

## RESEARCH ARTICLE

# Influence of behavioural and morphological group composition on pigeon flocking dynamics

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## ABSTRACT

Animals rely on movement to explore and exploit resources in their environment. While movement can provide energetic benefits, it also comes with energetic costs. This study examines how group phenotypic composition influences individual speed and energy expenditure during group travel in homing pigeons. We manipulated the composition of pigeon groups based on body mass and leadership rank. Our findings indicate that groups of 'leader' phenotypes show faster speeds and greater cohesion than 'follower' phenotype groups. Additionally, we show that groups of homogenous mass composition, whether all heavy or all light, were faster and expended less energy over the course of a whole flight than flocks composed of a mixture of heavy and light individuals. We highlight the importance of considering individual-level variation in social-level studies, and the interaction between individual and group-level traits in governing speed and the costs of travel.

**KEY WORDS:** Biologging, Collective motion, *Columba livia*, Flight, Flock structure

## INTRODUCTION

Energy budgets underlie the processes operating at every level of biological organization from the subcellular to entire communities. Energy is often considered the currency of life (Tolkamap et al., 2002). Therefore, any strategies that can offset and reduce energy expenditure are likely to be adaptive. Flying in flocks for birds has been shown to be both energetically costly and beneficial, depending on the shape of the flock (Usherwood et al., 2011; Portugal et al., 2014). At the individual level, behavioural strategies may have evolved to optimise travel through the optimal use of their 'energy landscape'. For example, birds that make use of predictable rising air (e.g. thermals – columns of rising air) (Wilson et al., 2012; Shepard et al., 2013) or adaptive combinations of active and passive dispersal through water currents in juvenile fish (Dingle, 2014). At the social level, behavioural interactions with conspecifics have evolved to optimise travel costs (Bill and Hermkind, 1976; Portugal et al., 2014; Voelkl et al., 2015). For example, in V-formation flights, vortices produced from the wingtips of leading individuals (Portugal et al., 2014; Voelkl et al., 2015) may explain decreased energetic expenditure of trailing individuals (Weimerskirch et al., 2001) when relative body position and the timing of their flaps are spatially and temporally 'in-phase' (Portugal et al., 2014). Similarly, fish have been shown to decrease


muscle activity in artificial vortices (Liao et al., 2003) and these mechanics may be utilised in response to vortices of conspecifics (Liao et al., 2003). However, current studies of social-level energy-saving strategies still largely ignore individual phenotypic variation, which is a foundational principle in evolutionary ecology (Wade et al., 2006; but see Ling et al., 2019). Furthermore, for social species, an individual's success is intrinsically tied not only to their own phenotype but also to the phenotypic composition of the surrounding group (Farine et al., 2015). Overall, how individual phenotype and group phenotypic composition interact to govern the speed and costs of travel is an important, but a hitherto understudied, aspect of the life history of animals which travel in groups.

Homing pigeons (*Columba livia*) are well suited to answer questions about speed and the costs of movement, and the interaction of individual-level phenotype and group phenotypic composition. Pigeons, like most birds, use flight, a costly form of locomotion (Schmidt-Nielsen, 1972), to navigate home and can do so alone (Meade et al., 2005; Biro et al., 2006; Pettit et al., 2015) or in groups (Nagy et al., 2010, 2013; Watts et al., 2016; Sankey et al., 2019). Group composition and group size are easy to manipulate in pigeons, by releasing birds in groups of predetermined phenotypes. Pigeons also exhibit high robustness to the application of animal-attached biologgers, which can be used to measure speed (using GPS; e.g. Pettit et al., 2013, 2015) and energetic proxies (using accelerometers; e.g. Taylor et al., 2017, 2019). Through the application of biologging technology, measures of morphological and behavioural phenotypes are attainable in pigeons, including repeatable 'in-flight' phenotyping, which is rare in biologging studies (Chmura et al., 2018). For example, repeatable measures of speed and leadership are measured with GPS loggers because of the reliability of pigeon homing (Nagy et al., 2010, 2013; Pettit et al., 2015) and the consistent transient leadership hierarchies shown to be stable in pigeon flocks (Nagy et al., 2010, 2013; Flack et al., 2012; Santos et al., 2014; Watts et al., 2016).

Unlike V-formation flocks, flying in a cluster flock has been shown to come at an energetic cost in pigeons (Usherwood et al., 2011). Furthermore, over long-duration flights in cluster flocks, pigeons have been found to reduce spatial density, providing further support for a proximate cost of flying close to conspecifics (Sankey and Portugal, 2019). How much an individual pays (energetically) may relate to both individual phenotype and the phenotypic composition in pigeon groups. In birds, the energetic output may be optimised (or minimised) by flying at an individually specific optimum speed (Tobalske et al., 2003), which may be characterised – in part – by morphological phenotype. For example, body mass has been shown to predict greater flight speeds in heavier pigeons (Pettit et al., 2015; Sankey et al., 2019). Flying at speeds outside of the optimum preferred solo flight speed entails not only increased energy output owing to the greater demand for chemical energy to power flight muscles (Tobalske, 2007) but also a shift in the proportion of lift generated by momentum (Tobalske et al., 2003). Sankey et al. (2019) found that pigeons compromised from their

