

Speed consensus and the ‘Goldilocks principle’ in flocking birds (*Columba livia*)

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The evolution of group living transformed the history of animal life on earth, yielding substantial selective benefits. Yet, without overcoming fundamental challenges such as how to coordinate movements with conspecifics, animals cannot maintain cohesion, and coordination is thus a prerequisite for the evolution of sociality. Although it has been considered that animal groups must coordinate the timing and direction of movements, coordinating speed is also essential to prevent the group from splitting. We investigated speed consensus in homing pigeon, *Columba livia*, flocks using high-resolution GPS.

Despite observable differences in average solo speed (which was positively correlated with bird mass) compromises of up to 6% from the preferred solo speed were made to reach consensus in flocks. These results match theory which suggests that groups fly at an intermediate of solo speeds, which suggests speed averaging. By virtue of minimizing extreme compromises, speed averaging can maximize selective benefits across the group, suggesting shared consensus for group speed could be ubiquitous across taxa. Nevertheless, despite group-wide advantages, contemporary flight models have suggested unequal energetic costs in favour of individuals with intermediate body mass/preferred speed (hence the ‘Goldilocks principle’).

Keywords: collective behaviour, coordination, flight dynamics, movement ecology, social behaviour, trade-offs

The evolution of social behaviour was a major step in the evolution of complex animal life on earth (Bourke, 2014; Maynard Smith & Szathmary, 1997; Sumpter, 2010) conferring many selective benefits to animals that achieved sociality (e.g. increased predator avoidance, Handegard et al., 2012; Kenward, 1978; Krause & Ruxton, 2002; Sumpter, 2010; energy conservation, Portugal et al., 2014; Weimerskirch et al., 2001; social information acquisition, Biro et al., 2006; Simons, 2004). Yet, achieving these advantages brought with it many challenges, such as how to coordinate movements and, therefore, remain spatially cohesive (Conradt & Roper, 2003, 2005, 2009). Coordination is widely discussed in terms of consensus building (Conradt & Roper, 2005; Seeley, 2003; Sumpter, 2010). Whether the group is led by particularly influential individuals (unshared; King et

al., 2008; Nagy et al., 2010) or decision making is distributed across multiple members (shared; Gall et al., 2017; Strandburg-Peshkin et al., 2015), groups that achieve coordination essentially make unanimous movement decisions (i.e. they come to a shared/unshared consensus) or risk losing cohesion (Conradt & Roper, 2005; Couzin et al., 2005; Ioannou et al., 2015). The dynamics of shared–unshared consensus have been shown to be impacted by intrinsic physical (Pettit et al., 2015) and behavioural (Sasaki et al., 2018) differences, the presence of uninformed individuals (Couzin et al., 2011), age (Lee & Teichroeb, 2016), dominance (King et al., 2008) and sex (Fischhoff et al., 2007). Nevertheless, despite our increasingly comprehensive understanding of collective decision making, thus far the field has largely focused on direction (‘where to go?’) and timing (‘when to leave?’) of movements (Conradt & Roper, 2005; Couzin et al., 2005; Sueur & Petit, 2008). These components, however, do not cover all scenarios. If groups do not reach a consensus on travelling speed (‘how fast to travel?’), the group will split regardless of whether a consensus on direction and timing was reached. Therefore, the dynamics of an integral aspect of coordinating group movements, attaining a consensus speed, are almost entirely unknown (but see Hedenström & Åkesson, 2017; Pettit et al., 2015).

Conflicts of interest regarding group travelling speed may arise as a result of heterogeneity in age, sex, experience and physiological or behavioural phenotypes within groups. Differences in preferred travelling speed will need to be resolved if the group is to remain cohesive (at least at the macroscopic level of the group’s movement; there is always the potential for faster individuals to take more tortuous pathways within the group borders and remain spatially cohesive). These conflict/resolution dynamics have parallels within

the current framework of collective decision making. Directional ('where?') preferences for foraging patches or travelling routes, for example, can often conflict among group members (Biro et al., 2006; King et al., 2008). While convergence of preferences can lead to beneficial (accurate) group decisions (Conradt & Roper, 2003; Simons, 2004; Strandburg-Peshkin et al., 2015), decisions are in many cases dictated by particular individuals, such as those more experienced (McComb et al., 2011; Prins, 1996), bolder (Jolles et al., 2017; Sasaki et al., 2018) or more dominant (King et al., 2008). Likewise, concerning decisions to set into motion ('when?'), individuals may differ in their preferred timing of departure, based on phenotypic differences such as physiological need for satiation (Conradt et al., 2009; Fischhoff et al., 2007; Rands et al., 2003) or personality differences (McDonald et al., 2016; Sih et al., 2012). Here, decisions may be governed by signalling mechanisms which can build a shared consensus for departure time (Ramseyer et al., 2009; Walker et al., 2017) or be dictated by movement initiators (Fischhoff et al., 2007; Rands et al., 2003).

The mechanism through which group speed is determined during collective movement is particularly important in bird flocks. Birds must increase their energetic output to fly either faster or slower than their individual optima (i.e. the speed at which work rate per unit distance or time is at its minimum; Fig. 1a; Hedenström, 2009; Pennycuik, 1968; Tobalske et al., 2003). These optima depend on an individual's unique morphology: heavier and structurally larger birds have been shown to have faster optimum speeds than smaller individuals, on both an intraspecific and an interspecific level (Fig. 1a; McFarlane et al., 2016; Norberg, 1995; Tobalske, 2007; Tobalske et al., 2003; Winter, 1999). Flying faster

in active flight necessarily costs more (Hedenström, 2009; Tobalske et al., 2003); an increased work rate of muscles is required to increase flap frequency or wingbeat amplitude to achieve faster speeds (Butler, 2016; Hedenström, 2009). Similarly, flying slower than an individual's optimum speed has also been shown to increase work rate, as the momentum of flight provides lift (Heerenbrink et al., 2015; Johansson et al., 2018). Furthermore, as flying is the most energetically demanding form of aerobic locomotion, any departure from an individual's preferred flight speed, be it faster or slower, may have significant implications for energy expenditure and overall fitness (Hedenström & Ålerstam, 1996; Schmidt-Nielsen, 1972; Tobalske et al., 2003).

Given that (1) an aligned and coordinated flock can only fly at one speed without fragmenting, and (2) flying at any speed other than individually variable energetic optima is costly, conflicts of preference regarding group speed are likely to arise in bird flocks. Presumably, if the costs of resolving the conflicts are too large, this will result in group fission (Fig. 1a). On the other hand, if conflicts are resolved and a consensus is reached, individuals may fare differently energetically (Fig. 1a). These costs of compromise ('consensus costs'; Conradt & Roper, 2005) will arise in any system when conflicts are resolved, whether in the context of timing, direction or speed, given that no decision outcome can be uniformly optimal for individuals that possess different preferences.

Using a mixed solo ($N = 30$) and group flight ($N = 18$) release plan to measure solo and group speeds, we aimed to investigate (1) the speed of group travel, with respect to the individual preferred speeds, and (2) the consequences of this adopted group speed on

individual flight costs, in a model species in avian navigation and aerodynamics, homing pigeons, *Columba livia*. Pigeons are able to home from release sites either solo or in groups, and have frequently been used in studies of collective behaviour (Biro et al., 2006; Nagy et al., 2010, 2013; Pettit et al., 2015) and aerodynamics, measuring the energetic cost of flight in both free-flying conditions (Taylor et al., 2017; Usherwood et al., 2011) and wind tunnels (Butler, 2016; Butler et al., 1977; Butler & Woakes, 1990; Rothe et al., 1987). The hypotheses we tested were, first, that body mass predicts solo flight speed in pigeons (Fig. 1b; McFarlane et al., 2016; Norberg, 1995; Tobalske, 2007; Tobalske et al., 2003; Winter, 1999), and, second, that, in group flights, the birds will not split (following Nagy et al., 2010, 2013; Watts et al., 2016) and so will compromise on speed. This second hypothesis is a set of three alternative hypotheses, depending on which birds compromise the most (see Fig. 1c).

