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Pigeon leadership hierarchies are not dependent on environmental contexts or individual phenotypes

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ABSTRACT

Remaining cohesive on the move can be beneficial for animal groups. As such, animal groups have evolved coordination mechanisms such as leadership to resolve navigational conflicts of interest. Consistent "leaders" may have an intrinsic advantage over "followers" which compromise on their preferred route to retain cohesion, which highlights the question of the inter-individual variation (phenotype) that can predict leadership. Studies in both birds and fish have revealed that intrinsically faster individuals can lead movements, and leading movements propagate from the front edge of the flock/shoal. However, these experiments are generally conducted in relatively "familiar" environments, where the degree of compromise between the "leaders" and "followers" is low. We suggested that inter-individual differences in route efficiency, while not explanatory of leadership from *familiar* locations, may emerge as predictors of leadership from *unfamiliar* locations. We tested this prediction – and the potential impact of multiple other behavioral, morphological and "in-flight" phenotypes on leadership – using two groups of homing pigeons (*Columba livia*) ($N = 16$), a classic model species of leadership. We recorded $N = 966$ unique GPS trajectories from birds in (i) solo and familiar, and (ii) solo and unfamiliar contexts to measure solo speed and solo route efficiency; and (iii) group and familiar, and (iv) group and unfamiliar contexts to assess group leadership. Pigeon leadership hierarchies were similar across environmental context (i.e., familiarity). However, we found that no covariates could consistently predict leadership score in either context.

1. Introduction

Social living can provide animals with substantial benefits (Ward and Webster, 2016), such as protection from predators (Kenward, 1978; Carere et al., 2009; Handegard et al., 2012; Ioannou et al., 2012), enhanced cognitive performance (Ashton et al., 2018) and greater collective-decision accuracy (Prins, 1996; Simons, 2004; Couzin et al., 2005; Berdahl et al., 2018). To retain these wide-ranging benefits, animals have evolved *coordination* mechanisms, which enable spatial *cohesion* on the move (Conradt and Roper, 2005; Couzin et al., 2005). Leadership provides such a mechanism to resolve conflicts of interest in the group members' navigational preferences (Conradt and Roper, 2005). Here, by following a leader, the group can retain spatial cohesion as a group changes direction (Conradt et al., 2009; Nagy et al., 2010; McComb et al., 2011). However, due to conflicting directional preferences – intrinsic in heterogeneous groups (Conradt and Roper, 2003) – the leader will have disproportionately low "consensus costs" (Conradt and Roper, 2005, 2010), essentially "getting its own way".

Theoretical models predict shared-consensus (shared leadership) should evolve more easily than unshared-consensus (consistent leadership) in animal groups on the move (Conradt and Roper, 2003, 2009). Shared-consensus decision making has been demonstrated empirically in olive baboons (*Papio anubis*; Strandburg-Peshkin et al., 2015), where leadership "initiations" are distributed relatively evenly across the troop (Strandburg-Peshkin et al., 2015). Nevertheless, many other taxa, such as homing pigeons (*Columba livia*; Nagy et al., 2010), common zebras

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(*Equus burchellii*; Fischhoff et al., 2007) and golden shiners (*Notemigonus crysoleucas*; Ioannou et al., 2015), demonstrate that certain individuals can exhibit consistent leadership. As such, investigating the phenotypic traits which govern leadership is currently undergoing intensive research (King et al., 2009; Ioannou et al., 2015; Pettit et al., 2015; Strandburg-Peshkin et al., 2018). Once thought to be related to consistent differences in dominance rank (Fossey, 1972; Peterson et al., 2002), many recent studies have found no correlation between leadership and dominance (Kurvers et al., 2009; Nagy et al., 2013; Strandburg-Peshkin et al., 2015), suggesting that these hierarchies can be context-dependent (Nagy et al., 2013).

Empirical work on homing pigeon flocks – which are known to exhibit consistent unshared leadership (Nagy et al., 2010, 2013; Flack et al., 2012, 2013) – has demonstrated that faster pigeons (from solo flights: Pettit et al., 2015; Sasaki et al., 2017), which fly at the front of the flock (in group flights: Nagy et al., 2010; Pettit et al., 2015; Yomosa et al., 2015), have a disproportionate navigational influence (i.e., leadership). This finding is consistent with studies of fish, where faster individuals also lead movements (Jolles et al., 2017), and individuals at the front of the shoal exhibit greater leadership (Herbert-Read et al., 2011; Katz et al., 2011). Route efficiency (or, closeness to a “beeline” trajectory) as a predictor of leadership in pigeons has more mixed support (Freeman et al., 2011; Flack et al., 2012, 2013; Watts et al., 2016). In two separate experiments by Flack et al., (2012, 2013), more route-efficient pigeons (through additional training) increased their leadership in one study (Flack et al., 2012) but had no effect in another (Flack et al., 2013). It is possible that route-efficiency has a plateauing effect on leadership; important in unfamiliar terrain, and then as birds become more familiar with the route home, becoming less important.

Other than speed (Pettit et al., 2015; Jolles et al., 2017; Sasaki et al., 2017) and route efficiency (Flack et al., 2012; Watts et al., 2016), leadership may be influenced by a multitude of phenotypic differences (Fischhoff et al., 2007; Kurvers et al., 2009; McComb et al., 2011; Ioannou et al., 2015; Jolles et al., 2017). Firstly, consistent inter-individual behavioral differences (“personalities”) in boldness (tendency to leave a shelter; e.g., Sasaki et al., 2018), neophilia (tendency to investigate novel objects; e.g., Kurvers et al., 2009), and exploration of a novel environment (Jolles et al., 2017) have all been shown to positively correlate with leadership. It is thought that these – often correlated (Sih et al., 2012) – “personalities” are likely a behavioral manifestation of internal tendencies to take risks (Wolf et al., 2007; Sih et al., 2012). Furthermore, how these “personalities” interact under different contexts may result in individuals that are more prone to taking risks becoming leaders under unfamiliar contexts, while aspects of dominance may determine leadership in familiar settings (e.g., Ioannou et al., 2015).

Other positive correlates of leadership have been found in demographic traits such as age (older individuals lead; e.g., McComb et al., 2011; Brent et al., 2015) and sex (females lead when lactating; Fischhoff et al., 2007), or other “in-flight” phenotypes such as route fidelity (the similarity of an individual’s solo homing paths in pigeons; Freeman et al., 2011). Nevertheless, despite such a broad range of phenotypic predictors, studies of pigeon-leadership tend to only focus on only a small subset (Freeman et al., 2011; Flack et al., 2012; Nagy et al., 2013; Pettit et al., 2015). We aimed to take a more comprehensive approach and measure multiple phenotypes in the (i) behavioral (i.e., boldness, neophilia, exploration, dominance), (ii) morphological and demographic (i.e., body and wing morphometrics, body mass and sex), and (iii) “in-flight” (i.e., solo speed, route efficiency, route fidelity) domains.

