Linking mechanism to function

in flocking birds

Thesis submitted for the degree of Doctor of Philosophy (PhD)

Royal Holloway University of London

September 18th 2019

Daniel W. E. Sankey

Author declaration

I declare that the following work is my own with the following exceptions. In Chapter 2, the majority of pigeon personality and dominance data were collected by Rhianna Ricketts, Joshua Brown, Joseph Deegan and Bryce Tidswell.

Acknowledgements

This thesis reflects not only my personal work but the indispensable contributions of others. I am thus highly indebted to several people, whom without I would not be in a position whereby I am finishing and submitting a thesis.

No one deserves more credit for this work and more of my appreciation than Steve Portugal. His attentive supervision and kind supportive nature have helped me develop both professionally and personally throughout the duration of my PhD. He is a fantastic mentor, and a highly intelligent and insightful researcher, whom I have taken pleasure in debating with. I trust that we will continue to work together to produce great science in the future, and I hope that I can repay him for his unbending dedication to my development.

I would also like to thank my co-supervisors Emily Shepard and Dora Biro for our useful meetings, and their critical assessments of my work and methods. Their expertise were crucial in the design of my early experiments, and the effective communication of Chapter 3.

I am greatly endebted to the late professor Percy Butler, who left money to the department of Biological Sciences at Royal Holloway, which directly funded my project. Unfortunately I did not get the chance to meet Percy, but I heard funny and inspiring anecdotes of Percy's life and personality stories from Dr. Graham Twigg – whom himself I thank for having facilitated the process of transferring Percy's funds to the department.

The following people provided useful intellectual discussion or career advice, and I would thus like to extend my thanks to Elli Leadbeater, Francesco Santi, Camilla Blasi-Foglietti, Harry Siviter, Sam Jones, Mark Brown, Lucy Taylor, Andrea Perna, Craig White, Chris Greenyer, Danai Papageorgiou Claudio Carere, Cecylia Watrobska, Rolf Storms, Robert Musters, Lena Grinsted, Vivek Sridhar, Damien Farine, Marie Attard, Matthew Hassenjager, Iain Couzin, Maté Nagy, Jade Hall, Alexzander Kochelnik, Christos Ioannou, Jake Chandler, Lucy Garrett, Vincent

Jansen, Stephen Lang, Gaelle Fehlmann, Anders Hedenström, Susanne Åkesson, Ariana Strandburg-Peshkin, Cini Gall, Simon Garnier, Lisa O'Bryan, Hannah Williams, Renaud Bastien, Jolle Jolles and Adrianna Muldonarro-Chapparo. I would also like to acknowledge and thank Cini Gall, Linda Garisson, Steven Lang and Francesco Santi for proof reading, helping me to improve and clarify parts of my work.

I would also like to thank members of our departmental Ecology, Evolution and Behaviour group (EEB) for attending my presentations and debating my work in departmental meetings; my close friends Camilla Blasi-Foglietti, Francesco Santi, Harry Siviter and Shannah Gates (in no particular order) for moral support; and members of the Portugal group: Stephanie McClelland, Sam Jones, Marie Attard, Jenny Cantlay, Jack Thirkell, Cecylia Watrobska, Molly Cordall, for excellent discussions about scientific papers, careers, and their helpful feedback on my ideas.

I also appreciate the amount of technical support I have received during my PhD. I would like to thank Elaine Turton, Tracey Jefferies, Rob Prouse, Linda Samways, Michelle Jux, Nicola Moss and Melanie Kiukkanen for help with pigeon logistics; Lara Nouri for her attentive pigeon husbandry and motivational conversation in my second field season; Shaun Gibson for his highly practical pigeon hatches; Robin Freeman for advice on GPS waterproofing methods; Lucy Bryce for her assistance attaining permissions at Chobham Common for my experiments in Chapter 6; Robert Musters for the building and skilful piloting of the robotic falcon used in Chapter 6; Rolf Storms for helping with the technical, methodological and conceptual aspects of Chapter 6; Maté Nagy, Lucy Taylor, Steve Portugal and Sarah Papworth for computer code; Tina Steinbrecher for helpfully speaking native German for me over the phone; and Tayla Sanders, Jack Thirkell, Marina Papadopoulou, Liz Greenyer and Drew Snow for help carrying pigeon baskets. I would also like to thank Rhianna Ricketts, Joshua Brown, Joseph Deegan and Bryce Tidswell for help collecting personality and dominance data used in Chapter 2.

Finally I would like to thank my family for their support, and my partner Liz Greenyer for inspiring me to follow my curiosity towards animal science, no matter where it took me. Her selfless support and inspirational ideas have got me through this project.

Abstract

A group of birds in coordinated flight is – perhaps owing to its success – a commonly observed phenomenon. This ubiquity suggests that bird species which fly together can achieve substantial evolutionary benefit. The proposed benefits of group flight include enhanced predator avoidance, the use of social information or even aerodynamic advantages. However, we still have little understanding of how these benefits will differ across ecological context or taxa. In this thesis, I argue that a good answer to this question can be found by considering how four response mechanisms interact to govern the selective benefits. The importance of birds' responses to 1) risk, 2) environmental/navigational information, 3) the aerodynamic environment, and 4) the social environment are mapped out conceptually in the Introduction. I then provide five Chapters of question-led empirical research in collective-flight model species homing pigeons (*Columba livia*), to manipulate and explicitly test all of the above factors. This empirical work included, in each data Chapter, the use of miniaturised, animal attached biologgers, such as GPS, to determine how the birds respond to these manipulations. The observed response mechanisms are discussed in light of evolutionary theory (in particular a behavioural ecological perspective) and thus are linked to the function for which the mechanism involved.

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Chapter 1: General Introduction

Flocking in birds: mechanism and function

For most people, seeing birds fly overhead in highly coordinated flocks is a common occurrence. The pattern and shape of flock formations may dazzle and engage onlookers visually and spectators may also ask deeper questions as to "how?" and "why?" such phenomena occur. These more curious observers would be in good company, as scientists and philosophers have asked these questions since the beginnings of natural history writing (Bostock and Riley 1900; Bajec and Heppner 2009). For example how do birds such as pigeons (*Columba livia*) perform apparently simultaneous manoeuvres (Bajec and Heppner 2009), and why do geese form stereotypic V-formation flock structures (Bostock and Riley 1900)? Early hypotheses – such as a rather peculiar suggestion of "telepathy" to explain synchronicity (Selous 1931) – have since been discounted in favour of newer alternatives (Reynolds 1987), and these will be discussed. Nevertheless, it is not the aim of this thesis the answer to such questions in isolation, but instead investigate the link between mechanisms "how?" and function "why?" in the evolution of collective flight.

My approach to this investigation is grounded in behavioural ecology (Davies et al. 2012): a modernised Darwinian logic, applied to the evolution of behaviour. Here,

successful behavioural mechanisms (the “how?”) are those which arrive at the best solution to pressures imposed by their evolutionary environment (the “why?”) (Tinbergen 1963; Davies et al. 2012). These successful behaviours need not be perfect optimisations; relative benefit alone will favour the survival and enhancement of successful behavioural mechanisms through evolutionary time (Dawkins and Krebs 1979). Behaviours which increase survival and/or reproduction of animals are thought to be passed forward, from generation to generation, through innate genetic programming (Lorenz 2003), social-cultural transfer (Aplin et al. 2015), or a combination of the two (Feldman and Laland 1996).

Perhaps unsurprisingly, the proposed benefits of flocking are as wide ranging as the evolutionary (or, selective) pressures imposed on bird groups. An understanding of these pressures provides a useful tool to understand the form and function of flocks. To use the classic example of V-formation flocks (found in larger bird species; Bajec and Heppner 2009) first, when a long and demanding migratory trip is demanded by the survival and/or reproductive needs of birds, it is their energetic reserves and often time which are the limited resource. V-formation flock dynamics can help save energy in through positive inter-individual aerodynamic interactions, and thus is likely to have evolved in response to energetic requirements (Portugal et al. 2014). Second, we know that predators can impose a great ecological challenge to the survival – and hence reproduction – of birds. Thus, behavioural mechanisms such as the highly aligned “cluster swarms” of starlings (*Sturnus vulgaris*) may function to confuse visual predators (Carere et al. 2009; Procaccini et al. 2011). Finally, when resources are limited, birds may rely on the knowledgeable individuals, or a “wisdom of the crowd” whereby multiple uninformed individuals

converge on an effective solution (Simons 2004; Dell'Ariccia et al. 2008). Flocks which predominantly face such a *knowledge deficit* may form less densely packed "cluster travelling flocks", to share information on the move.

Nevertheless, ecological pressures are not fixed throughout the duration of an animal's life history. Take a hypothetical example of a flock of birds which are *i)* naïve to the distribution of resources in their environment, *ii*) have limited energetic resources, and then once decided upon a response to the first two pressures, *iii*) encounter a predator on the way. How such a (potentially unlucky) group of birds respond flexibly to these proximate pressures in their environment (*Section 1*) is not well understood. I will argue that a good answer to this question can be found by considering how four response mechanisms – and how they interact with ecological or species-specific differences – govern the benefits of group flight (*Section 2*). I will briefly discuss responses to 1) the aerodynamic environment, 2) risk, 3) environmental/navigational information, stressing the importance of their links to 4) the social environment. I will then consider the social environment separately. Throughout, I will make reference to how these mechanisms could influence an individual's fitness both directly (*Section 2*), and by forming the group-level structure, or "flocking type" which can exhibit functional capacity beyond that achievable at the individual-level (Sumpter 2006, 2010). As above we define three broad categories of "flocking type", namely V-formations (Weimerskirch et al. 2001; Portugal et al. 2014), cluster travelling flocks (Jolles et al. 2013; Ling et al. 2019) and cluster swarms (Ballerini et al. 2008; Storms et al. 2019) (*Section 3*).

In order to study the benefits of group flight across context, I propose to measure the responses of individuals and groups to manipulations of the *i*) social/aerodynamic environment, *ii*) risk environment and *iii)* navigational familiarity. I will use animal attached biologging technology to measure spatial position (using GPS) and energy expenditure (using accelerometers) (*Section 4*), which can be used to inform how evolution has shaped behavioural phenotype and flexibility. Fundamental to the study of natural selection is the need to understand individual phenotypic variation and flexibility, as variation is the raw-material necessary for selection to act upon (Dall et al. 2012). Thus I will measure phenotype in behaviour (e.g. dominance, "personality", navigational route efficiency, flight speed, and group leadership) and morphology (e.g. body mass, structural morphometrics) at the individual level.

The study of consistent inter-individual phenotypic differences will be introduced in *Section 5*, and its relationship to leadership and group movement more broadly discussed. Following this, in *Section 6*, I will discuss how a combination of *individual phenotypes* generate *group phenotypic compositions*, and how this collective phenotype can impact the fitness of individuals. Insights which arise from this are that an "optimal group phenotypic composition" may be dependent on the environmental context, giving rise to "context dependent optimal compositions" (or CDOCs). This is introduced in *Section 7*, where I discuss potential implications for CDOCs in a changing ecology and artificial (i.e. captive) contexts. There are few data or empirical studies within a group composition framework on which to draw from. Nevertheless, the potential applications of beneficial group compositions to conservation or captive management strategies are briefly discussed.

Finally, in *Section 8*, the model species for the PhD, domestic pigeons (*Columba livia domestica*, Gmelin 1789) will be introduced and their suitability of linking mechanism to the functions of flocking, via experimental manipulations, will be discussed. Specifically, I will describe the ecology of their closest wild cousins, rock doves (*Columba livia*), and typical housing and husbandry conditions of pigeons kept for the purpose of homing. Their flight characteristics and morphological features are discussed, the ethical implications of attaching biologging devices for flight experiments, as well as their suitability as a model system to test the link between mechanism and function in birds flocks (*Section 9*).

1. Living in groups

Behavioural strategies to remain spatially cohesive with congeners are thought to have evolved when selective benefits to grouping outweigh any costs (Krause and Ruxton 2002; Sueur et al. 2011). There is an extensive literature of the benefits of group living, many of which are relevant in a stationary context – or movement within a relatively small and stable space – and are not explicitly related to moving groups. These benefits, such as thermoregulation (e.g. emperor penguins, *Aptenodytes forsteri*, huddle to conserve heat energy (Ancel et al. 1997)) and communal defence (e.g. black headed gulls, *Larus ridibundus*, mob predators (Kruuk 1964)) are dependent on groups remaining spatially cohesive. This suggests an additional importance to remaining cohesive on the move, because if the group split when travelling, they may reduce these stationary benefits at the arrival site.