<H1>Methods

<H2>Subjects and Morphological Measurements

Homing pigeons ($N = 18$), all aged 1–1.5 years, were used in the experiments. They were housed in two separate groups of nine, in purpose-built lofts (7 x 6 ft) at Royal Holloway, University of London, U.K. (see Portugal, Ricketts, et al., 2017; Portugal, Sivess, et al., 2017 for further husbandry details). Food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, U.K.), water and grit (Versele-Laga–Colombine Grit and Redstone, Deinze, Belgium) were provided ad libitum. Birds were weighed regularly, and their structural size measured (for full details, see the Appendix).

<H2>Biologgers

Each bird was tagged with commercially available GPS loggers (QStarz BT-Q1300ST, Düsseldorf, Germany) which recorded latitude, longitude and time (GMT), 5 times/s (5 Hz). The outer casing was replaced with resealable bags and additional clear tape to reduce mass while retaining waterproofing. Logger loading totalled 21 g which was 4.2–5.6% as a relative value of the pigeon's mass (mean = 4.8%). The loggers were attached by trimming feathers on the bird's back and attaching Velcro strips to the bird (hook side) using Araldite epoxy glue (Biro et al., 2006; Taylor et al., 2017). Velcro strips (loop side) were also attached to either the loggers or the modified casing (for GPS) for easy attachment and removal per flight. The loggers were removed from the birds as soon as they came back into the lofts following an experimental release.

<H2>Flight plan

Pigeons were released from a northerly bearing (only group 1; five males and four females, randomly chosen) or an easterly bearing (only group 2; five females and four males, randomly chosen), from two sites per group away from traffic at 5 km and 9 km by road (see the Appendix). Sites were named N5, N9, E5 and E9, based on flight bearing (e.g. N or E) and distance (e.g. 5 km or 9 km; Appendix Fig. A1). Each individual flew solo ($N = 15$ flights per site) and in their respective groups ($N = 9$ flights per site; Table 1).

Solo/group condition was staggered to control for temporal variation in wind speed and direction (Table 1). Additionally, the solo stage was extended for the first set of releases

from each site (see Table 1 for full flight order, dates and further site information). This was to ensure the route was learned, so that group flights were not at a navigational familiarity advantage, thus avoiding atypical flight speeds associated with unfamiliarity, a phenomenon found in a recent study of pigeon flight speeds (Taylor et al., 2017).

Analyses were run on solo speeds from all available flights and all group speed data. An alternative analysis, omitting data before the seventh flight from each site (where unfamiliarity could play a larger role), was also conducted.

<H2>Missing Data

Two birds, both from group 1, a male and a female, did not return home following a scheduled release from site N5. The first individual was lost following its fourth release, and the second was lost on its seventh release from this site. Neither had participated in any group flights, so both were removed from the data set. For more information on missing data and data processing see the Appendix. The final number of flights per individual is documented in Appendix Table A1.

<H2>Theoretical Speed Estimates

The library ‘afpt’ (Heerenbrink et al., 2015) was used to estimate the minimum power speed of birds given the morphological metrics that we measured. To compare these theoretical estimates to observed data we converted the data to % values. Unlike in the observed data, where the relative speed was a comparison between solo and group flying speed (given as %), we had to define an appropriate theoretical flock speed $S_{\text{flock_theor}}$. (Fig.

2a). For this, we deduced how close (i.e. how many standard deviations) the mean of observed solo speeds was to the observed group speed (0.18 standard deviations from the mean), and then subtracted this number of standard deviations from the mean of the theoretical estimates (Fig. 2a). Then all theoretical speed estimates were converted into % values relative to $S_{\text{flock_theor}}$. (Fig. 2b). Minimum power speeds in free-flying pigeons are likely to be much higher than their theoretical equivalents, perhaps due to theoretical work being based on wind tunnel data (see Discussion and Taylor et al., 2017; Usherwood et al., 2011). Therefore, direct comparison of observed/theoretical speeds was not possible. Our assumption when comparing our theoretical speed estimates with observed data was that individuals were flying at the speed of minimum power in solo flights. (See Discussion for a break-down of this assumption, and how the interpretation of the results would differ if the birds were flying at different optimal speeds (i.e. maximum range speed)). These theoretical estimates allowed us to make comparisons between data and theory and estimate the intragroup energetic increase as a result of speed compromise; importantly, theoretical estimated speed was not used in any of the tests of our main hypotheses.

<H2>Speed

Ground speed from solo flights was calculated using the distance between locations at each GPS time step (5 Hz) using GPS data (see the Appendix). Ground speed of group flights was given by the speed between locations of the group's centroid (after individuals that split from the group had been removed; see the Appendix). See Appendix Table A2 for the resulting statistics, had we not used the centroid and instead used individual trajectories.

To calculate airspeed, we integrated wind data (provided by a wireless weather station at the home loft) with ground speed from GPS trajectories, following methods detailed in Safi et al. (2013). From each flight trajectory (both solo and centroid data, i.e. group flight), we took a mean of all airspeed data. Airspeed had no obvious deviation either throughout a flight or across all flights (Fig. 3a-g). Means of airspeed per flight were collated, and a median of these airspeeds was used as an individual's preferred speed (Fig. 3e). A mean was used for the intraflight (per flight) speed data as initial observations of the speed frequency histograms across individual flights yielded both long- and short-tailed distributions, which mean-averages more accurately estimate (Fay & Gerow, 2013). Capturing long and short tails is important when estimating energetic costs and speed capability. For example, medians will omit data for extreme bursts of speed which might be characteristic of an individual and which probably have a very high cost (Tobalske et al., 2003); mean-averages, on the other hand, use all the data in the estimate. We did, however, run all statistical models using medians instead of means (these statistics are reported in Appendix Table A2). The median of interflight speeds was chosen to remove erroneous airspeeds, for example, a reading of approximately 31.5 m/s was observed for each individual in group 2 from their ninth group flight; this is more than twice a normal airspeed estimate for that group (13.9 m/s). The weather station may have picked up large gusts and distorted airspeed estimates in some cases. See the Appendix for additional methods on how airspeed was calculated in solo and group flight contexts.

Despite a staggered group/solo flight protocol as a control, support-winds (see Appendix) were stronger for group flights (Appendix Fig. A2a). This further justifies our use of airspeed, a measure that controls for differences in wind parameters, in the final analysis (see further investigation into the impact of these support-wind deviations and further information regarding our release protocol in the Appendix).

<H2>Statistics

For our statistical analysis we first needed to account for the differences in airspeed across the two groups (Fig. 3e, Appendix Fig. A3), probably caused by the differences in support-wind commensurate with each release direction (see discussion in the Appendix). Our questions were not related to actual flight speeds, only relative to the group speed. At first, both groups were treated individually to test for outliers which may skew the results. Individual ‘P’ (see Fig. 3e) held significant influence over the direction of the predicted linear model. It had a Cook’s D of 1.11, which is over the generally accepted thresholds: (1) $3 \times$ the mean of Cook’s $D = 0.38$ and (2) a score of over 1.00 (Kim & Storer, 1996). Following the removal of this individual, we found no difference between the gradient of the two groups’ slopes for individual speed (ANCOVA: $N = 2$, $F_1 = 0.07$, $P = 0.80$); as expected significant differences were found between the intercepts (ANOVA: $N = 2$, $F_1 = 491.5$, $P < 0.001$). When this individual was not removed from the data, the direction or significance values of the ANOVA slope and intercept did not change (see Appendix Table A2 for the summary statistics from each model where this individual was not removed). Therefore, both groups were included together in our models to test our two key questions: (1) whether body mass predicts preferred solo flight speed and (2) how divergence from mean body mass (mass residual) impacts speed compromise within groups (see Fig. 1).

