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Animal behaviour

Misinformed leaders lose influence over pigeon flocks

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In animal groups where certain individuals have disproportionate influence over collective decisions, the whole group's performance may suffer if these individuals possess inaccurate information. Whether in such situations leaders can be replaced in their roles by better-informed group mates represents an important question in understanding the adaptive consequences of collective decision-making. Here, we use a clock-shifting procedure to predictably manipulate the directional error in navigational information possessed by established leaders within hierarchically structured flocks of homing pigeons (*Columba livia*). We demonstrate that in the majority of cases when leaders hold inaccurate information they lose their influence over the flock. In these cases, inaccurate information is filtered out through the rearrangement of hierarchical positions, preventing errors by former leaders from propagating down the hierarchy. Our study demonstrates that flexible decision-making structures can be valuable in situations where 'bad' information is introduced by otherwise influential individuals.

1. Introduction

Animal groups faced with making joint decisions can exploit variation in members' personal information by sharing decision-making: when navigating, for example, they can pool their personal knowledge to reduce overall navigational error (e.g. [1]). However, in some groups, decisions are not shared entirely 'democratically', meaning that individuals do not contribute equally to decisions [2,3]. The group's performance then becomes disproportionately dependent on leaders' information quality. Because leadership does not necessarily correlate with competence [2,4] the question arises whether (i) followers and/or leaders are sensitive to the quality of leaders' input, and, if so, (ii) whether groups have any scope for 'overruling' inaccurate leadership.

Homing pigeon flocks form transitive leadership hierarchies where some individuals consistently contribute more to directional decisions than others [3], although a degree of decision-sharing is also evident among members [5,6]. These hierarchies are stable across time [7], and important factors structuring them include individual differences in, e.g. navigational experience [8,9] and speed [4]. Recent modelling work has shown that multi-level hierarchies can compensate for an increase in navigational error better than random networks [10]; however, this advantage disappears when the most influential individuals have the highest error, as errors then propagate down the hierarchy. In such situations, hierarchical structuring could be detrimental.

Here, we examined whether this model prediction holds true in real homing pigeon flocks, by experimentally increasing the navigational error of an identified leader. We manipulated leaders' personal information through 'clock-shifting': a procedure known to systematically interfere with pigeons' use of the sun-compass