However, for the purposes of understanding the benefits of flocking – and how mechanism governs the emergence of form and function in bird flocks – these additional benefits, which cannot be measured in flight will receive little further attention. Additionally, the benefits of grouping on communal hunting (increased prey capture), although present in moving groups (Stander 1992; Lang and Farine 2017) including birds (Götmark et al. 1986) will not be considered, because of the limited relevance of testing these functions with a flock of prey animals (i.e. pigeons Kenward 1978; Henderson et al. 2004). The benefits which can be achieved by groups in motion generally fall under three broad categories, 1) decreased predation, 2) information sharing and 3) energy conservation. Each of which will be discussed in greater detail below.

1.1. Decreased predation

The reduction of predation risk for individuals in groups has been widely researched (Hamilton 1971; Kenward 1978; Treherne and Foster 1980; Foster and Treherne 1981). Firstly individuals may benefit from a simple "dilution" effect (Hamilton 1971). Here, it is reasoned that for each predator attack, an individual's predation risk will decrease linearly with group size, simply, one divided by group size. This was demonstrated in a study of fish predator (*Sardinops sagax*) attacks on ocean skaters (*Halobates robustus*), the observed number of attacks per individual decreased at a similar rate to that expected (Foster and Treherne 1981). Another anti-predator benefit associated with increased group size is increased collective

vigilance which may impart earlier detection of predators (Bertram 1980; Treherne and Foster 1980; Portugal and Guillemain 2011), presumably because the chances of at least one individual detecting the predator increases when more individuals are present. This was illustrated by work of Kenward (1978), in which goshawks (*Accipiter gentilis*) approaching woodpigeons (*Columba palumbus*) elicited a fleeing response from greater distances in larger flocks. This difference in fleeing distance also accounted for some, but not all, of the variation in attack success decrease in larger flocks. The author suggested that a "visual confusion" – whereby the predator finds it hard to pick out a target in larger prey groups (Neill and Cullen 1974; Jeschke and Tollrian 2007) – may explain the additional variation. Further evidence of the confusion effect comes from decreased survival of "odd" individuals (the oddity effect) (Landeau and Terborgh 1986). Predators may find it easier to target prey of an unusual colour (Landeau and Terborgh 1986), size (Rodgers et al. 2011) or even behaviour (Szulkin et al. 2006). Find more discussion on the confusion effect in *Section 2.4: Social environment*.

1.2. Information use

When resources are unevenly distributed, the benefits of information sharing are thought to favour group living (Ward and Zahavi 1973; Evans et al. 2016). Here, it posited that a larger group has a greater chance of finding at least one large food item or patch, and that once food is found, naïve individuals follow knowledgeable individuals to food sources. This was originally proposed by Ward and Zahavi

(1973), who presented many observational studies as evidence of this "information centre" hypothesis. This early theory has been updated to give more understanding to the benefits this can provide to an active signaller. Richner and Heeb (1996) suggest that decreased predation, resulting from the recruitment of more group members, could explain the evolution of active signals. Further, whether active signalling is even necessary has been debated, suggesting that previous success alone could elicit followers (Evans et al. 2016). Foraging success could be gauged by colony members through cues such as feeding young, arrival time, or fatness (Bijleveld et al. 2010; Evans et al. 2016). Regardless of the mechanism, it seems that naïve individuals can follow knowledgeable individuals to food patches, and that this may be widespread in social birds (Ward and Zahavi 1973; Thiebault et al. 2014; Evans et al. 2016). Shared navigation (Couzin et al. 2005) is a potential mechanistic solution to sharing information, and is discussed in *Section 2.2: Navigational environment*.

1.3. Energy conservation

Moving in group can decrease energetic expenditure for animals in the assemblage, particularly for those species moving in a fluid (Killen et al. 2012). This may be (*i*) regardless of spatial position in the group, as observed in grey mullets (*Liza aurata*; Marras et al. 2015), where it is posited that even leading individuals can benefit from zones of high pressure created by trailing individuals, or (*ii*) dependent on spatial positioning, for example in V-formation flocks of birds, where trailing

individuals have been shown to reduce energetic output (Weimerskirch et al. 2001). Regardless of the spatial inequalities in benefit, trailing individuals are thought to optimise travel by exploiting vortices (Portugal et al. 2014; Marras et al. 2015). In birds this may require optimal "phasing" of wingbeats relative to the flap frequencies and spatial positions of the birds in front (Portugal et al. 2014) (see more below in *Link to social environment*).

There is also evidence that flying in groups can increase energy expenditure (Usherwood et al. 2011; Taylor et al. 2019). Here, pigeons flying in "cluster travelling flocks" (see *Section 3*), may increase flight costs to avoid collisions (Usherwood et al. 2011; Taylor et al. 2019), or through the emergence of an uneven localised air environment left in the wake of other birds (Usherwood et al. 2011). In pigeons, therefore, energetic concerns may be more linked with "cost mitigation" than "energy conservation" (Taylor et al. 2019). This is not a dead end in a study of the function of cluster flocks. On the contrary, as flying solo (Taylor et al. 2019) and in less dense clusters (Usherwood et al. 2011) can reduce flight costs in pigeons, a motivation to reduce energy expenditure is likely to trade off with other benefits of flocking such as protection against predators (Kenward 1978). Therefore, optimal decisions to separate from the group, or gain additional space (reducing cluster density), may be dependent on predation risk (Chapter 6), or the duration of flight (Chapter 4). Additionally, mechanisms to reduce the uneven localised air environment could emerge by individuals remaining stable in their inter-individual flock positioning (Chapter 5).

2. Individual level mechanisms and the social environment

2.1. Risk environment

2.1.1. Individual mechanism

Ecological theory suggests animals should behave to minimise predation (Lima and Dill 1990). Animals may benefit by responding appropriately to a risk environment (e.g. uneven distribution of predation risk; Laundré et al. 2001) through behavioural patterns such as space use, and specific behaviours such as vigilance (Elgar 1989; Lima and Dill 1990). Evidence of adaptive space use in response to predation risk was found by Hernández & Laundré (2005), who observed – as predicted – a shift in the movement of elks (*Cervus elaphus*) from highly conspicuous open areas to forest edges following the reintroduction of wolves (*Canis lupis*) to Yellowstone National Park. There is also evidence that vigilance behaviours can decrease predation (Krause and Godin 1996). In one study, fish which foraged with their head down (and therefore presumed to have a smaller field of vision) took significantly longer to respond to a model predator, suggesting a trade-off between foraging and vigilance behaviours (Krause and Godin 1996). Vigilance may therefore impose constraints on food acquisition, and this is perhaps exacerbated in bird which use visual cues to forage.

2.1.2. Link to social environment

The constraint which vigilance places on foragers can be minimised by grouping with other foragers. When prey animals group together, the probability of detecting a predator increases (Bertram 1980). Although not linearly as was expected in an early model (Pulliam 1973), but rather, it seems animals can respond to the social environment by decreasing vigilance (Bertram 1980) or adjusting vigilance according to perceived threat through public information (Beauchamp et al. 2011). While noteworthy, feeding is not related, for the most part, to groups on the move in flocks (except see: Pelletier et al. 2007). See more information on social-level anti-predator strategies, with regards to social "interaction rules" in *Section 2.4: Social environment.*

2.2. Navigational environment

2.2.1. Individual mechanism

Much of what we know about navigation in animals has been gleamed from the study of homing in pigeons (Wallraff 2005; Gagliardo 2013). The major current paradigm identifies the need for two main components for successful navigation; a map and a compass (Kramer 1953; Gagliardo 2013; Biro 2018). Here, it is reasoned that animals have a general sense of their spatial position with regards to their target (the "map"). After a general direction is chosen, animals will use sensory cues to remain on track (the "compass"). The broad paradigm has remained unchanged since 1953 (Kramer 1953), nevertheless the specifics in homing pigeons

are highly debated (Casper 2009). The “compass” component is mostly resolved: simply put, pigeons appear to use the sun as a compass corrected by an internal-clock (Biro et al. 2007), and then, under heavy cloud cover, draw on magnetic field sense organs, potentially located in the right eye or upper mandible (Wiltschko and Wiltschko 2017). The “map” component remains especially contentious, particularly around the role of olfaction in determining positional information. Anosmic pigeons (i.e. those unable to smell or deprived of odours) are disoriented upon release from unfamiliar sites (Papi et al. 1971, 1972; Jorge et al. 2009), and, thus some role of olfaction is undisputed (Gagliardo 2013; Wallraff 2014; Wiltschko and Wiltschko 2017). However, the controversial claim is that the olfaction thus provides an accurate “map” of an individual’s position in space (Jorge et al. 2009; Wiltschko and Wiltschko 2017), as meteorological data do not support the necessary stable distributions of volatile chemicals for accurate positional information for this hypothesis (Waldvogel 1987). Indeed, the role of olfaction has recently been hypothesised to provide nothing more that the “activation” of other non-olfactory navigational maps (Jorge et al. 2009), such as visual landmarks (Biro et al. 2007) and detections of the magnetic field (Wiltschko and Wiltschko 2017). Jorge et al. (2009) first confirmed that anosmic pigeons were disoriented, then subsequently showed that pigeons exposed to artificial odours such as lavender – which could not provide navigational information – demonstrated homing capacities indistinguishable from those exposed to the natural odours of the release site.

2.2.2. Link to the social environment

The field of social learning has provided evidence that group members can benefit from travelling with experienced congeners (Mueller et al. 2013; Berdahl et al. 2018). Mueller et al. (2013) trained a group of captive-bred whooping cranes (*Grus americana*) to take a specific migration route, following a manned aircraft. Following the training, the birds continued to make the same journey each year. Younger individuals – not present during the training flights – had a greater journey accuracy if they flew with older (trained) birds compared to groups which flew without older birds (Mueller et al. 2013). Moreover this study, and another in pigeons (Pettit et al. 2013a), found that the improved routes *when following experienced individuals* remained in the *absence of this leader*. These studies support a local enhancement hypothesis, whereby the following of more experienced conspecifics can bring inexperienced individuals into contact with spatial cues associated with shorter flight paths (Hoppitt and Laland 2008). Additionally, as the route was remembered, these studies seem to contradict earlier notions that followers simply "scrounge" successful routes from informed individuals (Beauchamp and Kacelnik 1991; De Perera and Guilford 1999). However, later work does suggest that learning in followers is compromised relative to leaders. Pettit et al. (2015) found that after a series of group flights, birds which were consistent leaders had increased navigational efficiency upon further solo releases. This may be a result of increased learning by individuals which favoured navigational over social information (Guttal and Couzin 2010; Pettit et al. 2013a).

When individuals in groups differ in *i*) information (i.e. informed or uniformed) or in *ii*) their preferences for particular sites, collective decisions involving the social transfer of information must be made for the group to remain cohesive on the move (Couzin et al. 2005). Firstly, Couzin et al. (2005) showed, in simulation models, that a relatively small proportion of informed individuals can transfer (potentially pertinent) information to uninformed individuals via emergent leadership. The importance of this work was that it demonstrated the potential significance of social cues in collective decision making (i.e. there was no active signalling in this system). Later empirical studies support consensus decision making by *cues* (Biro et al. 2006; Strandburg-Peshkin et al. 2015) but do not test predictions based on the alternative, intention *signalling*, hypothesis (Couzin and King 2010). Second, alternative intra-group directional preferences can lead to conflicts of interest (Conradt and Roper 2009). This could lead to a minority of highly motivated individuals dominating directional movement (Conradt et al. 2009; Couzin et al. 2011). Though this would increase the "consensus costs" (the cost of following against your own preference) for most individuals in the group (Conradt and Roper 2005; King et al. 2008), favouring the evolution of shared decision making (Conradt and Roper 2005).

An increase in group size may increase the accuracy of collective decisions. Simons (2004) proposed that "many wrongs" could make a right; that the navigational inaccuracies inherent in one individual could be ameliorated by travelling with larger groups. The mechanism governing this process is based on the notion that by combining many inaccurate compasses or guesses, one more accurate guess emerges. Similar to the "wisdom of the crowd" phenomenon, which originated

when Francis Galton (1907) collected many individual guesses of an ox's weight at a county fair in 1907, and the median average of the guesses was remarkably close to the actual weight of the ox. The many wrongs hypothesis is supported by studies of group flight in pigeons, whereby the GPS route of a group's centroid was more accurate than individual flight paths (Biro et al. 2006; Dell'Ariccia et al. 2008; Mehlhorn and Rehkaemper 2016).