To test the first question, whether mass predicts speed was run both as a linear model (LM, on the median of airspeeds for each of 16 individuals) and as a mixed model including a data point for each flight ($N = 299$ flight trajectories). In this latter model we used ground speed as the dependent variable, bird mass, support- and cross-wind components, flight order and sex as fixed factors, and group ID and pigeon ID as random factors. Ground speed, and not airspeed, was used because support- and cross-winds, both used in the airspeed calculation, are present in the model. The resulting model had normally distributed residuals (Appendix Fig. A4).

To test the second question (see Fig. 1c; i.e. identifying which individuals compromise least to fly as a flock), we ran a comparison of a linear fit of absolute speed compromise against mass (relative to mean mass), with an LM with an anchor at zero (mean mass; Fig 1c). If a linear fit predicts speed compromise, this will suggest that heavy or light individuals were compromising the least (if the slope of the model is negative or positive, respectively; Fig. 1c). If, however, an LM does not explain the relationship, whereas the model with an anchor does, then we have evidence that birds closer to the mean mass compromise less on speed in flock flight (Fig. 1c). This conclusion can only be reached if the two slopes on the anchor model are negative and positive, respectively, forming a ‘V’ shape (Fig. 1c), showing that greater deviance from mean mass necessitates larger compromises to remain cohesive. We also ran, post hoc, an LM on speed compromise against absolute divergence from mean mass, as this may be more intuitive given our

eventual findings (see Results). Linear mixed models (LMM) could not be run on these data, as the hypothesis requires that data are transformed to absolute values. This would require transforming some of the data, but not others, which violates the requirements of the mixed models. This is an interesting challenge for statistics, specifically using mixed models on absolute data.

We were also able to estimate the increased work rate from flying in a flock compared with flying solo. Using the intercept of our constructed power curves with theoretical flock speed $S_{\text{flock_theor}}$ for each individual, we then fitted a second-order polynomial of work rate as a function of mass to these data, to examine whether deviations in mass could have a superlinear impact on work rate in our flocks. Statistics, as well as all data manipulation processes, were conducted in R version 3.4.3 (R Core Team, 2017). All statistical test values reported are from two-tailed tests.

<H2>Ethical note

Experimental protocols were approved by Royal Holloway University of London Ethical Review Board.

<H1>Results

The observed relationship between individual body mass and preferred solo speed was positive and linear (Fig. 4a-d; model 1: per individual – airspeed – LM: $N = 15$, $t_{13} = 5.28$,

$R^2 = 0.68$, $P < 0.001$; model 2: per flight – ground speed with wind covariates – LMM: $N = 299$, $t = 3.25$, confidence interval, CI = [0.006, 0.024]), which is consistent with our predictions (Fig. 1b), and follows the same pattern predicted by our theoretical estimates (Heerenbrink et al., 2015; Fig. 2b; LM: $N = 15$, $t_{13} = 5.46$, $P < 0.001$). Support-wind and flight order were also significant predictors of flight speed (LMM: $N = 299$; support-wind: $t = 2.58$, CI = [0.023, 0.160]; flight order: $t = 3.00$, CI = [0.024, 0.117]). This was unlike morphometrics (Alerstam et al., 2007) and cross-winds which had no significant predictive power of the birds' flight speeds (tarsus length: LM: $N = 15$, $t_{13} = 1.61$, $P = 0.13$; wing area: LM: $N = 15$, $t_{13} = -0.05$, $P = 0.96$; cross-winds: LMM: $N = 299$, $t = -0.67$, CI = [-0.147, 0.072]).

Heavier individuals (ca. 500 g) slowed down by as much as 1.4 m/s compared to their preferred solo flight speed, from 15.5 m/s to 14.1 m/s. Similarly, lighter individuals (ca. 380 g) sped up to maintain group cohesion, with a maximum flight speed increase of 1.5 m/s from their preferred solo speed (see Fig. 3e for full range of flying speeds). The closer an individual pigeon was to the mean body mass of the group, the closer it flew to its usual preferred solo speed (Fig. 5a; LM: $N = 15$, $f_{2, 12} = 13.49$; $R^2 = 0.64$, $P < 0.001$). The slope of the model was negative for values below the mean mass ($t = -5.09$, $P < 0.001$) and positive for values above the mean mass ($t = 4.959$, $P < 0.001$), which creates the characteristic 'V' shape (Fig. 5a). This matches the prediction that intermediate individuals compromise on speed the least (Fig. 1c). Appendix Table A3 shows that under each change to the analysis methods, the 'V' shape persists. The overall relationship held when

considering just females (LM: $N = 8$, $F_{2,5} = 16.34$, $R^2 = 0.81$, $P < 0.01$) but was not statistically significant for just males (LM: $N = 7$, $F_{2,4} = 5.85$, $R^2 = 0.62$, $P = 0.06$).

Our estimates of theoretical work rate show a significant minimum work rate for birds weighing around 430 g (Fig. 4c; second-order polynomial regression: $N = 15$, $t_{12} = 6.93$, $P < 0.001$). Birds that are heavier or lighter than this minimum are thus likely to expend more energy per unit time at the group's observed speeds.

<H1>Discussion

To maintain group cohesion, heavier individuals slowed down, lighter individuals sped up and intermediate mass individuals flew closer to their usual and presumably optimal flight speeds (Alerstam et al., 2007; Hedenström & Alerstam, 1996). Speed compromise for birds in between these extremes could be predicted by a linear relationship (see Results). The 'Goldilocks principle' (named after Robert Southey's classic fairy tale in which the protagonist, Goldilocks, finds a group of bear characters' food and sleeping arrangements to be 'just right' at intermediate and not extreme ends of a spectrum; Zalasiewicz & Williams, 2012) has been used as an analogy in various fields of science to highlight the benefits of intermediate qualities (Kagan, 1990; Zalasiewicz & Williams, 2012). For example, in astrophysics, it is used to quantify habitable areas that are neither too far from nor too close to the sun to support life (Zalasiewicz & Williams, 2012) and in developmental psychology, rate of learning is thought to be maximized by educational

material that is neither too difficult nor too easy (Kagan, 1990). Here, we adopt the term for use in collective animal movement, where the consensus outcome is favourable for intermediate individuals across any continuum of phenotypic measurement, for example body mass, but, equally, potentially other behavioural (Sasaki et al., 2018), morphological (King et al., 2008) or physiological (Fischhoff et al., 2007) traits.

An averaging of speed preferences will minimize extreme speed compromises, and hence large increases in work rate associated with large speed adjustments (Fig. 1, 4c). This strategy may, therefore, reduce the likelihood of group fission (particularly by individuals with extreme values for preferred speed that might otherwise be unable or too fatigued to remain cohesive). Reduced group fission will result in larger group sizes, believed to help maximize selective benefits such as protection from predators (Conradt & Roper, 2003) and homing accuracy (Biro et al., 2006; Dell'Arciccia et al., 2008), although interestingly not the costs of locomotion in pigeons (Usherwood et al., 2011). Therefore, travelling at potentially compromised speeds with the group, rather than risking flying solo at a different, but energetically favourable speed, could maximize the benefits for each individual in the collective (Conradt & Roper, 2003, 2009).