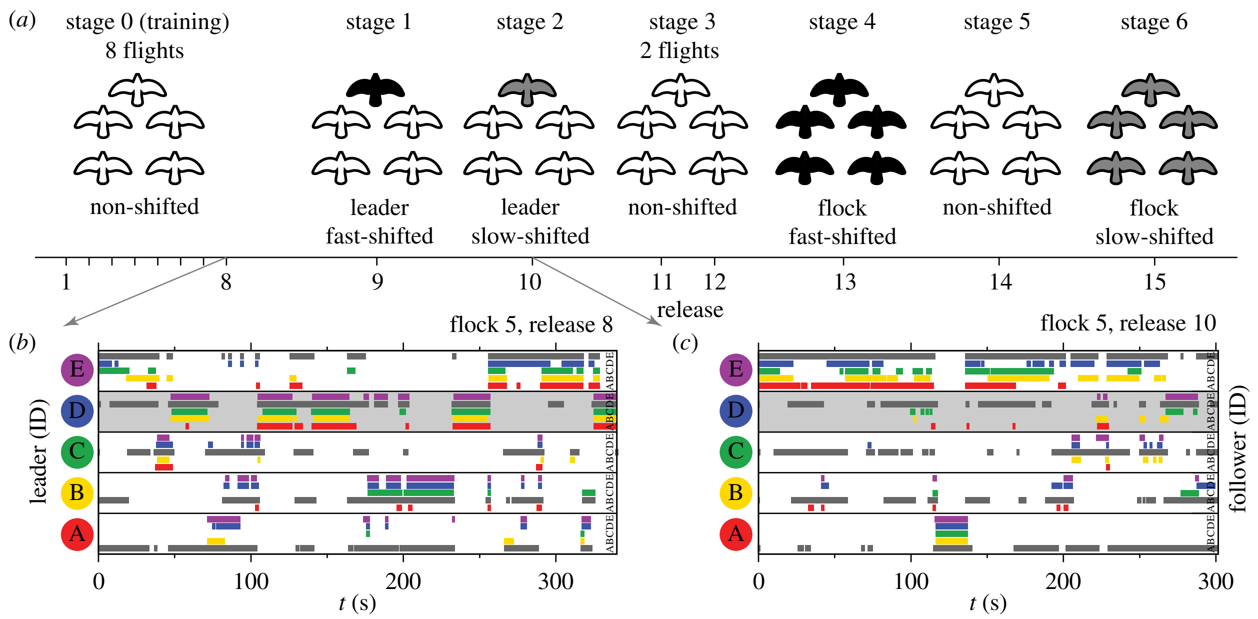

Figure 1. Experimental design and leadership analysis. (*a*) Release protocol for the eight experimental flocks. (*b*,*c*) Momentary leader–follower interactions over 10 s time windows for an example flock in releases 8 and 10, respectively. Coloured bands indicate who is following the given individual at each time step. Dark grey indicates that a bird is not following other birds, either because it is top of the hierarchy or flying alone, or because interactions cannot be resolved using our time resolution. The stage 0 leader (D) is highlighted with a light grey background; note the disappearance of most of its leadership (coloured bands in (*b*)) when clock-shifted (*c*).

for directional guidance, where clock-shifted ('misinformed') birds fly a predictably deviated route home [11]. We asked whether stable leadership results in such errors propagating down the hierarchy (i.e. the whole flock flies the incorrect, shifted route) or if some compensatory mechanism allows flocks to maintain a correct (non-shifted) route.

2. Material and methods

We assigned 40 homing pigeons (age = 2–5 years) to eight flocks of five birds, ensuring a comparable age distribution across flocks. During all flights, positional data were logged using 5 Hz GPS loggers (Qstarz BT-Q1300ST) attached to the birds' backs via Velcro strips.

We trained flocks from our chosen site (Bladon, 51°49′23.48″ N 1°21′26.29″ W; distance and direction from home: 5.27 km, 149.5°) through eight consecutive releases ('stage 0'; figure 1*a*). We calculated leadership ranks for each member in each flock based on spatial positioning (with leaders nearer the front and followers nearer the back) and confirmed these through directional correlation delay analysis (electronic supplementary material, figure S1; see [3] for details of both methods). We designated as 'stage 0 leaders' birds with the highest average rank over the last four training releases.

After training, we conducted six experimental stages. We performed four clock-shifts (stages 1, 2, 4 and 6; figure 1*a*), during which selected birds were placed in light-tight chambers until their internal clocks readjusted to an artificially shifted day–night cycle. All shifts corresponded to either an anticlockwise (fast) or clockwise (slow) 70° shift in the Sun's azimuth on the dates of release. Birds were then released in their original flocks. stages 3 and 5 were control flights, not involving clock-shift.

GPS tracks were analysed in MATLAB (Mathworks 2012b) and R (0.98.1014). We explored the effect of misinformed (i.e. clock-shifted) leaders and flocks by assessing, post-clock-shift (i) changes to the leadership hierarchy and (ii) deviations in the route flown. See the electronic supplementary material for detailed Methods. All data were made available on the Dryad Digital Repository [12].