2.3. Aerodynamic/energetic environment

2.3.1. Individual mechanism

For birds to fly they need to have (*i*) sufficient lift (upward movement) to overcome gravity and, (*ii*) sufficient force (forward movement) to overcome drag. Flight is costly (Schmidt-Nielsen 1972), but there are means by which to make it less so. Shepard et al. (2013) suggest that following wind gradients and thermal uplifts of air constitute adaptive use of the "energy landscape". Empirical support is growing for this hypothesis, and current examples include 1) evidence that herring gulls (*Larus argentatus)* and lesser black-backed gulls (*L. fuscus*) adjusted their flight trajectories to make use of small scale updrafts from buildings (Shepard et al. 2016) and 2) the (perhaps better known) use of thermals by soaring vultures (Harel et al. 2016). The evidence suggests a strong selection pressure to respond to the aerodynamic environment (Wilson et al. 2012). These species, however, do not form distinctly coordinated flocks (Heppner 1974), and hence, while our

investigations will make use of this theory (Chapter 5), we apply a synergised approach with respect to the social environment.

2.3.2. Link to social environment

The social environment can also affect the aerodynamic environment, and responding to the movements of other birds can influence the localised air environment. Ibis have been shown to exploit upwash and avoid downwash created by neighbours (Portugal et al. 2014). The results of this study found not only that the birds achieved spatial positions predicted by theoretical models, but that the timing of a focal individual's wing flap could be predicted by the relative position and angle to their neighbour, maximising areas of predicted upwash and avoiding downwash from the neighbours' wing flap (Portugal et al. 2014). Evidence of adaptive use of the social/aerodynamic environment in cluster travelling flight types (*Section 3*) is lacking (but see Chapter 5).

In-flight, power requirements – the energy required for flapping flight – have been shown to have a U-shaped relationship with speed (Fig 1.1; (Tobalske et al. 2003)). The speed of flight which costs the least energy – the minima in these U-shaped relationships – is given as U_{mp}. Faster flight is more costly because of the energy necessary to beat wings more regularly, or increase the amplitude of the wing beat, necessary to displace more air (Heerenbrink et al. 2015; Johansson et al. 2018). Slower flight is also thought to be more costly. Although less immediately obvious, it is for similar reasons: the faster the bird is moving, the more air passes through each wingbeat, so at slow speeds, more effort is needed to provide sufficient lift

(Heerenbrink et al. 2015; Johansson et al. 2018). This same logic can be applied when understanding why heavier birds will have a higher U_{mp}. When a bird is heavier, it will require a faster air flow to produce the same amount of lift. This is thought to cause a right shift in the U-shaped relationship for heavier birds (Fig. 1.1; Tobalske et al. 2003). The flight speed which minimises energy expenditure per unit distance, speed of maximum range (U_{mr}), can be found from the smallest gradient which touches the curve and goes through intercepts of zero on both the x and y axis (Fig. 1.1). Depending on ecological context, animals may be expected to fly closer to the U_{mr} or the U_{mp}. Evidence that animals may actually behave this way is given by Hedenström & Alerstam (1996), who found a shift from U_{mp} toward velocities predicted from the U_{mr} in skylarks (*Alauda arvensis*) flying in a migration context, presumably to maximise distance, rather than decrease general costs of being airborne U_{mp}.

For birds flying in groups – which must speed match to achieve this feat (Chapter 3) – any discontinuities in structural size or body mass amongst the group could lead to unequal power requirements (see Chapter 3). Recent findings – that average flight speed of a group increases with group size (Åkesson et al. 2016; Hedenström and Åkesson 2016) – suggest that larger groups have a higher proportion of large (and hence fast) individuals, and smaller birds may pay a higher cost than the larger faster birds to be in that flock (Hedenström and Åkesson 2016; Fig. 1.1). However, there are alternative explanations. Firstly, birds may benefit from upwash created by individuals at the front. This seems unlikely in cluster travelling flight types (see *Section 3*) as cluster flocking birds have been shown to have high, and costly, flapping frequencies in pairs (Taylor et al. 2019) and in denser flocks (Usherwood et

al. 2011). It is also possible that larger groups exploit and share information about positive tailwinds, either because more individuals may have more collective knowledge about beneficial airspace, or more simply, because the flock is larger and therefore encounter a larger mix of air currents.

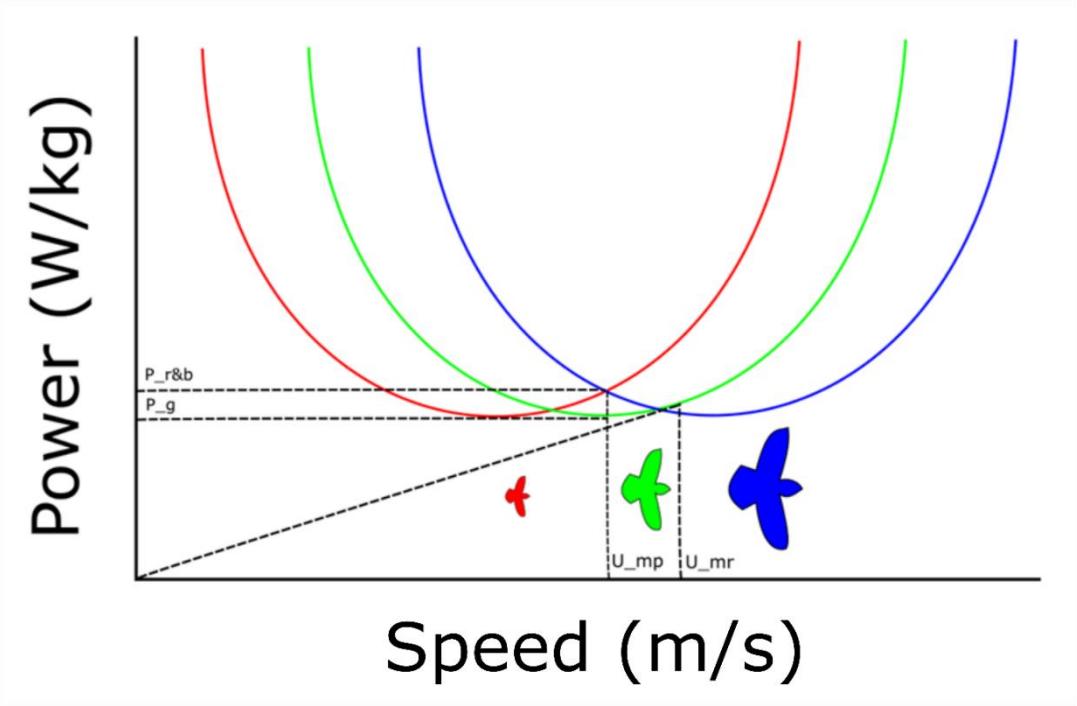

Figure 1. 1. Power curves in bird flight

Larger birds (red/green/blue are progressively larger) are expected to have a right shifted, U-shaped relationship between power and velocity. If the group were travelling at the speed dictated by the minimum power requirement for the medium bird (vertical dashed line on figure) the predicted power output for the medium sized bird (P_g) would be lower than the predicted values for the small and large birds (P_r&b). The velocity at which power costs are minimised per unit time, and unit distance is given (U_{mp} and U_{mr} respectively) for the medium sized (green) bird.

2.4. Social environment

2.4.1. Interaction rules

As mentioned in the introductory paragraph, telepathy is no longer considered as a hypothesis for the coordination of collective behaviour. If "thought transference" (Selous 1931) is out, then social "interaction rules" are in (Breder 1954; Herbert-Read et al. 2011; Herbert-Read 2016; King et al. 2018). It is presently believed that coordinated collective motion can be achieved by social interaction rules at the local level, i.e. collectively moving animals need not know the positions and/or orientations of all group members, only those close to them (Breder 1954; Herbert-Read 2016). Indeed, groups of interacting agents, programmed with simple rules, demonstrate that interactions at the local level can produce collective motion patterns similar to those found in nature (e.g. fish shoals and bird flocks) (Reynolds 1987). Perhaps the most successful implementation has been of three rules: 1) repulsion: when the focal individual is too close to one or another neighbour, 2) attraction: towards neighbours in the focal individual's sensory field and 3) alignment: with neighbours at specific distance or sensory related "zones" (Fig. 1.2; Reynolds 1987; Couzin et al. 2002). If these rules *i*) really are how animals interact in flocks/shoals, and *ii*) are divisible, having evolved at least partially independently of one another, then we might see ecological benefits to behaving according to different rules independently, or in certain combinations (Ioannou et al. 2012). It is immediately obvious that repulsion is important to avoid clumping with neighbours (if attraction rules are present), and potentially on a larger scale, solitary animals may use repulsion heuristics to avoid crossing territories with conspecifics,

effectively maximising available resources (Quinn and Graves 1999). However, only attraction and alignment rules are further discussed in this section due to the greater body of evidence of their roles in ecological processes. For a critique of the "interaction rules" hypothesis, separating behaviours into unitary "traits" (Gould and Lewontin 1979), and future outlook, see Chapter 7.

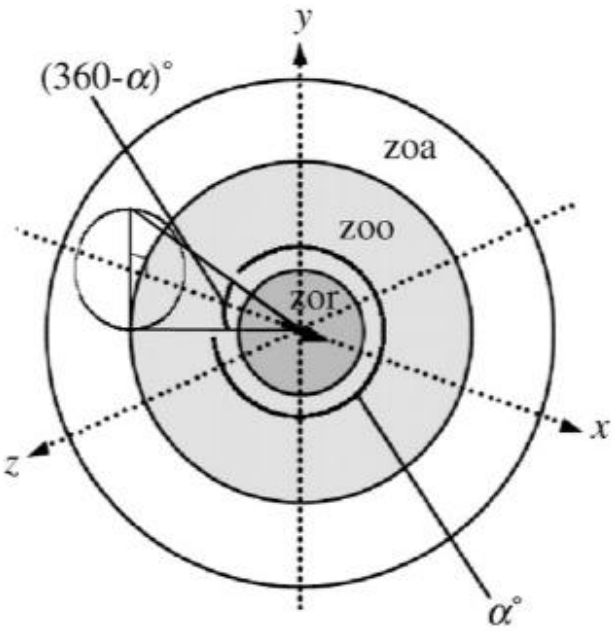

Figure 1. 2. Interaction "rules" which can reproduce collective motion

A focal individual is located at (0,0,0, on x, y and z axes). Firstly, this focal individual will attract toward a neighbour within a zone of attraction (zoa), and the centroid of neighbours in this zone if there are more than one neighbour. Second, the focal individual will align its body orientation with neighbour(s) within the zone of orientation (zoo). Finally when neighbours get too close, in the zone of repulsion (zor), focal individuals are repelled from their neighbour. Figure taken from (Couzin et al. 2002).

2.4.2. Cohesion – attraction

A behavioural heuristic to attract toward conspecifics, and to remain cohesive, can potentially provide benefits at the individual level (Hamilton 1971). Firstly, from an individual perspective, there may be less chance of being predated in larger groups. This is known as the dilution effect (Foster and Treherne 1981; discussed in *Section 1*). Second, attraction to the centre of large groups may provide unshared benefits through "selfish herd" effects (Hamilton 1971; King et al. 2012). Finally, attraction "rules" may also increase predator confusion (Ruxton et al. 2007; Ioannou et al. 2012; Hogan et al. 2017a) a selective benefit at the mutualistic level (Farine et al. 2015), i.e. all individuals benefitting in tandem (Sumpter 2006, 2010), but see below section: *Coordination – alignment*, for a more detailed discussion. Additional benefits from cohesion include *i*) social information regarding foraging (Ward and Zahavi 1973), *ii*) breeding opportunities (Emlen and Oring 1977), *iii*) predator defence (Evans et al. 2016), and *iv*) effective group decision making (Couzin et al. 2011) as discussed in *Section 1.2: Information use*.

2.4.3. Coordination – alignment

Coordination of an individual's movements to both the direction and the timing of their neighbours movements are considered important to the function of group flight. Directional coordination (or alignment) may improve the accuracy of collective decisions (Couzin et al. 2005), provide aerodynamic advantages (inferred from: Portugal et al. 2014), and enhance anti-predator benefits (Ioannou et al.

2012; Herbert-Read et al. 2015). Information regarding the predator location can be passed from individual to individual by aligning with the orientation of fleeing individuals (Herbert-Read et al. 2015). Additionally, aligned groups can "move faster in the same direction" than groups with high "attraction" (Wood and Ackland 2007; Couzin et al. 2011), enhancing a collective escape response (Ioannou et al. 2012). Finally, the confusion effect may be enhanced by turning movements with high alignment, such as propagating "waves" in starlings (Procaccini et al. 2011).