While an averaging of speed may represent a parsimonious overall strategy for all group members, intermediate group flight speeds are intrinsically likely to best suit individuals of an intermediate body mass (Fig. 5a). Thus, although speed compromise increases linearly for larger/smaller individuals (Fig. 5b), the energetic cost of compromise may follow a superlinear pattern (Fig. 4c). The predicted difference in work rate in our flock

was just under 0.02 J/s for both the largest and smallest individuals in the group. Over the course of a long duration flight, particularly for species that migrate in groups, this could have significant impacts on the costs of flight, and the fitness of the individuals that pay this cost of compromise (Flack et al., 2018; Hedenström & Åkesson, 2017).

The models that predict U-shaped power curves, while the best supported (Heerenbrink et al., 2015; Pennycuick, 1968; Tobalske et al., 2003), are contested by some findings (e.g. Johansson et al., 2018; Torre-Bueno & Larochelle, 1978). These latter studies suggest, at least in some species, that for intermediate flight speeds, flight costs remain relatively stable (Johansson et al., 2018; Torre-Bueno & Larochelle, 1978). Nevertheless, most studies demonstrating flat power output only measure a speed range of ca. 5 m/s, and increases in energetic costs would still be likely for extreme speed changes (Engel et al., 2010). If the hypothesis that energetic costs are relatively flat at intermediate speeds is correct (and assuming all adult members of the same species fly within these bounds), this would still not rule out the potential usefulness of the present work in predicting the composition of mixed-species or mixed-age flocks. In the sea, fish are often found to be cohesive with others that are orders of magnitude larger (e.g. some species of shark and pilot fish travel together for mutual benefit; Magnuson & Gooding, 1971), and this is not found in birds, which could be due to differences in speed optima (which are largely governed by mass; Alerstam et al., 2007). Altogether, the most up-to-date evidence suggests (1) there is likely to be an energetic cost (albeit potentially small) to pigeons that compromise on speed to fly in a flock, and (2) that despite the contention between

competing flight cost hypotheses, our conceptual advance remains potentially powerful as a tool to help explain group composition.

There is strong evidence, given the number of solo flights ($N = 299$) in our multivariate model, that female pigeons were not slower than the males, despite having significantly lower body mass (sexual dimorphism). Both sexes were still estimated to compromise more at greater deviances from the mean mass of the group, although not significantly in the case of males. With only eight males and eight females in our study, this latter result would require further testing to come to any strong conclusions. Given no observable sex differences in solo speed, an argument for speed compromise as a mechanism to remain cohesive with the opposite sex seems unlikely at this stage.

The predicted increase in power output for birds of different body masses is only valid if the assumption that pigeons were flying at the speed of minimum power (V_{mp}) when flying solo is correct. Theoretical estimates of V_{mp} (Heerenbrink et al., 2015) range from 10.0 to 11.0 m/s (Fig. 2a), which are similar to estimates from multiple wind tunnel experiments (approximately 11 m/s; reviewed in Butler, 2016). However, two field studies that measured energetic proxies in free-flying pigeons showed a minima in a work rate proxy (flap frequency) close to 14.5 m/s (Usherwood et al., 2011) and 21.5 m/s (Taylor et al., 2017) respectively, which strongly suggests optimum speeds (e.g. V_{mp}) will be at higher values than those predicted by the models. Our observed airspeeds, which varied from 8.4 to 23.9 m/s (mean = 15.8; data from all solo flights), are more consistent with these latter field studies. While these findings make our assumptions broadly applicable, there is

insufficient evidence of whether the birds are flying at either V_{mp} or V_{mr} (maximum range speed). Further investigation into the aerodynamics of free-flying birds is necessary to elucidate the costs of flight in free-flying conditions, as well as any differences between a solo and group-flying context (but see Usherwood et al., 2011). Despite the paucity of current knowledge in a free-flying context, we have noteworthy evidence that intermediates have reduced energetic cost when flying in average-speed flocks. If pigeons were flying at their maximum range speed (V_{mr}), intermediates would still benefit from the Goldilocks principle, albeit in terms of optimizing their distance per unit energy, rather than energy per unit time (Hedenström & Ålerstam, 1996).

To further consider how group speed is governed and maintained, that is, whether the consensus is shared or unshared, it is worth noting that unshared consensus, dictated by intermediates, while potentially less intuitive than a shared consensus, cannot be ruled out in the present study. In migrating birds, faster group speeds were found in larger groups in three species of migrating birds (Eurasian oystercatcher, *Haematopus ostralegus*, red knots, *Calidris canutus*, and dunlin, *Calidris alpina*; Hedenström & Åkesson, 2017). This suggests that in these species, larger and/or heavier (and therefore possibly faster) individuals were setting the pace (Hedenström & Åkesson, 2017). Disproportionate influence has also been found in pigeons regarding flight direction consensus; here, faster homing pigeons were shown to have a greater impact on group navigational decisions, suggesting an unshared consensus system (Pettit et al., 2015). To determine whether each individual contributes to flock speed, or whether the decision is under majority control (Strandburg-Peshkin et al., 2015), future work should focus on manipulations of the

group's phenotypic composition, specifically modifying its mass/speed distribution. Moving forwards, teasing apart whether apparently 'shared' decisions reflect 'leadership' from intermediates will be a challenging but insightful avenue for further research across all modes of collective decision making (i.e. speed, direction and timing). Testing predictions from evolutionary collective decision-making models (e.g. Conradt & Roper, 2010) may aid future research on this topic.

Local 'interaction rules', which are commonplace in the collective behaviour literature, could account for average speeds. Here, animals are hypothesized to respond to neighbours according to their absolute or relative distance by (1) moving closer to them (at further distances), (2) moving away from them (at close distances) or (3) aligning with them (at intermediate distances; Couzin et al., 2002). Potentially, slower individuals will not fall out behind (unless they cannot physically keep up), as they will be attracted back towards the flock by these social forces, despite the increased energetic cost (Herbert-Read et al., 2011; Jolles et al., 2017; Katz et al., 2011). Likewise, for faster individuals, as their distance in front of the flock starts to increase, interaction rules may govern a deceleration response which keeps the individual close to the group (Jolles et al., 2017). Indeed, agent-based models, which replicate flocking behaviour by incorporating these rules, already implicitly assume a sharing of speed preferences: 'agents' average the movement vector (direction/speed) of their neighbours (Couzin et al., 2002; Jolles et al., 2017).

Using pairs of pigeons, Pettit et al. (2013) found interaction rules were mediated by turning responses, not acceleration/deceleration. This suggests a scenario whereby all individuals

could fly at their preferred speeds, with faster individuals taking more tortuous trajectories, and the group remaining cohesive regardless. However, if this were the case, heavier individuals should have faster speeds from flights in a group context too, which was not observed. The exact mechanism governing speed averaging, therefore, remains elusive. Nevertheless, given the success of simulations based on interaction rules to predict the qualitative (Couzin et al., 2002; Sumpter et al., 2012) and quantitative (Herbert-Read et al., 2011; Katz et al., 2011) aspects of other components of collective movement, more rigorous testing of this hypothesis would be beneficial.

