual field covers (to attend to flock partners).

3) Analysis of the two additional solo flight sessions (solo-2 and solo-3)

To check that any key difference observed across the solo-1, pair and flock flight sessions was not caused by continued route learning over repeated flights, we examined whether birds returned to their previous solo-1 levels of head movement in the solo flights conducted after the pair and flock flights (solo-2 and solo-3). The model structure was identical to that used to compare the main flight sessions (subsection 1). Comparing the paired flights and the solo flights conducted after the paired flights (solo-2) revealed significant increases in all head movement parameters (head turning rate: $\chi^2_1 = 48.22$, $P < 10^{-4}$; saccade frequency: $\chi^2_1 = 325.68$, $P < 10^{-4}$; saccade amplitude: $\chi^2_1 = 129.98$, $P < 10^{-4}$). Comparing the flock flights and the solo flights conducted after the flock flights (solo-3) also revealed significant increases in all head movement parameters (head turning rate: $\chi^2_1 = 68.57$, $P < 10^{-4}$; saccade frequency, $\chi^2_1 = 306.2$, $P < 10^{-4}$; saccade amplitude: $\chi^2_1 = 147.69$, $P < 10^{-4}$; also see Table A1).

4) Comparison across the three solo flight sessions (solo 1-3)

We next examined whether and to what extent birds changed their head movement across the three solo flight sessions (solo 1-3) due to any learning effect. The model structure was identical to that used to compare the main flight sessions (subsection 1). We found moderate decreases in all head movement parameters particularly in the last solo flight (solo-3) sessions (Table 1; head turning rate: $\chi^2_2 = 22.60$, $P < 10^{-4}$; saccade frequency: $\chi^2_2 = 25.56$, $P < 10^{-4}$; saccade amplitude: $\chi^2_2 = 12.12$, $P = 0.0023$; also see Table A1). Overall, however, these observed decreases in head movement across the solo flight sessions were far more moderate than those observed across the main flight sessions (i.e. solo-1, pair, and flock flight sessions; see Table 1).

5) Homing efficiency

We also tested whether birds changed their homing efficiency (straightness of flight path) across the main flight sessions (solo-1, pair, and flock) and the three solo flight sessions (solo 1-3). The model structure was identical to that used to compare the main flight sessions (subsection 1) except that homing efficiency was included as a response (this response was logit-transformed to achieve approximate normality (Warton & Hui, 2011)). We found that homing efficiency increased across the flight sessions, both across the three main flight sessions (solo-1, pair, and flock; $\chi^2_2 = 82.66$, $P < 10^{-4}$) and across the three solo flight sessions (solo 1-3; $\chi^2_2 = 52.62$, $P < 10^{-4}$; also see Table A1). Overall, homing efficiency was slightly higher when birds flew as a flock compared to when they flew individually (see Table 1).

(Appendix Summary) Non-homing flights

In our follow-up experiment, we also examined pigeons' head movements as a function of flock size during non-homing flights, i.e. circling flights around the birds' home loft (see Appendix text; Table A2 and Figure A2). We found that, although saccade amplitude decreased significantly as a function of flock size, head turning rate did not change significantly, and saccade frequency increased significantly as a function of flock size. It is likely that the observed increase in saccade frequency was associated with the increase in flight turning rate (birds in larger flocks flew more circular paths around the loft, as indicated by the increased flight turning rate as a function of flock size) and is thus a situational artifact. On the other hand, the observed decrease in saccade amplitude may reflect an effect of flock size on attention. However, overall, the degree of observed decrease in saccade amplitude was more moderate than that observed in homing flights; specifically, saccade amplitude was on average 12.35 degree/saccade in the initial solo homing flights and decreased to 7.35 degree/saccade in the flock homing flights (a flock of ~10), while it ranged only between 12.11 (solo) to 11.36 (a flock of 9-14) degree/saccade in the flights around the loft.

Individual differences observed during flock flights

6) Head movement as a function of individual spatial position in the flock

We examined the relationship between individuals' spatial positions (front-back, left-right, and distance from the flock centre) and head movement patterns (head turning rate, saccade frequency and amplitude) during flock flights. We included in the model the trial means of each head movement parameter (either head turning rate, saccade frequency or saccade amplitude) as the response variable (the trial means, but not the subject means, were used due to the randomization of flock members across trials), the trial means of front-back position (m), left-right position (m), and distance from the flock centre (m; log-transformed to achieve approximate normality) as fixed terms, and the subject ID and individual flight ID as random terms. We also included the trial means of flight turning rate, the number of individuals in a flock (9-11), and the flight days (1-11) as control fixed terms (because we found in the former analyses that these factors potentially affect head movement). As this model (and also the other models in this subsection) included more than one test predictor, to avoid issues arising from multiple testing, we first compared the full model with the null model excluding all test predictors (while keeping all control predictors and random effects) and then proceeded with the tests of individual test predictors only if this full-null comparison was significant. The full-null comparison revealed significance for head turning rate as the response variable ($\chi^2_3 = 8.45$, $P = 0.038$), but no significance for saccade frequency ($\chi^2_3 = 4.25$, $P = 0.24$) or amplitude ($\chi^2_3 = 5.78$, $P = 0.12$) as a response variable. We thus tested the effect of each spatial position variable as a predictor of head turning rate as the response variable. Birds positioned more centrally in the flock showed larger head turning rates (Figure 4: $\chi^2_1 = 6.74$, $P = 0.009$). Birds positioned more frontally in the flock showed larger head turning rates (Figure 5; $\chi^2_1 = 6.74$, $P = 0.009$). Birds positioned more leftward in the flock did not differ from those positioned more rightward ($\chi^2_1 = 0.26$, $P = 0.61$). See Table A3 for the details about the model structures and statistical results (formula, estimates, SE, and CI).

7) Head movement as a function of individual leadership rank

We first examined the relationship between leadership rank and head movement patterns during flock flights. We included in the model the trial means of each head movement parameter (either head turning rate, saccade frequency or saccade amplitude) as the response variable, individuals' leadership rank (calculated per trial) as a fixed term, and the subject ID and individual flight ID as random terms. We also included the control terms (the trial means of flight turning rate, the number of individuals in a flock, and the flight days) as described above. Birds with higher leadership ranks tended to show larger head turning rates, although this effect did not reach statistical significance (Figure 6; $\chi^2_1 = 3.02$, $P = 0.082$). No significant relationship between leadership rank and saccade frequency ($\chi^2_1 = 2.63$, $P = 0.11$) or saccade amplitude ($\chi^2_1 = 0.93$, $P = 0.33$; also see Table A3) was found.

We next examined the relationship between individuals' leadership ranks and spatial positions (front-back, left-right, distance from the flock centre) in a flock. We included in the model individuals' leadership rank as the response variable, the trial means of front-back position (m), left-right position (m), and distance from the flock centre (m; log-transformed) as fixed terms, and the subject ID and individual flight ID as random terms. The full-null comparison revealed significance for this model ($\chi^2_3 = 16.92$, $P < 10^{-3}$). Consistent with previous studies (Nagy et al., 2010; Pettit et al., 2015), leaders were positioned more frontally than followers in the flock (Figure 7a; CLMM, $\chi^2_1 = 16.60$, $P < 10^{-3}$). We also found that followers tended to be positioned more peripherally in the flock than leaders (CLMM, $\chi^2_1 = 9.58$, $P = 0.002$). No significant relationship was found between leadership rank and individuals' left-right position (CLMM, $\chi^2_1 = 0.33$, $P = 0.56$; also see Table A3).

8) The relationship between flight performance during the initial solo flights and head movement/flight performance during the flock flights

We examined whether individual differences in flight performance (ground speed, homing efficiency) observed during the initial solo flights (solo-1), known to affect leader-follower dynamics and flight formations in subsequent flock flights (Flack, Pettit, Freeman, Guilford, & Biro, 2012; Pettit et al., 2015), were related to individuals' head movement parameters observed during the flock flights. We included in the model the trial means of each head movement parameter (either head turning rate, saccade frequency or saccade amplitude) during the flock flights as the response variable, individuals' mean ground speed and homing efficiency during the solo-1 flights as fixed terms and the subject ID and individual flight ID as random terms. We also included the control terms (the trial means of flight turning rate, the number of individuals in a flock, and the flight days) as described above. The full-null comparison revealed significance for the model with head turning rate as the response ($\chi^2_2 = 6.67$, $P = 0.036$), while it did not reveal significance for the model with saccade frequency as the response ($\chi^2_2 = 5.12$, $P = 0.077$) or the model with saccade amplitude as the response ($\chi^2_2 = 4.33$, $P = 0.11$). We thus tested the effects of each predictor for the model with head turning rate as the response. Birds with higher ground speed in the solo-1 flights showed higher head turning rate ($\chi^2_1 = 6.45$, $P = 0.011$) in the flock flights. No significant relationship was found between homing efficiency and head turning rate ($\chi^2_1 = 0.04$, $P = 0.85$; also see Table A3).