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preferred speed to fly at a consistent speed with their whole group (the time-averaged speed of a whole group), which highlights that the benefits of grouping (e.g. anti-predator benefits (Kenward, 1978; Carere et al., 2009) or enhanced decision making accuracy (Biro et al., 2006; Dell'Arciccia et al., 2008) may outweigh these costly compromises. Both heavier and lighter pigeons may, therefore, have to increase their relative energetic output to fly (and stay) together in a group. This suggests that an individual of a given body mass (individual phenotype) would benefit energetically by flying in groups of similar mass (homogeneous group phenotypic composition) as the group may fly closer to the individual's preferred speed, which would require less of an energetically costly compromise. This highlights the potential of individual-level and social-level behavioural traits that may result in more efficient travel. Social level traits also extend to leadership–follower dynamics, with theoretical models suggesting groups comprising a higher proportion of leaders could form less-dense flocks, as leaders try to initiate collective movements in their preferred direction (Johnstone and Manica, 2011), which in pigeons could result in flying faster and further per unit energy owing to this reduction in density (Usherwood et al., 2011).

Here, we ask how individual-level phenotype and group phenotypic compositions may interact to govern the speed and the energetic costs of bird flight, via experimental manipulations. We experimentally manipulated group leadership composition, and the group body-mass composition of homing pigeon flocks to test *a priori* predictions (in brackets) through experimental manipulations over two separate experiments (summarised in Table 1). In experiment 1, following flights to predetermine leadership hierarchies, we separated birds into groups of leaders and followers. We predicted that (1) groups of leaders would show reduced density (following Johnstone and Manica, 2011) and (2) there would be a reduction in speed and/or energy expenditure proxies in denser, presumably follower, phenotype flocks (Usherwood et al., 2011; Taylor et al., 2019; see further rationale for all predictions in Table 1). In experiment 2, we predicted that (3) group flights composed of more heavy individuals would exhibit greater flock speed and (4) heterogeneous groups (i.e. those with a

mixture of heavy and light individuals) would experience greater costs of group flight relative to flying in homogenous groups.

## MATERIALS AND METHODS

### Experiments and general protocol

Homing pigeons ( $N=49$ ) were kept in purpose-built lofts at Royal Holloway University of London (Surrey, UK; latitude=51.416, longitude=-0.572), and provided with food (Johnstone and Jeff Four Season Pigeon Corn, Gilberdyke, UK), water and grit (Versele-Laga, Grit and Redstone, Deinze, Belgium) *ad libitum* throughout the course of the study period (April–September, 2018) (see Portugal et al. 2017a,b for full husbandry details).

All birds were weighed (CoffeeHit, Coffee Gear Digital Bench Scale; 2 kg limit/0.1 g accuracy) weekly, providing a key morphological covariate ('natural' bird mass), while simultaneously monitoring the welfare (Angelier et al., 2016; Portugal and White, 2022). The repeatability of body mass (g) was deduced using likelihood ratio tests, with 95% confidence intervals estimated using 10,000 parametric bootstrap iterations (see Portugal et al., 2017a; 2020).

The study comprised two experiments. Experiment 1: group leadership composition ( $N=33$  birds, age=9 months), conducted between July and September, 2018. Birds had no experience of the release site at the beginning of the study. Experiment 2: group body mass composition, consisted of  $N=12$  birds, age=9 months, assorted by body mass into categories of either 'heavy' or 'light', using the same birds as in experiment 1. This study was conducted throughout September 2018.

The key parameters were flight speed ( $m\ s^{-1}$ ) and energetic proxies: flap frequency (Hz), and the amplitude of the vertical movement in the pigeon's body as it flaps in flight (dorsal body amplitude in mm) (Usherwood et al., 2011; Taylor et al., 2017; 2019; Sankey and Portugal, 2019). To record these variables, we adopted a biologging approach, using GPS (speed; 5 Hz, QStarz BT-Q1300ST, Düsseldorf, Germany; mass=12.5 g) and accelerometers (flap frequency and dorsal body amplitude; 200 Hz; AX3, Axivity Ltd, Newcastle upon Tyne, UK; 8 g). See Ricketts et al., 2021 and supplementary Materials and Methods for further

**Table 1. Summary of experimental predictions, rationale and results of homing pigeon flock dynamics analysis**

Prediction	Supporting evidence and/or rationale	Results	Prediction match?
1 Groups of leaders will show decreased flock density	Reduced coordination, resulting in increased flock-spread, in groups of leaders in an evolutionary model, via too many leaders attempting to dominate movement decisions (Johnstone and Manica, 2011).	Flock spread: n.s. Dorso-ventral spread: decreased Cranio-caudal spread: n.s.	No – measure of group spread from left–right had opposite trend.
2 Denser flocks will demonstrate decreases in speed and/or increases in energy expenditure proxies	Speed reductions: Taylor et al. (2019) suggest that energy costs of flying close to others is driven by the need to coordinate and avoid collisions, which is likely to slow birds down (Safi et al., 2013). Energetic proxies: pigeons in denser flocks have increased energy expenditure after accounting for speed (Usherwood et al., 2011).	Speed: Increased Flap frequency: n.s. Amplitude: n.s.	No – the opposite trend was observed for speed.
3 Groups comprising more heavy individuals will exhibit greater flock speeds	Body mass predicts pigeon speed in solo flights (Pettit et al., 2015; Sankey et al., 2019; see also supplementary Materials and Methods).	Speed: n.s.	No – but homogenous groups were faster.
4 Heterogeneous mass groups will experience greater costs of flight relative to homogeneous groups	Groups need to reach speed consensus (Sankey et al., 2019), which involves potentially costly speed compromise.	Flap frequency: n.s. Amplitude: n.s. Total flaps: increased Sum of amplitude: increased	No – per unit time step. Yes – over the course of the whole flight.