We aimed to test the following predictions in flocks of homing pigeons released multiple times from sites with a similar bearing (“familiar” flights – after a plateau in route efficiency) and subsequently from alternative sites (“unfamiliar”), with distinct differences in the release bearing of the sites. Prediction (1): in familiar flight releases, only speed and route fidelity will be predictive of higher leadership (following Pettit et al., 2015 and Freeman et al., 2011). Prediction (2): from unfamiliar release sites, where all individuals may have, on-average, lower route efficiencies, intrinsic inter-individual differences in homing competency will remain, and will predict higher leadership ranks, in addition to their differences in speed. We did not manipulate efficiency via extra training flights (“experience”) of individuals, as our questions relate to intrinsic phenotypic predictors of leadership across environmental context. Prediction (3): the influence of (potentially correlated) behavioral phenotypes such as “boldness”, “neophilia” and “exploration”, will have a stronger impact on leadership in “unfamiliar” flights, than in “familiar” flights, given that individuals prone to taking risks might initiate more leadership movements (Ioannou et al., 2015).

2. Methods

2.1. Subjects and materials

2.1.1. Housing

A group of 18 homing pigeons (aged 11 – 15 months old) were kept in two flocks of nine pigeons at Royal Holloway University of London, U.K (51°25′32″N, 00°33′47″W). Group 1 was originally composed of four males and five females, however, following losses of two individuals (one female and one male) in early flights, these individuals were removed from the data, and thus group 1 comprised seven individuals (three male and four females). Group 2 was composed of five males and four females. Sex was determined via genetic testing of feather samples (Animal Genetics, Cornwall, U.K.). Each flock was housed in a separate loft (7 ft × 6 ft) (see Portugal et al. 2017a for further husbandry details). The pigeons were provided with ad libitum access to food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, U.K.), water and grit.

2.1.2. Biologgers

Flight metrics measured were as follows: speed and route efficiency (solo flights), and leadership and spatial positioning within the flock (group flights). To measure these parameters we deployed miniaturized GPS loggers (QStarz BT-Q1300ST, Düsseldorf, Germany’ 5 Hz; 12.5 g) attached to the back of the birds (Taylor et al., 2019; Sankey et al., 2021; Papadopoulou et al., 2022a) (for full attachment and biologger methods, see Supplemental material).

2.2. Familiar/unfamiliar experiment

2.2.1. “Familiar” releases

To assess solo and group responses to differences in familiarity of homing route and terrain, we first established a “familiar” flight bearing (Fig. 1) (June-August 2017; Supplemental Material, Supplementary Table 1). We flew each individual from the same release bearing in the following order: (1) 12 solo flights from the same release site (5 km), (2) six group flights from the same release site, (3) 12 solo flights from a further site (9 km) in the same direction (bearing) beyond the 5 km original release site, and finally (4) six group flights from the latter release site (9 km) (see Supplemental material, Supplementary Tables 1 and 2 for full release protocol). “Familiar” flights were classified as flight trajectories after the first nine flights from each location, given previous work showing that pigeons gain striking recapitulation of their routes before the ninth flight (Flack et al., 2012; Taylor et al., 2017). The flight bearing for group 1 was north (actual bearing = −8.02°), and the flight bearing for group 2 was east (actual bearing = 45.26°; Fig. 1). This was to avoid confounding aspects associated with (i) flights across a latitudinal gradient, as pigeons have been shown to detect latitudinal gradients via magnetic field detection; (Walker et al., 2002), or (ii) local conditions intrinsic to the terrain (e.g., altitudinal climbs, or wind properties of the site/release-bearing more generally). Following the “unfamiliar” phase (below) we conducted a final three solo and group flights from each of the “familiar” release sites (in the same order as above), to control for effects of learning or fatigue associated with the

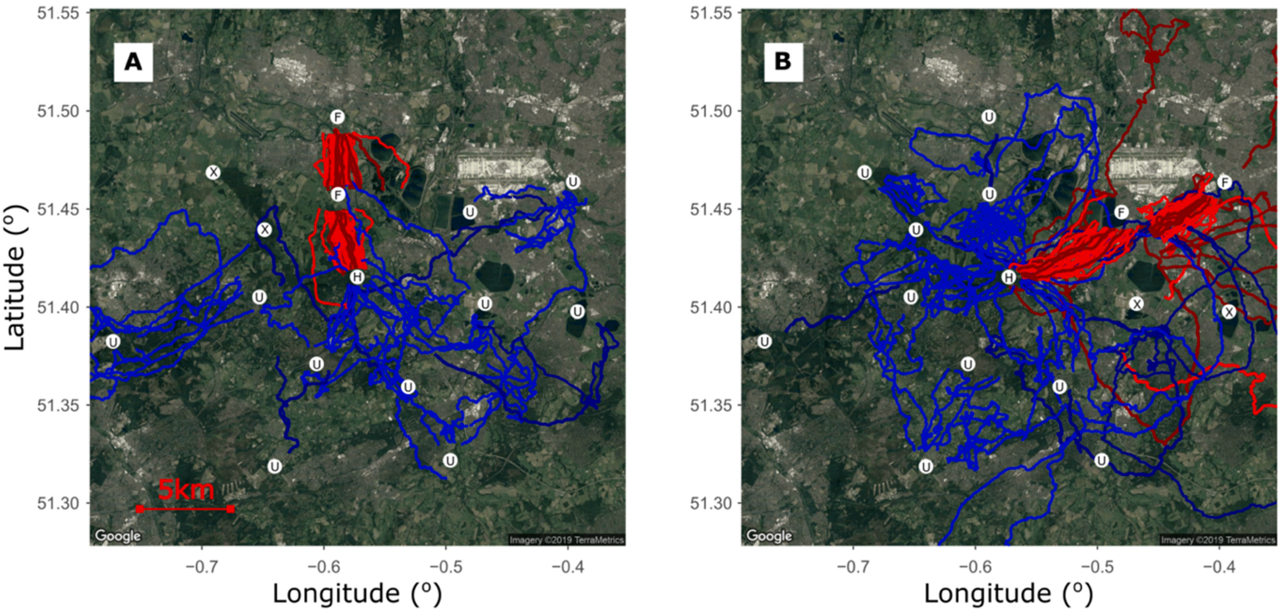

Fig. 1. "Familiar/unfamiliar" pigeon flight releases. GPS trajectories from "Familiar" (F) release sites (>9 flights from a given location) are colored red; trajectories from "unfamiliar" (U) sites are colored blue. 5 km trajectories (inner circle of sites around home; H). Each bird undertook only one release from each unfamiliar site, either as a group ($N = 5$), or solo ($N = 5$). Solo flights are given as bright red/blue lines and group flights are colored dark red/blue. (A) Group 1 flight trajectories, where "familiar" release bearing was north (−8.02°). (B) Group 2 flight trajectories, where "familiar" release bearing was east (45.26°). Two sites – with the closest bearing to the "familiar sites" – were never visited by each pigeon/group (marked as X). The observable gaps in the trajectories are from the trimming of the GPS data (see Supplemental material). Maps were created using Google Maps © using R package "ggmap" (Kahle and Wickham, 2013).

experimental flight season.