We next examined whether individual differences in flight performance (ground speed, homing efficiency) observed during solo-1 flights were related to individuals' spatial positions (front-back, left-right, and distance from the flock centre) and leadership during the flock flights. We included in the model each of these parameters observed during the flock flights in turn as the response variable, individuals' mean ground speed and homing efficiency during the solo-1 flights as fixed terms and the subject ID and individual flight ID as random terms. The full-null comparison revealed significance for the model with front-back position as the response ($\chi^2_2 = 10.54$, $P = 0.005$), while it did not show significance for the model with left-right position ($\chi^2_2 = 5.16$, $P = 0.076$), leadership rank ($\chi^2_2 = 1.71$, $P = 0.42$), or distance from the flock centre as the response ($\chi^2_2 = 0.08$, $P = 0.96$). We thus tested the effect of each test predictor for the model with front-back position as the response. Consistent with Pettit et al. (2015), birds with higher ground speeds in the solo-1 flights positioned more frontally during the flock flights (Figure 7b; $\chi^2_1 = 9.96$,

$P = 0.002$). No relationship was found between front-back position and homing efficiency ($\chi^2_1 = 0.17$, $P = 0.68$; also see Table A3).

(Appendix Summary) Individual differences during paired flights

Finally, we subjected the data from the paired flights to the same analyses as those described above. The results were largely consistent with those from the flock flights, although we also found several interesting differences (see Appendix text for details). First, unlike in the flock flights (which indicated a small effect of distance from the flock centre), we found that those pairs that flew at greater inter-individual distances in the paired flights showed slightly larger (instead of smaller) head movements (Figure A3). Second, leaders showed slightly larger head movements than followers (Figure A4), while the relationship between head movement and front-back position was not significant (although we found that those frontally-positioned birds were more likely to be leaders, consistent with the results from the flock flights; Figure A5a). Third, we found that those birds that flew more efficiently (rather than those that flew faster) in the solo-1 flights were positioned more frontally in the paired flights (Figure A5b).

Discussion

We examined if the group size effect, a key characteristic of collective attention, can be observed in the head movements of free-flying pigeons in the context of homing navigation. We also tested whether individuals that occupy different spatial and leadership positions within a flock differ in their patterns of attention. We found that birds sharply decreased head movement as a function of flock size: the degree of head turning per unit time decreased by 35% when the same birds switched from solo to paired flights, and decreased by a further 39% when they switched from paired to flock flights (~10 individuals). Given that previous studies have shown decreased head movement to be primarily a consequence of a decrease in the visual scanning of landmarks (or increase in attention to particular landmarks) and/or of an increase in attention to flock partners (Kano et al., 2018; Taylor, Portugal, & Biro, 2017), our results suggest that the group size effect we observed was due to individual birds progressively decreasing visual scanning of landmarks while increasing attention to flock partners as a function of flock size. This observed flock size effect is also likely driven by specific demands associated with the homing/large-scale navigational context because our follow-up experiment indicated that this group size effect was far less pronounced during non-homing flights (flights around the loft) than during homing flights.

During flock flights, individual differences in head movement within a flock were small relative to the large overall decrease between solo and flock flights that all birds exhibited in parallel. Thus, it is likely that the observed individual differences are affected by factors other than those that caused the overall flock size effects. It should also be noted that the observed relatively small individual differences require further testing in future studies under different conditions (different release sites, number of releases, etc.) to examine the robustness of these findings. Nonetheless, some preliminary discussions are helpful here to suggest the nature of the observed individual differences and their relations to the flock size effect. Specifically, we found that birds positioned more frontally made significantly larger head movements than those positioned more towards the back, and those positioned more centrally also made larger head movements than those positioned more peripherally. Although we initially expected that leader birds would make larger head movements than follower birds, and indeed this was the case to a certain degree, this observation was only supported by a nonsignificant trend. As we found that leader birds were positioned more frontally in a flock than follower birds, these results overall suggest that individuals' patterns of head movement were influenced by their spatial positions in the flock, presumably rather than leadership per se.

The relationship between front-back position and leadership was consistently detected in previous studies with homing pigeons (Nagy et al., 2010; Pettit et al., 2015; Pettit et al., 2013) and also other species (Katz, Tunstrøm, Ioannou, Huepe, & Couzin, 2011). We also found that fast-flying birds in the solo flights were positioned more frontally during flock flights, which is consistent with Pettit et al. (2015), while we did not find a significant relationship between solo flight speed and flock leadership, unlike that previous study. It should be noted, however, that our birds had flown from the same release location many times before the flock flights, and thus they were already highly familiar with the route (as indicated by relatively high homing efficiency in our results; Table 1), which may have weakened individual differences in flight performance (and likely also in head movement) during the flock flights. Thus, further studies are necessary to examine individual differences in flight performance and head movement by minimizing the number of releases (as in Pettit et al., 2015). Notably, Pettit et al. (2015) additionally found that those leader and frontally-positioned birds followed more efficient routes in subsequent solo flights than follower birds, suggesting that leadership either causes or is correlated with enhanced route learning. Our results cannot distinguish between these alternatives, but they do provide a simple mechanistic explanation: fast-flying birds not only tend to position more frontally and become leaders in a flock, but we have also shown that they actively attend to visual landmarks to a greater degree than back-positioned birds, which could ultimately lead to better route learning by frontally-positioned/leader birds.

Previous studies on predator vigilance found that the best strategy for a predator to attack a moving group is a pursuit of peripheral or isolated individuals (Demšar & Lebar Bajec, 2014; Ioannou et al., 2012; Nishimura, 2002), and, during foraging, peripheral individuals in a flock tend to increase their vigilance, leading to the so-called ‘edge effect’ (Beauchamp & Ruxton, 2008; Elgar, 1989; Hirsch, 2007; Krause & Ruxton, 2002). Our homing data indicated just the opposite of what would be expected from these previous vigilance studies; namely peripherally-positioned birds within a flock showed smaller head movements than centrally-positioned birds. Nishimura (2002) has suggested that an alternative (but less supported) strategy for a predator to attack a moving flock is a pursuit of the nearest bird; in our study, likely one of the back-positioned birds. If this were the case, from the perspective of prey, those back-positioned birds would have to be more vigilant (scan more widely) than the rest of the flock, because the space behind them is not occupied by any other flock member and therefore they are open to attack. However, again, this expectation does not accord with our finding that back-positioned birds within flocks showed smaller head movement than frontally-positioned birds. Thus, our results better fit the idea that, during flock flights, peripheral or back-positioned individuals may prioritize maintaining flock cohesion (which leads to increased attention to flock partners and inhibition of visual scanning) rather than to increase their own efforts of vigilance. This is likely because maintenance of flock cohesion may be a more imminent task for back-positioned individuals (so as to avoid lagging behind the flock) and peripheral individuals (so as to maintain distance from the flock centre) than for frontally-positioned and central individuals. It is likely that, for both central and peripheral individuals, simply maintaining flock cohesion leads to anti-predatory benefits, such as diluting predation risk and confusing a predator (and also navigational benefits by pooling their navigational knowledge). Importantly, unlike in the foraging context (Inglis & Lazarus, 1981), the proportional decrease in peripheral individuals associated with increase in flock size does not account for the observed flock size effects in this study.

We reason that the flock size effect we found emerged most likely because individuals inhibited their head movement to attend to other flock members during flock flights; and this increased attention was necessary mainly to maintain cohesion (while also avoiding collisions and aligning with other members). Previous studies measuring head movements of homing pigeons

(Kano et al., 2018; Taylor et al., 2019) found that, during paired flights, birds attenuated their head movement (head saccades as well as vertical oscillatory head displacements) likely to attend more closely to their flight partner. The observed effect of flock size in this study additionally indicates that birds need to attenuate their head movement further in a larger flock, likely to improve the visual tracking of multiple flight partners. Therefore, this interpretation may extend the idea that flock-flying is costly for homing pigeons, not only energetically (Taylor et al., 2019; Usherwood et al., 2011) but also attentionally.

Alternative to this interpretation, decreased efforts of predator vigilance and landmark search (or a decrease in perceived predation risk or navigational demands) could have caused birds to decrease their head movement because, as mentioned, flying in a large flock could lead to both navigational and vigilance benefits and hence may have relaxed the need for predator detection and landmark search in individual birds. However, during the non-homing flights, where the actual predation risks and navigational demands were likely lower, we observed only a minimal effect of flock size. One key difference between the homing and non-homing flights in our study was that birds maintained much tighter flock cohesion in the former than the latter (see Appendix). Therefore, the observed flock size effects during the homing flights can be most parsimoniously explained as follows. (1) Individual birds may experience increased motivation to maintain flock cohesion during homing because staying in a flock can reduce navigational demands and predation risk. (2) Individual birds may face increased demands to follow a larger number of flock partners, both attentionally (Kano et al., 2018; Taylor et al., 2019) and physically (Taylor et al., 2019; Usherwood et al., 2011). (3) As a consequence, individual birds may decrease their baseline level of visual scanning (for both landmark search and predator vigilance) and instead increase reliance on the flock's collective sensory capacities and knowledge. Importantly, inhibition of head movement is likely accompanied by potential loss in navigational information (e.g. visual landmarks) acquired by individuals. However, our results show that such potential loss can ultimately be compensated for by the flock’s collective efforts because individual birds in our experiments continued to improve in their homing efficiency across flights sessions (see Table 1).