<sup>1</sup>'Amplitude' represents dorsal body amplitude. n.s., no significant difference.

information on logger treatment and attachment. The total mass of the loggers was 21 g (see Portugal and White, 2018; 2022).

Each flight experiment comprised releasing the homing pigeons from a site between Windsor Castle and Eton (coordinates: latitude=51.497, longitude=-0.589) away from their home lofts at Royal Holloway University of London (coordinates: latitude=51.415, longitude=-0.573). Firstly, birds were gathered from their home loft and placed in wicker carrying baskets (dimensions=80 cm×40 cm×22 cm) for transportation to the release site. Following this, the birds were driven 8.90 km north (exact bearing=-0.07 rad) to the release site. The birds were typically in transit for 15–25 min. At the release site, GPS loggers were switched on at least 5 min before deployment to ensure an accurate signal was being received from the satellites (Sankey et al., 2021; see supplementary Materials and Methods for further biologging protocol information). Following this, GPS and accelerometers were attached to the back of each bird (see Sankey et al., 2021; Ricketts et al., 2021 for full logger attachment details). The birds were released as groups by opening the side hatch on the wicker basket following at least a 15 min delay from the release of a previous group. This time delay ensured birds were not subsequently meeting up en route from the release site to the home lofts. These delays worked every time, as groups never joined during a flight (<50 m distance; see supplementary Materials and Methods).

### Training flights

All 33 birds in this study were trained using the same protocol as follows. Firstly, they were trained to enter the loft via a hatch on the front side, using a small cardboard box (roughly ten times the volume of a pigeon) with windows cut out (to see the surrounding area) and a flap leading from the box to the hatch. This protocol was carried out many times over the course of 3–4 weeks. Following this, all birds were released (following protocol for group flights) from locations at the following distances from the loft, all in the direction of the release site (all distances are approximate; 0 m, 500 m, 2100 m, 4700 m, 6000 m, 7200 m and finally the release site at 8900 m). Releases from each successive location were repeated until all individuals returned home. Losses from the first two release sites totalled nine birds (these are not included in the  $N=33$ ). Following this, there was only one more loss, at the 6000 m site. During training, all birds wore a Velcro strip with wheel-balancing bicycle weights (see above) equivalent in weight to the loggers (20 g) to acclimatise to the mass and general presence of the logging device.

### Experiment 1: group leadership composition

For experiment 1 (group leadership composition manipulations), we firstly randomly allocated 33 pigeons into three separate groups. Following a training phase (see supplementary Materials and Methods for details on training), each of the three pigeon groups ( $N=11$ ,  $N=11$ ,  $N=10$  for each group, respectively, following one loss in training flights at the 6000 m release site) were released 10 times from the standard Windsor/Eton release site to establish leadership hierarchies (Nagy et al., 2010, 2013; Flack et al., 2013; Pettit et al., 2015; Watts et al., 2016).

Following the allocation of leadership ranks (following Nagy et al., 2010; also see below), each group was subdivided into leaders (top 5 leadership scores) and followers (bottom 5 scores). In the groups of 11 ( $N=2$  groups), the individual with the middle score (at leadership rank 6) were subsequently left out of further study. The new groups ( $N=6$  groups; three groups of  $N=5$  leaders and three

groups of  $N=5$  followers) were released a further 10–11 times (Tables S1–S3) to assess differences in group dynamics between groups of leaders and groups of followers (subsequently referred to as ‘leadership manipulation flights’). Bird losses (i.e. birds that did not return from a particular flight;  $N=3$ ), as well as all logger failures ( $N=6$ ) and flights where one or more groups did not participate, are documented in Table S3. Groups were not changed because of losses but instead, group size (which was thus diminished in some cases) was treated as a categorical variable with fixed effects in our models (see ‘Statistics’).