2.2.2. *"Unfamiliar" releases*

The second phase – following the first phase of "familiar" releases, but before the final phase of "familiar" flights – were the "unfamiliar" flight releases (July-August 2017; Supplemental material, Supplementary Table 2). Here we used a series of five additional release bearings per group, all spaced > 45° from the "familiar" release bearing (see Fig. 1). The closest "unfamiliar" release bearing to the "familiar" flight bearing was 53.45° for both groups, between bearing "N" and bearing "E".

Each "unfamiliar" flight bearing ($N = 5$) had two sites (at ~5 km and ~9 km), totaling $N = 10$ "unfamiliar" release sites. This was divided evenly into $N = 5$ "unfamiliar" solo flights, and $N = 5$ "unfamiliar" group flights (for order of all flight releases see Supplemental material, Table S1). Group and solo flights were divided as evenly as possible between 5 km sites and 9 km flights (see Supplemental material, Supplementary Table 2).

After all flights had been conducted we visually assessed the trajectories (Fig. 1; Supplemental material, Supplementary Fig. 1)). There was very little cross over between the trajectories for "familiar" and "unfamiliar" flight paths, validating our choice to analyse these trajectories separately.

2.3. *Phenotype assessment*

2.3.1. *In-flight phenotype*

2.3.1.1. Solo speed. Following initial treatment of the data (see Supplemental Material), ground speed was calculated for solo "familiar" flights, after the first nine flights from each site; total $N = 12$ flights per individual). Speed was given as the mean speed between successive GPS points throughout the flight (see detailed methods and justification of mean values in Sankey and Portugal, 2019). Airspeed was then calculated using the wind vector, as measured by the weather station (Greenfrog Scientific, Doncaster, U.K) placed at the home lofts (Longitude = −0.5726, Latitude = 51.4154; height = 7.84 m from the ground). The wind vector at the start of each flight was taken for airspeed calculation.

2.3.1.2. Solo route efficiency. The distance for perfect accuracy (or, beeline) was divided by the total distance traveled for each bird to provide a measure of route efficiency between 0 (did not return home) to 1 (perfect accuracy, straight line) (Meade et al., 2005). "Unfamiliar route efficiency" was measured at the first flight from a site ($N = 5$ per bird) and "familiar route efficiency" after 9 flights from a site ($N = 12$ per bird).

2.3.1.3. Leadership. In all group flights ("familiar" – $N = 18$; "unfamiliar" – $N = 5$) we measured leadership using correlation of time lags in the vector movement of the pigeons trajectories (Nagy et al., 2010). Specifically we used a quadratic interpolation of directional correlation time delay values (s) that maximizes correlation estimate to a more precise degree than our loggers are capable of (5 Hz) (see methods in Pettit et al., 2015). The "leadership score" for each individual is provided as the mean time-delay in their movements relative to the group (following: Nagy et al., 2010; Pettit et al., 2015). For example, a leadership score of 0.2 s will mean, on average, turning 0.2 s before the rest of the group (for full details, see Supplemental material).

2.3.1.4. Cranio-caudal distance to centroid. Distance in front/behind the flock (or, cranio-caudal distance with respect to the centroid), shown to be predictive of leadership (Nagy et al., 2010; Pettit et al., 2015; Yomosa et al., 2015) was calculated for each individual, at each time step, with respect to the average heading of the group (for centroid calculation see Portugal et al., 2014, and Supplemental material).

2.3.1.5. Route fidelity. A variance of distance to each individuals' solo mean path (Fig. S2.1) was calculated for each bird, for "familiar" flight paths, from each of the two "familiar" sites. The average variance around the mean path was termed "mean fidelity" and the bottom 5% of the variance was termed "peak fidelity" (following: Freeman et al., 2011). Peak fidelity was a key predictor of leadership, in Freeman et al. (2011), and was thus measured (1) as a potential "in-flight" phenotypic predictor of leadership, and (2) to control for its potentially confounding effect on the other key variables from our predictions. See Supplemental Material for more detailed information on the calculation.

2.3.2. Morphological phenotypes

Various measures of morphology were taken for each pigeon. Wing measurements were taken by tracing the outline of the wing onto A4 graph paper. Wing length, wing area and wing width were calculated by counting the number of squares more than 50% covered by the wing outline (see Pennycuick, 2008 for detailed methods). Toe and tarsometatarsus length were measured using a flexible tape measure, as was body width (mm). Body mass (grams) was measured using metric measuring scales (CoffeeHit: Coffee Gear Digital Bench Scale – 2 kg/0.1 g limit/accuracy) on a regular basis (total = 12 per bird; taken biweekly throughout the study period, June-August 2017), both for analysis, and as part of their routine care and husbandry.

2.3.3. Behavioral phenotype

2.3.3.1. Personality. To measure individual differences in behavior, we assessed exploration of a testing arena (180 × 150 cm loft; divided into nine equal rectangles of 50 ×60 cm using tape, see Portugal et al. 2017b). A novel object was either *present* (neophilia trials; e.g,. Kurvers et al., 2009; Schuett et al., 2011) in the center of the bottom-right square, or *absent* (boldness trials; Kurvers et al., 2009; Cote et al., 2011). Novel objects used were a backpack wrapped in pearlescent wrapping paper, a large water bottle painted with neon colors, and a helium balloon. Each pigeon in group 1 completed five 20-min trials (of both boldness and neophilia), and in group 2 each pigeon completed four trials for both (see Supplemental material for full protocol). "Boldness" was defined as the time (s) of the first emergence from the box in trials with novel object absent, with earlier exits indicating greater "boldness". "Neophilia" was defined as the time (s) spent in the bottom right zone (with the novel object) in trials with novel object present. "Exploration" was defined as the value X^2 from a chi-squared test on a null distribution, where exactly equal spread of time spent between each of the zones would give a X^2 value of zero, and increasingly unequal distributions providing greater X^2 values. Thus low values of X^2 correspond to more "exploratory" individuals. "Exploration" was calculated in trials with novel object *absent*, to help reduce a potential confounding effect of the object. "Boldness" and "neophilia" were given as a proportion of the total trial time (20 mins), and all three "personality" metrics were transformed to reduced skewedness, using Shapiro-Wilks tests in base R (R Core Team, 2017), (see Supplemental material, Supplementary Figure 2).