In conclusion, our results show that collective attention in homing pigeons is characterized by the group size effect and is accompanied by individual differences in visual scanning behaviour as a function of birds’ spatial position within the flock. We have therefore demonstrated that the group size effect on visual scanning emerges not only in foraging contexts, but also during large-scale visually-mediated navigation. Notably, however, the apparently similar group size effect across these contexts seems to emerge via distinct mechanisms; specifically, in the former, the group size effect may be driven by decreased necessity for predator vigilance (and constant necessity for foraging), while, in the latter, it may be driven by increased necessity for maintaining flock cohesion. Overall, our results suggest that, during collective navigation, individuals increase reliance on social cues as the number of group members increases, while simultaneously inhibiting environmental monitoring. Reduced environmental monitoring at the individual level may, nonetheless, be ultimately compensated for by the group’s collective efforts, likely through one or more suggested mechanisms such as ‘many wrongs’ (Simons, 2004) and collective sensing (Berdahl et al., 2013). Finally, given that we have shown that such attentional adjustments by individuals occur not only as a function of the number of nearby individuals but also as a function of context (e.g. homing vs. non-homing flights), heterogeneity of individual characteristics (e.g. differences in individuals’ flight speeds) and the characteristics of the local environment that individuals are experiencing (e.g. at different spatial positions in a flock), we suggest that future studies of group size effects should go beyond treating collective phenomena as a linear ‘numbers game’.

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Appendix text

Habituation to the mask

The following section, taken from our previous study using an identical experimental methodology (Kano et al., 2018), describes the protocol employed to habituate subjects to wearing the equipment used in the present study.

‘All birds were habituated to wearing the custom-made mask and backpack prior to flight testing. Backpacks were individually fitted to birds following established procedures (Nagy et al., 2010), to be worn for the duration of the study, and we verified that birds were able to walk and fly normally whilst wearing them. Many of the current subjects were already familiar with these backpacks from recent experiments (Sasaki & Biro, 2017; Taylor et al., 2017; Watts, Nagy, Burt de Perera, & Biro, 2016). Birds typically preened the elastic straps into their breast feathers; we checked these daily to ensure they had not slipped. Mask habituation lasted a minimum of 7 days (with each daily session lasting a maximum of 4 h) inside or around the birds’ home loft. For safety and comfort, masks were designed such that birds could take them off by themselves using their feet, so the purpose of the habituation sessions was to accustom them to masks to the point that they stopped removing them. The criterion for a bird passing habituation was that it did not take the mask off on two consecutive days out of a total of 7 days. No bird was dropped from the study for failing to meet this criterion. After 7 days of habituation, birds rarely removed the mask, although they occasionally made apparent attempts to do so (e.g. by shaking their head), particularly at the beginning of a daily session. However, we confirmed that the frequency of such attempts decreased considerably within the first hour of the session (typically 4 times per hour in the first hour to 0–1 times per hour in the remaining hours). Importantly, after the 7 days of mask habituation, we confirmed that all birds exhibited normal locomotive patterns (e.g. walking, flying, landing, taking off) and other essential activities (e.g. drinking, eating, tending to chicks/eggs) inside and around the loft.'

Follow-up experiment: Flights around the home loft

We examined the flock size effect while birds were flying around their loft. Fifteen birds participated in this follow-up experiment, conducted three months after the main experiment. Ten of these birds had also participated in the main experiment (homing) and the remaining 5 birds participated only in this follow-up experiment (habituated to the mask following the same procedures described above). We released flocks of 13 to 14 pigeons above their home loft, once per day and over a total of 30 days. One bird did not coordinate with the flock (flew only as solo) and was replaced with another bird on the 5th day. Another bird stopped participating in flights later on during the series of trials, and was not released on the last 5 days of the experiment. The data from one additional day were dropped because one of the loggers malfunctioned.

In each trial, the flock was released just outside the loft and allowed to engage in any activity for 30 minutes, while the entrance to the loft was temporarily blocked. During these 30-minute periods, subjects performed intermittent flights circling the loft, either solo or with a varying number of other birds. Solo flight was defined as the focal bird flying (> 20 km/s ground speed for a minimum of 10 seconds) a minimum of 200-m away from any other flying bird (a presumed interaction limit). Coordination with a given partner was defined as the focal bird flying cohesively (within a 50-m distance) with the partner in the same direction (within 45 degrees). Due to the fission-fusion pattern of flocking in this context, flock size was defined as ordinal scores; either 1-'small' (2-4 birds), 2-'medium' (5-8 birds), or 3-'large' (9-14 birds). If a bird did not fly for longer than 10 seconds on a given day, all of that bird's data was dropped from the analyses. On average, total sample duration was 1.0 ± 1.2, 1.4 ± 1.2, 0.7 ± 0.6, and 0.7 ± 0.5 minutes (mean ± s.d.) per trial in the solo, small-, medium-, and large-flock flights, respectively.

We included in the model the subject means of each head movement parameter (head turning rate, saccade frequency, or saccade amplitude) as the response variable, the flock size (solo, small, medium, large) as a fixed term and the subject ID as a random term. See Table A4 for the details about the model structures and statistical results (formula, estimate, SE, and CI). Birds did not change their head turning rate (degree/s) as a function of flock size (Table A2 and Figure A2; $\chi^2_1 = 0.88$, $P = 0.35$). They showed opposite patterns in saccade frequency and amplitude: they increased saccade frequency ($\chi^2_1 = 14.47$, $P = 0.00014$) while decreasing saccade amplitude ($\chi^2_1 = 8.80$, $P = 0.0030$) as a function of flock size.

Thus, unlike during homing flights (see main text), birds did not show clear decreasing tendencies with flock size in all head movement parameters during these around-the-loft flights. The observed overall pattern across the three head movement parameters was somewhat puzzling, in that saccade frequency increased while saccade amplitude decreased as a function of flock size, and these opposing changes in saccade frequency and amplitude offset the change in head turning rate. These results can be explained by the fact that birds increased flight turning rate as a function of flock size (Table A2) because larger flocks tended to fly more circular paths around the loft; and our main results have shown that birds tend to increase saccade frequency (but not saccade amplitude) in response to an increase in flight turning rate during flock flights (Figure 3). Thus, the observed increase in saccade frequency may be a situational artifact, while the decrease in saccade amplitude may reflect a genuine effect of flock size. However, it should be noted that the observed decrease in saccade amplitude during the loft flights was far more moderate than that observed during the homing flights (compare Tables 1 and A3). One critical difference which might explain this observed difference between homing and loft flights may be the cohesiveness of flock, namely that, while birds flew with partners cohesively during homing flights (flying with a partner/partners for longer than 80% of the total duration where each flight lasted around 5 minutes; see Methods), they flew with partners only occasionally during the loft flights (flying with a partner/partners for around 1-2 minutes during the 30-minute observation period). This may have been due to a perceived reduction in the benefits of flying as a flock, both for the anti-predatory and navigational benefits, when in close proximity to the loft.

Individual differences observed during paired flights

We examined individual differences in head movement and flight performance in paired flights using the same analyses that we conducted on flock flight data. See Table A5 for the details about the model structures and statistical results.

First, we examined the relationship between individuals' head movement and relative positions with respect to the centre of the two birds during the paired flights. We included in the model the trial means of each head movement parameter (either head turning rate, saccade frequency or saccade amplitude) as the response variable, the trial means of front-back position (m), left-right position (m), and distance from the pair centre (m; log-transformed to achieve approximate normality) as fixed terms, and the subject ID and individual flight ID as random terms. We also included the trial means of flight turning rate and the flight days (1-11) as control fixed terms. The full-null comparison revealed significance for the model with saccade frequency (χ^2_3 = 8.58, P = 0.035) but not for the model with head turning rate (χ^2_3 = 7.75, P = 0.052) or with saccade amplitude (χ^2_3 = 4.60, P = 0.20). We thus analysed the model with saccade frequency further. We found that birds positioned more distantly from the partner bird showed higher saccade frequency

($\chi^2_1 = 8.00$, $P = 0.0047$) (Figure A3); the opposite tendency from that observed during the flock flights. The other test predictors (front-back and left-right position) were not significant.

Second, we examined the relationship between individuals' head movement and leadership quantified through directional correlation delay analysis. We included in the model the trial means of each head movement parameter (either head turning rate, saccade frequency or saccade amplitude) as the response variable, individuals' leadership rank (calculated per trial) as a fixed term, and the subject ID and individual flight ID as random terms. We also included the trial means of flight turning rate as an additional control term. We found leader birds showed higher saccade frequency (Figure 4b; $\chi^2_1 = 6.17$, $P = 0.013$) with a similar level of head turning rate (Figure 4a; $\chi^2_1 = 3.63$, $P = 0.057$) and saccade amplitude (Figure 4c; $\chi^2_1 = 1.18$, $P = 0.28$). We also examined the relationship between individuals' leadership and spatial position in the pair. We included in the model individuals' leadership rank as the response variable, the trial means of front-back position (m), left-right position (m), and distance from the pair centre (m; log-transformed) as fixed terms, and the subject ID and individual flight ID as random terms. The full-null comparison revealed significance ($\chi^2_3 = 18.74$, $P = 0.00031$). Testing each test predictor revealed that frontally-positioned birds were also leaders in a pair (Figure A5a; $\chi^2_1 = 18.51$, $P < 10^{-4}$), consistent with the results from the flock flights. The other test predictors (left-right position, distance from the pair centre) were not significant.