2.4.4. Linking mechanism to function: attraction and alignment

"Interaction rules" are not often discussed with relation to their function (Bajec and Heppner 2009), with notable exceptions (Buhl et al. 2006; Ruxton et al. 2007; Sumpter 2010; Ioannou et al. 2012). Ruxton et al. (2007) found that "attraction", but not "alignment" rules increase survival in a study of human (*Homo sapiens*) "predators" mouse clicking on simulated particles or "prey". However, in a more realistic study, Ioannou et al. (2012) used real fish predators to peck at similarly programmed particles on a screen in their tanks. Simulated particles with alignment rules preferentially survived to the next simulation (generation) compared with particles with only attraction or repulsion rules alone. Thus, alignment behaviour in the virtual prey was selected for by the predator (Ioannou et al. 2012). This suggests that under selective pressure from predators, alignment rules should evolve, and that individuals which cannot match these effective rules (termed conformity; *Section 5.5: Conformity*) may be preferentially predated on. This is termed the oddity effect, and is a well-supported example of social selection in

shoaling fish, and although this functional link is missing in birds, could be prevalent in the evolution of highly coordinated flocking types like that of starlings (Landeau and Terborgh 1986).

While there is evidence that individuals should balance "alignment" and "attraction" rules (Ioannou et al. 2012), the optimal response could be context dependent (Chapter 6). Individuals may move to the centre (King et al. 2012), as predation risk may be lower here (Okamura 1986; Rayor and Uetz 1990; Salek and Smilauer 2002; Stankowich 2003; Morrell and Romey 2008). This "selfish herd" behaviour (Hamilton 1971) can provide individual-level selective benefits (King et al. 2012). The mechanism for selfish herd behaviour ideally involves individuals actively moving toward the group's centroid wherever possible (i.e. when not constrained by other individuals or environmental features), although it is understood that an animals estimation of the centroid may be somewhat skewed (King et al. 2012). Secondly, another documented possibility is that animals increase their coordinated behaviours (Bode et al. 2010) under higher perceived threat levels, maximising information transfer (Herbert-Read et al. 2015), collective escape speed (Ioannou et al. 2012) and potentially predator confusion (Procaccini et al. 2011) , and so maximising benefits at the group level (Sumpter 2006, 2010; Sumpter et al. 2018).

To my knowledge, investigating the trade-off between (sometimes mutually exclusive) mechanisms 1) "attract to centroid" and 2) "increase alignment" has not been achieved in any study system. Therefore, we need predictions whose patterns separate the hypotheses to formally test the mechanisms. A decreasing distance to

centroid may appear to validate selfish herd theory (King et al. 2012), but it is possible that the group are condensing to increase effective "alignment" responses, i.e. they may get closer to one another to facilitate coordinated behaviours. There is much evidence that this is in fact the case, and studies of collective behaviour often assume individuals need to be in close proximity to perform highly coordinated behaviours (Couzin et al. 2002; Ballerini et al. 2008; Bode et al. 2010). The crucial difference will be that once the group has reduced in size, do individuals on the outer edge still aim to achieve central positions? Simply, if "centroid attraction" was the primary goal, individuals on the right would attempt to turn left, and individuals on the left would attempt to turn right more strongly or more often when the group perceives higher levels of threat (see Chapter 6). Whether this latter prediction is congruent with just coordination and not selfish herd dynamics may require model validation. To my understanding, a description of a basic agent-based model involving a moving flock (Couzin et al. 2002) with additional motivations to 1) turn and 2) accelerate/decelerate toward the group's centroid is missing from the literature (but see Chapter 7 for more details on a proposed model).

3. Flocking types

By utilising the aforementioned mechanisms, responses to 1) risk, 2) aerodynamics, 3) navigational cues and perhaps most importantly, 4) social information, interactions with neighbours and/or the environment may create emergent group-

level structures or behaviours. These can then have their own properties that can or cannot be independent of the individual phenotypic differences which comprise them (Voelkl et al. 2015; Sumpter et al. 2018).

3.1. Model species and "flocking types"

Some species and their associated flocking types can be used as good models for understanding flocking function (Sumpter et al. 2008; Zoratto et al. 2010; Portugal et al. 2014). This is generally achieved by attempting to isolate the following three functional benefits of group flight: 1) decreasing the costs of flight through adaptive use of the local air environment (Portugal et al. 2014); 2) adaptive use of social information (Sumpter et al. 2008) and 3) decreased risk of predation (Zoratto et al. 2010). I will propose that these three functions may have distinct flocking structures associated with maximising benefits. This is also intuitive, as one would expect different solutions to evolve in the face of different ecological problems. Firstly, V-formations (Fig. 1.3A) have a relative focus on energy conservation (Weimerskirch et al. 2001; Portugal et al. 2014). Second, "cluster travelling flight" (Fig. 1.3B) may emerge through an adaptive blend of navigational and social information (Guttal and Couzin 2010; Ling et al. 2019). "Travelling flight" is defined so as to highlight the polarised, goal-oriented nature of such phenomena in contrast to the final flocking type: "cluster swarms" (Fig. 1.3C), which again is new nomenclature, to distinguish differences in structure and function, which may be

the result of a relative emphasis on anti-predator benefits (Carere et al. 2009; Zoratto et al. 2010; Storms et al. 2019).

Isolating the functional benefits is discussed in relative terms, as perhaps all three selective pressures operate in any one given system/ flocking type. For example, V-formation flocks, which have a relative emphasis on energy conservation (Weimerskirch et al. 2001; Portugal et al. 2014), also show benefits of social learning (informational benefits) from travelling with more experienced conspecifics (Mueller et al. 2013). Additionally, smaller V-formation flocking birds (e.g. plovers; sub-family: Charadriinae, small ibis; sub-family: Threskiornithinae) are prey species to aerial predators (Parrish and Hamner 1997). Secondly, "cluster travelling flight", I have posited are formed when informational deficit is a strong selective pressure. In response, species such as jackdaws (*Corvus monedula*) and rooks (*Corvus frugilegus*) which roost together in "information centres" (Ward and Zahavi 1973), and follow other (potentially more knowledgeable) individuals in group movements. Nevertheless, there are energetic constraints to flying in cluster flocks (Usherwood et al. 2011; Ling et al. 2019; Taylor et al. 2019), which may be exacerbated by unstable movement within the flock (Ling et al. 2019; and Chapter 5) or flying at the back of the flock (Usherwood et al. 2011). Additionally, there may be anti-predator benefits to "cluster travelling flight" (Sumpter 2010; Woods et al. 2018; Taylor et al. 2019). Though, such flocking types may sometimes be poor at responding to predators, due to strong social-pair (presumably mating-pair) interactions (Jolles et al. 2013; Ling et al. 2019), which inhibit efficient information transfer (Ling et al. 2019) (but see Chapter 6). While I do not have any direct evidence that the final flocking type, "cluster swarms", have an anti-predator

advantage over the other two types, there is evidence that synchronised aerial manoeuvres such as “wave events” have been shown to reduce predator success in attacks on starlings (Procaccini et al. 2011). Additionally, the greater densities associated with this flocking type (Storms et al. 2019) may decrease predation risk, relative to other flight types (Hogan et al. 2017a; Storms et al. 2019). “Cluster swarms”, flying around their roosts and hence not travelling, have little or no need for navigational information, and presumably could land if they were fatigued, so no obvious energetic constraint also (Carere et al. 2009).

Figure 1. 3. "Flocking types"

"Flocking types" are proposed to emerge from different relative selective pressures on groups, **(A)** "V-formation" flight, proposed to function for energetic benefits, relative to other flocking types. Photo: Simon Colenut, accessed on 30/3/2017, accessible from: http://thedeskboundbirder.blogspot.co.uk/. Species: unknown. **(B)** "Cluster travelling flight", proposed to function for informational benefits, relative to other flight types. Photo: Simon Colenut, accessed on 30/3/2017, accessible from: http://thedeskboundbirder. blogspot.co.uk/. Species: Mixed flock of grey plovers (*Pluvialis squatarola*), knots (*Calidris canutus*), turnstones (genus: *Arenaria*) and bar-tailed godwits (*Limosa lapponica*). **(C)** "Cluster swarm" flight, may confer increased anti-predator benefits, potentially related to "predator confusion". Photo: Amir Cohen, accessed on 30/3/17, accessible from: https://www.theatlantic.com/photo/2014/02/the-murmurations-of-starlings/100690/. Species: common starlings (*S. vulgaris*).

3.2. Mechanism and the plasticity of "interaction rules"

The different forms of flight proposed may be mediated by interaction rules present at the individual level (Bajec and Heppner 2009). There exists two ways in which an animal system can modify its interaction rules. Either *i*) over long periods of time through natural selection; as already discussed, Ioannou et al. (2012) found evidence of selection for coordinated motion in virtual prey. Alternatively, *ii*) a

species may exhibit plasticity in its “interaction rules”, which can lead to emergence of qualitatively different emergent structures. This was demonstrated theoretically by Couzin et al. (2002), who showed that a group of agents in a simulation could effectively shift from a swarm, to a torus, to schooling like behaviour by increasing the alignment zone respectively (Fig. 1.4). This study illustrates the possibility that depending on the context, species could modify their interaction rules, and effectively the three-dimensional structure of the group, to adaptively respond to situations at the group level.

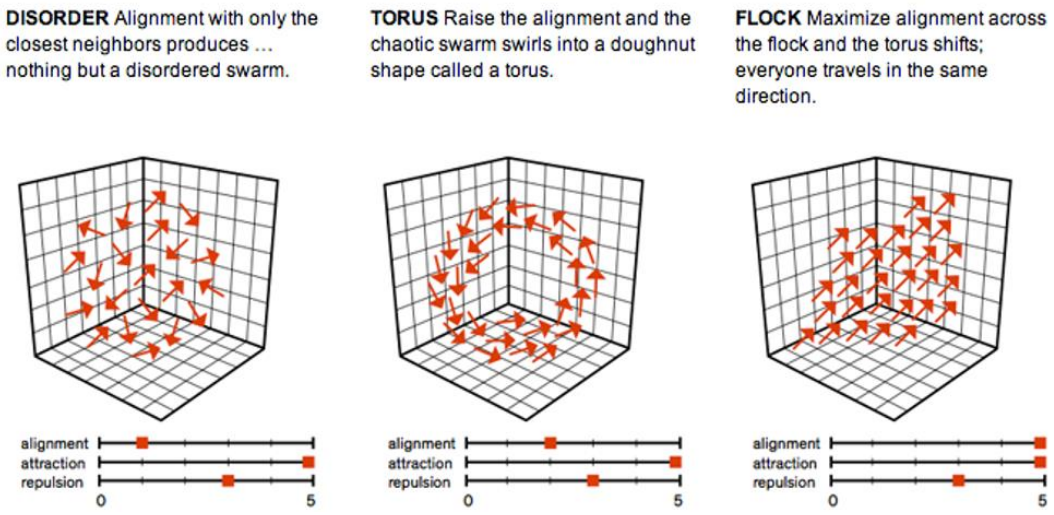

Figure 1. 4. Plastic interaction rules?

A simulated model from Couzin et al. (2002) showed that as an alignment parameter was increased, the structure of the group transformed qualitatively between three stable states; disorder, torus and flock. This suggests the different emergent structures of bird flocks (“flocking types”) could result from a simple changing of decision mechanisms at the individual level.

4. Measuring benefits/costs of group flight

4.1. Traditional methods

Measurement of the costs/benefits of group flight has traditionally been based upon 1) observations of predation rates (Cresswell 1994; Carere et al. 2009; Zoratto et al. 2010), 2) studies of information acquisition at breeding grounds (Ward and Zahavi 1973; Evans et al. 2016) and 3) inferences of energetic savings from photographs/films of formation flights (Hainsworth 1987; Cutts and Speakman 1994). Firstly, observational studies of predation risk under different group sizes has provided evidence that group living can minimise the risk of predation. For example, starlings in groups were less likely to be predated than were individuals (Zoratto et al. 2010), as were larger, denser groups, compared with smaller, less dense groups (Carere et al. 2009). Secondly, studies of information acquisition at breeding grounds identify birds as they enter and exit roosts, documenting the recruitment of followers (Evans et al. 2016). However, despite advances in our understanding of recruitment behaviour – and hence, an understanding of in-flight composition of identified individuals – these studies tell us little about information transfer on the move. Finally, studies investigating energetic benefits using photographs and films can reveal startlingly quantitative data (Cutts and Speakman 1994), though they are based on predicted positions of vortices (upwash created from flying birds' wingtips) from potentially imperfect theoretical models.