3. Results

Birds identified as stage 0 leaders occupied hierarchical positions where they had high influence (rank 1 or 2) on flocks' directional decisions in the majority of stage 0 flights (electronic supplementary material, figure S2). Although ranks initially showed fluctuations, as stage 0 progressed these leaders' positions exhibited increasing stability, particularly in the final two flights (electronic supplementary material, figures S3 and S4). Following clock-shifting of stage 0 leaders (stages 1 and 2), most of these birds' average time delay values (reflecting whether and how soon their directional changes were copied by others) decreased (figure 2*a*) meaning that they were located significantly less often, than during stage 0, in positions of high influence both within (figure 1*b*,*c*) and averaged across flights (generalized linear mixed model (GLMM) family binomial with *flock* as random factor a) rank 1: $Z = -2.75$, effect $= -2.12$, $p = 0.006$, b) rank 1 or 2: $Z = -3.76$, effect $= -3.05$, $p < 0.001$; electronic supplementary material, figures S2–S4). This was accompanied by a significant, two-place decrease in stage 0 leaders' median rank (with only three of the eight stage 0 leaders remaining top-ranked during the first clock-shifted flight, and none during the second), and while their ranks increased again during stage 3, they did not recover fully (figure 2*b*). Other birds in the flock also showed changes in rank, but in none of them were these significantly in a consistent direction (electronic supplementary material, figure S5). During the two flock clock-shift releases (stages 4 and 6), flocks frequently split up, leaving too small a sample size to assess changes in leadership hierarchies statistically. Out of eight flights in which the stage 0 leader did not split and where at least three birds remained in the flock, on three occasions the stage 0 leader assumed leadership.

To detect clock-shift deviation in tracks, we used 'virtual vanishing bearings', calculated as the subjects' heading at given points with respect to the release point [13]. For each