Third, we examined whether individual differences observed in the solo-1 flights were related to individuals' head movement patterns, spatial positions and leadership observed in the paired flights. We included in the model the trial means of each head movement parameter (either head turning rate, saccade frequency or saccade amplitude) during the paired flights as the response variable, individuals' mean ground speed and homing efficiency during the solo-1 flights as fixed terms and the subject ID and individual flight ID as random terms. We also included the trial means of flight turning rate as an additional control term. The full-null comparison did not reveal significance for the model with any head movement parameter. We next examined whether individual differences in flight performance (ground speed, homing efficiency) observed during solo-1 flights were related to individuals' spatial positions (front-back, left-right, and distance from the pair centre) and leadership during the paired flights. We included in the model either of these parameters observed during the paired flights as the response variable, individuals' mean ground speed and homing efficiency during the solo-1 flights as fixed terms and the subject ID and individual flight ID as random terms. The full-null comparison revealed significance for the model with front-back position ($\chi^2_2 = 7.73$, $P = 0.021$) and no significance with left-right position ($\chi^2_2 = 1.05$, $P = 0.59$), distance from the pair centre ($\chi^2_2 = 1.87$, $P = 0.39$; as the distance from the pair centre was identical for the two birds in any given flight, to analyse this response, we randomly resampled one bird from each flight 500 times, and the mean of the χ^2 scores was used), or leadership as the response ($\chi^2_2 = 5.44$, $P = 0.066$). We thus analysed the model with front-back position further. We found that those birds with higher homing efficiency in the initial solo flights positioned more frontally in the paired flights (Figure A5b; $\chi^2_1 = 6.45$, $P = 0.011$; note that, although one bird showed particularly low homing efficiency, we confirmed that removal of this bird yielded a similar result). The effect of solo ground speed was not significant.

Therefore, although overall patterns seemed consistent between the paired and flock flights, we found several interesting differences. Specifically, first, in the paired flights, birds that flew at greater inter-individual distances (rather than those that flew closer to each other) showed larger head movements. One explanation for this result is that distance from the partner may correlate with motivation rather than ability (e.g. speed) to coordinate with the partner in the paired flights, and hence distantly-flying birds may have also had a reduced motivation to attend to that partner. On the other hand, in the flock flights, distantly-flying birds (those that may have been lagging behind due to slower speed) had an increased motivation to keep up with the rest of flock and hence more strongly attended to the partners. Second, leaders, rather than frontally-positioned birds, showed larger head movements in the paired flights. Moreover, the birds that flew more efficiently (i.e. followed straighter routes) rather than those that flew faster in the initial solo flights became both leaders and frontally-positioned birds in the (subsequent) paired flights. These results may indicate that route knowledge (as indicated by homing efficiency), rather than individual flight characteristics of subjects (e.g. speed), may have influenced the triadic relationship among leadership, front-back position, and head movement in the paired flights. These potential differences between paired and flock flights may be simply explained by the fact that we conducted the flock flights after the paired flights, and thus all individuals were less familiar with the routes in the paired flights in this study. However, it is also possible that, as pair-flying birds, unlike flock-flying birds, had to compromise only two potentially-conflicting route preferences, and both birds had to follow only one partner bird, the individual differences in route knowledge rather than flight kinematic characteristics became a dominant factor in the paired flights.

Effect of solo route fidelity on head movement and flight performance observed during flock flights

We were asked whether there was a relationship between individuals' route fidelity observed during solo flights and their head movements and flight performances (observed during the solo, paired or flock flights). Relatedly, a previous study found that birds with higher fidelity to their own routes tended to become leaders in subsequent paired flights (Freeman, Mann, Guilford, & Biro, 2011) (note that a leader in this previous study was defined as the bird flying closer to its habitual route during the paired flights, while a leader in this study was defined using the directional correlation delay analysis in both paired and flock flights). To answer this question, we conducted additional analyses. Route fidelity was a single measure for a given bird, defined here as the mean of all possible pairwise nearest-neighbour distances among the last 5 solo flights of that bird (we chose those last 5 flights because birds established their own habitual routes after the first 4 flights; see Kano et al. (2018) for details); the nearest-neighbour distance of a given pair of paths was calculated by first choosing the path which was shorter in duration as the reference path, then measuring the closest distance from each positional fix on the reference path to the other path, and finally averaging those values. We then tested the effect of route fidelity on head movement and flight performance observed during the last 5 solo flights (after the birds established their own habitual routes), paired flights, and flock flights using the same statistical methods described in the main text; specifically, we used the same model structure as that used to test the effect of solo speed and homing efficiency (on the head movement and flight performance observed during the flock flights), except that we replaced those test factors with the route fidelity. We observed no significant effect of route fidelity on the head movement patterns observed during the solo (the last 5 flights), paired or flock flights. It thus appears that higher route fidelity does not imply more attention to the landscape, at least not in a way that is detectable in birds' head movements. Notably, although not significant, birds with higher route fidelities tended to be leaders during the paired flights ($\chi^2_1 = 3.72$, $P = 0.054$), partly replicating the results from Freeman et al. (2011). Moreover, we found that birds with higher route fidelities were positioned more leftward in a flock during both paired ($\chi^2_1 = 9.48$, $P = 0.002$) and flock flights ($\chi^2_1 = 4.11$, $P = 0.043$); the other relationships in the models were not significant. Although it remains unclear what this latter result suggests, one possibility is that there are covert (non-significant) relationships between fidelity, leadership, and the side- (or perceptual-)bias in our data (as suggested by the previous studies; Freeman et al., 2011; Nagy et al., 2010). Further studies are necessary to confirm those possible effects.

Tables

Table 1. Data summary and the means (s.d. in parentheses; across flights) of head movement and flight path parameters in each flight session.

	Solo-1	Pair (2 birds)	Solo-2	Flock (8-11 birds)	Solo-3
N of subjects / *N* excluded	22 / 0	22 / 0	22 / 0	22 / 0[*1]	20 / 2
N of releases per subject	8	9	2	11	2
N of individual flights / *N* excluded	172 / 4	178 / 20	44 / 0	217 / 25	40 / 0
Flight time per release (min)	6.1 (2.3)	5.3 (0.7)	4.5 (0.9)	4.4 (0.5)	4.3 (0.6)
Excluded time (%) per release due to non-coordination	-	17.1 (26.4)	-	17.2 (24.1)	-
Head turning rate (deg/s)	22.55 (4.21)	14.65 (3.03)	22.89 (4.49)	8.91 (2.23)	20.29 (3.95)
Saccade frequency (saccades/s)	1.81 (0.17)	1.54 (0.16)	1.84 (± 0.16)	1.20 (0.20)	1.70 (0.16)
Saccade amplitude (deg/saccade)	12.35 (1.64)	9.41 (1.14)	12.36 (1.79)	7.35 (0.84)	11.83 (1.57)
Flight turning rate (deg/s)	11.08 (0.47)	11.15 (0.28)	10.19 (0.68)	10.43 (0.34)	10.27 (0.57)
Ground speed (km/h)	55.88 (2.46)	51.50 (1.76)	63.77 (3.6)	58.71 (1.72)	61.16 (2.62)
Homing efficiency (proportion)	0.73 (0.09)	0.84 (0.03)	0.82 (0.09)	0.90 (0.02)	0.88 (0.05)

*1 Two birds were dropped from the experiment from the 2nd and 4th releases onward in the flock-flight session (see the main text for details).

Table A1. Summary of the statistics used to examine behavioural changes observed across flight sessions.

Test	Model as a R formula	Response	Term	Estimate	SE	CI $_{\text{lower}}$	CI $_{\text{upper}}$	χ^2	d.f.	*P*
Changes in head movement across the main flight sessions (solo-1, pair, and flock) on head movement	Response ~ Session + (1 + Session_A + Session_B || Subject) [*1]	Head turning rate	Session (solo-1 vs. pair) [*2]	-7.9	0.59	-9.04	-6.79	116.87	2	$< 10^{-4}$
			Session (solo-1 vs. flock) [*2]	-13.65	0.59	-14.71	-12.43			
		Saccade frequency	Session (solo-1 vs. pair) [*2]	-0.27	0.03	-0.33	-0.21	85.16	2	$< 10^{-4}$
			Session (solo-1 vs. flock) [*2]	-0.61	0.04	-0.68	-0.54			
		Saccade amplitude	Session (solo-1 vs. pair) [*2]	-2.94	0.23	-3.39	-2.53	112.7	2	$< 10^{-4}$
			Session (solo-1 vs. flock) [*2]	-5.01	0.23	-5.47	-4.59			
Effect of flight maneuvers (and flight sessions) on head movement	Response ~ Bin*Session + (1 + Bin*Session_A + Bin*Session_B || Subject) [*3]	Head turning rate	Bin:Session (solo-1 vs. pair) [*2]	2.58	0.33	1.98	3.29	71.34	2	$< 10^{-4}$
			Bin:Session (solo-1 vs. flock) [*2]	4.05	0.32	3.45	4.76			
		Saccade frequency	Bin:Session (solo-1 vs. pair) [*2]	0.18	0.02	0.13	0.22	75.67	2	$< 10^{-4}$
			Bin:Session (solo-1 vs. flock) [*2]	0.38	0.03	0.32	0.44			
		Saccade amplitude	Bin:Session (solo-1 vs. pair) [*2]	0.6	0.1	0.41	0.79	54.52	2	$< 10^{-4}$
			Bin:Session (solo-1 vs. flock) [*2]	0.74	0.08	0.59	0.89			
Changes in head movement across the two additional solo flight sessions (pair vs. solo-2)	Response ~ Session + (1 + Session || Subject)	Head turning rate	Session	8.24	0.65	6.95	9.57	48.22	1	$< 10^{-4}$
		Saccade frequency	Session	0.3	0.03	0.24	0.35	325.68	1	$< 10^{-4}$
		Saccade amplitude	Session	2.95	0.26	2.45	3.43	129.98	1	$< 10^{-4}$
Changes in head movement across the two additional solo flight sessions (flock vs. solo-3)	Response ~ Session + (1 + Session || Subject)	Head turning rate	Session	11.27	0.67	9.91	12.51	68.57	1	$< 10^{-4}$
		Saccade frequency	Session	0.5	0.04	0.42	0.57	306.2	1	$< 10^{-4}$
		Saccade amplitude	Session	4.43	0.25	3.92	4.97	147.69	1	$< 10^{-4}$
Changes in head movement across the three solo flight sessions (solo 1-3)	Resonse ~ Session + (1 + Session_A + Session_B || Subject)	Head turning rate	Session (solo-1 vs. solo-2) [*2]	0.34	0.62	-0.94	1.47	22.6	2	$< 10^{-4}$
			Session (solo-1 vs. solo-3) [*2]	-2.45	0.47	-3.42	-1.46			