4.2. Biologging technology

Fairly recent advances in animal attached data loggers (biologgers) have provided researchers with highly quantified temporal streams of data, and represent a success story in the study of the mechanisms, and functions of group flight (Rutz and Hays 2009; Portugal et al. 2014; Berdahl et al. 2018). For example, data from Global Positioning System (GPS) loggers have revealed that domestic pigeons groups, trained to home and released from familiar sites, generally take a more direct route home than individuals (Biro et al. 2006; Dell'Ariccia et al. 2008; Mehlhorn and Rehkaemper 2016). This suggests increased accuracy of collective decisions associated with information sharing in group flight (Simons 2004; Biro et al. 2006; Sumpter et al. 2008; Mehlhorn and Rehkaemper 2016).

High resolution accelerometer loggers can provide acceleration (*g*) in three dimensions (Fig. 1.5). Streams of animal attached accelerometry data can provide, through simple calculations, a bird's flapping frequency and dorsal body amplitude (a proxy for wingbeat amplitude) (Usherwood et al. 2011; Taylor et al. 2017, 2019) discussed in *Section 2.3: Aerodynamic/energetic environment*. These two variables provide indirect – but highly relevant (Tobalske 2007) – measures of energy expenditure in flap powered bird flight (Usherwood 2016). This technology has been used to estimate flight costs in cluster flocking birds (pigeons; Usherwood et al. 2011) and V-formation flocks (Northern bald ibis *Geronticus eremita*; Portugal et al. 2014).

The combination of accelerometers and GPS (attached to the same animal) provides further insight into the mechanism and function of bird flocks. Such studies have shown that 1) spatial positioning (GPS) and flap phasing (accelerometer) combine to govern the energetic benefits of V-formation flocks, as discussed in *Section 2.3: Aerodynamic/energetic environment*; (Portugal et al. 2014). Additionally, it has been shown, using these technologies that cluster flocking pigeons may experience greater energetic costs (accelerometer), especially in denser clusters (GPS) (Usherwood et al. 2011).

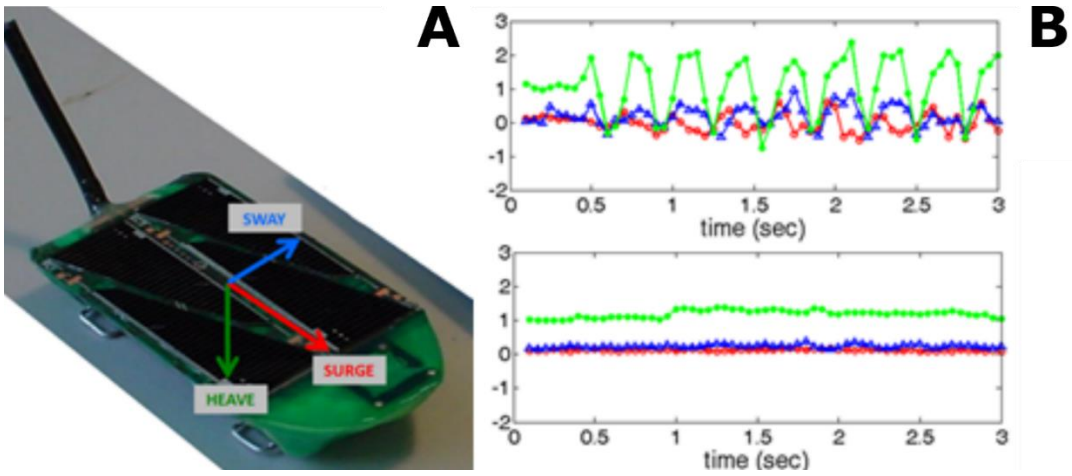

Figure 1. 5. Accelerometers

Accelerometer trace (20 data per second for each axis, surge heave and sway) from flapping flight (data and figure from UvA Bird Tracking System website: http://www.uva-bits.nl/gps-trackers/; species not provided). **(A)** Flapping flight creates a stronger signal in vertical axis (heave, or z), as each flap produces vertical movement in the birds body. Amplitude (height of peak) and flap frequency (number of peaks) can be measured using these data. **(B)** A running mean of the

data in **A**). This shows the influence of gravity on the tag and hence the posture or orientation of the tag in three dimensions.

4.3. Linking technology to function

Spatial positioning (measured by GPS) is thought to govern some fitness advantages, such as the protective benefits, afforded by central positions to predators (Hamilton 1971; King et al. 2012); high energy consumption (measured by proxy from accelerometers) can negatively impact an individual's state, or condition (Kays et al. 2015), this may in turn, indirectly impact an individual's fitness. Indeed, differences in intra-group energy expenditure may create a positive feedback loop, whereby individuals in better condition (i.e. state) can consistently outperform others in worse condition. State to behaviour feedbacks are discussed in the next section where their role in the maintenance of consistent inter-individual differences in behaviour (cf. personality) are considered (Sih et al. 2015).

5. Consistent inter-individual phenotype

5.1. Animal "personality"

Recently, there has been much attention paid to understanding the phenomenon that many animals differ consistently – from other members of their species – in a number of measurable behavioural traits when tested under laboratory (Dyer et al. 2009; Grinsted et al. 2013; Siviter et al. 2016) or field conditions (Carter et al.

2012b, a). More specifically, these differences can exist irrespective of other phenotypic similarities such as sex and age (Dall et al. 2012). "Personalities" – as these consistent individual behavioural differences are often referred to – are simply repeatable and measurable behavioural differences between individuals. I will not use terms like "boldness" (often used to describe the willingness to leave a shelter, e.g. Mcdonald et al. 2016), "neophilia" (willingness to investigate a novel object, e.g. Kurvers et al. 2009) or "exploration" (range or distance travelled through a testing arena, e.g. Smith and Blumstein 2010) as if the observed "personalities" evolved independently of other processes. Unlike morphological characteristics (e.g. secondary sexual traits, Emlen and Oring 1977), "personalities" are statistical phenomena that likely correlate with more fundamental differences in internal physiological mechanisms (Biro and Stamps 2010), which may be driven by genetics (Patrick et al. 2013) and/or development (Bierbach et al. 2017). Nevertheless, repeatable behavioural differences between animals of the same species is uncontroversial (David and Dall 2016), despite previous theory which predicted that behaviour, for all members of a species, should be flexible to ecological conditions (Sih et al. 2015). Therefore the explanation of these differences has been critical to understanding evolutionary and ecological processes (Dall et al. 2012). A previous dichotomy, that either proximate (e.g. behaviour is constrained by state; Careau et al. 2008) or adaptive (e.g. an individual's phenotype is successful when relatively rare; Dall et al. 2004) processes can explain animal personality, is perhaps being replaced by an integration of the two (e.g. adaptive decisions which depend on the individual's state; Sih et al. 2015). Initial differences in state may diverge the costs and benefits of particular

behaviours, which can feedback into the individual's state; strengthening (positive feedback), or stabilising (negative feedback) the behavioural differences between individuals in a population (Sih et al. 2015).

There is increasing evidence that consistent individual differences on-the-ground (which are independent of age, sex, etc.) can be explained by frequency dependent trade-offs in life history productivity (Wolf et al. 2007), which may be mediated by an animals physiology (Biro and Stamps 2010). It was suggested that some individuals have a higher metabolic rate, and as a result, need to take more risks, but also may potentially achieve more rewards (Wolf et al. 2007; Biro and Stamps 2010). The culmination of such a mechanism may result in frequency dependent selection (Dall et al. 2004) for "risk taking" individuals which "live fast and die young" (Wolf et al. 2007), mediated by state and/or metabolic rate (Sih et al. 2015). For example, Killen et al. (2012) found a direct relationship between metabolic rate and risk taking in seabass *Dicentrarchus labrax*. Additionally orb-weaving spiders: *Larinioides cornutus* and *L. patagiatus* with higher heart rates take more risks (Shearer & Pruitt 2014). However frequency-dependence alone is not likely to predict behavioural consistency (Wolf et al. 2010), a recent review argues that a combination of frequency-dependent selection, with adaptive decisions based on current state (e.g. energy levels; Houston and McNamara 1999) may be useful in our understanding of "personality" emergence (Sih et al. 2015). A recent meta-analysis of over 70 studies suggests that metabolic rate positively covary with behaviours with greater energetic turnover (e.g. foraging behaviour and dominance interactions) but not those with weak or inconsistent energetic return (e.g. exploration, sociability) (Mathot et al. 2019). While this study (Mathot et al. 2019)

no doubt represents the largest dataset at present on the link between metabolic rate and “personality”, the authors mention neither risk-taking nor frequency-dependence, and thus this work can contribute only indirectly to a synthesis of proximate and ultimate personality explanations (unlike Sih et al. 2015).

5.2. Leadership

Consistent leadership, is a now well-documented phenotype in many taxa such as birds (Nagy et al. 2010), fish (Burns et al. 2012) and mammals (King et al. 2008; McComb et al. 2011; Brent et al. 2015). Consistent leadership can logically be defined as having a consistent and disproportionally large influence on group-level decisions. In moving groups this can be simplified to movement decisions to change direction which are then copied – within a defined time period – by neighbours (Nagy et al. 2010). The methods for assessing leadership involve pairwise correlation of movement or speed vectors, and finding the movement forwards or backwards in time which correspond to the greatest correlation value. If a focal individual’s movement vector best correlates with that of their neighbours when the vector is pushed forward in time, this means the focal individual made this decision first, and thus “leads” the movement (Nagy et al. 2010). Such “time-shifts” are generally averaged over an entire flight, producing a pairwise correlation value between the potential “leader” and “follower” for each possible time interval (see Fig. 1.6 for an example of pairwise correlation values between pigeons in a group; taken from: Nagy et al. 2010).

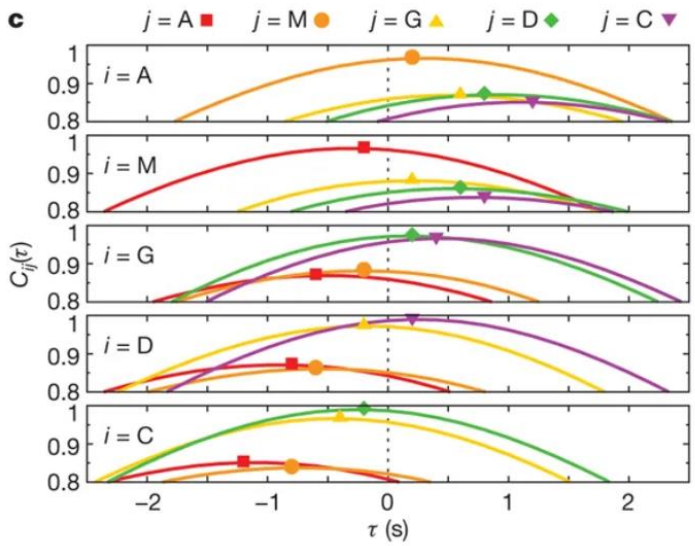

Figure 1. 6. Correlation curves in pigeon leadership

In cohesive animal groups, followers will make movements as leaders, but they will be delayed in time. In this example (taken from Nagy et al. 2010), individual "A" (red), generally makes movements before others in the flock. The greatest correlation between the movement vector of "A" and the vector of any other individual occur when individual A's trajectory is *moved forward* in time.

5.2.1. Adaptive leadership hypothesis

Theory suggests that consistent differences in leadership could be adaptive, i.e. there may be negative frequency dependent selection (see Davies et al. 2012) for different "leadership" phenotypes(Johnstone and Manica 2011). Johnstone and Manica (2011) suggested that entire groups of *socially-oriented* individual "followers" would not explore their environment for novel resources, whereas groups of *goal-oriented* individuals "leaders" could not achieve coordination, and hence the benefits of group living (Krause and Ruxton 2002). The result was the

evolution of stable ratios of leaders and followers (Johnstone and Manica 2011). In support of their model assumptions, Freeman et al. (2011) found that *goal-oriented* pigeons, i.e. those with high route-fidelity during solo homing flights, were significantly more likely to lead paired movements (Biro et al. 2006; Freeman et al. 2011). This provides tentative evidence for frequency dependent ratios of leadership between goal-oriented pigeons (site loyal; leader) and socially-oriented pigeons (less site loyal; follower). Additionally, goal-oriented fish have been shown to take up higher leadership ranks (Ioannou et al. 2015). Nevertheless, the most successful leaders were those that traded-off goal-orientedness for some degree of social-orientedness. Individuals too goal-oriented would often split from the group, and hence could not lead movements (Ioannou et al. 2015).