### Experiment 2: group mass composition

For experiment 2, we took 27 of the 33 pigeons used in experiment 1 (Fig S1) – with unmanipulated body mass distribution approximately normal (Shapiro–Wilk test;  $W=0.962$ ,  $P=0.392$ ) – and formed two subsequent groups: ‘light’ and ‘heavy’ (Table S1). Six light individuals and six heavy individuals (randomly selected from the bottom/top eight of the 27 birds, respectively) were selected, leaving a difference of 46.9 g between the heaviest bird from the light group (mean±s.d.: 374.3±19.3 g) and lightest bird from the heavy group (455.3±15.4 g). On a given flight/day the groups were either flown as complete but separate heavy/light groups (homogeneous mass groups) or with two individuals swapped into the other group (heterogeneous mass groups) before flights. See supplementary Materials and Methods and Table S2 for the randomisation of group compositions. Therefore, we utilised four distinct mass compositions: (1) ‘all light’ ( $N=6$  ‘light’ birds), (2) ‘predominantly light’ ( $N=4$  ‘light’ birds;  $N=2$  ‘heavy’ birds), (3) ‘predominantly heavy’ ( $N=4$  ‘heavy’ birds;  $N=2$  ‘light’ birds) and (4) ‘all heavy’ ( $N=6$  ‘heavy’ birds). We flew each composition eight times, totalling 192 trajectories, with no missing data or birds. We express these conditions as the proportion of heavy individuals in the flock; therefore, we had eight group flights with each [0], [0.33], [0.67] and [1], as a proportion of heavy birds where square brackets are used to denote the proportion of heavy birds in this study throughout.

### Computational methods

#### Fission, cohesion and sensitivity algorithms

We removed all GPS timestamps for the first and last 1000 m of the flights (following Taylor et al., 2017) to compare only relatively steady sections of the return flight home (8.9 km total before subtracting 2000 m to make 6.9 km of analysed flight). Further, in group flights, we removed individual data where the distance of an individual was over 50 m to the centroid (mean of latitude and longitude across group at each timestamp; see supplementary Materials and Methods and Sankey et al., 2021). We also ran statistics on centroid distances of 25 m and 75 m to test the sensitivity of the statistics to our arbitrary choices of parameters (see supplementary Materials and Methods). Fission – the proportion of flight an individual is separated from the group – was then calculated by dividing the total number of timestamps removed by the total number of steps.

We only recorded further metrics for each flight if a group remained stable in their composition. This was defined as unchanged group membership for a proportion of over 0.1 (10%) of the flight (subsequently referred to as ‘minimum flight proportion’). This allowed us to reduce erroneous readings, which may be caused by different group sizes or different group compositions, which arise by fission and/or fusion of birds. However, it was possible, therefore, to record multiple readings of a single metric in one flight (i.e. a reading for each of the different group compositions which remained stable

for over 10% of the flight). Therefore, we recorded the date and unique flight ID to use as random intercepts (see ‘Statistics’), to deal with the pseudoreplication (Davies and Gray, 2015). We tested the sensitivity of our subsequent analyses to our arbitrary choice of ‘minimum flight proportion’, by testing ‘minimum flight proportion’ values of 0.05 and 0.25, as well as 0.1 (see supplementary Materials and Methods).

### Leadership

To assess leadership, we used pairwise correlations analysis on the merged trajectories (see methods in Nagy et al., 2010), whereby time-lags of similar movements are used to quantify the directional correlation delay of their turns (and hence the leadership). For example, if one individual turns (on average) 0.2 s before the rest of the flock, it would be considered a leader; whereas another individual who turns 0.2 s after the rest of the flock, would be considered a follower. Leadership analysis was not considered if individuals did not remain cohesive (<50 m; following Pettit et al., 2015) for over 50% of the flight. If the resulting ‘leadership’ matrix from all flights demonstrates a significant transitive hierarchy (following Nagy et al., 2010, 2013; Flack et al., 2012, 2013; Pettit et al., 2015; Watts et al., 2016), we can separate flocks by leadership rank to test our hypotheses (i.e. to test the relationship between leadership, flock composition and flock density and the efficiency of travel; see ‘Predictions’).

### Speed and wind variables

We measured ground speed using the point-to-point distance travelled between GPS coordinates at each time step (5 Hz). We took a median of speed for sections of flight with different but stable group compositions (see above). The route efficiency of each flight was classically calculated as the perfect beeline (the straightest possible line between the site and the loft) divided by the total distance travelled (Biro et al., 2006; Freeman et al., 2011). This metric (route efficiency) was calculated for each individual/group for each flight.

As speed can be influenced by wind speed and direction relative to the direction of travel (Safi et al., 2013), in order to control for the impact of wind in our statistical models we recorded wind speed (accuracy  $\pm 0.1 \text{ m s}^{-1}$ ) and direction (accuracy  $\pm 22.5 \text{ deg}$ ) every 0.5 h at the home loft using a weather station (Aercus Instruments WS2083 Pro Wireless Weather Station; Greenfrog Scientific, Doncaster, UK). Using the nearest time stamp of wind data to the first time stamp of trimmed GPS pigeon data, we calculated wind currents parallel (support wind) and perpendicular (crosswind) to the direction of travel (following Safi et al., 2013). A mean of support and cross-wind components were calculated across the whole flight (solo) or for periods of flight with stable group composition as above (group).