2.3.3.2. Dominance. We video recorded and analysed the agoniztic interactions in nine "dominance trials" to determine the dominance hierarchy in each of the two flocks (for full protocol see Supplemental Material, and Ricketts et al., 2022). Agonistic behaviors measured were: chasing, feather pulling, wing slaps and neck grabs (Nagy et al., 2013; Portugal et al., 2017b, 2020). These were recorded into a matrix with an initiator (winner) and receiver (loser) for each instance of a behavior. All interactions from the nine video trials for each group were totaled, as pigeons have been shown to have dominance hierarchies that are highly stable over time (Nagy et al., 2013; Portugal et al., 2020). We calculated normalized David's Score (dominance score) (Curley, 2016), and the hierarchy's linearity using Landau's linearity index (h′) (Landau, 1953). David score biases the win/losses of pairs by an overall score, so that "wins" over high-ranking individuals are given greater weight (De Vries et al., 2006). Landau's (h′) estimates the transitivity of the matrix, for example, high linearity would mean that if A beats B, and B beats C, then A is likely to beat C (Landau, 1953).

2.4. Statistics

2.4.1. Repeatability

If a given behavioral/flight phenotype was repeatable, we used a mean average of all values as a measure of *phenotype* in this domain for further analysis. We measured the repeatability using likelihood ratio tests with 1000 parametric bootstrap permutations to estimate 95% confidence intervals (Portugal et al., 2017b). Results from all repeatability analyses are detailed in the Supplemental material. If variables were found to be unrepeatable, we removed them from the analysis.

2.4.2. Principal component analysis (PCA)

To answer our main question of what variables can predict leadership, and whether this differs across familiar and unfamiliar terrain, we ran principal component analyses on each of the subcategories of repeatable phenotype separately (i.e., (i) "morphological", (ii) "behavioral" and (iii) "in-flight" phenotypes as described above). The resulting variables were a condensed depiction of how individuals differed in each of these three domains of inquiry, while also providing loadings, i.e., the extent to which each of the initial variables contributed to the variance between individuals. PCA was chosen for this analysis to increase the degrees of freedom (independent observations) (Budaev, 2010). Standard multivariate regression (Pinheiro et al., 2012) of our phenotypes of interest ($N = 15$), given the number of birds in the study ($N = 16$), would provide zero degrees of freedom. PCA loadings and summary statistics can be found in Supplemental material (Supplementary Table 3).

2.4.3. Models

To test our predictions as to whether flight variables such as speed and route efficiency determined leadership, we ran both (i) a linear model (LM; R Core Team, 2017) with the data of group 1 and group 2 combined, and (ii) a linear mixed model (LME; Pinheiro et al., 2012) with groups as random intercepts. The dependent variable was always leadership score (as above), and the independent variable was different (according to predictions). We further ran an ANOVA (R Core Team, 2017) on the two resulting models, which determined whether we accepted or rejected random intercepts (p value < 0.05). We describe results from the LME if the random intercepts were accepted, and LM if they were rejected. In either case, we ran separate linear models (LM) on each group. We investigated our first two predictions in this way.

For the PCA analysis (to assess our third prediction and for additional, exploratory analyses) we ran an LME on leadership over the first three principal components from all PCAs ($N = 9$; 3× morphological/behavioral/flight). We then used multimodel inference (using "dredge" function from R package MuMIn; Allwood et al., 2007; see dredge output in Supplementary material, Supplementary Table 4) containing all possible combinations of the PCA, which were then ranked by Akaike information criteria (AIC) score. The most highly predictive PCA variables were then applied in the same manner as above, with a comparison between LM and LME. Data and code are available at: https://github.com/sankeydan/famUnfam.

3. Results

Group 1, released from a northerly bearing, had higher overall route efficiencies than group 2 released from an easterly bearing ($t-$*test*: DF = 10.713, $t = 9.987$, $p < 0.001$; Fig. 2A-B), and additionally had faster airspeeds ($t-$test: DF = 168.85, $t = 16.071$, $p < 0.001$; Fig. 2C-D). This confound could have influenced our understanding of the differences between "familiar" and "unfamiliar" locations, validating our decision to run the "familiar" segment from different release bearings.

Leadership hierarchies were significantly transitive (interactions down the hierarchy point in the same direction) and linear (no large "jumps" between the scores of individuals in consecutive ranks) in familiar flights and unfamiliar flights (familiar flights; group 1:

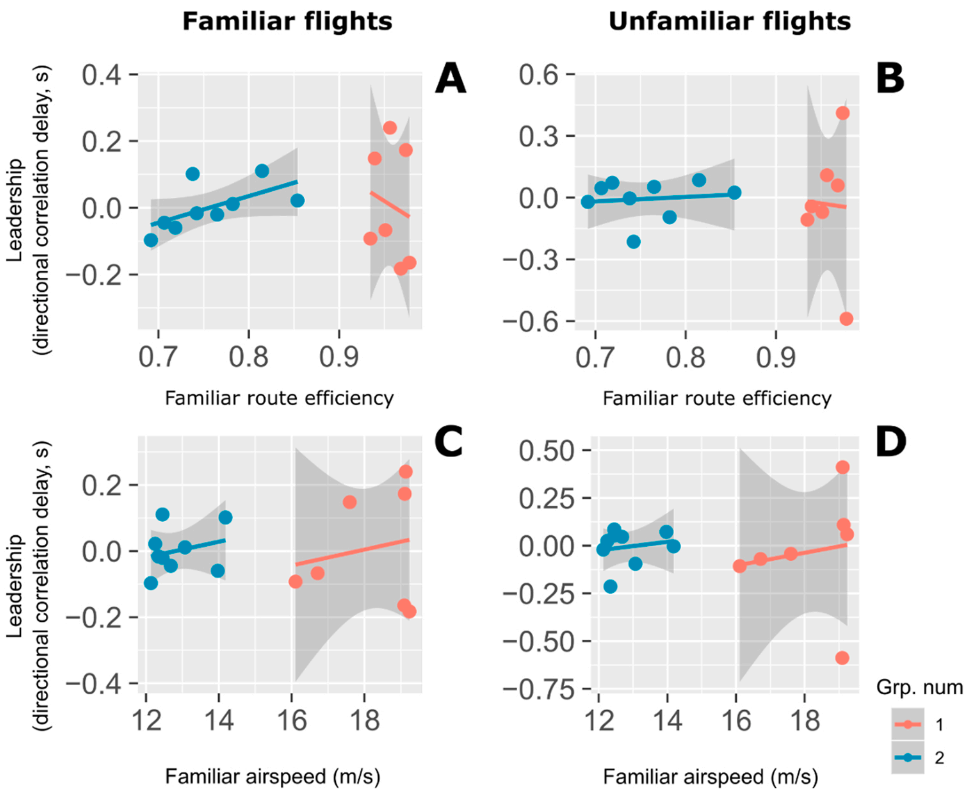

Fig. 2. Leadership, speed and route efficiency: results following predictions. Route efficiency from 0 (did not return home) to 1 (perfect "beeline") (A and B) from "familiar" flights was not predictive of leadership (directional correlation delay, s, Pettit et al., 2015) from either (A) "familiar" (number of solo flights from a site >9), or (B) "unfamiliar" flight locations (solo flight from a site = 1). Solo airspeed (m/s) (C and D) was also not predictive of leadership from either "familiar" (C) or "unfamiliar" (D) release sites. There were large differences in the airspeed and route efficiency from individuals in groups 1 and 2, presumably due to differences in the release site bearing with group 1 (red points and lines; see legend), from a northerly bearing and group 2 (blue points and lines) from an easterly bearing (Supplementary material Supplementary Tables 1 and 2). Plots were generated in ggplot2 with 95% confidence intervals around a predicted linear model per group.

transitivity (T) = 1, $p = 0.002$; group 2: $T = 1$, $p < 0.001$; unfamiliar flights; group 1: $T = 0.771$, $p = 0.017$; group 2: $T = 1$, $p < 0.001$).). Leadership was consistent across context, i.e., "familiar/unfamiliar" flights (LM; DF = 14, $t = 2.39$, $p = 0.033$).

3.1. Prediction 1: Solo speed, and route fidelity, but not route efficiency, govern leadership in familiar flights

Our first prediction, that in familiar flights, solo speed would predict enhanced leadership rank was not supported (LME: DF = 13, $t = 0.728$, $p = 0.480$; Fig. 2 C); and an individual's peak route fidelity had no impact on leadership (LM; DF = 13, $t = -0.717$, $p = 0.486$). Similarly, solo route efficiency from familiar flight locations was not predictive of leadership rank in group flights (LME: DF = 13, $t = 0.757$, $p = 0.423$; Fig. 2). However, group 2 showed a positive – yet statistically non-significant – relationship between leadership score and solo route efficiency (LM: DF = 7, $t = 2.012$, $p = 0.084$; Fig. 2A). Individuals which flew more often at the front of the flock (higher cranio-caudal distances) had higher, but not significantly higher, leadership scores (LM; DF = 14, $t = 1.978$, $p = 0.070$).

3.2. Prediction 2: Both route efficiency and speed govern leadership in unfamiliar flights

Ascertaining – in response to our second prediction – whether solo route efficiency from unfamiliar locations is predictive of enhanced leadership in unfamiliar flights was not possible, as solo route efficiencies were not repeatable across individuals (R = <0.001, ± 0.058 (SE), 95% CI: 0–0.019, $p = 0.516$; see Supplemental material for all repeatability analyses). We did, however, attempt to correlate *familiar* route efficiencies with *unfamiliar* leadership ranks, and also found them to not be predictive (LM: DF = 14, $t = 0.121$, $p = 0.905$; Fig. 2B).

Solo speed from familiar flights – contrary to our second prediction – was not supported as a predictor of leadership in unfamiliar flights (LME: DF = 13, $t = 0.809$, $p = 0.433$; Fig. 2D). Thus, the consistent and repeatable differences in individual preferred speed in solo familiar flights ($R = 0.346 \pm 0.104$ (SE), 95% CI: 0.139–0.531, $p < 0.001$) did not equate to leadership in group flights from either familiar or unfamiliar locations.

3.3. Prediction 3: risk-taking "personalities" have stronger influence in "unfamiliar" flights

Boldness and neophilia scores, which may reflect inter-individual differences in "risk taking" (Wolf et al., 2007), positively covaried (LM: DF = 14, $t = 2.607$, $p = 0.021$; Fig. 3), though neither variable was predictive of exploration score (neophilia – LM: DF = 14, $t = -0.678$, $p = 0.509$; boldness – LM: DF = 14, $t = -0.33$, $p = 0.974$). Combined in principle component analyses (PCA; Budaev, 2010), no personality covariates were predictive of leadership. Behavioral PC2 – corresponding mostly to the inverse of exploration (PCA loading = −0.94795, maximum range = −1 to 1) – was the greatest predictor of the behavioral components on leadership (Supplementary material, Supplementary Tables 3 and 4). Nevertheless, exploration was not predictive of leadership in either "familiar" (LM: DF = 14, $t = 1.03$, $p = 0.321$; Fig. 3) or "unfamiliar" flights (LM: DF = 14, $t = -0.744$, $p = 0.469$).

3.4. Personality, morphology and dominance

Dominance – a potential variable of interest in leadership (Peterson et al., 2002; King et al., 2008; Nagy et al., 2013; Strandburg-Peshkin et al., 2015) – was not predictive of leadership across context (familiar – LM: DF = 14, $t = -0.138$, $p = 0.892$; unfamiliar – LM: DF = 14, $t = -0.754$, $p = 0.463$). Body mass showed no relationship with dominance (LM: DF = 14, $t = 0.775$, $p = 0.451$; Fig. 3, Fig. 4), but sex did (LM; DF = 14, $t = 2.457$, $p = 0.026$; Fig. 2.4), with males being more aggressive than females. Neophilia was highly predictive of greater dominance rank (LM: DF = 14, $t = 4.484$, $p < 0.001$; Fig. 3), whereas (the correlated trait of) boldness was not (LM: DF = 14, $t = 1.389$, $p = 0.186$). This indicates that individuals more willing to investigate