Two questions emerge from our arguments. First, it is still unknown how the costs of speed compromise interacts with other costly aerodynamic interactions in group flight. We know from previous work that pigeons pay an extra energetic cost when flying in a flock above the cost of flying solo (Taylor et al., 2019). Unlike in V-formation flocks, where aerodynamic upwash from neighbouring birds can be utilized via effective positioning and flap phasing to save energy (Portugal et al., 2014), cluster-flocking birds like pigeons are thought to either experience more unpredictable air environments (Usherwood et al., 2011) or need greater control to avoid collisions and stay cohesive (Taylor et al., 2019; Usherwood et al., 2011). It seems likely that the effects of speed compromise and flying in a flock are additive, that is, compromising comes at a cost, as does flying in a flock, and these costs are summed. Nevertheless, there could also be an interaction, whereby some individuals can offset some of the cost through behavioural adjustments. Flying at the front of the flock, for example, has been shown to offset energetic costs (Usherwood et al., 2011). A second question that has arisen is: how does speed compromise play out on a moment-

to-moment basis? Our study looked at the average speed of individuals and groups, which gives us a broad understanding of the overall costs of speed consensus, although the phenomenon is dynamic. It is possible for individuals to have the same average speed but nevertheless split due to individual differences in intraflight speed distributions. Both these questions are logical starting points for future investigation into speed consensus.

The present study represents a foundation for the investigation of individual and group level mechanisms that influence the determinants and consequences of group speed, applicable not only to birds but also, more broadly, to comparisons of animal groups across taxa. Terrestrial animals, which are not in persistent motion when travelling, and for which locomotion is less costly (Schmidt-Nielsen, 1972), may make trade-offs in terms of minimizing overall time to reach a given destination rather than moment-by-moment optimization of energy expenditure. The problem of ‘how fast to travel’ is likely to generate conflicts of interest in any given animal group, owing to the intrinsic heterogeneity of group-living animals across multiple taxa (e.g. Johnston, 1990; McFarlane et al., 2016; Pruitt & Riechert, 2011). Questions such as (1) how different species solve this problem, (2) whether inter- or intraspecific differences in preferred speeds play a role in the composition or spatial distribution of groups and (3) at what levels of conflict compromise becomes unattainable (resulting in group fission) provide exciting novel avenues for further research.

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Appendix

Morphological Measurements

Body mass measurements (total = 12 per bird) were taken biweekly throughout the study (June–August 2017), using scales (CoffeeHit, Belvedere, U.K.: Coffee Gear Digital Bench Scale; 2 kg/0.1 g limit/accuracy). A mean of all body mass measurements was used for analysis. Mean body mass (g) was likely to be a reliable indicator of body mass overall, as mass was significantly repeatable ($r = 0.76$, 95% CI = [0.54, 0.85], $P < 0.001$). We used likelihood ratio tests with 10 000 parametric bootstraps to estimate 95% CIs for repeatability. The repeatability was even more pronounced when individual bird mass was compared with the mean mass of the group on a given weighing session (i.e. removing temporal fluctuations; $r = 0.863$, CI = [0.72, 0.92], $P < 0.001$). Altogether, this indicates a high consistency in body mass differences across a group. A measurement of the tarsometatarsus and all subsequent morphological measures were taken on 22 August 2017. We used a permanent marker to draw a dot at the intertarsal joint and the top of the metatarsal pad, then, using a flexible tape measure, we measured the length between the

two dots. Using A4 graph paper (0.5 cm squares) and a pencil, we drew the outline of the right wing of each bird. The squares were counted and converted into cm^2 which gave an approximation of the area of one wing (following Pennycuick, 1969). Additionally, to calculate the body area, the width of the bird's body was measured, and multiplied by the root chord (the width at the base of the measured wing). Twice the area of the right wing, plus the body area, gave an estimate for each bird's wing area (Pennycuick, 1989). Two separate measurements of the birds' wing lengths were taken. First, using a flexible tape measure, we measured from the glenoid fossa to the end of the furthest reaching primary feather. Additionally, we measured wing length from our outline sketch of each wing (above). A mean-average of the two measurements was used in analyses.

Additional Release Protocol Information

The birds were transported (usually in transit for less than 20 min) in a wicker pigeon racing box (80 x 40 cm and 22 cm deep). When the pigeons returned to the loft, the loggers were retrieved, and the data were inspected via Google Earth to check for any logger malfunctions.

No releases were conducted in rainy conditions, when cloud cover was over 50% or at wind speeds of over 7 m/s. Nevertheless, despite this latter criterion, some higher wind speeds were recorded (see Airspeed) if the wind increased after the start of the experiment (after leaving the home loft). Birds were released as early as 0600 hours and as late as 2 h before sunset (depending on the date). The maximum number of releases per day was three from 5 km sites and two from 9 km sites.

At the release site, the birds were released in the order they were randomly selected from the box. A minimum 7 min interval between solo releases was used to reduce the chance of birds pairing up. This period was extended if the previously released bird was still in sight. During group releases, the side hatch to the wicker box was opened, allowing all birds to fly out at once.

Ground Speed Calculation

The equation used to calculate instantaneous ground speed (S m/s) for each time stamp (t Hz) is as follows:

$$a = \sin\left(\frac{(x_2 - x_1) \times \frac{\pi}{180}}{2}\right)^2 + \cos(y_2) + \cos(y_1) + \sin\left(\frac{(y_2 - y_1) \times \frac{\pi}{180}}{2}\right)^2 \quad (1)$$

$$S_{t1} \left(\frac{\text{m}}{\text{s}}\right) = \text{Hz}(1/\text{s}) \times R(\text{m}) \times 2 \times \text{atan2}(\sqrt{a}, \sqrt{1-a}) \quad (2)$$

where x_2 is longitude at $t=1$, x_1 is longitude at $t=-1$, y_2 is latitude at $t=1$, y_1 is latitude at $t=-1$, R is the estimated radius of the earth, 63 710 000 m (Bullard, 1948), and Hz is the number of GPS fixes/s. We verified the equations by estimating the distance between one of the release sites in the study (N5) and the home loft (= 4.54 km) and comparing this with an estimate from Google Maps (= 4.44 km). The difference between these estimates was small (2.2%).

Wind Data

For the calculation of airspeed, wind data were recorded using an Aercus Instruments WS2083 Pro Wireless Weather Station (Greenfrog Scientific, Doncaster, U.K.). The device was positioned at the university building next to the home loft (longitude = -0.5726, latitude = 51.4154, height = 7.84 m from the ground) provided a reading of wind bearing (± 22.5 degrees) and wind speed (accuracy ± 0.1 m/s) every half an hour during the study. For each flight, the first reading of the individual's time stamp from the GPS (after the first 1000 m from the release site had been removed from the trajectory) was chosen as the time point to integrate with wind data.

Airspeed

Airspeed was calculated as follows. First, we calculated the difference between the wind direction (as described above) and the heading from the bird's track (Nagy et al., 2010). Then, by integrating wind speed, the cross- and support-winds could be estimated for each time step. Finally, combining estimates for the cross- and support-winds with ground speed (for ground speed see equations 1 and 2 above) at each time step provided an estimate of how much of the observed ground speed was due to wind, and how much was the flight of the bird (airspeed).

For each bird on each flight, a mean of airspeed (for airspeeds of over 4.5 m/s, the chosen parameter for identifying stationary birds) was recorded. Airspeeds of less than 4.5 m/s were considered stationary as this was the midpoint between a fast on-the-ground pace (1 m/s; Fujita, 2002) and the lowest horizontal flapping flight airspeeds recorded from two

wind tunnel experiments (8 m/s; Rothe et al., 1987; Pennycuick 1968; also see Butler 2016 for a synthesis of these earlier works and others).

Group Airspeed

Centroid ground speed was converted to airspeed, as in the previous section, but gave qualitatively similar estimates to a simple median of all individual's airspeeds from a group flight context (data are given in Fig. 3c). For groups 1 and 2, respectively, the medians of centroid airspeeds were 13.91 m/s (SD = 4.66, $N = 16$) and 17.56 m/s (SD = 3.35, $N = 16$) and the medians from all individual flights in a group context were 13.90 m/s (SD = 3.10, $N = 117$) and 17.74 m/s (SD = 1.92, $N = 150$; Fig. 3c). The similarity of these values is compatible with the finding that fission was rare (% fission per flight: median = 0%, mean = 7%; across all individuals/flights).