		Saccade frequency	Session (solo-1 vs. solo-2) [*2]	0.03	0.03	-0.02	0.08	25.56	2	$< 10^{-4}$
			Session (solo-1 vs. solo-3) [*2]	-0.12	0.03	-0.17	-0.07			
		Saccade amplitude	Session (solo-1 vs. solo-2) [*2]	0.01	0.22	-0.41	0.43	12.12	2	0.0023
			Session (solo-1 vs. solo-3) [*2]	-0.54	0.14	-0.81	-0.27			
Changes in homing efficiency across the main flight sessions (solo-1, pair, vs. flock)	Response ~ Session + (1 + Session_A + Session_B || Subject)	Homing efficiency[*4]	Session (solo-1 vs. pair) [*2]	0.69	0.09	0.5	0.88	82.66	2	$< 10^{-4}$
			Session (solo-1 vs. flock) [*2]	1.19	0.09	1	1.37			
Changes in homing efficiency across the three solo flight sessions (solo 1, 2, vs. 3)	Response ~ Session + (1 + Session_A + Session_B || Subject)	Homing efficiency[*4]	Session (solo-1 vs. solo-2) [*2]	0.58	0.1	0.37	0.79	52.62	2	$< 10^{-4}$
			Session (solo-1 vs. solo-3) [*2]	0.94	0.09	0.74	1.11			

*1 Session_A and Session_B are dummy-coded variables for Session (solo-1, pair, flock).

*2 The term Session has three levels and thus model estimates are calculated for the two pairs (with solo-1 as a control). Yet note that the effect of Session is tested in a likelihood ratio test by comparing the full model with the reduced model dropping only that term from the full model.

*3 Bin is flight turning-rate bin (0 to 30 degree/sec in 6 bins).

*4 Homing efficiency is logit transformed to achieve approximate normality.

Table A2. Data summary and the means (s.d. in parentheses; across flights) of each head movement and flight parameter as a function of flock size.

	Solo	Small (2-4 birds)	Medium (5-8 birds)	Large (9-14 birds)
Duration (min) of flights per subject (*N* = 15) in a trial (30 trials in total)	1.0 (1.2)	1.4 (1.2)	0.7 (0.6)	0.7 (0.5)
Head turning rate (deg/s)	24.39 (3.10)	24.68 (2.18)	25.23 (2.51)	24.51 (1.72)
Saccade frequency (saccades/s)	2.01 (0.16)	2.07 (0.14)	2.17 (0.13)	2.16 (0.09)
Saccade amplitude (deg/saccade)	12.11 (0.92)	11.92 (0.47)	11.62 (0.71)	11.36 (0.57)
Flight turning rate (deg/s)	14.60 (2.28)	15.02 (0.72)	15.92 (0.52)	15.81 (0.53)
Ground speed (km/h)	42.54 (3.80)	42.62 (1.29)	41.83 (1.44)	40.60 (0.78)

Table A3. Summary of the statistics used to test for individual differences during flock flights.

Test	Model as a R formula	Response	Term	Estimate	SE	CI $_{\text{lower}}$	CI $_{\text{upper}}$	χ^2	d.f.	*P*
Effects of individual spatial position on head movement	Response ~ Front-Back + Left-Right + log(Centre) + TurnRate + NofFlock + Day + (1 + Front-Back + Left-Right + log(Centre) + TurnRate + NofFlock + Day || Subject) + (1 | FlightID) ^{*1}	Head turning rate	log(Centre)	-0.62	0.2	-1.13	-0.13	6.74	1	0.009
			Front-Back	0.57	0.22	0.16	0.95	6.74	1	0.009
			Left-Right	-0.092	0.18	-0.4	0.26	0.26	1	0.61 (n.s.)
		Saccade frequency^{*2}	-	-	-	-	-	-	-	-
		Saccade amplitude^{*2}	-	-	-	-	-	-	-	-
Effects of individual leadership rank on head movement	Response ~ Leadership + TurnRate + NofFlock + Day + (1 + Leadership + TurnRate + NofFlock + Day || Subject) + (1 | FlightID) ^{*3}	Head turning rate	Leadership	-0.23	0.13	-0.5	0.04	3.02	1	0.082 (n.s.)
		Saccade frequency	Leadership	-0.02	0.01	-0.05	-0.003	2.63	1	0.11 (n.s.)
		Saccade amplitude	Leadership	-0.06	0.06	-0.17	0.05	0.93	1	0.33 (n.s.)
Effects of individual spatial position on leadership	Response ~ Front-Back + Left-Right + log(Centre) + (1 + Front-Back + Left-Right + log(Centre) + || Subject) + (1 | FlightID)	Leadership	log(Centre)	1.28	0.36	0.56	1.99	9.58	1	0.002
			Front-Back	-1.78	0.42	-2.61	-0.95	16.6	1	$<10^{-3}$
			Left-Right	-0.11	0.2	-0.49	0.27	0.33	1	0.56 (n.s.)
Relationship between flight performance during the solo-1 flights and head movement during the flock flights	Response ~ SoloSpeed + SoloEfficiency + TurnRate + NofFlock + Day + (1 + TurnRate + NofFlock + Day || Subject) + (1 | FlightID) ^{*3}	Head turning rate	SoloSpeed	1.11	0.4	0.28	1.93	6.45	1	0.011
			SoloEfficiency	0.06	0.33	-0.56	0.73	0.04	1	0.85 (n.s.)
		Saccade frequency^{*2}	-	-	-	-	-	-	-	-
		Saccade amplitude^{*2}	-	-	-	-	-	-	-	-
Relationship between flight performance during the solo-1 flights and the flock flights	Response ~ SoloSpeed + SoloEfficiency + Day + (1 + Day || Subject) + (1 | FlightID)	log(Centre)^{*2}	-	-	-	-	-	-	-	-
		Front-Back	SoloSpeed	2	0.56	0.81	3.01	9.96	1	0.002
			Solo_Efficiency	0.23	0.56	-0.96	1.38	0.17	1	0.68
		Left-Right^{*2}	-	-	-	-	-	-	-	-
		Leadership^{*2}	-	-	-	-	-	-	-	-

*1 Front-Back, Left-Right, and log(Centre) are the trial means of front-back position (m), left-right position (m), and distance from the flock centre (m; log-transformed to achieve approximate normality), respectively. FlightID is the unique ID of individual flock flights. TurnRate, NofFlock and Day are the trial means of flight turning rate, the number of individuals in a flock (9-11), and the flight days (1-11), respectively.

*2 The effect of each term is not tested because the full-null comparison did not reveal significance.

*3 Solo_Speed and Solo_Efficiency are the subject means of ground speed and homing efficiency (logit-transformed) observed during the solo-1 sessions, respectively.

Table A4. Summary of the statistics used to test for the flock size effect during flights around the loft (non-homing flights).

Test	Model as a R formula	Response	Term	Estimate	SE	CI $_{\text{lower}}$	CI $_{\text{upper}}$	χ^2	d.f.	*P*
Effect of flock size	Response ~ FlockSize (1 + FlockSize | Subject)[*1]	Head turning rate	FlockSize	0.19	0.2	-0.21	0.62	0.88	1	0.35
		Saccade frequency	FlockSize	0.06	0.01	0.03	0.08	14.47	1	0.00014
		Saccade amplitude	FlockSize	-0.24	0.06	-0.37	-0.12	8.8	1	0.003

*1 FlockSize is defined as ordinal scores; 1-‘small’ (2-4 birds), 2-‘medium’ (5-8 birds), and 3-‘large’ (9-14 birds).

Table A5. Summary of the statistics used to test for individual differences during pair flights.