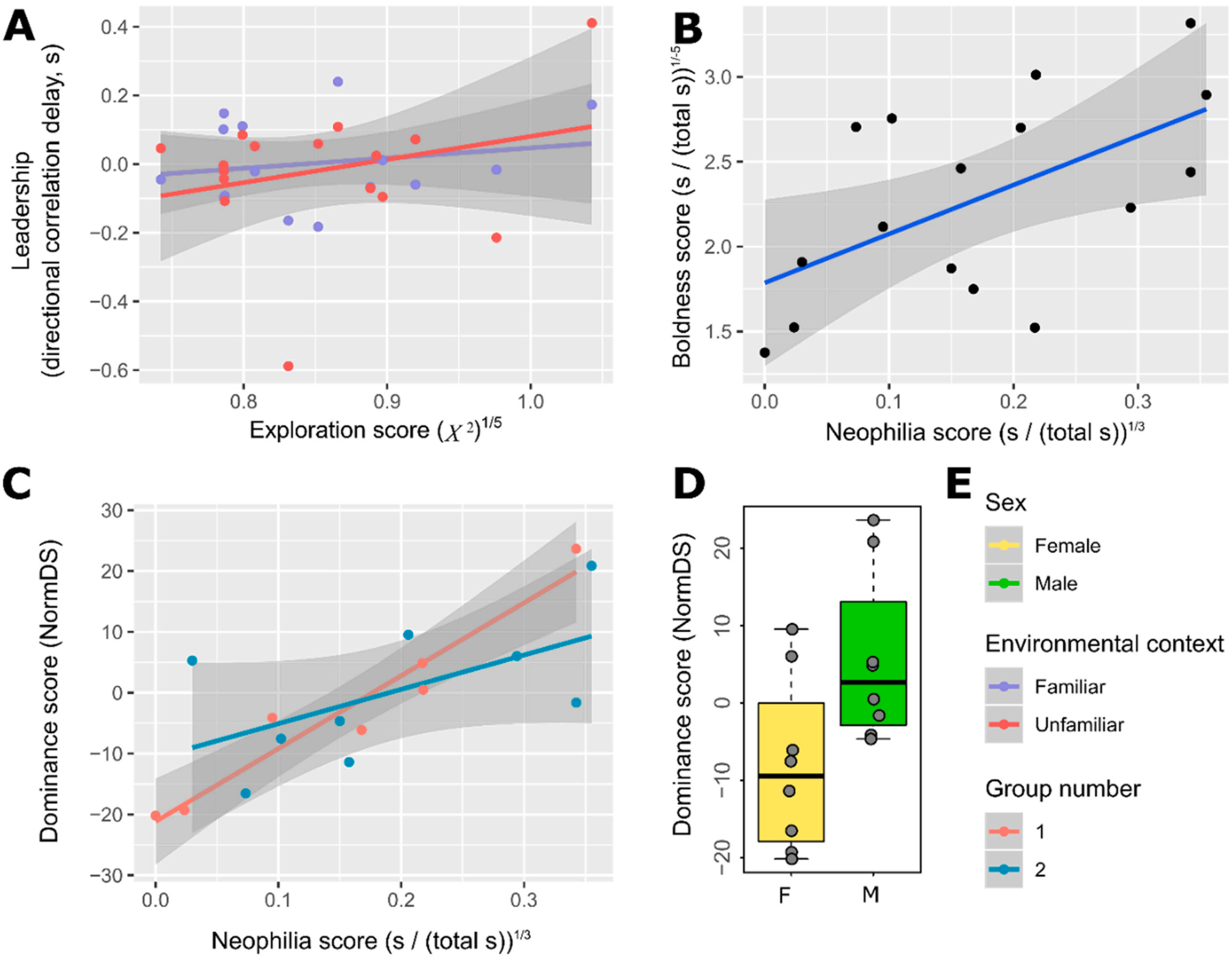

Fig. 3. Pigeon "personality" results. (A) Leadership score (directional correlation delay, s) against exploration score – the evenness of individual time budget spread across testing arena (chi-squared score $(X^2)^{1/5}$; see Supplemental material for transformations). Purple and red lines reflect environmental contexts "familiar" and "unfamiliar" respectively (see legend in (E)). (B) Boldness score – latency to leave the box (s / (total s)$^{1/-5}$), against neophilia score – time spent in experimental sector with a novel object (s / total s)$^{1/3}$ (see Supplemental material). Both groups were treated together, here, as observations were measured individually (i.e. not in a group context). (C) Dominance score – calculated using normalized David's score (NormDS) (Gammell et al., 2003) from a matrix of aggressive interactions for each group (group 1 = orange/red; group 1 = turquoise) against neophilia score (s / total s)$^{1/3}$. (D) Box and whisker plots, and individual data points (gray) illustrating dominance score (NormDS) against bird sex (yellow = female; green = male). (E) Legends for previous plots.

novel objects took up higher dominance ranks, but not those with decreased latency to leave the box.

3.5. *Other phenotypic predictors of leadership*

Results from a model selection (see *Methods: Statistics*) across the PCA analysis scores showed that PC1 from the morphological dataset (corresponding mostly to body mass, PCA loading = −0.535; Supplementary material, Supplementary Table 3) was the best predictive covariate of leadership. Body mass, when tested post-hoc, was a positive significant predictor of leadership score in familiar flights (LM; DF = 14, $t = 2.94$, $p = 0.011$; Fig. 4) and unfamiliar flights (LM; DF = 14, $t = 2.659$, $p = 0.020$). However, in familiar flights, this relationship was driven only by group 1 (LM; DF = 5, $t = 3.063$, $p = 0.028$; Fig. 4), and was not present in group 2 (LM; DF = 7, $t = -0.474$, $p = 0.650$; Fig. 4). Furthermore, in unfamiliar flights, body mass did not have significant effect on leadership score in either group, when treated independently (LM; group 1: DF = 5, $t = 1.992$, $p = 0.103$; group 2: DF = 7, $t = 0.459$, $p = 0.660$). The range of body mass in group 1 was more than twice as large as the range in group 2 (117 g vs 56 g); while the mean body mass of the groups were similar (group 1 = 438 g; group 2 = 437 g). Body mass was significantly correlated with familiar route flight airspeed (LME; DF = 13, $t = 3.088$, $p = 0.009$), with heavier individuals exhibiting faster speeds. Heavier individuals additionally showed significant increases in cranio-caudal (front-back) distance in "familiar" flights (LM; DF = 14, $t = 3.518$, $p = 0.003$; Fig. 2) but not in "unfamiliar" flights (LM; DF = 14, $t = 1.481$, $p = 0.161$; Fig. 4).

4. Discussion

We did not find any evidence for context-dependent leadership hierarchies across environmental context (flights from "unfamiliar" and "familiar" terrain). Leadership across the two conditions was consistent across all data. However, no phenotypic traits were universally predictive of leadership either between experimental flock's or across environmental contexts. Therefore, we find no support for our three core hypotheses; (1) that phenotypic differences in solo speed are predictive of leadership across context (contrasting with Pettit et al., 2015; Sasaki et al., 2018), (2) that route efficiency could govern leadership in "unfamiliar" flights, or (3) that "personalities" associated with risk-taking has a larger influence on leadership in "unfamiliar" flights.