Data Drop Out

The first four releases were not recorded with GPS. Instead, dummy loggers were attached to habituate the birds to the increased mass load ($N = 64$ flights; 4 flights x 16 birds). This was due to an increased risk of losing birds in the first few releases. Other GPS data were lost due to logger failure ($N = 35$), and 10 flights were lost as two pigeons developed symptoms of canker (watery eyes and raspy breathing) and thus were quarantined and treated (five flights of data were missing per affected bird). Once symptoms were absent, and birds were flying circles around the home loft, they were reintroduced into the group and the study. For solo flights, data were removed from further analysis if individuals paired up and flew together despite the interval of time left between releases ($N = 85$; 13.8%

of all solo flights). The criterion for exclusion was that birds flew together (distance <50 m; Pettit et al., 2015) for more than 5% of the homing flight. Other files were lost if the battery ran out before the pigeon returned home ($N = 8$). The total flights ($N = 768$) minus the missing flights ($64 + 45 + 85 + 8$) left 566 flights in total: 299 solo and 267 group flights. The final number of flights per individual is documented in Appendix Table A1.

Some GPS data dropped out from individual time stamps, rather than a whole corrupt file. In these cases, rather than interpolate from data before and after the missing rows due to possible measurement error, we left such rows blank. Other data processing included trimming the data from the start and end of each trajectory at distances 1000 m from the release site and from the home loft. This process removes unwanted speeds from both climbing and descent at the start and end of the flight (following Taylor et al., 2017).

Release Site Distance

Release sites at two different distances (5 km and 9 km) were chosen to investigate any potential impact of site distance on flight speed, and to avoid over-familiarizing birds to one site (which can have an impact on airspeed; Taylor et al., 2017). There was a small decrease in airspeed with increasing distance (from a mean of 16.20 m/s from 5 km release sites to 15.7 m/s from 9 km sites), although this result was not statistically significant (t test: $N = 566$, $t_{559,61} = 1.69$, $P = 0.09$). As the flight release treatment was the same across both groups (Table 1), we included airspeeds from both release distances as equal in our results statistics.

Support-wind Deviations in Solo/Group Flights

Despite our efforts to control for potential temporal differences in wind speed and direction (Table 1) there was a statistically significant deviation in the support-wind component (for calculation and methods see Airspeed in main text) between solo and group flights (solo $N = 267$, group $N = 384$, $t_{443.43} = 3.38$, $P < 0.001$; Fig. A2a), with groups, on average, experiencing a faster support-wind (median = 0.23 m/s) than solo individuals (median = -0.29 m/s; negative support-winds are head-winds). As airspeed and support-winds were strongly negatively correlated (LM: $N = 566$, $t_{531} = -17.42$, $P < 0.001$; Fig. A2b), we took the median value of support-wind for each condition (i.e. group or solo) and used the LM to interpret what the extent of this deviation in support-wind would be, in terms of m/s (0.344 m/s; Fig. A2b). We added this value to all solo flight speeds and reperformed the main analysis. As the effect size of the deviation in support-wind component was small, the resulting reanalysis of speed compromise and mass deviation (from Fig. 2d) was similar (Table A2). Therefore, we have not included this speed modification in our final regression.

Centroid and Fission Analysis

Fission

To identify fission events, the centroid of the group was identified through a multistep process. First, the mean of each individual's longitude and latitude was taken as a preliminary centroid, then if any individuals were outside a radius of 50 m to the centroid, the furthest individual was removed for that time step. The centroid was then recalculated and the process repeated. The reason one individual needed to be removed at a time was because in the case of fission the centroid of the initial 'group' could lie outside the group

itself. For example, if one individual in a group of five split from the group and was 1 km away at a given time step, the identified ‘centroid’ would be placed 200 m away from the actual group. Subsequently, all individuals would meet the threshold for having undergone fission. Therefore, it is important, if using this method, to remove one individual (the furthest individual) at a time and recalculate the centroid, in a jack-knife fashion (Portugal et al., 2014). Fission was comparatively rare (median percentage of time split from the group per flight was 0% and the mean was 7% across all individuals). An ANOVA of fission data revealed no consistent interindividual differences in fission propensity (group 1: $N = 118$, $F_{115} = 2.08$, $P = 0.15$; group 2: $N = 145$, $F_{142} = 0.39$, $P = 0.53$).

Intergroup Differences in Airspeed

For our statistics, we needed to account for the intergroup difference in airspeeds (t test: $t_{507.39} = 10.53$, $P < 0.001$). We reason this may have been due to a prevailing easterly wind direction (circular mean = 1.02 rad; observed from our weather station) in Surrey and west London (also documented in Lee, 1977), the extent of which might not have been fully captured by our weather station (and hence airspeed). Group 2, flying against the prevailing wind direction (group 2 sites: E5 = 0.79 rad and E9 = 0.87 rad), had lower overall airspeeds than group 1 (group 1 sites: N5 = -0.14 rad and N9 = -0.07 rad) when comparing all observed flights (Fig. 3e; t test: group 1: $N = 276$; group 2: $N = 257$; $t_{507.39} = 10.53$, $P < 0.001$).

Additional Models

Our per-individual model of how divergence from mean mass of the group affects the compromise our birds made to fly in a flock was treated in three ways: using all individuals, using just lighter individuals (LM: $N = 9$, $t_7 = 4.10$, $R^2 = 0.66$, $P < 0.01$) and using just heavier individuals (LM: $N = 6$, $t_4 = 6.75$, $R^2 = 0.90$, $P < 0.01$) as confirmatory analyses.

We treated the other morphological covariates (tarsometatarsus, length and wing span) in the same fashion and found no interaction with group number (ANCOVA: tarsometatarsus length: $F_1 = 0.84$, $P = 0.38$; wing span: $F_1 = 0.46$, $P = 0.51$). Thus, intergroup comparison was also possible with these morphological covariates.

Table 1. Release order and number of flights from each of the homing pigeon release sites

Site	Condition	No. of flights	Dates
N5/E5	Solo	12	1 Jun 2017 – 30 Jun 2017
N5/E5	Group	6	1 Jul 2017 – 7 Jul 2017
N9/E9	Solo	12	7 Jul 2017 – 17 Jul 2017
N9/E9	Group	6	17 Jul 2017 – 25 Jul 2017
N5/E5	Solo	3	11 Aug 2017 – 13 Aug 2017
N5/E5	Group	3	14 Aug 2017 – 17 Aug 2017
N9/E9	Solo	3	18 Aug 2017 – 20 Aug 2017
N9/E9	Group	3	23 Aug 2017 – 25 Aug 2017

Group 1 were consistently released from a northerly bearing (sites N5 and N9) and group 2 were released from easterly sites (E5 and E9). The numerical value in the site names represents approximate distance; actual distances were N5 = 4.54 km, N9 = 8.90 km, E5 = 5 and E9 = 9.10 km. The alphabetic character of site names represents bearing; actual site bearings were N5 = -0.14 rad, N9 = -0.07 rad, E5 = 0.79 rad and E9 = 0.87 rad. Condition, solo or group, refers to whether the birds were released alone or in their respective groups. Dates are provided for each phase of the study.