### Energetic proxies: accelerometer measures

Data were downloaded from the accelerometry loggers as .svg files, and then processed to .csv files in OMGUI (<https://github.com/digitalinteraction/openmovement/wiki/AX3-GUI>), before exporting to R (<https://www.r-project.org/>). We then trimmed accelerometer data to match the start and end of the timestamps from the trimmed GPS (see above). Following this, we calculated flap frequency and dorsal body amplitude for each pigeon, for each flight. Flapping frequency was calculated using smoothed dorsal acceleration (z-axis of the accelerometer; smoothed over 0.025 s), and removing static acceleration (over 15 wingbeat cycles, >2 s; see Taylor et al., 2017) before estimating the upper reversal point (see Portugal et al., 2014)

as a measure of each flapping cycle. This measure was calculated at each wingbeat (i.e. the time between one flap and the next, in flaps per second, Hz). The amplitude (mm) of the dorsal body acceleration (‘dorsal body amplitude’) was estimated via double integration of the acceleration curve, before passing through a Butterworth filter with a cut-off frequency 2.5 Hz (see Usherwood et al., 2011 and Taylor et al., 2017, for further information). Again, this measure was calculated at each wingbeat. Medians of accelerometer measures were taken per bird, per flight, in all experimental treatments.

### Flock density

We calculated a further series of covariates describing the flock density. Across the flock, all neighbour-to-neighbour distances (in metres) were collated and averaged (mean average) at each time step distance. Flock spread was defined as the median value of these per-time-step values across sections of flight where group composition remained stable (see above). Dorso-ventral and cranio-caudal spread were defined as the distance (in metres) between the furthest individuals to the left/right or front/back, respectively, with regard to the heading of the centroid (Sankey and Portugal, 2019; Sankey et al., 2022). Consistent with flock spread, this was recorded at each time step, and then further reduced to a median value across cohesive sections of flight to provide measures of dorso-ventral spread and cranio-caudal spread for further analysis.

### Statistics

We used linear mixed models (R package ‘nlme’: <https://CRAN.R-project.org/package=nlme>) to estimate the explanatory power of various covariates on dependent variables; speed, flap frequency, total flaps for the entire flight, dorsal body amplitude, sum of dorsal body amplitude over the entire flight and flock density parameters. Fixed effects were as follows: group composition was provided as categorical variable; support-wind and cross-wind components were included as numeric covariates to control for their effect (Sankey et al., 2022); our random effects included: pigeon ID; group number (in experiment 1 only; as the same treatment was conducted across six separate groups: three leader and three follower groups); unique flight ID and date (unique flight ID and date picking up smaller and larger scale local perturbations in temporal environmental conditions). All model fits were tested for a fit to the assumption of parametric residuals, and, depending on the greatest visual coherence of model residuals with a fitted qq-norm plot (<https://www.r-project.org/>) were treated with: (i) no transformation, (ii) Box–Cox transformations (Sakia, 1992) or (iii) log transformations. All data and code are available via GitHub at <https://github.com/sankeydan/pigeonGPC>.

## RESULTS

### Experiment 1: group leadership composition

In experiment 1, involving the manipulation of group leadership composition, we initially needed to determine the establishment of leadership hierarchies. We assigned a total of 33 pigeons to three distinct groups consisting of 11, 11 and 10 pigeons, respectively. These groups were released 10 times from the standard Windsor/Eton release site to determine leadership rank. All three groups exhibited significantly transitive leadership hierarchies (methods from Nagy et al., 2013;  $T_1=1.000$ ,  $T_1=1.000$ ,  $T_1=0.890$ ;  $P<0.001$  for all groups) and so were divided into groups with the five lowest and five highest leadership scores (directional correlation delay; see Materials and Methods) per group. Body mass was not predictive of leadership score in any of the three groups (LM; d.f.=8; Group 1:  $t=-0.494$ ,  $P=0.635$ ; Group 2:  $t=0.334$ ,  $P=0.747$ ; Group 3:  $t=2.254$ ,

$P=0.054$ ), nor was there any significant difference in the mean body mass of leaders and followers (followers=403.03 g, leaders=413.16 g;  $t$ -test  $t=0.841$ , d.f.=26.624,  $P=0.408$ ), thus suggesting body mass was not a significant factor in determining leadership.

Contrary to our expectations in prediction 1, leader flocks had increased density relative to follower flocks in two of our three measures of flock density, with decreased flock spread (LME with negative Box–Cox transformation, d.f.=15,  $t=1.975$ ,  $P=0.067$ ), and significant decreases observed in dorso-ventral spread (LME with negative Box–Cox transformation, d.f.=15,  $t=2.376$ ,  $P=0.031$ ), but with no observed difference in cranio-caudal spread (LME with negative Box–Cox transformation, d.f.=15,  $t=0.743$ ,  $P=0.469$ ).

Prediction 2 was also not supported, as the leader flocks, which were denser (dorso-ventrally), demonstrated greater speeds than follower flocks (Fig. 1A; LME, d.f.=28,  $t=-6.087$ ,  $P<0.001$ ), with an estimated speed increase of approximately  $1.19 \text{ m s}^{-1}$  for leader groups, from  $18.11 \pm 1.98 \text{ m s}^{-1}$  (mean  $\pm$  s.d.) to  $19.30 \pm 1.53 \text{ m s}^{-1}$ . Flock speeds for training flights were closer to the speed of followers at  $18.13 \pm 1.53 \text{ m s}^{-1}$ . We found no effect of leadership composition on the energetic proxy of flap frequency (Fig. 1B; LME, d.f.=27,  $t=0.9607$ ,  $P=0.345$ ) or dorsal body amplitude (Fig. 1C; LME, d.f.=27,  $t=0.212$ ,  $P=0.833$ ).