Body mass was the only predictor of leadership across "familiar" and

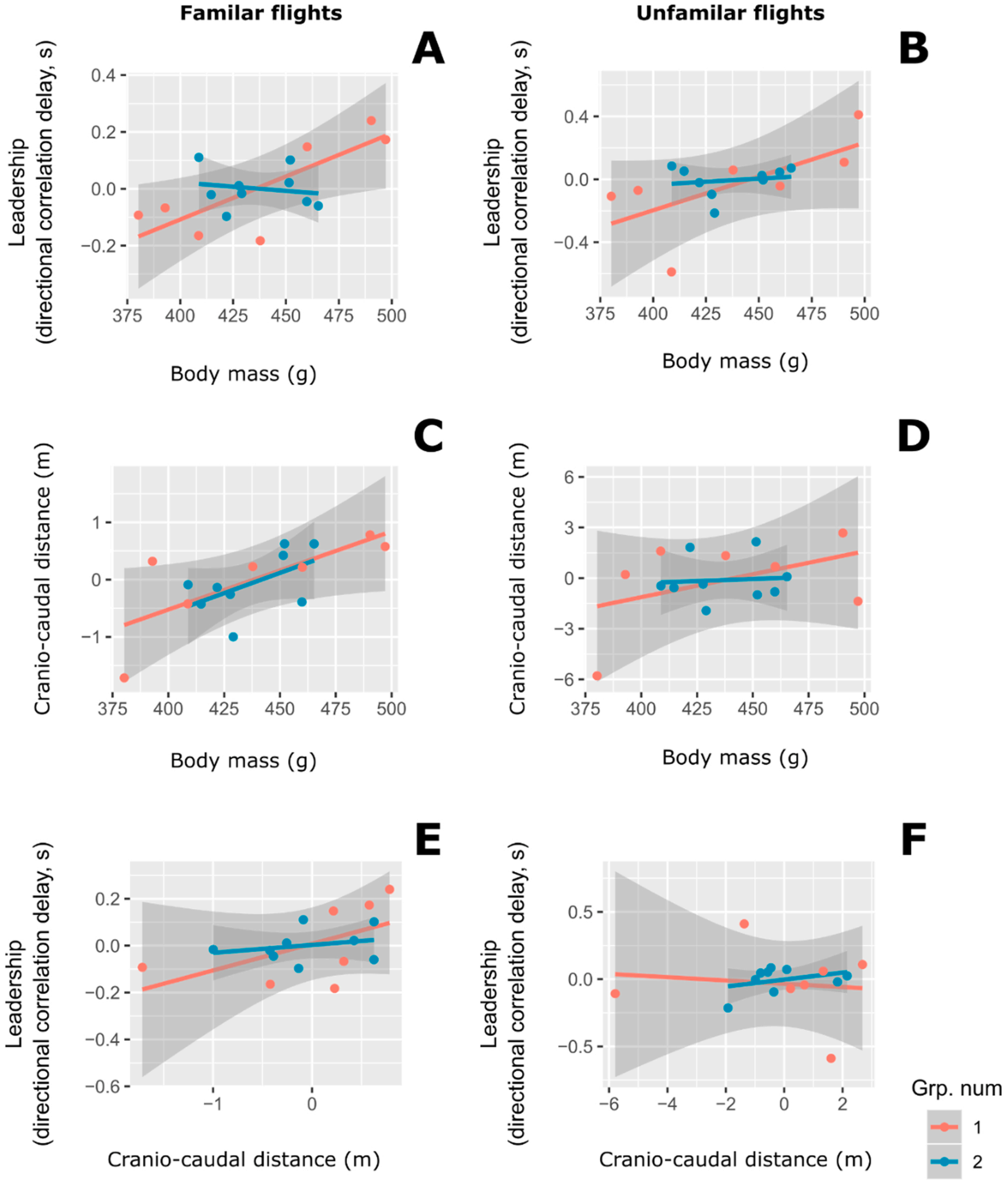

Fig. 4. Body mass, airspeed, and cranio-caudal distance in “familiar” and “unfamiliar” flights. (A-B) Body mass (g) was predictive of leadership score (directional correlation delay, s, Pettit et al., 2015) in (A) “familiar” flights, and (B) “unfamiliar” flights when data were grouped together, but only in group 1 when not (red; see *Results*; see legend in (F)). Group 2 (blue) showed no such relationship, though this may be due to their much smaller range in body mass. C-D) Increased mean body mass (g) was significantly positively correlated with cranio-caudal (front-back) distances to flock centroid (m) in (C) “familiar” flights, but not in (D) “unfamiliar flights. E-F) Individuals with greater cranio-caudal distances (m) did not show increased leadership score in (E) ”familiar” flights, or (F) “unfamiliar” flights. The effect of body mass (g) on C) cranio-caudal distance (m), and D) airspeed (m/s), was positive and significant.

“unfamiliar” flight contexts, and this was only in one group (group 1). Of potential significance, here, is that group 1 had a range of body mass twice as large as group 2, in which leadership was not predicted by body mass. Potentially, the addition of heavy and light individuals to group 2 (smaller mass range) group would have led to the same relationship as observed in group 1 (larger mass range). As body mass typically predicts solo flight speed (Pettit et al., 2015; Sankey et al., 2019), it is not clear why body mass would predict leadership while solo flight speed did not.

As there was no consistency in the inter-individual route efficiencies from "unfamiliar" release sites, we cannot confirm or reject prediction (*2*): that more efficient homers will take up higher leadership ranks in "unfamiliar" terrain. To understand how route efficiency governs leadership, it is perhaps more useful to use individuals with additional training as was conducted by Flack et al., (2012, 2013). Nevertheless, additional training may introduce confounding variables beyond increases in route efficiency. For example, Taylor et al. (2017) found that site familiarity was associated with changes in wingbeat kinematics. They found that wingbeat frequency (flaps per unit time) reduced and dorsal body amplitude (a proxy for the wingbeat amplitude) increased while route efficiencies were stabilizing. This was followed by a reversal of the trend for additional releases after the individuals' idiosyncratic routes had formed (Taylor et al., 2017). To reduce the bias in the assessment of route efficiency effects on leadership in unfamiliar contexts, future work will need to retain "unfamiliarity", while incorporating inter-individual differences in route efficiencies. We suggest that either differences in age (Santos et al., 2014), satiation (Rands et al., 2003), or lineage (Gazda et al., 2018) may provide a better test, albeit still with intrinsic biases. In particular, genetic lineage is highly regarded in pigeon racing (Gazda et al., 2018), with faster homers selling for higher prices. However, it would be important to establish whether these superior homers demonstrate increased route efficiencies, with differences not explained by speed alone. Following the results of Gazda et al. (2018), this may be very difficult, as homing pigeons, despite remarkable similarities in their genetic architecture, demonstrate modest selection towards *both* increased muscle growth (potentially, for speed) and brain function (potentially, for navigation) (Gazda et al., 2018). Nevertheless, the onset of high-resolution biologging technology provides a method to tease apart these variables (speed, route efficiency) across breeds, and provides potentially fruitful ground for further research.