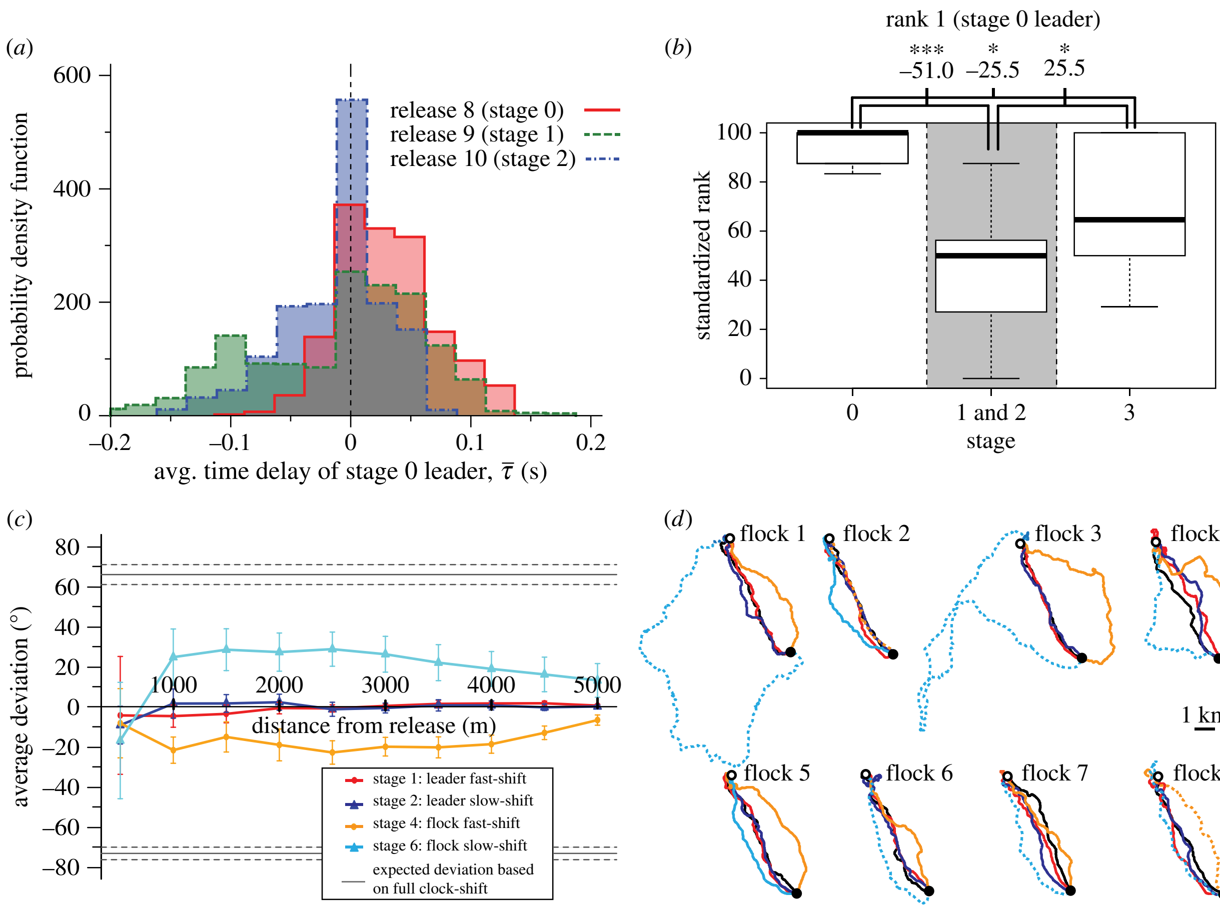

Figure 2. Effect of clock-shift on time delays, leadership ranks and routes. (*a*) Distribution of momentary time delay values (τ) for stage 0 leaders for releases 8–10, averaged for each time step over the eight flocks. Positive values indicate being ahead of the mean of the flock. (*b*) Boxplots of median standardized ranks of stage 0 leaders. Asterisk indicates significance level between stages (* < 0.5, *** < 0.001) and the numbers the effect sizes from post hoc Tukey tests, only after a significant effect of *stage* in a LMM with *flock* as a random effect was found (see electronic supplementary material, figure S4 for boxplots of the other ranked birds). Standardized rank 100 is equivalent to rank 1 (top). (*c*) Median deviation in virtual vanishing bearings in the tracks of the four clock-shifted stages compared with the same birds' final training flight. Bars indicate standard errors across all flocks. Dashed grey lines indicate the standard error of expected clock-shift across the four stages. (*d*) Flight tracks of the stage 0 leaders during their last training flight (black) and the four clock-shift releases. Colouring of lines matches panel (*c*); dashed lines indicate the leader flew alone or the flock split (i.e. three or fewer birds remained). White circles show release site; black circles show home loft.

500 m concentric boundary centred around the release site, we calculated the flock medians of the difference in each individual's heading between their last training release (non-shifted control) and test release for stages 1, 2, 4 and 6 (figure 2*c*,*d*). A deviation of zero indicates that the track is, at the given distance from release, identical to the training track, i.e. displays no effect of clock-shift.

When all birds in the flock were clock-shifted (stages 4 and 6), virtual vanishing bearings were significantly different from the null expectation (table 1) in the expected direction of deviation for compass control (i.e. anticlockwise for the stage 4 fast-shift and clockwise for the stage 6 slow-shift). However, when only the stage 0 leader was clock-shifted (stages 1 and 2) flock virtual vanishing bearing deviations were not significantly different from the null expectation. This was also true for the stage 3 and 5 controls (table 1).

4. Discussion

Previous theoretical work predicted that in hierarchically structured decision-making errors by leaders propagate downwards, resulting in inaccurate collective decisions [10]. By introducing inaccurate navigational information of a specific magnitude at the top of the hierarchy, we found this disadvantage could be overcome in pigeon flocks: our results showed that when only leaders were misinformed flocks retained their existing routes, whereas when entire flocks were shifted they displayed deviated routes (albeit with a smaller-than-predicted deviation, as is common in birds familiar with the landscape, [14]; although see [15]). Thus, we can infer that clock-shifting was successful, but that leaders alone were not able to 'mislead' their flocks on erroneous routes.