In additional analyses, we found no evidence that leader groups exhibited different amounts of fission than follower groups (mean 19% and 12% of flights spent separated from the group in follower and leader groups, respectively; LME with negative Box–Cox transformation, d.f.=50,  $t=1.562$ ,  $P=0.125$ ). There were no significant differences in route efficiency between leader and follower groups (LME, d.f.=50,  $t=1.200$ ,  $P=0.236$ ), with follower group mean efficiencies at approximately 0.73 and leaders at 0.79 (where the efficiency of a beeline is 1).

### Experiment 2: group mass composition

We investigated the effects of four different mass compositions on flight behaviour: (1) ‘all light’ ( $N=6$  ‘light’ birds), (2) ‘predominantly light’ ( $N=4$  ‘light’ birds;  $N=2$  ‘heavy’ birds), (3) ‘predominantly heavy’ ( $N=4$  ‘heavy’ birds;  $N=2$  ‘light’ birds) and (4) ‘all heavy’ ( $N=6$  ‘heavy’ birds). Each mass composition was flown eight times. The mass compositions are expressed as the proportion of heavy individuals in the flock, denoted by square brackets, with eight group flights conducted for each proportion [0], [0.33], [0.67] and [1]. We found no support for prediction 3, that flocks with a greater number of heavy individuals, by proportion, would fly faster (Fig. 1D; LME, d.f.=136,  $t=1.000$ ,  $P=0.319$ ). However, in *post hoc* tests we did find that certain group mass compositions were predictive of speed over others (Fig. 1D; LME with Tukey’s pairwise *post hoc* test, d.f.=134; comparisons are as follows: [0–0.67],  $t_{\text{ratio}}=3.287$ ,  $P=0.007$ ; [0.33–1],  $t_{\text{ratio}}=-3.341$ ,  $P=0.006$ ; [0.67–1],  $t_{\text{ratio}}=-4.402$ ,  $P<0.001$ , see Table S4 for all statistics). The most significant differences were observed between homogeneous groups ([0] and [1]) and heterogeneous groups ([0.33] and [0.67]), where a *post hoc* test between these two groups revealed significantly higher speeds in homogeneous groups (LME, d.f.=136,  $t=4.466$ ,  $P<0.001$ ). The homogeneous mass groups flew an estimated  $1.56 \text{ m s}^{-1}$  faster (using mean values).

We found mixed support for prediction 4, which posited that energetic proxies (flap frequency and dorsal body amplitude) would be reduced in groups of homogeneous composition. When analysed per unit time step, there was no significant difference in either flap frequency (Fig. 1E; LME, d.f.=28,  $t=0.396$ ,  $P=0.694$ ) or dorsal body amplitude (Fig. 1F; LME, d.f.=28,  $t=0.396$ ,  $P=0.480$ ) in

homogeneous groups. However, when considering the entire duration of the flight, where the dependent variables were: (i) total flaps and (ii) the sum of dorsal body amplitude, energetic proxies were reduced in homogeneous mass groups (LME, total flaps:  $N=163$ ,  $t=-3.977$ ,  $P<0.001$ ; total amplitude: d.f.=163,  $t=-3.265$ ,  $P=0.001$ ). This is probably because homogeneous mass groups demonstrated greater speeds but at similar per-time-step energy expenditures, as there were no observable differences in route efficiencies (Table S5).

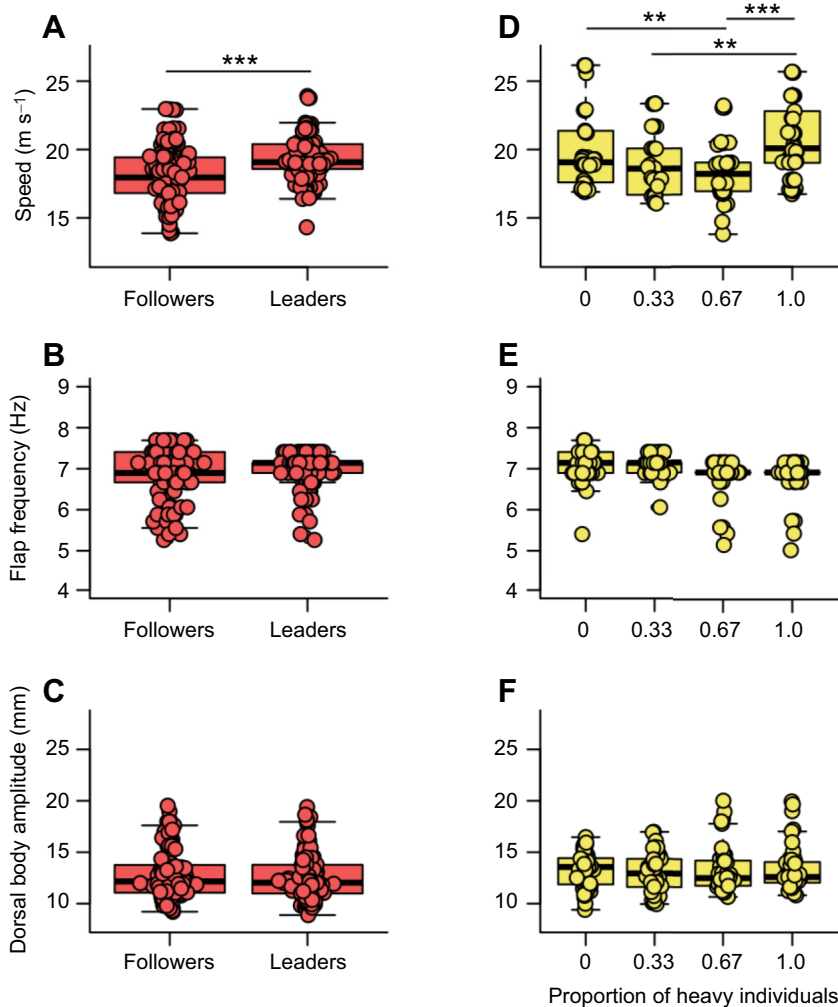
In additional analyses, fission was not found to be different across groups of differing mass composition. The mean fission for each mass-composition group was: [0]=7%, [0.33]=9%, [0.67]=11%, [1]=15% (see Table S5 for all statistics). There were no differences in route efficiency between groups of different mass composition, with mean route efficiency for each group: [0]=0.95, [0.33]=0.94, [0.67]=0.92, [1]=0.95 (see statistics in Table S5).