Test	Model as a R formula	Response	Term	Estimate	SE	CI $_{lower}$	CI $_{upper}$	χ^2	d.f.	*P*
Effects of individual spatial position on head movement	Response ~ Front-Back + Left-Right + log(Centre) + TurnRate + Day + (1 + Front-Back + Left-Right + log(Centre) + TurnRate + Day || Subject) + (1 | FlightID)^{*1}	Head turning rate^{*2}	-	-	-	-	-	-	-	-
		Saccade frequency	log(Centre)	0.04	0.01	0.02	0.06	8	1	0.0047
			Front-Back	-0.005	0.009	-0.03	0.01	0.32	1	0.57 (n.s.)
			Left-Right	0.004	0.01	-0.02	0.03	0.11	1	0.75 (n.s.)
		Saccade amplitude^{*2}	-	-	-	-	-	-	-	-
Effects of individual leadership rank on head movement	Response ~ Leadership + TurnRate + Day + (1 + Leadership + TurnRate + Day || Subject) + (1 | FlightID)^{*3}	Head turning rate	Leadership	0.39	0.2	0.001	0.8	3.63	1	0.057 (n.s.)
		Saccade frequency	Leadership	0.03	0.01	0.009	0.06	6.17	1	0.013
		Saccade amplitude	Leadership	0.08	0.07	-0.05	0.21	1.18	1	0.28 (n.s.)
Effects of individual spatial position on leadership	Response ~ Front-Back + Left-Right + log(Centre) + (1 + Front-Back + Left-Right + log(Centre) + || Subject) + (1 | FlightID)	Leadership	log(Centre)	-0.14	0.25	-0.63	0.35	0.32	1	0.57 (n.s.)
			Front-Back	-1.81	0.5	-2.79	-0.82	18.51	1	$< 10^{-4}$
			Left-Right	0.2	0.28	-0.34	0.75	0.54	1	0.46 (n.s.)
Relationship between flight performance during the solo-1 flights and head movement during the pair flights	Response ~ Solo_Speed + Solo_Efficiency + TurnRate + Day + (1 + TurnRate + Day || Subject) + (1 | FlightID)^{*3}	Head turning rate^{*2}	-	-	-	-	-	-	-	-
		Saccade frequency^{*2}	-	-	-	-	-	-	-	-
		Saccade amplitude^{*2}	-	-	-	-	-	-	-	-
Relationship between flight performance during the solo-1 flights and the pair flights	Response ~ Solo_Speed + Solo_Efficiency + Day + (1 + Day || Subject) + (1 | FlightID)	log(Centre)^{*2}	-	-	-	-	-	-	-	-
		Front-Back	Solo_Speed							
			Solo_Efficiency	0.54	0.2	0.17	0.94	6.45	1	0.011
		Left-Right^{*2}	-	-	-	-	-	-	-	-
		Leadership^{*2}	-	-	-	-	-	-	-	-

*1 Front-Back, Left-Right, and log(Centre) are the trial means of front-back position (m), left-right position (m), and distance from the flock centre (m; log-transformed to achieve approximate normality), respectively. FlightID is the unique ID of individual flock flights. TurnRate, and Day are the trial means of flight turning rate, and the flight days (1-11), respectively.

*2 The effect of each term is not tested because the full-null comparison did not reveal significance.

*3 Solo_Speed and Solo_Efficiency are the subject means of ground speed and homing efficiency (logit-transformed) observed during the solo-1 sessions, respectively.

Figure legends

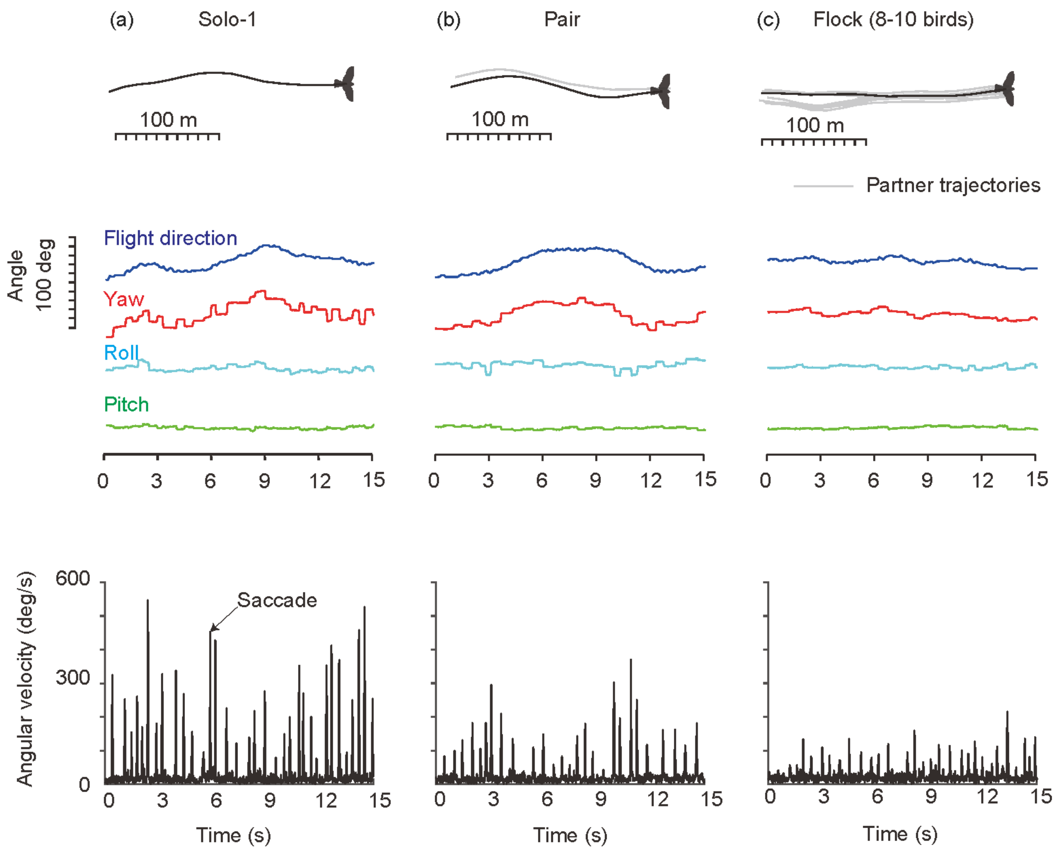

Figure 1. Examples of flight trajectories (recorded by GPS), flight directions (recorded by GPS), head angles (yaw, roll, and pitch; recorded by IMU), and the combined angular velocity (deg/s; combining changes in yaw, roll, and pitch angles) performed by the same bird during solo-1 (a), pair (b), and flock flights (c).

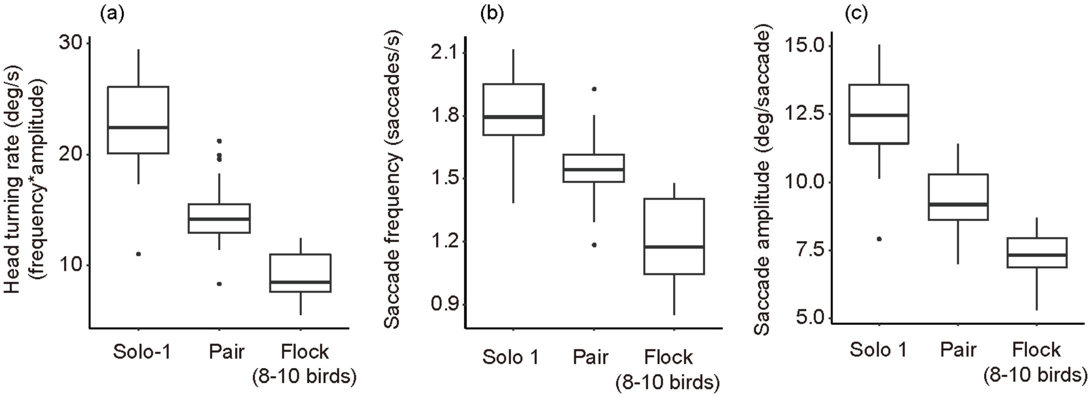

Figure 2. Head turning rate (deg/s), saccade frequency (saccades/s), and saccade amplitude (deg/saccade) across the main flight sessions (solo-1, pair, flock). Head turning rate is given as saccade frequency × amplitude. Box plots show the median, interquartile range (IQR), and 1.5 × IQR, with outliers plotted individually.

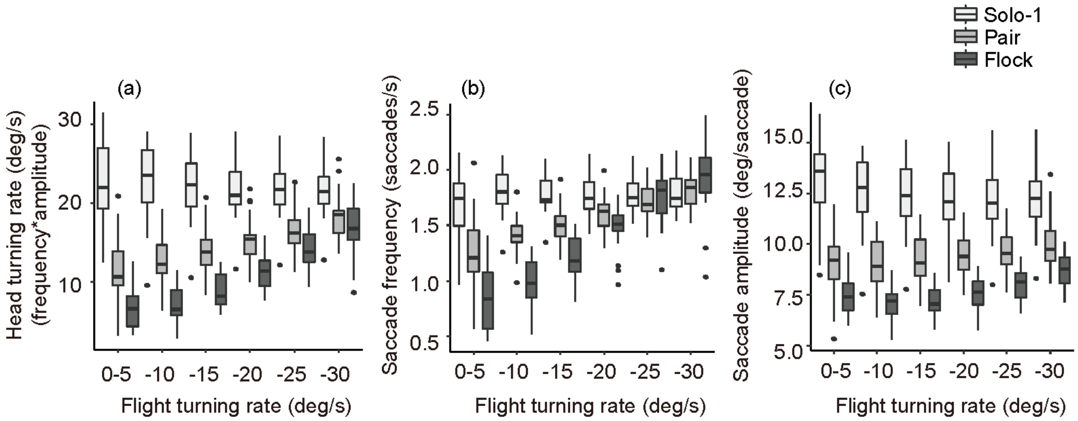

Figure 3. Head turning rate (degree/s), saccade frequency (saccades/s), saccade amplitude (degree/saccade) across the main flight sessions (solo-1, pair, flock) as a function of flight turning rate (in 5-degree/s bins). Box plots show the median, interquartile range (IQR), and 1.5 × IQR, with outliers plotted individually.