5.2.2. Physiological leadership hypothesis

Leadership differences may also be dependent on an animals physiological state (Rands et al. 2003; Fischhoff et al. 2007; Conradt et al. 2009). For example, lactating female plains zebra (*Equus burchellii*) are shown to have disproportionately high leadership ranks, which could be explained by their greater relative food requirements (Fischhoff et al. 2007). Additionally, recent evidence in pigeons suggests that speed can predict leadership (Pettit et al. 2015), while speed, in turn, may be governed by physiological differences. This may also explain the positive relationship between speed and leadership in fish (Jolles et al. 2017). However, refuting an adaptive frequency-dependent hypothesis for leadership in pigeons has not been achieved. This is because the internal differences in "goal-orientedness",

as predicted by models (Johnstone and Manica 2011), implicitly assumes some level of conflict in the preferred routes of the pigeons (Biro et al. 2006; Freeman et al. 2011), and most studies of leadership release over "familiar" terrain, i.e. from a site they had already been previously released from (but see (Sasaki et al. 2018)). In these cases, pigeons most probably already know the way home (i.e. have proved it by returning at least once) (Flack et al. 2012, 2013; Pettit et al. 2015; Watts et al. 2016). So, in the context of familiar landscape, individuals may follow faster birds (Pettit et al. 2015), but only when they are accurate enough (Watts et al. 2016) (see Chapter 2 for further discussion and a formal test of these hypotheses).

5.2.3. Phenotypic predictors of leadership rank

The question of whether either hypothesis (i.e. adaptive or state-dependent) can explain consistent differences in leadership, is likely to come from an understanding of other phenotypic differences between individuals. In fish, boldness predicted leadership in pairs of three-spined sticklebacks, *Gasterosteus aculeatus* (Jolles et al. 2015) . Likewise in a study of barnacle geese *Branta leucopsis*, bolder, less neophobic individuals lead group movements, but this was on the ground, and not in the context of flight (Kurvers et al. 2009). The only study of on-the-ground phenotypic differences, as a means of predicting leadership in pigeons, was of their dominance rank, and this did not correlate with leadership (Nagy et al. 2013). Termed, context-dependent hierarchies, pigeons are thought to specialise on being either dominants or leaders. This is surprising, considering larger birds were socially dominant (Nagy et al. 2013), and theory predicts should also fly faster (Hedenström

and Åkesson 2016), and therefore lead (Pettit et al. 2015). Many factors, both on the ground and in flight, were however not studied (e.g. association networks, personality), and may hold explanatory potential. Dominance and the presence or absence of its capacity to predict leadership is addressed again in *Section 5.5: Dominance*.

5.3. Morphological differences

As already discussed in *Section 2*, structural size and body mass differences can affect flight speed at which power requirements are minimised (Fig. 1.1; Tobalske et al. 2003; Hedenström and Åkesson 2016). Larger birds, may therefore be faster, and faster birds may end up at the front more often, where pigeons effectively lead from (Yomosa et al. 2015).

5.4. Dominance

Dominance hierarchies are ubiquitous within social animal groups, and are proposed to be the result of competition for limited resources (Murton et al. 1972), and/or mating opportunities (Dewsbury 1982). The benefit to having a high dominance rank, which can be roughly defined as being the more likely winner of agonistic encounters against lower ranked individuals, is a disproportionately large share of the resources or mating opportunities (Landau 1951; De Vries et al. 2006). Although, these two factors may be intrinsically linked as the distribution of

resources is correlated with conspecifics of the opposite sex (Emlen and Oring 1977), and successful defence of high resource territories can result in increased individual fitness (Wells 1977).

With regards to decision making, dominance does not appear to predict leadership in pigeons, a system with consistent unshared leadership (Nagy et al. 2013), or olive baboons (*Papio Anubis*) which demonstrated weak consistent leadership (Strandburg-Peshkin et al. 2015). These findings have overturned earlier assumptions (see Strandburg-Peshkin et al. 2018); past reviews described consistent leadership as synonymous with dominance (Conradt and Roper 2003, 2009). This was because they have a disproportionately large (dominant) share of decisions, and made sense to converge the terms. However, this, and empirical studies which demonstrated a positive relationship between dominance and leadership (Schaller 1963; Peterson et al. 2002; King et al. 2008) may have led to the underlying assumption that dominance and leadership would be stable hierarchies with high correlation (Strandburg-Peshkin et al. 2018). Nagy et al. 2013, used a social networks approach and found, although both hierarchies were present and stable, there was no correlation between the two. As discussed in *Section 5.2: Leadership*, this may be the result of individual specialisation toward either flight or dominance.

5.5. Conformity

It is thought that when the selective pressure from predators is high, individuals in moving groups should behave similarly (to reduce costs associated with being the odd-one-out) and with high coordination to others (to increase benefits associated with predator confusion) (Farine et al. 2015). In general, group-level emergent properties (and hence their functions), are thought to be governed by simple and *similar* interactions (Biro et al. 2016). The fact that animals in moving groups often behave differently (Nagy et al. 2010; Jolles et al. 2013) could suggest alternative selective pressures (e.g. information or energetics), or differences based upon state or morphology (Herbert-Read et al. 2013). There is evidence of conformity in fish: Mcdonald et al. (2016) found that in groups, the importance of shared collective decisions outweighed a bold individual's tendency to lead shoals in less risky conditions. Herbert-Read et al. (2013) provide interesting evidence for conformity of speed in fish groups despite consistent individual differences in speed. They show that consistent preferred individual speeds are almost, but not completely, lost in the context of group movements.

6. Group phenotypic composition

The distribution or ratios of the individuals' phenotypes in groups either on-the-ground or in-flight could make a difference to the resulting group-level phenotype of the group, and the associated costs and benefits for individuals in the group (Farine et al. 2015). Examples of how the composition of the group can affect the

overall group phenotype are amounting. Kurvers et al. (2009) showed that time of arrival at a novel food patch could be predicted by both the focal individual's neophobia score (individual phenotype) and its companion's neophobia score (group phenotypic composition), with lower scores predicting reduced arrival times, and hence, potentially enhances net acquisition of food. Fish containing a mix of both bold and shy phenotypes approached food and achieved a greater overall yield per individual than groups of all bold or all shy individuals (Dyer et al. 2009). Another example is of ibis juveniles (phenotype), which cannot form V-formations (group phenotype) (Biro et al. 2016). Having not yet had the required hours of practice, the group level property – V-formation – cannot form, and the group level benefit – saved energy through aerodynamic advantages – is not achieved (see Chapter 5 for further discourse).

So, it may be expected that animals should evolve to make adaptive decisions about who to associate with, or how to behave according to the group's phenotypic composition, thus changing the group composition. For example, dominant meerkats (*Suricata suricatta*) evict subordinates of breeding age and condition from their groups, changing the composition of the group, which may maximise their own reproductive benefit (Stephens et al. 2004). Also, individuals could choose to join or leave a group, depending on the social context (Farine et al. 2015). Individuals have been shown to preferentially join flocks depending on the composition. Both downy woodpeckers (*Picoides pubescens*) and white-breasted nuthatches (*Sitta carolinensis*), were preferentially found to join mixed species flocks in the presence of parid species (tufted titmouse; *Baeolophus bicolor*, Carolina chickadee; *Poecile carolinensis*, black-capped chickadee; *P. atriacapillus*)

(Dolby and Grubb 1999). The presence of the tits is thought to enhance anti-predator or foraging benefits in the group, by taking advantage of their food locating and/or predator detection mechanisms (Morse 1970).

Already discussed are anti-predator benefits at the group level. It seems that if individuals are similar (assorted by phenotype), or at least can behave that way temporarily (can conform their behaviours; see *Section 5.5: Conformity*), they may achieve anti-predator benefits (Bode et al. 2010; Mcdonald et al. 2016). Potentially pushing in the opposite direction, intrinsic differences (i.e. heterogeneity) between individuals may lead to better collective decisions (Simons 2004; Couzin et al. 2011). This suggests that the context (i.e. navigational or anti-predator contexts) could be important to consider when considering the adaptive function of assortative grouping.

7. Context dependent optimal compositions (CDOCs)

7.1. Background

Another notable area for exploration would be how beneficial group phenotypic compositions may differ across context, here referred to as contest dependent optimal compositions (CDOC). While adaptive responses to modify the group's phenotypic composition or its collective phenotype is theoretically sound (Farine et al. 2015) and evidence is amounting (*Section 6*), there is little or no work investigating changes in optimal compositions given a specific ecological context. It

is likely that advances in this area will come from sorting groups by phenotypic composition (see Szorkovszky et al. 2016, and Chapter 5). Any consistent changes in individual level or group level measure (e.g. spatial positioning, leadership or energetic expenditure) which can be predicted by a combination of both social group and context (e.g. familiarity, risk, or social/aerodynamic context; *Section 2*) would be noteworthy. Such results may provide the first formal evidence of group compositions which increase fitness in different contexts. This could be a productive area of research, as changes in ecological factors (e.g. seasonality in temperate species) could provide a selective pressure for a reorganisation of group structure.

7.2. Potential applications

Progressing our understanding of context dependent optimal compositions (CDOCs) may have applications for welfare and conservation. Optimal group phenotypic compositions have already been elucidated (Sih and Watters 2005; Dyer et al. 2009; Keiser and Pruitt 2014), and theory has already applied in welfare (Bøe and Færevik 2003) and conservation work (Creel et al. 2013a; West et al. 2016). Group or individual level outputs such as stress, can be lowered providing benefits to both welfare and conservation (Creel et al. 2013a, b). Additional knowledge of how the benefits of GPC change with changing environmental context (CDOC) may be useful to practitioners.

8. Pigeons as a model system to test functions of flocking

8.1. Pigeons: ecology and flight

The domestic pigeon (*Columba livia domestica*, Gmelin 1789), birds of the family Columbidae, are the domesticated form of rock doves (*Columba livia*). Wild rock doves were found to feed on mainly lentiscus fruits for the duration of the study by Baldaccini, Giunchi, Mongini, & Ragionieri (2000), though the domestic pigeon is usually fed a combination of the following fruits (maize), cereals (wheat, barley, millet and sorghum), seeds (canary, sunflower and hemp seeds) and legumes (peas and lentils) (Sales and Janssens 2003). Domestic pigeons are prey to woodland-living Eurasian sparrowhawks (*Accipiter nisus*) and peregrine falcons (*Falco peregrinus*) which occupy coastal and inland areas, including cities (Henderson et al. 2004). Both rock doves and feral pigeons live in breeding groups, though rock doves breed mostly in coastal areas and cliffs (Johnston et al. 1988), whereas feral pigeons have adapted to breeding in cities from elevated building spaces, perhaps to remain as inaccessible to cats (*Felis catus*) as possible (Wheater 1999).

With an average of a pigeon's body mass (0.350 kg), wing span (0.665 m) and wing area (0.0649 m^2) (provided in Bruderer and Boldt 2001), theoretical predictions of flight speed estimated from general models of Pennycuick (1995) are U_{mp} 8.9 m/s and U_{mr} 14.7 m/s (from: Bruderer and Boldt 2001). Estimated speeds from radar tracking of rock doves in Israel found speeds between 14 and 22 m/s, and homing pigeon flight speeds were estimated as 19 m/s from a helicopter (Bruderer and Boldt 2001). This is remarkably close to a recent study on homing pigeons in which

GPS loggers were attached either to a Velcro strip on their back, or to an elasticated harness (Pettit et al. 2015; Fig. 1.7). The average of the bird's mean speeds was not given in the publication but appears to be close to 19 m/s (Fig. 1.7). These values are relatively high compared with the theoretical prediction. Alerstam et al. (2007) suggest this is due to the ecological need to fly fast. Pigeons are prey species which could suggest a *higher than predicted* speed (and therefore power) could trade off with the ecological necessity to out-run their predators, which, themselves can achieve remarkable speeds during dives, which have been estimated to be as high as 157 m/s in peregrine falcons (Tucker 1998).

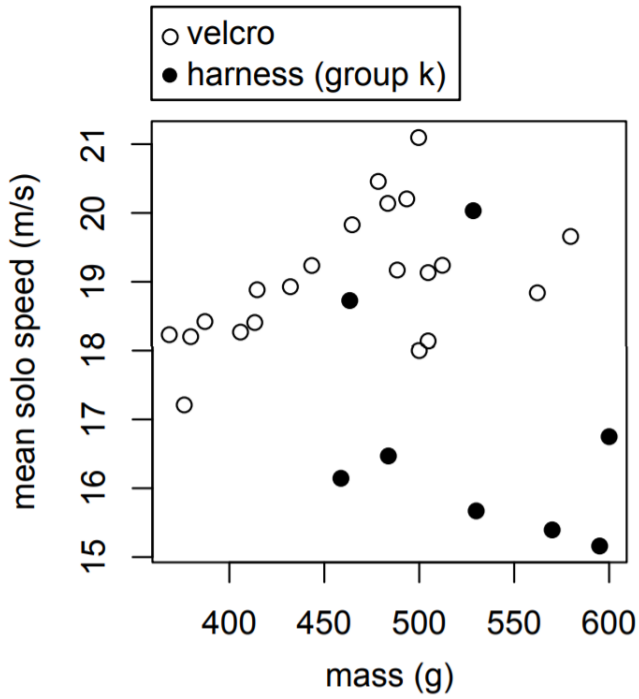

Figure 1. 7. Pigeon speed

Taken from Pettit et al. (2015), pigeons with Velcro attached loggers appear to have a mean speed of roughly 19 m/s during homing flights, when displaced 4-5 km from the home loft.