Leadership cannot emerge without individuals being followed (King, 2010), and thus group decision making ultimately relies on the response of potential "followers" (King, 2010; Strandburg-Peshkin et al., 2018). "Following" may represent a trade-off between (1) the costs of splitting (e.g., risk of predation; Hogan et al., 2017; Papadopoulou et al., 2022b) and (2) the *costs* of route compromise (i.e. going in an undesirable direction; Conradt and Roper, 2005; Sueur et al., 2011). This "trade-off of costs" suggests that following may never be as beneficial as leading, which demands an evolutionary explanation. We suggest that trading-off these two options *optimally* may represent the best possible strategy given their intrinsic handicap (Nagy et al., 2013). "Making the best of a bad job" is a well explored concept in behavioral ecology, which can explain how differences in fitness payoff can be maintained (Eberhard, 1982; Dominey, 1984; Emlen, 1996; David and Dall, 2016). Alternatively there may be additional predation costs of leadership (Ioannou et al., 2019). Ioannou et al. (2019) projected virtual prey onto the wall of a tank containing predatory fish (potentially of mixed species with mean length 26.6 mm ± 3.60 SD), and found that individuals on the leading edge were preferentially predated. Another possibility is that "leadership" and "followership" are personalities themselves and remain evolutionarily stable via frequency dependent benefits (Johnstone and Manica, 2011).

Leadership across environmental context was not predicted by any axis of "personality". Our findings contrast with previous results finding a positive influence of "boldness" on leadership across "familiar" and "unfamiliar" (first six releases from a novel site) context (Sasaki et al., 2017). Why this was the case, we cannot be sure, although the experimental set-up testing boldness (and hence potentially the motivational context) were different. Sasaki et al. (2018) used a system whereby individuals latency to leave the box may have been driven by a container of food placed in the testing arena. We reason that food motivation may be a better axis with which to quantify the potential motivations of individuals (i.e. a "reason" to lead the group). Leadership has been shown to correlate with intake of food quality (in barnacle geese, *Branta leucopsis*; Black et al., 1992), and quantity (in chacma baboons, *Papio ursinus*; King et al., 2008). Despite many calls for consistency in "personality" measurement across taxa (Vazire et al., 2007; Carter et al., 2013; David and Dall, 2016), researchers still tailor the methods to their own hypotheses and the feasibility of the methods given their specific system and set up (Dall and Griffith, 2014). Our aims were to test "risk taking" as a potential explanatory variable for leadership (Ioannou et al., 2015). It seems, however, given current evidence, that "food motivation" (which may be governed by internal physiology) could drive collective dynamics (Killen et al., 2017). Manipulating satiation, via food deprivation, could be an appropriate test of this hypothesis.

Previously it has been demonstrated that solo flight speed and route efficiency can be predictors of leadership in pigeons (Flack et al., 2012; Pettit et al., 2015), contrasting with the results in the present study. However, these two factors as determinants of leadership are not entirely ubiquitous. Pettit et al. (2015), for example, found that while solo flight speed did predict leadership in a group scenario, solo flight efficiency did not. Flack et al., (2012, 2013) determined that increases in flight efficiency, through direct manipulation of homing of specific individuals, was not accompanied by improvements in hierarchical position. In contrast again to our present findings, Sasaki et al. (2018) found that bold pigeons were flock leaders in both familiar and unfamiliar group flight contexts. Bold individuals were also more likely to occupy all subsequent upper ranks within the flight leadership hierarchy, not just the lead. Interestingly, however, bold and shy individuals did not differ significantly in their solo route efficiency or solo flight speed, but they did differ in how they improved over subsequent releases. From familiar sites, there was a gradual decline observed in proportion of times each rank was occupied by a bold bird, from highest to lowest. From unfamiliar release sites, however, this change was more abrupt, with a distinct switch between ranks Sasaki et al. (2018).

The pigeon flocks created for the Sasaki et al. (2018) study where allocated based on their personality scores, ensuring an approximate 50/50 split of bold and shy birds. The flocks in the present study were embedded together as a group two years prior to the commencement of this study and the personality phenotyping. It is feasible, therefore, that variable ratios of bold/shy birds within a flock may be responsible for the difference in our findings. Similarly, group size has been demonstrated to impact leadership and general flock dynamics, with individual movement characteristics becoming increasingly homogenized in larger groups. The precise impact of group size on leadership influence and behavior has not been fully established, nor whether any effects scale linearly with flock size or exhibit a sudden step change. Thus it is possible that differences in flock size are driving these variations in findings regarding leadership in pigeon flocks, and thus determining the full impact of flock size on flight dynamics is a fruitful avenue for future research.

Consistent with previous results, in contrast, is the stability of leadership across multiple flights in the present study. Leadership being consistent over time and social context has been established in pigeon flocks (Nagy et al., 2010; Santos et al., 2014), yet within these there are context dependent hierarchies (Nagy et al., 2013). A possible explanation for the difference in findings in the present study may be that there was a further context present that we were unaware of, or was not identified. Typically, knowledge of a specific release site is less critical for homing pigeons than general homing experience (Wallraff, 1978). Prior studies (e.g., Pettit et al., 2015; Sasaki et al., 2018) have used pigeon flocks of mixed overall ages and homing experience. In the present study, both pigeon age and prior overall homing experience where more homogenous, and this again may contribute to the difference in results we find in the present study to previous work.

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CRediT authorship contribution statement

Daniel Sankey: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Dora Biro:** Conceptualization, Methodology, Writing – review & editing. **Rhianna Ricketts:** Investigation, Methodology. Writing – review & editing.**Emily Shepard:** Conceptualization, Methodology, Writing – review & editing. **Steven Portugal:** Conceptualization, Methodology, Funding acquisition, Supervision, Writing, Writing – review & editing.

Declarations of Competing Interest

None.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2022.104629.

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