### DISCUSSION

We have found several ways in which group phenotypic composition influences the speed–energy trade-offs in flocking pigeons. Despite our predictions being almost categorically unsupported, this study reveals many ways in which the group phenotypic composition can affect the cost of transport. Overall, we found that flocks of leader pigeons are denser and faster than flocks of followers. Furthermore, groups composed of individuals with homogeneous mass, either all heavy or all light, demonstrated increased speed and reduced energy expenditure compared to groups with a mixture of heavy and light individuals. These results highlight the interplay between group phenotypic composition and flight dynamics in pigeons.

We found that the groups composed of individuals with higher leader scores, referred to as ‘leader groups’, exhibited higher density compared with the groups composed of individuals with lower leader scores, referred to as ‘follower groups’, despite our initial predictions suggesting otherwise. We initially reasoned that leaders would attempt more initiations (Johnstone and Manica, 2011; Ramos et al., 2015), and that this, in turn, would result in reduced flock density. However, contrary to our predictions, we observed that leaders exhibited significantly more compact flock formations along the dorso-ventral plane. As our birds were all flown from the same site, this may have reduced the conflict in navigational decision-making (Conradt and Roper, 2003; Biro et al., 2006). Furthermore, as leaders have been shown to learn routes better than followers (see Pettit et al., 2015), this navigational conflict may have actually reduced in leader flocks that all know the route better than individuals in follower flocks. Therefore, we suggest that with reduced conflict in route direction, the ‘leader groups’ were able to optimise their flock dynamics, rather than attempt initiations toward their preferred direction of travel.

Leader pigeons may also exhibit a more goal-oriented individual-level phenotype (Freeman et al., 2011; Sasaki et al., 2018). Pigeons with greater ‘peak-fidelity’ – a measure of coherence in their solo flight routes – predicted leadership in pigeon pairs (Freeman et al., 2011). Goal-orientedness was also shown to have a positive impact on leadership in fish, however, only when balanced with moderate levels of social tendency, as fish which were highly goal-oriented would split from the group, reducing their influence (Ioannou et al., 2015). As goal-orientedness is thought to represent a trade-off between the propensity to risk isolation and the safety of the group (Ioannou et al., 2008), such behaviour may correlate with individual differences in boldness (Ioannou et al., 2008; Jolles et al., 2017). Notably, studies have shown that boldness predicts leadership



**Fig. 1. Individual-level flight metrics from experiments on group leadership composition and group mass composition of homing pigeon flocks.** (A–C) Group leadership composition: metrics for individuals in groups of followers or leaders. (D–F) Group mass composition: group flights with different proportions of heavy individuals; either 0 (6 light individuals), 0.33 (4 light and 2 heavy individuals), 0.67 (2 light and 4 heavy individuals) or 1 (6 heavy individuals). Median flight speeds (m s<sup>-1</sup>; top row), flapping frequencies (Hz; middle row) and dorsal body acceleration values (mm; bottom row) are given as points with box and whisker plots for each experiment. Boxes represent the interquartile interval with median line; whiskers are 5th and 95th percentiles. Statistically significantly different responses between groups are provided from a Tukey *post hoc* test of a linear mixed-effects model (see Materials and Methods), where \*\**P*<0.01; \*\*\**P*<0.001.

propensity in fish (Jolles et al., 2017) and pigeons (Sasaki et al., 2018). While our study did not directly assess the goal-orientedness or boldness of the leaders, it presents an avenue for future research to explore these potential factors.