Importantly, we also documented a drop in leaders' hierarchical ranks (i.e. in the majority of flocks their input into the flock's navigational decisions diminished) when they alone were clock-shifted. In considering this result, however, it is worth noting that stage 0 leaders were not entirely stable in their leadership during training (electronic supplementary material, figures S3 and S4). Nonetheless, stability was greatest in releases 7–8, where all stage 0 leaders ranked either in the top two (release 7) or the top (release 8) hierarchical positions. Thus, the comparison with stages 1 and 2 is clearest when considering the latter part of stage 0. That leadership stability was gradually established is also supported by the observation that stage 0 routes showed a clear learning curve, asymptoting also around releases 7–8 (electronic supplementary material, figure S7). We therefore suggest that although there is noise in the

Table 1. Comparisons between the median flock virtual vanishing bearings for each stage and their corresponding null expectation. Null expectation was calculated as a track with a mean deviation of 0, and a standard deviation exactly equal to that of each flock for the different stages. We compared a linear mixed model (LMM) with *stage*, and *distance* as fixed effects and *flock* as a random effect to a LMM without *stage* (maximum-likelihood test: $\chi^2 = 130.8$, $p < 0.001$), then used post hoc Tukey tests for pairwise comparisons between combinations of interest.

stage comparison	estimate	*z*-value	Bonferroni corrected *p*-value
stage 1, null	−3.40	−0.929	1
stage 2, null	−1.63	−0.446	1
stage 4, null	−13.5	−3.68	0.0024
stage 6, null	24.6	6.71	<0.001
stage 3 release 1, null	1.17	0.320	1
stage 3 release 2, null	−4.05	−1.10	1
stage 5, null	1.88	0.364	1
stage 4, stage 3 release 1	−16.8	−4.59	<0.0001
stage 4, stage 3 release 2	−17.3	−4.73	<0.0001
stage 6, stage 5	22.7	5.01	<0.0001

system in the form of (i) flocks gradually settling on both leaders and routes and (ii) leaders varying in the extent to which they drop in rank, the combination of overall patterns within the leadership hierarchical data and analyses of route structures pre- and post-clock-shifting provide a sufficiently high signal-to-noise ratio for our conclusions.

We hypothesize that where a decrease was observed in leaders' hierarchical rank, this could have been due to two non-mutually exclusive mechanisms. First, clock-shifting may have caused leaders to become uncertain in the quality of their own information. Clock-shifting places the sun-compass, an important navigational cue, in conflict with all other directional cues (e.g. visual, magnetic) in the bird's environment. This conflict may have prompted leaders to place less weight on their personal information and more on social information (i.e. the copying of flockmates). Uncertainty may also have reduced the flight speed of the clock-shifted leader, and because speed is associated with leadership in pigeons [4], slower flight may result in birds dropping down the hierarchy (although see electronic supplementary material, figure S6, showing that loss of leadership cannot be explained purely by changes in speed). This mechanism requires no recognition by followers that their leader has inaccurate information. Alternatively, flock members may have actively 'filtered out' the low quality information, by reducing their reliance on social information received from leaders. This could have been due to recognizing the increased conflict between their and the leader's directional preference, or to detecting a cue (e.g. reduced speed) indicating uncertainty in the leader. Thus, the latter mechanism corresponds to followers 'choosing' not to follow, and the former to leaders 'choosing' not to lead. At present, we cannot distinguish between these alternatives.

Our study demonstrated that flexible decision-making structures can be valuable in situations where information with high error may be introduced by otherwise influential individuals. Our results have implications for both theoretical and empirical studies of collective motion and navigation, and highlight the importance of considering the effects of information quality and individual certainty in shaping inter-individual interactions during collective actions.

Ethics. Protocols used in this paper were approved by the Local Ethical Review Committee of Oxford University's Department of Zoology, reference number APA/1/5/ZOO/NASPA/Biro, 2013.

Data accessibility. Data are available via Dryad: http://dx.doi.org/10.5061/dryad.508j2 [12].

Authors' contributions. I.W., T.B.d.P. and D.B. designed the study, I.W. collected the data, I.W. and M.N. analysed the data, and all authors contributed to writing the manuscript. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare no competing interests.

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