Table A1. Total usable flights for solo and group flights per individual

Pigeon	Group number	No. of usable solo flights	No. of usable group flights
32	1	23	18
39	1	22	15
55	1	24	14
56	1	22	17
58	1	21	18
59	1	23	17
81	1	24	18
46	2	21	17
47	2	13	17
53	2	16	18
67	2	17	11
69	2	18	17
74	2	23	18
76	2	7	18
78	2	10	16
95	2	15	18

Total number of flights was 30 solo and 18 group, although data are missing for any of the following reasons: (1) first flights not recorded with biologgers, (2) logger failure, (3) temporary illness, (4) paired flight or (5) flight took longer than battery length.

Table A2. Statistics: different outcomes for each model under a range of changes to the analytical methods

Model	Standard methods			Individual speeds			Remove individuals using Cook's distance			Remove first six flights			Add solo-group differences in wind support			Median instead of mean		
	R^2	t or (F)	P [or CI]	R^2	t or (F)	P [or CI]	R^2	t or (F)	P [or CI]	R^2	t or (F)	P [or CI]	R^2	t or (F)	P [or CI]	R^2	t or (F)	P [or CI]
Slope	0.147	(0.269)		0.147	(0.269)		0.147	(0.498)	0.494	0.139	(0.065)	0.803	0.147	(0.269)	0.614	0.117	(0.25)	0.627
Intercept	0.147	(287.42)	<0.001	0.147	(287.42)	<0.001	0.147	(178.365)	<0.001	0.139	(491.5)	<0.001	0.147	(287.42)	<0.001	0.117	(740.812)	<0.001
LM 1	0.682	5.284	<0.001	0.64	4.81	<0.001	0.585	4.446	0.001	0.744	6.15	<0.001	0.694	5.433	<0.001	0.605	4.459	0.001
LM 2	0.674	5.179	<0.001	0.569	4.142	0.001	0.313	2.525	0.024	0.466	3.371	0.005	0.357	2.684	0.019	0.303	2.376	0.034
Polynomial	0.827	7.409	<0.001	0.827	7.409	<0.001	0.363	2.38	0.033	0.827	7.409	<0.001	0.827	7.409	<0.001	0.827	7.409	<0.001
LMM	0.744	4.274	[0.008 0.023]	0.744	4.274	[0.008 0.023]	0.745	4.568	[0.009 0.023]	0.744	4.274	[0.008 0.023]	0.744	4.274	[0.008 0.023]	0.744	4.274	[0.008 0.023]
Anchor	0.692	(13.489)	0.001	0.748	(17.801)	<0.001	0.313	(2.961)	0.087	0.457	(5.052)	0.026	0.646	(10.97)	0.002	0.555	(7.487)	0.008
LM	0.061	-0.921	0.374	0.189	-1.739	0.106	0.001	0.134	0.895	0.018	0.495	0.629	0.287	-2.287	0.04	0.217	-1.897	0.08

R^2 , t values (or F values if in parentheses) and P values [or confidence intervals, CI, if in brackets] are given for each model, and for each iteration of the main methodology as follows (from left to right). ‘Standard methods’ is the base methodology, as justified in the Methods. ‘Individual speeds’, gives group speed as calculated from each individual trajectory instead of from the centroid speed. ‘Remove individuals using Cook’s distance’ refers to removing those that exceeded the chosen parameter: $3 \times$ mean Cook’s distance. Note that this is one of the only two methodological changes that changed the significance of any model (here the Anchor model), where the P value rises to 0.082. ‘Remove first six flights’ takes data from only after the sixth flight from each site (to help control for

familiarity). ‘Add solo–group differences in wind support’ accounts for the observed variation in wind condition between release conditions. This was not used in the standard methods because using airspeed, as opposed to ground speed, already accounts for much of this variation. Additionally, airspeed uses wind parameters in the calculation. This pseudoreplication is why a change in one summary statistic (for the linear model), is not interpreted further. Finally, ‘median instead of mean’ uses median values of speed per flight trajectory rather than mean values. Statistics are provided for the following models: (1) slope of ANOVA (Slope); (2) intercept of ANOVA (Intercept); (3) linear model: speed vs mass (LM 1); (4) linear model: speed compromise vs mass residual (LM 2); (5) second-order polynomial: work rate vs mass (Polynomial); (6) linear mixed models: speed vs mass (LMM); (7) linear model between speed compromise and mass residual (Anchor, where an anchor was specified at $x = 0$ (mean mass)); (8) linear model between speed compromise and mass residual (LM; see Fig 5a, b). For all models see Methods for details. *P* values and CIs that are significant to 95% confidence are given in bold.

Table A3. Anchor model output

		Estimate	SE	<i>t</i>	<i>P</i>
Standard methods	Intercept	1.03	0.85	2.64	0.02
	x.minus	-0.08	0.03	-5.09	<0.01
	x.plus	0.16	0.05	4.96	<0.01
Individual speeds	Intercept	0.92	0.80	1.15	0.27
	x.minus	-0.10	0.03	-3.25	0.01
	x.plus	0.17	0.05	3.47	<0.01
Remove individuals using Cook's distance	Intercept	1.43	1.35	1.06	0.31
	x.minus	-0.06	0.05	-1.29	0.22
	x.plus	0.17	0.08	2.06	0.06
Remove first six flights	Intercept	1.44	0.54	1.22	0.25
	x.minus	-0.10	0.02	-2.42	0.03
	x.plus	0.17	0.03	3.11	0.01
Add solo-group differences in wind support	Intercept	0.52	0.71	0.73	0.48
	x.minus	-0.14	0.03	-5.25	<0.01
	x.plus	0.20	0.04	4.54	<0.01
Median instead of mean	Intercept	1.57	0.80	1.97	0.07
	x.minus	-0.11	0.03	-3.81	<0.01
	x.plus	0.15	0.05	3.02	0.01

Linear model output from each change to the analysis methods (see Fig. 5a) All slopes for mass values below the mean are negative; all slopes for values above the mean are positive, indicating that each model shows a characteristic 'V' shape as seen in Fig. 1 (main text). All significant *P* values are highlighted in bold; the only *P* values that did not reach significance were for when the individual was not removed due to the extreme Cook's distance (see Fig. A5a, b).

Figure legends

Figure 1. Concept and hypotheses. (a) Larger, heavier birds (yellow, through green to purple indicates birds with larger mass and/or structural size; colour scale from Garnier, 2017) are known to have energetic optima at faster speeds than relatively smaller or lighter birds (grey segmented lines from right to left of the x axis: speed; Tobalske et al., 2003). Birds could split (fission; at the top), and fly solo at energetically optimal (low on energetic costs scale) but opposing speeds. Alternatively, the birds could come to a consensus on travelling speed (consensus; at the bottom), and benefit from decreased risk of predation and enhanced navigational efficiency associated with grouping (Krause & Ruxton, 2002). Within a consensus context, we provide scenarios where the group travels at the preferred speed of the small, the medium and the large bird (from left to right). Energetic cost increases as the deviation from an individual's optimum speed increases, whether flying faster or slower (Hedenström, 2009; Tobalske et al., 2003). Therefore, both large and small individuals would probably pay a large cost to fly at one another's preferred speed (coloured deep red for energetic costs). Flying at the preferred speed of medium birds, which is also the result of an averaging of preferences, reduces overall compromise (there are no birds high/red on the energetic costs scale at this intermediate speed). If adopted group-wide, this strategy could reduce the probability of group fission, and hence reduce ultimate costs for each flock member. (b, c) Predictions of our study. Hypothesis lines are coloured **to correspond with mass (as in (a); Garnier, 2017)**. (b) First, we predicted a positive influence of body mass (x-axis) on speed (y-axis) regardless of the group travelling speed (the first hypothesis; see main text). (c) Second, if the birds do not split, and compromise on speed (the second set of hypotheses), they may fly at the preferred speed of the heaviest or lightest or average-sized individuals. These hypotheses are represented as regression lines: either straight and increasing/decreasing (where light and heavy individuals have the lowest speed compromise, respectively), or with an anchor point at zero (where

average-mass individuals compromise least). This latter scenario indicates that any divergence from mean mass (either higher or lower) will have a positive impact on speed compromise. Predicted relationships are shown here as lines for simplicity; however, note that linearity is not specifically expected on a theoretical basis