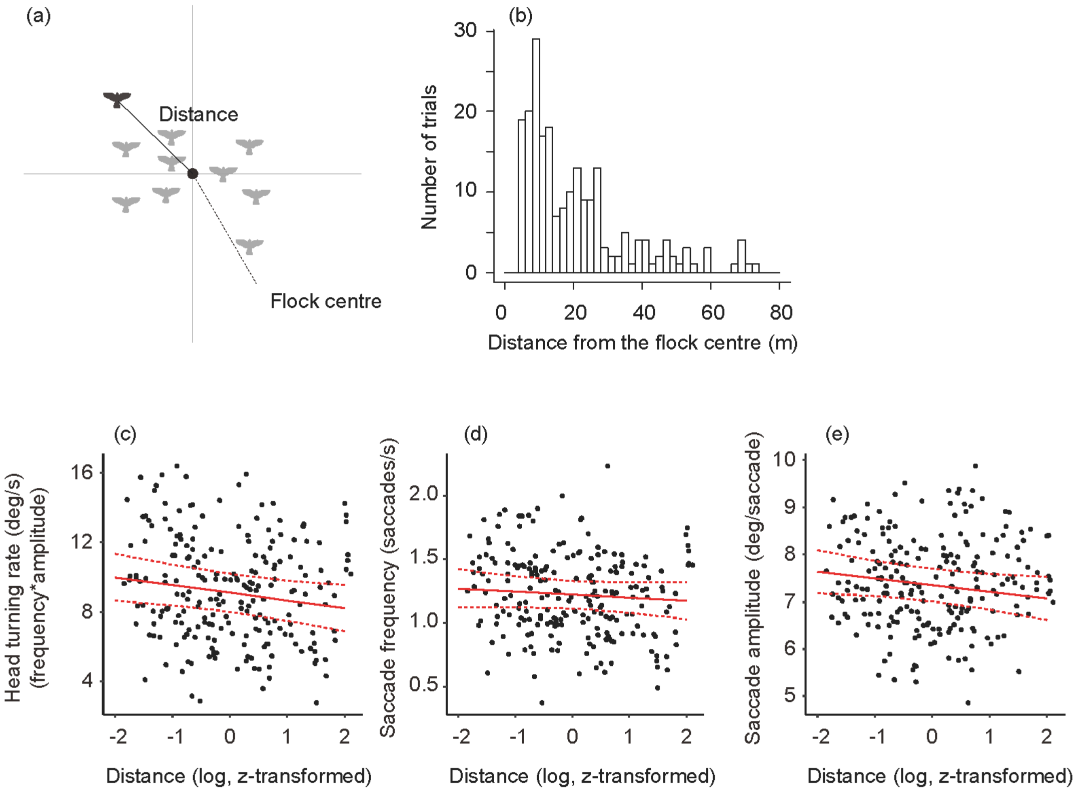

Figure 4. Effect of distance from the flock centre on individual head movement. (a) Example of distance calculation from the centroid of all birds' GPS positions. (b) Histogram of these data across all flock flights. (c-e) Head movement as a function of mean distance from the flock centre (log and z-transformed); (c) head turning rate (deg/s; frequency × amplitude), (d) saccade frequency (saccades/s), and (e) saccade amplitude (deg/saccade). Solid and dashed lines indicate predicted values and 95% confidence intervals, respectively.

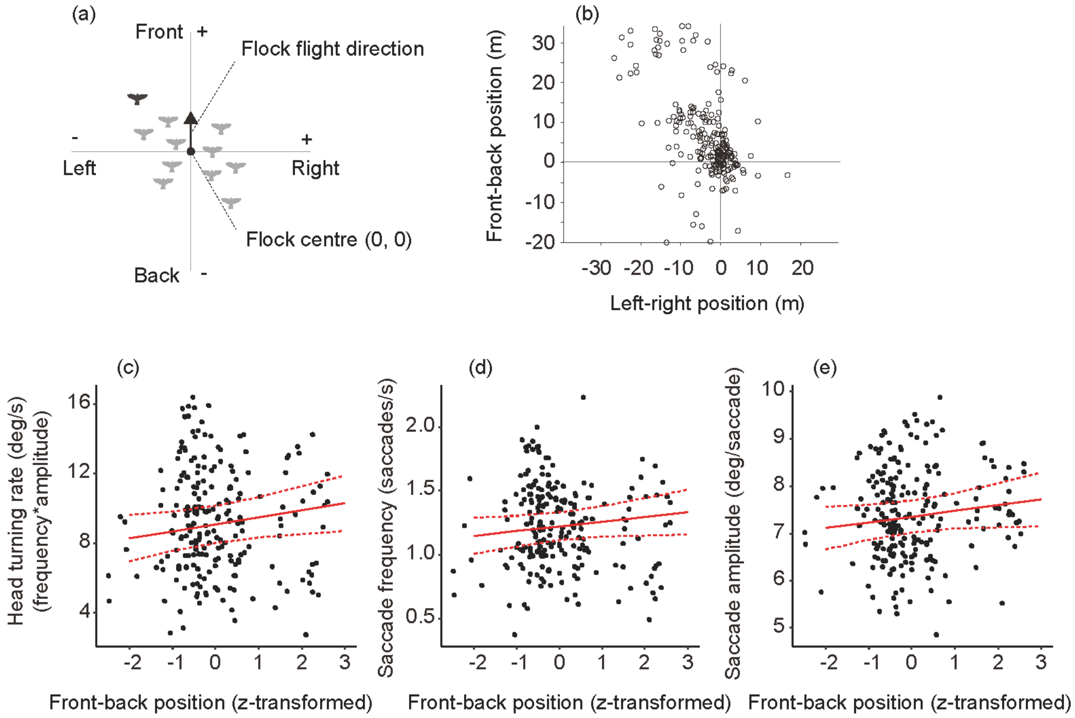

Figure 5. Effect of spatial position within the flock on individual head movement. (a) Example of front-back and left-right position calculation with respect to the flock centre and to the flock's mean flight direction. (b) The distribution of these data across all flock flights. (c-e) Head movement as a function of front-back positions (z-transformed); (c) head turning rate (deg/s; frequency × amplitude), (d) saccade frequency (saccades/s), and (e) saccade amplitude (deg/saccade). Solid and dashed lines indicate predicted values and 95% confidence intervals, respectively.

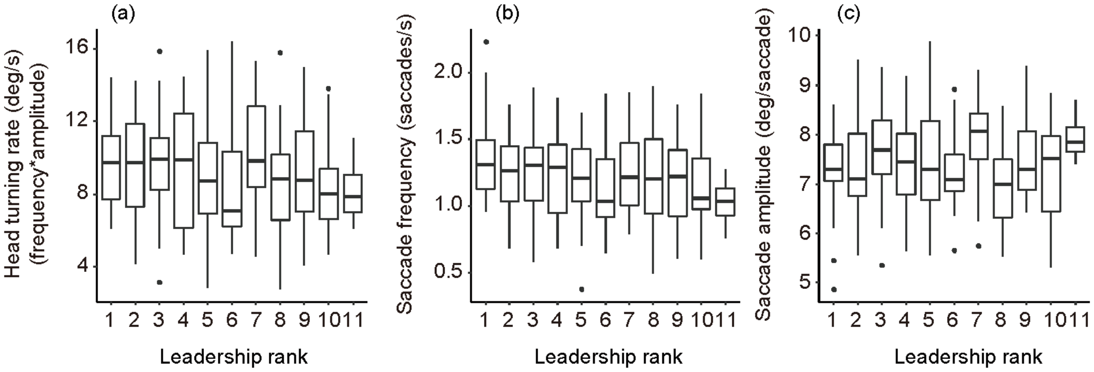

Figure 6. Head turning rate (deg/s; frequency × amplitude), saccade frequency (saccades/s), and saccade amplitude (deg/saccade) as a function of birds' leadership ranks during flock flights. Box plots show the median, interquartile range (IQR), and 1.5 × IQR, with outliers plotted individually.

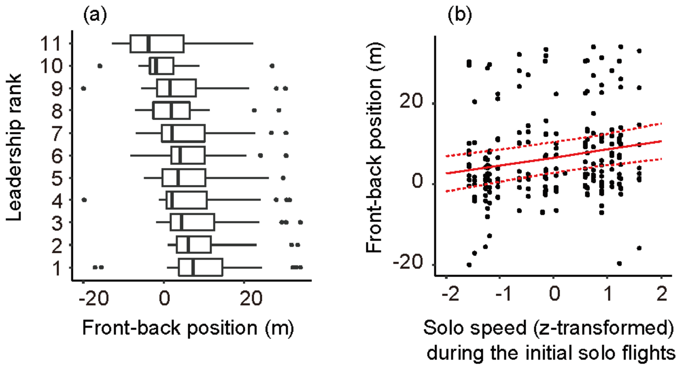

Figure 7. Relationships among leadership, front-back positioning, and solo-1 flight speed. (a) Leadership rank as a function of front-back position during flock flights. Box plots show the median, interquartile range (IQR), and 1.5 × IQR, with outliers plotted individually. (b) Front-back position during the flock flights as a function of individual mean ground speeds (km/h; z-transformed) observed during the solo-1 flights. Solid and dashed lines indicate predicted values and 95% confidence intervals, respectively.