8.2. Pigeons, biologgers and welfare

The semi-captive housing and husbandry conditions, as well as the physiological traits of homing pigeons, may minimise the impact of biologging technologies to animal welfare (Portugal and White 2018). The attachment of external biologging devices has been demonstrated to negatively impact body condition, metabolism, survival and reproduction in free living birds (White et al. 2012). The findings suggest that the additional mass or drag (energetic cost) of the device decreases the fitness of individuals when released into natural and competitive environments. With regards to the mass of our loggers (21 g; see Chapters 2-6; Fig. 1.8), pigeons, which are small birds (weighing roughly 350-550 g), will carry an additional 3.8%-6% of their body weight. Welfare impact of such loadings may be mitigated by the short-term deployment, and continuous food supply provided for our pigeons (see Chapters 2-6).

Figure 1. 8. Biologger attachment

Taken from Taylor et al. (2017). Accelerometer (upper back) and GPS logger (lower back) can be attached via a Velcro strip to homing pigeons to record their movement patterns and wingbeat kinematics during flight.

8.3. Pigeon homing

The ability of the domestic pigeon to find its way home has long been utilised by humans for message carrying (Denny 2015), sport (Wallraff 2005) and research (Wiltschko and Wiltschko 2017). They have been known to home from previously unknown locations of up to 1000 km away (Ioalé et al. 1983). The mechanisms pigeons utilise to home from unknown locations are discussed in detail in *Section 1.2: Navigational environment*. Such reliability in their homing provides a study system which enables manipulations, vital to test our ideas of mechanistic

responses to environmental context (Chapters 2, 5 and 6). Additionally, the opportunity to release birds multiple times in the same conditions provides repeatability in our dataset (Chapters 2, 3, 5 and 6).

8.4. Suitability of pigeons in linking mechanism to function in bird flocking

Pigeons have provided evidence that fitness costs can differ at the individual level for the three proposed selective pressures/ functions of group flight (information use: Mehlhorn and Rehkaemper 2016; predator avoidance: Santos et al. 2015; energetics: Usherwood et al. 2011). Pigeons provide the opportunity to manipulate conditions and test predictions in a free-flying environment. By manipulating parameters, such as the 1) risk (Chapter 6), 2) familiarity of release site (Chapter 2) or 3) social/aerodynamic environment (Chapter 5), we may find that the strategies of individuals change, influencing fitness directly, or by having an impact on the emergent group spatial structure or energetics.

9. Research plan

Given their suitability to test the overarching questions of the thesis, I proposed that by manipulating the flight context, the relative weight of each of these three challenges could also be modified. The effect of experimental manipulations on the individual and group level processes may reveal how individuals respond

mechanistically to the imposed pressures, shedding light on the evolution of collective flight.

Chapter 2: Are flock dynamics responsive to the navigational environment? By manipulating the navigational context (i.e. route familiarity), I investigated the influence of individual phenotype on leadership dynamics. I suggested that the predictive power of a route-efficient phenotype on leadership may be masked in current studies, which predominantly release birds in only a "familiar" context (see *Section 5.2.2: Physiological leadership hypothesis*).

Chapter 3: Are there any "winners" and "losers" when birds come to a "speed consensus"? Also, is flock speed a shared outcome or dictated by influential individuals? Flocks need to speed match to retain cohesion, and hence the selective benefits of grouping on the move. I investigated which individuals were compromising the least/most, and whether compromise was linked to body mass or structural morphometrics (see *Section 2.3.2: Aerodynamic/energetic environment: Link to social environment*).

Chapter 4: Following an incident where a released group of my pigeons took an unexpected 177 km round trip from a release site only 9 km away, I investigated whether long-term energetic fatigue would have an influence on flock structure, reflecting a trade-off between energetic costs and other flocking benefits (i.e. protection from predators; Kenward 1978). I predicted that flocks would decrease in density over time (following Usherwood et al. 2011) (see *Section 1.3: Energy conservation*).

Chapter 5: Can the social context modify flock structure and function? Here, I assorted groups of pigeons by “leadership rank” or “mass”, testing the impact of the group phenotypic composition on flocking dynamics such as flock spread, stability, speed, and the energetic expenditure of the individual birds (see *Section 1.3: Energy conservation* and *Section 6: Group phenotypic composition*).

Chapter 6: How do individuals in flocks respond to predation threat, and what are the collective outcomes of these individual responses? Using a robotic peregrine falcon, I tested game-theoretic principles on individual decision making, to elucidate how individuals respond to predators, and whether their decisions are more aligned with “cooperative” or “selfish” benefits (see *Section 2.4.4: Social environment: Linking mechanism to function – attraction and alignment*).

Chapter 7: General Discussion: I tie up the results in the context of current literature, and provide some novel insights from my three years studying bird flocks. I critique many of our current philosophical and experimental paradigms, and suggest research question for future work on collective bird flight.

Chapter 2: Pigeon leadership hierarchies are not dependent on environmental contexts or individual phenotypes

Daniel. W. E. Sankey[1], Dora. Biro[2], Rhianna. L. Ricketts[1],

Emily. L. C. Shepard[3] and Steven. J. Portugal[1]

Author affiliations:

[1] *School of Biological Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, U.K.*

[2] *Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, U.K.*

[3] *Swansea Laboratory for Animal Movement, Biosciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, Wales, U.K.*

Abstract

Remaining cohesive on the move can be beneficial for animal groups, and 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 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 have 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 behavioural, morphological and "in-flight" phenotypes on leadership – using homing pigeons (*Columba livia*) (N = 16), a classic model species of leadership, divided into two groups (N = 7 and N = 9). We flew birds in *i*) solo and familiar (N = 6), *ii*) solo and unfamiliar (N = 5) contexts to measure solo speed and solo route efficiency (using GPS biologgers; 5 Hz). Further, we flew *iii*) group and familiar (N = 12), and *iv*) group and unfamiliar (N = 5), to asses group leadership across environmental context. Pigeon leadership hierarchies were similar across environmental context. However, we found that no covariates could predict

leadership score in either context, besides body mass, with heavier individuals leading group movements more often than lighter individuals. Even body mass was predictive of leadership in only one group, though this group had more than twice the range in body mass than the other group (117 g vs 56 g), which could potentially explain the difference. Our results highlight a discordance between empirical work and current theoretical hypotheses of leadership mechanisms. We provide suggestions for improved methodologies, and ideas for future work to test hypotheses regarding phenotypic variation and leadership.

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). For example, pigeons which navigate in groups take more accurate trajectories in comparison to solo fliers (Biro et al. 2006; Dell'Ariccia et al. 2008; Taylor et al. 2019). 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 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) or speed (Sankey et al. 2019; Chapter 3). 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), and this has 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 pigeons (*Columba livia*; Nagy et al. 2010), common zebra (*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 the hierarchies can be context-dependent (Nagy et al. 2013). We ask 1) whether leadership structure is also context-dependent with regards to the environmental conditions in which the observations are made, and 2) whether phenotypic predictors of leadership differ accordingly.

Empirical work on homing pigeon (*Columba livia*) 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 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). A key difference between these two studies was the level of experience from the release site in the less knowledgeable individuals (Table 2.1). Relatively more trained (and more efficient) individuals show enhancements in their leadership rank when "inexperienced" individuals had *three* training flights (relatively "unfamiliar") from a site, but did not when they had *eight* (relatively "familiar") (Table 2.1). The total difference between the number of flights between "inexperienced" and the "experienced" individuals was similar (Table 2.1), however, an essential point here is that gains in route efficiency with number of flights from a site is non-linear (Meade et al. 2005; Guilford and Biro 2014; Taylor et al. 2017). The impact of repeated flights on route efficiency are typified by an initial *steep rise*, followed by a *plateau* (Freeman et al. 2011; Taylor et al. 2017), whereby a "stereotypic route" is formed (Meade et al.

2005; Sasaki and Biro 2017). The estimate for when efficiency plateaus ranges from six flights (Flack et al. 2012; Taylor et al. 2017), through to between eight and ten flights (Guilford and Biro 2014), with typical route efficiencies plateauing at between 0.75 (Flack et al. 2012) and 0.8 (Flack et al. 2012; Guilford and Biro 2014) (relative to a perfect beeline trajectory at a value of 1). Therefore, the route efficiency of "inexperienced" individuals with *three* training flights (Flack et al. 2012) is likely to be markedly lower that those with *eight* training flights (Flack et al. 2013) (Table 2.1).

Similarly to how route efficiencies plateau, their impact on flock leadership may also reach a point at which no additional influence is conferred (Fig. 2.1). Experimental manipulations which increased the directional error – and simultaneously decreased the influence of previously established leaders – has demonstrated the potential impact of route efficiency on leadership elegantly (Watts et al. 2016). Given that pigeons use a "sun compass" as part of their navigational toolkit (reviewed in Wallraff 2005), clock-shifting procedures can be used to reliably decrease route efficiency (Biro et al. 2007). Watts et al. (2016) used such procedures to show that "misinformed" leaders lose influence in pigeon flocks. Additionally, pigeons with more efficient idiosyncratic "familiar" routes were *not* shown to have greater influence in pigeon pairs (Table 2.1; Freeman et al. 2011), shedding further doubt on the impact of route efficiency on leadership from "familiar" flight locations, where route efficiencies may be high across the group. With respect to our initial questions, i.e. whether leadership is context dependent, and whether phenotype can predict the respective hierarchy, we have identified "familiarity" as a potentially relevant environmental context. Further we suggest

that the predictive power of phenotypic differences of homing ability (or route efficiency) on leadership could be masked by the comparatively low degrees of compromise in "familiar" flights, but could influence leadership in an "unfamiliar" context.

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, across a host of different taxa (Fischhoff et al. 2007; Kurvers et al. 2009; McComb et al. 2011; Ioannou et al. 2015; Jolles et al. 2017). Firstly, consistent inter-individual behavioural 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 behavioural manifestation of internal tendencies to take risks (Wolf et al. 2007; Sih et al. 2012), which may reflect an individual's position on a "pace of life" spectrum (Réale et al. 2010). This spectrum, ranging from "fast reproduction, but low survival" to "slow reproduction, but high survival", is potentially governed by internal physiological mechanisms (Réale et al. 2010; Sih et al. 2014), like faster metabolic rates (Biro and Stamps 2010). Greater risk-taking may result in flock leadership by increasing an individual's "initiation attempts" (King 2010; Ioannou et al. 2015) in a preferred direction of travel (Ioannou et al. 2015). Also, faster metabolic rates could lead to increased speed (and hence leadership (Pettit et al. 2015; Sasaki et al. 2017)) by providing a greater supply of chemical energy to wing muscles (Tobalske 2007), and/or through enhanced

growth-rate, conferring greater body mass and structural size (Biro and Stamps 2010). Body mass and structural size are known to be associated with flying speed across species (Alerstam et al. 2007), and body mass has been shown to predict speed in pigeons (Pettit et al. 2015). Sasaki et al. (Sasaki et al. 2018) found that "bolder" pigeons occupied higher leadership ranks in pigeons and that this was consistent across "familiar" and "unfamiliar" release flights. Nevertheless, the criteria for "unfamiliar" in this study was <7 flights from the same location (Sasaki et al. 2018). If behavioural traits are governed by a "risk taking" mechanism, it might be expected that their influence on leadership will be greater in the *first release* from a truly novel, "unfamiliar", and presumably riskier (Lima 1998) site, than releases from "familiar" locations.

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 many phenotypes in the aforementioned *i*) behavioural (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 (Fig. 2.2). Prediction (1): in familiar flight releases, only speed will be predictive of higher leadership (following Pettit et al. 2015). Prediction (2): from unfamiliar release sites, where all individuals may have on-average lower route efficiencies (Fig. 2.1), 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) behavioural 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).