Our methods were designed to decrease flock density, and hence modify the speed/energetic trade-off, by forming groups with high conflict through increases in their natural goal-orientedness (Johnstone and Manica, 2011). Our attempted density manipulations may have not been successful, owing to the potential decreases in conflict through enhanced route learning (as mentioned above). To increase route conflict, future work should potentially (i) train individuals from different sites (before releasing in groups) or (ii) fly the leaders of one group with the leaders from another group (each group may have conflict in their ‘preferred’ path). Nevertheless, by chance alone, intrinsic leaders (potentially bolder, more goal-oriented individuals) could be unevenly distributed across experimental groups and mixing across groups could introduce unaccountable bias. This bias would need to be taken into account if our protocol is used for further work, which may be achievable by measuring boldness in personality assays (Portugal et al., 2017a) and goal-orientedness in solo flights (Freeman et al., 2011).

We predicted that denser flocks would be slower, but instead, we found the opposite. It is conceivable that flying in a more cohesive flock (which for pigeons is a more costly flock; Usherwood et al., 2011) could result in birds increasing their flying speed, as faster

flight can help minimize the overall cost of transport. This is unlikely given that the flocks of leader birds, despite flying closer together and flying faster – both expected to increase energetic output – did not show such a trend. However, an alternative explanation is that the presence of leaders, who are known to be faster birds (Pettit et al., 2015), contribute to the overall increased speed of the denser leader flocks. These leaders also may possess a greater familiarity with the flight route (Pettit et al., 2015), enabling them to lower the cost of transport. However, the absence of solo flight data for the birds in our study prevents us from directly confirming these hypotheses. Nevertheless, the potential influence of flock cohesion, individual characteristics such as leader status, and the birds’ familiarity with the flight route provide intriguing avenues for future experimental investigation and modelling into the relationship between flying speed and group dynamics in avian flocks (e.g. Papadopoulou et al., 2022a,b).

Although pigeon mass is a significant predictor of solo flight speed (Fig. S1; Sankey et al., 2019; Pettit et al., 2015), groups of heavy birds did not fly faster than groups of slower birds. It was in fact the homogenous profile of the group phenotypic compositions (whether light or heavy) that predicted greater speed. We hereby hypothesise the following: (i) the general morphological profile of individuals (e.g. wingspan, structural size) which has been shown to correlate with body mass in birds (Alerstam et al., 2007; Sullivan et al., 2019), will affect the flow rate and magnitude of air currents

left in their wake and (ii) individuals can achieve a more optimal trade-off between downwash avoidance and upwash exploitation (Portugal et al., 2014) in the wake of similar-sized individuals. This is highly speculative, as no present evidence can confirm or reject this claim, particularly in cluster-flocking species. However, a recent study suggests that a previous dichotomy between costly cluster flocks (Usherwood et al., 2011) and energetically beneficial V-formation flight mechanisms (Portugal et al., 2014) might not be as straightforward as first thought, after observations of ‘compound V’ flock shapes within the cluster formations of shorebirds (Corcoran and Hedrick, 2019). We know that flying in a flock comes at a cost in pigeons, but this does not rule out the possibility of relative savings when individuals are matched in size and/or gait, as supported here.

Decreased energy expenditure in homogeneous mass groups was found as expected; nevertheless, our results suggest a different mechanism than the one proposed. We expected that: (1) in groups of a similar mass, we would find an intrinsic reduction in costly speed compromise between the birds (*sensu* Sankey et al., 2019) and also (2) acceleration/deceleration responses would be less common (or indeed necessary), and thus, energy savings achieved via moving around less. Following our results, this now seems unlikely. Instead, it appears to be that because the homogenous mass groups are flying home faster at a similar cost per time step, it is this that allows them to achieve a reduced total energy expenditure.

The fact that homogeneous mass groups flew faster than heterogeneous groups and leader flocks flew faster than follower flocks, both without additional cost, contributes to the ongoing discussion about how group phenotypic composition can affect fitness (Farine et al., 2015). It is also important to note that the fitness of individuals will rarely be driven by one facet (e.g. speed/energy optimisation) alone. Instead, the benefits conferred to different individuals/phenotypes will likely be context dependent (Dyer et al., 2009; Nagy et al., 2013; Ioannou et al., 2019). Demonstrating the benefits of an optimal phenotype (or phenotypic composition) in one context could not provide a genuine inference of fitness in the tested animals, whether wild or captive/semi-captive. Nevertheless, in captive animal systems, we can identify a known evolutionary pressure in birds (here, the costs of flight; Schmidt-Nielsen, 1972) and test, via manipulations, the influence of individual phenotype and group phenotypic composition (e.g. Dyer et al., 2009). Therefore, we demonstrate that we can learn about one important component of life history in isolation and derive conclusions about individual and group-level success (Farine et al., 2015).

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: D.W.E.S., S.J.P.; Methodology: D.W.E.S., S.J.P.; Validation: D.W.E.S., S.J.P.; Formal analysis: D.W.E.S.; Investigation: D.W.E.S., S.J.P.; Resources: S.J.P.; Data curation: D.W.E.S.; Writing - original draft: D.W.E.S.; Writing - review & editing: D.W.E.S., S.J.P.; Visualization: D.W.E.S.; Supervision: S.J.P.; Project administration: D.W.E.S., S.J.P.; Funding acquisition: S.J.P.

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#### Data availability

All data are available via GitHub at <https://github.com/sankeydan/pigeonGPC>.

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