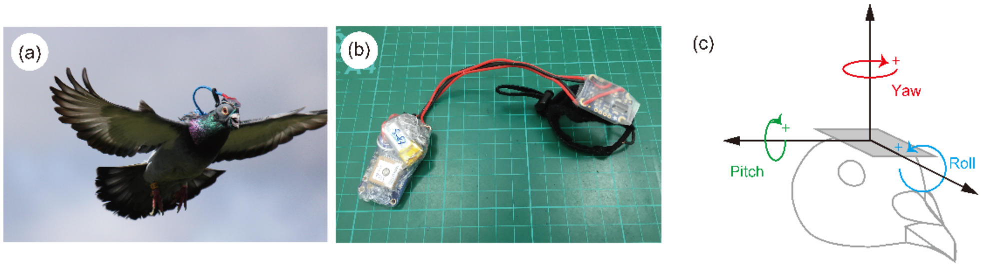

Figure A1. Experimental apparatus. (a) A pigeon wearing the logger. (b) The logger incorporating a head-mounted IMU (attached to a custom-made mask to fit the pigeon's head) and a back-mounted GPS attached to a microcomputer, micro-SD card and battery (to be installed in a backpack). (c) Yaw, roll, and pitch axes in the IMU device. The arrows indicate the direction of rotation.

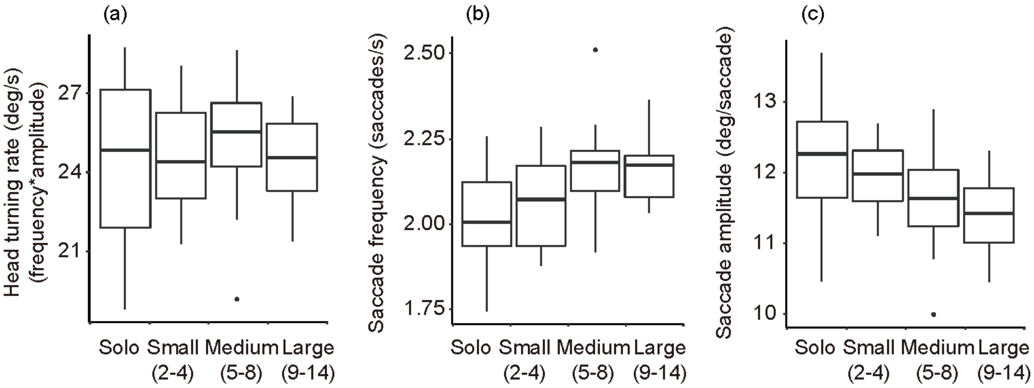

Figure A2. Head movement as a function of flock size across all around-the-loft flights; (a) head turning rate (deg/s), (b) saccade frequency (saccades/s), and (c) saccade amplitude (deg/saccade) Box plots show the median, interquartile range (IQR), and 1.5 × IQR, with outliers plotted individually.

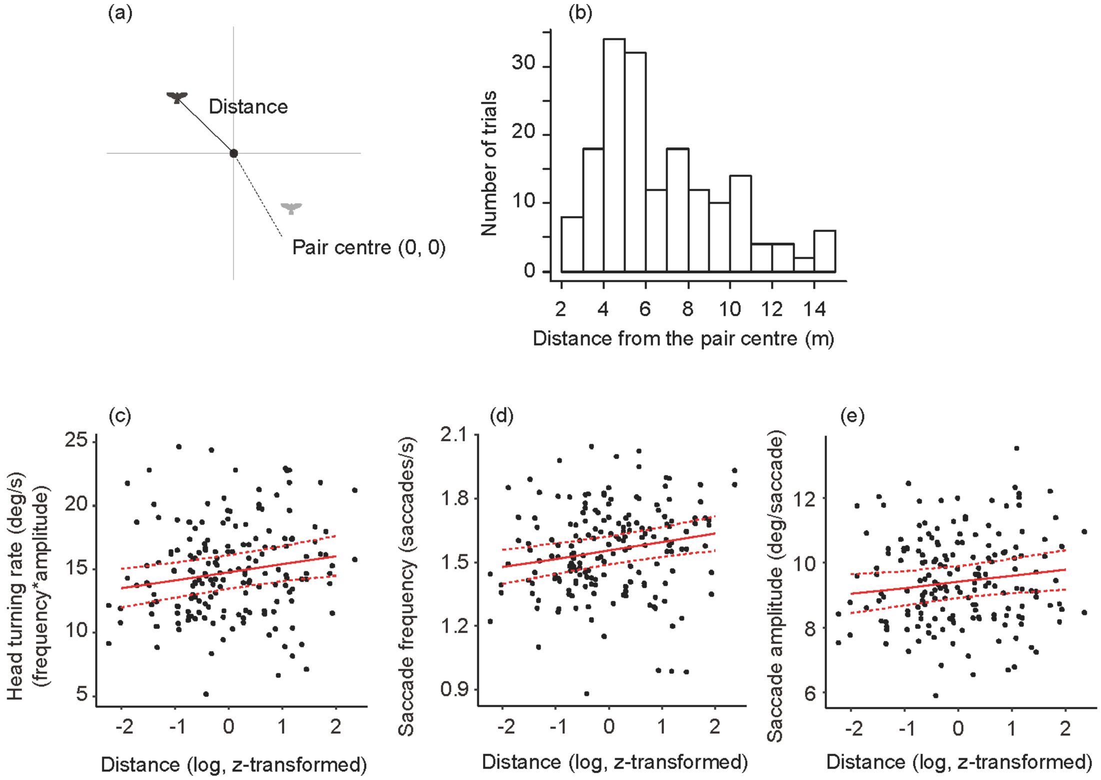

Figure A3. Effect of spatial position within the pair on individual head movement. (a) Example of front-back and left-right position calculation with respect to the pair centre and to the pair's mean flight direction. (b) Histogram of these data across all paired flights. (c-e) Head movement as a function of mean distance from the centre of the two birds (log and z-transformed); (c) head turning rate (deg/s; frequency × amplitude), (d) saccade frequency (saccades/s), and (e) saccade amplitude (deg/saccade).

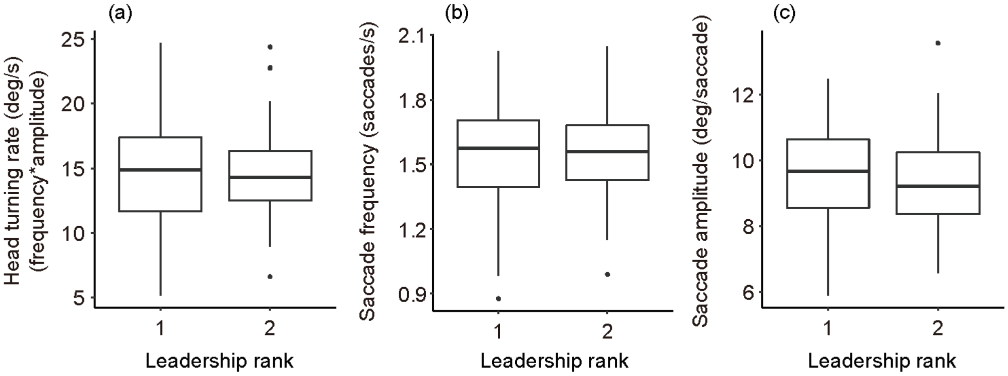

Figure A4. Head movement as a function of birds' leadership ranks during the paired flights; (a) head turning rate (deg/s; frequency × amplitude), (b) saccade frequency (saccades/s), and (c) saccade amplitude (deg/saccade). Box plots show the median, interquartile range (IQR), and 1.5 × IQR, with outliers plotted individually.

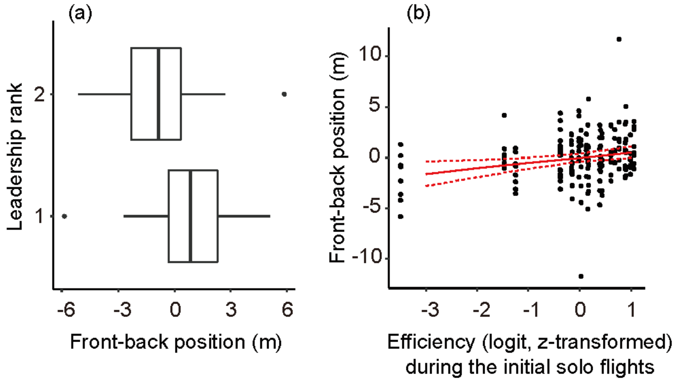

Figure A5. Relationships among leadership, front-back positioning, and solo-1 homing efficiency. (a) Leadership rank as a function of front-back positions in the paired flights. Box plots show the median, interquartile range (IQR), and 1.5 × IQR, with outliers plotted individually. (b) Front-back positions (m) observed in the paired flights as a function of the individual means of homing efficiency (logit and z-transformed) observed in the initial solo flights.