Figure 2. Theoretical predictions and observed speeds. (a) Theoretical relative power output (J/m) for each bird based on morphological metrics (R library ‘afpt’; Heerenbrink et al., 2015) over a range of flight speeds (m/s). Each individual is represented by a curve (coloured according to increasing mass; colour scale from Garnier, 2017). All curves are transposed on the y-axis about the minimum power speed V_{mp} (minima of each curve) so that relative power output, the extra cost of flying at different, nonoptimal speeds, is transposed to equal zero at this point. The mean of minimum power speeds (solid vertical line) is given, as is the theoretical flock speed $S_{flock_theor.}$. This theoretical flock speed was estimated using the difference (in standard deviations) from observed flock speed to the mean of the observed solo speeds (see Methods for further details). (b) Each individual’s predicted speed, the speed of minimum power (see Discussion), relative to $S_{flock_theor.}$ is plotted against the bird’s mass (g).

Figure 3. Speed data. Centroid airspeeds (relative to the mean value of speed per flight; m/s) are represented as (a-b) frequency histograms and (c-d) speed traces for each group flight (up to a maximum of 600 s flight duration) for (a, c) group 1 and (b, d) group 2. (e) Individual airspeeds in solo (orange) and group (purple) contexts, given as box plots for observed airspeed for pigeons A–P in both solo and group contexts. Pigeons A–G were in group 1 and pigeons H–P were in group 2. Birds are ordered first by group and second by increasing mass. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and circles are given for all raw data. (f)

63 Combined frequency histogram of group airspeed (from centroid) from (a) and (b). (g)

64 Combined frequency histogram for solo airspeeds, following methods used to generate (f).

65
66 Figure 4. The ‘Goldilocks’ principle in pigeon flocks. Individuals are identified by mass using
67 the colour scale from Garnier (2017; see key in (d)). Bird images in (b) are both coloured and
68 scaled according to mass (using bird mass (g) minus 350, divided by 150; numerical values
69 350 and 150 are arbitrary, and chosen to best fit the plot). (a) Theoretical predictions (solid
70 lines; R package ‘afpt’; Heerenbrink et al., 2015) showing predicted relative work rate (Δ J/s)
71 across a range of flight speeds (%) in the heaviest (purple; $N = 23$ flights), the lightest (yellow;
72 $N = 22$ flights) and the closest-to-the-mean body mass (purple/yellow blend; $N = 21$ flights)
73 individuals. Observed solo speeds relative to observed flock speed (%) are given as dashed
74 lines (data as in (c)). (b) Median observed speed in solo flights (for N flights per individual, see
75 Table A1), expressed as relative (%) to the average observed speed of the flock ($S_{\text{flock_obs.}}$;
76 segmented black line, $N = 36$ group flights) for each individual bird used in the analysis. (c)
77 Theoretical relative power output at S_{flock} (Δ J/s) against body mass (g) for each pigeon ($N =$
78 15). This is the intersection of curves and the theoretical flock speed $S_{\text{flock_theor.}}$ from (a)). The
79 solid black line is a fitted polynomial regression line. The segmented black line is the mean
80 mass of the birds. (d) Speed compromise (absolute value of solo speed, relative to group speed
81 %) versus the divergence from mean mass (absolute difference of an individual’s mass from
82 the mean mass of its respective group, g) for each individual ($N = 15$). The solid black line is
83 a fitted linear model.

84
85 Figure 5. Matching predictions to data. (a) Absolute speed compromise (%) against body
86 mass (g), relative to the mean mass of the birds’ respective groups (grey points). Following
87 the rejection of the hypotheses that either heavier or lighter individuals were compromising

least (linear model: $N = 15$, $F_{2, 12} = -0.92$, $R^2 = 0.06$, $P = 0.37$), a linear model with two slopes and one intercept (see Fig. 1c and the Methods) was fitted to the data ($N = 15$, $F_{2, 12} = 13.49$; $R^2 = 0.64$, $P < 0.001$), and is provided here (solid line). (b) Solo speed, given as (%) relative to observed group speed against mass (relative to mean mass). A linear model is fitted to the data with 95% confidence intervals, CI, using ggplot2 (Kahle & Wickham, 2013). The actual statistical test was a linear mixed model ($N = 299$, $t = 3.25$, $CI = [0.006, 0.024]$). To keep consistency with our predictions (Fig. 1b), we have not included individual data points here. Instead, this variation can be found in Fig. 3e.

Figure A1. Satellite image depicting the four release sites (N5, N9, E5 and E9) made with GoogleMaps. Flight bearing is indicated by the letter (N = north; E = east) and the number indicates approximate distance from the home loft (i.e. 5 or 9 km; for accurate distances and more information see the main text). Red lines are the trajectories of four solo flights from respective locations (examples selected for directness and clarity). Different release bearings were chosen for each group (group 1: north; group 2: east) to reduce any confounding impact of terrain; different distances were chosen to investigate possible impact of distance on flight speed.

Figure A2. (a) Box plots showing the differences in support-wind (m/s; recorded via a weather station: Aercus Instruments WS2083 Pro, Greenfrog Scientific, Doncaster, U.K.), at the home loft (longitude = -0.5726, latitude = 51.4154; height = 7.84 m from the ground) across group and solo flights. Group flights had faster associated support-winds, despite attempts to control for seasonal and temporal differences in weather. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the

interquartile range and the circles are outliers. (b) Airspeed (m/s) against support-wind. The linear relationship between the variables (black line) allowed us to interpret the difference (red/blue horizontal lines) that faster support-winds (for group flights) might have had using median values of group flight (red vertical line) and solo flight (blue vertical line) support-wind. This interpreted difference was 0.344 m/s which was added to all solo flight speeds and the main analysis was reconducted, without finding any difference in the main statistics and thus conclusions.

Figure A3. Speed (m/s) for each bird (points) against body mass (g) relative to the mean mass (vertical segmented line) of the group. Linear models are fitted using ggplot2 (Wickham & Wickham, 2007). Data points and models are colour coded by group (see key). Upper and lower horizontal segmented lines represent average flock speed for group 1 and group 2, respectively.

Figure A4. Normal quantile–quantile plot for the linear mixed model. A close match of our residuals to the quantile–quantile line (qq line) reveals that the variation in speed (dependent variable) is normally distributed around the fitted model line ($N = 299$ speed recordings). There is perhaps evidence of a slight heavy tail (points above qq line in the top right), which would suggest some (roughly 6–10 flights) recordings of speed were relatively high. However, this is a minority of data points (ca. $< 2.5\%$ of total flights)

Figure A5. Effect of not removing an individual with an extreme Cook's distance. (a) Output statistics show the linear model for speed compromise (%) over body mass relative to mean mass (red line) was not significantly different from a null distribution. This was probably due to the extreme solo speed found for the third heaviest bird, as this individual had an extreme Cook's D (1.11), which is over the generally accepted thresholds of (1) $3 \times$ mean of Cook's $D = 0.38$ and (2) a value greater than 1.00 (Kim & Storer, 1996). (b) This causes the qq-plot to

138 skew and have an arced shape, with few values below the qq-normal line (dotted line). This
139 means that the assumption of normally distributed residuals (an explicit assumption of linear
140 models) has been violated, and therefore is not an accurate representation of the data.

141