Table 2. 1. Previous studies on route efficiency and pigeon homing

First column: authors and citation. Second column: number of training flights for less route efficient pigeons. Efficiency differed due to either less experience (first and second row), increased directional error, via a clock-shifting procedure (third row) or intrinsic inter-individual differences (fourth row). Third column: number of training flights for birds with greater efficiency for each respective study. Fourth column: whether a positive impact of route efficiency on leadership was found in statistical tests employed by the authors of the respective studies (Y/N).

Study	Number of flights – lower route efficiency	Number of flights – greater route efficiency	Observable effect of route efficiency on leadership?
(Flack et al. 2012)	3	15	Y
(Flack et al. 2013)	8	18	N
(Watts et al. 2016)	8, but "misinformed"	8	Y
(Freeman et al. 2011)	20, intrinsically less efficient	20, intrinsically more efficient	N

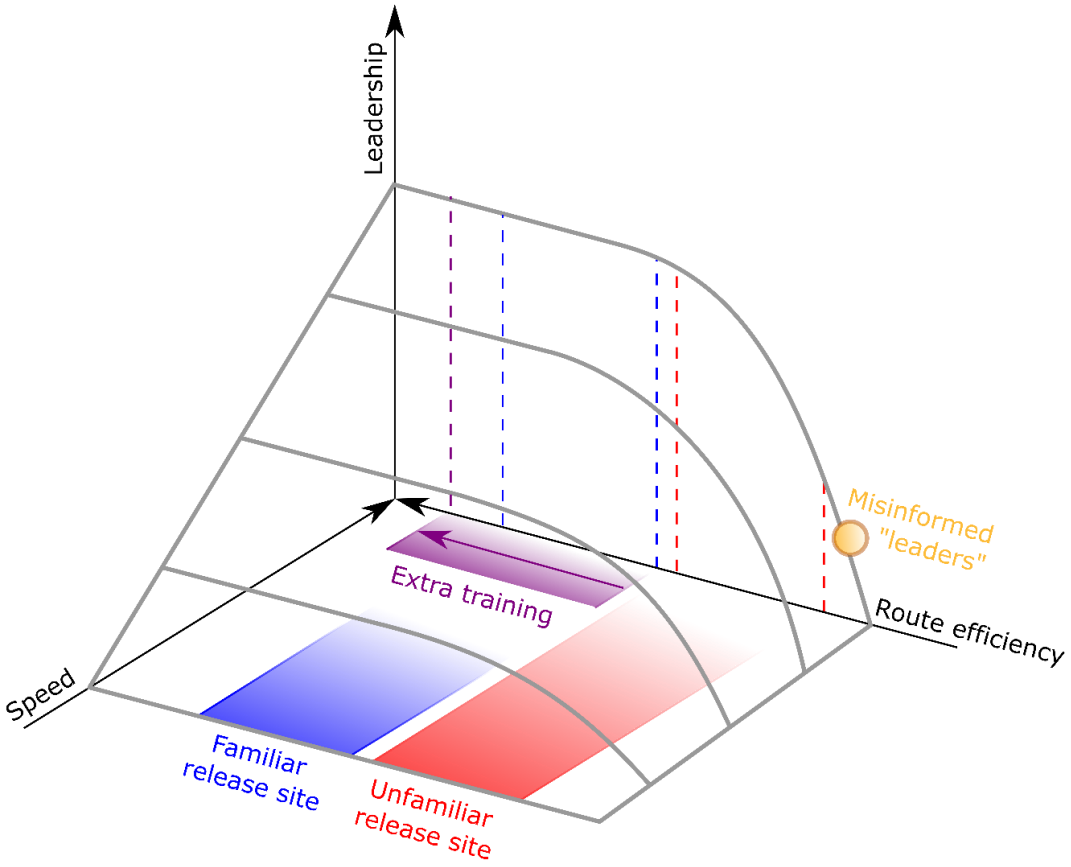

Figure 2. 1. Speed, route efficiency and leadership: a summary of previous findings

Leadership (y-axis) has been shown to positively covary with increasing relative speed (left side of figure; Pettit et al. 2015; Jolles et al. 2017a). Leadership may increase with greater individual route efficiencies, but with a plateau (right side of figure; evidence from Flack et al. 2012, 2013; Watts et al. 2016). Previously "leading" pigeons with artificially reduced route efficiencies ("misinformed leaders"; yellow/orange orb) have been shown to diminish in navigational influence (Watts et al. 2016). While we do not know the relative solo speed of these "misinformed leaders", we have placed this observation in hypothetical space with high speed and low efficiency. When birds are familiar with a release site, they demonstrate high but variable route efficiencies (blue shaded area) (Freeman et al. 2011; Flack et al. 2012; Taylor et al. 2017). If the leadership/route efficiency relationship plateaus, this may explain why leadership does not covary with

additional route efficiency gains from familiar release sites either through extra training (purple shaded area; Flack et al. 2013), or through intrinsic inter-individual differences in route efficiency from familiar sites (Freeman et al. 2011). Subsequently, this relationship would explain why larger differences in experience (where some individuals were "unfamiliar"; red shaded area) showed a positive impact of route efficiency on leadership (Flack et al. 2012). We predicted that, from "unfamiliar" release sites, intrinsic phenotypic differences in *i*) speed and *ii*) homing competence (greater normal route efficiencies) would increase leadership; whereas only speed would predict leadership from "familiar" release sites.

Methods

Subjects and materials

Housing

A group of 18 homing pigeons (*Columba livia*) aged 11 – 15 months old were kept in two flocks of nine pigeons at Royal Holloway University of London, U.K. 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 (7ft x 6ft). The pigeons were provided with *ad libitum* access to food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, U.K.), water and grit.

Biologgers

For flight metrics – speed and route efficiency (solo flights), and leadership and spatial positioning within the flock (group flights) – we deployed miniaturised GPS loggers (QStarz BT-Q1300ST, Düsseldorf, Germany' 5 Hz; 12.5 g) attached to the back of the birds (Sasaki et al. 2018; Taylor et al. 2019) (for full attachment and biologger methods, see *Supplemental Material*). We also attached accelerometers (AX3, Axivity Ltd, Newcastle upon Tyne, U.K.; 200 Hz; 8 g), the data of which were not used in the present study.

Familiar/unfamiliar experiment

"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. 2.2) (June-August 2017; Table S2.2). 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 Table S2.2 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 (see *Introduction* and Flack et al. 2012; Taylor et al. 2017). The flight bearing for group 1 was north (actual bearing = -0.14rad), and the flight bearing for group 2 was east (actual bearing = 0.79rad; Fig. 2.2). This was to avoid confounding aspects associated with *i*) flights across a latitudinal gradient (e.g. 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 experimental flight season.

"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; Table S2.2). Here we used a series of five additional release bearings per group, all spaced >45° from the "familiar" release bearing (see Fig. 2.2). The closest "unfamiliar" release bearing to the "familiar" flight bearing was 0.93rad (53.45°) for both groups, between bearing "N" and bearing "E" (see Table S2.1). Each "unfamiliar" flight bearing had two sites (at ~5 km and ~9 km), totalling 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 Table

S2.2). Group and solo flights were divided as evenly as possible between 5 km sites and 9 km flights (Table S2.2).

After all flights had been conducted we visually assessed the trajectories (Fig. 2.2). There was very little cross over between the trajectories for "familiar" and "unfamiliar" flight paths, validating our choice to analyse these trajectories separately.

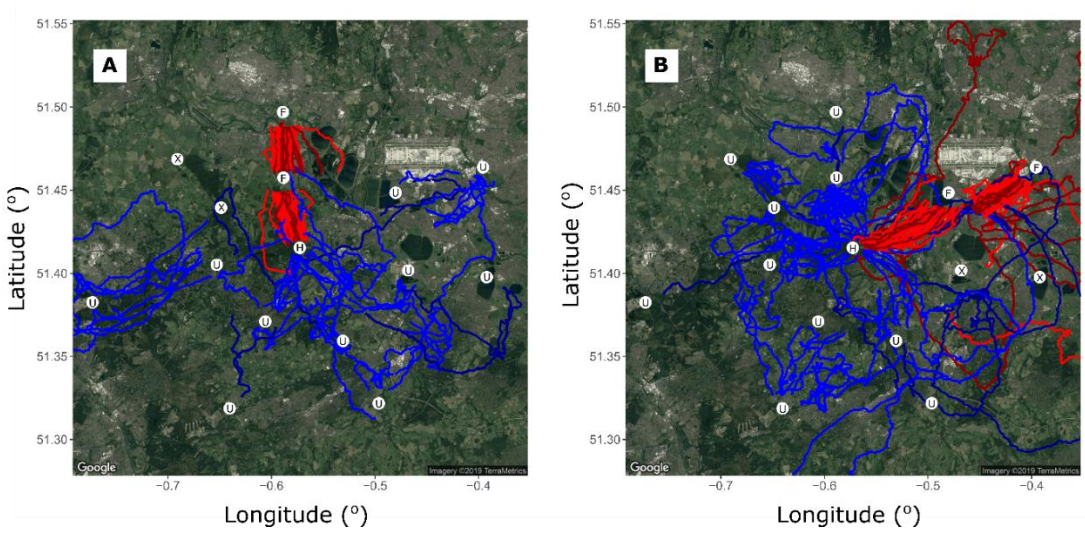

Figure 2. 2. "Familiar/unfamiliar" pigeon flight releases

GPS trajectories from "Familiar" (F) release sites (>9 flights from a given location) are coloured red; trajectories from "unfamiliar" (U) sites are coloured 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 coloured dark red/blue. **(A)** Group 1 flight trajectories, where "familiar" release bearing was north (-0.14rad). **(B)** Group 2 flight trajectories, where "familiar" release bearing was east (0.79rad). 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).

Phenotype assessment

In-flight phenotype

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 Chapter 3). 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. For detailed methods see Chapter 3, and Safi et al. (2013).

Solo route efficiency

The distance for perfect accuracy (or, beeline) was divided by the total distance travelled 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).

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 maximises 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. See more detail on leadership calculations in *Supplemental Material*.

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 *Supplemental Material*). See more detail on this calculation, see Chapter 4.

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.

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 estimated 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.

Behavioural phenotype

Personality

To measure individual differences in behaviour, we assessed exploration of a testing arena (180 x 150cm loft; divided into nine equal rectangles of 50 x 60 cm

using tape; Fig. 2.1). A novel object was either *present* (neophilia trials; e.g. Kurvers et al. 2009; Schuett et al. 2011) in the centre of the bottom-right square, or *absent* (boldness trials; Kurvers et al. 2009; Cote et al. 2011). Novel objects used included a backpack wrapped in pearlescent wrapping paper, a large water bottle painted with neon colours, 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: Transforming "personality" data*).

Dominance

We video recorded and analysed the agonistic interactions in nine "dominance trials" dominance in each of the two flocks (for full protocol see *Supplemental Material*). Agonistic behaviours: chasing, feather pulling, wing slaps and neck grabs (Nagy et al. 2013; Portugal et al. 2017b) were recorded into a matrix with an initiator (winner) and receiver (loser) for each instance of a behaviour. We repeated the protocol, and all interactions from the nine videos for each group were totalled – as pigeons have dominance hierarchies that are highly stable (Nagy et al. 2013; Portugal et al. 2017b). We calculated normalised 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).

Statistics

Repeatability

If a given behavioural/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.

2017a). Results from all repeatability analyses are detailed in the *Supplemental Material*.

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*) "behavioural" 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 enquiry, 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 (i.e. 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 Table S2.3.

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. For the PCA analysis, we ran an LME on leadership over the first three principal components from all PCAs (N = 9; 3x morphological/behavioural/flight). We then used multimodel inference (using "dredge" function from R package MuMIn; Allwood et al. 2007; see dredge output in Table S2.4) 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.

Results

Leadership hierarchies were significantly transitive (i.e. interactions down the hierarchy point in the same direction) and linear (i.e. no large "jumps" between the scores of individuals in consecutive ranks) in familiar flights and unfamiliar flights (familiar flights; group 1: 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). Transitivity for group 1 was low in unfamiliar flights, which may be due to a paucity of data where the flock remained cohesive (N = 5 "unfamiliar" group flights, vs. N =

18 “familiar” group flights), though transitivity for group 2 “unfamiliar” was still high (T = 1). Leadership was consistent across context, i.e. “familiar/unfamiliar” flights (LM; DF = 14, t = 2.39, p = 0.033), though, not if each flock was treated separately (LM; group 1: DF = 5, t = 1.745, p = 0.141; group 2: DF = 7, t = 0.331, p = 0.750). The results from our predictions follow (Fig. 2.3A-D)

Prediction 1: solo speed, and 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. 2.3C). 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. 2.3). However, group 2, which had lower overall route efficiencies than group 1 (*t – test*: DF = 10.713, t = 9.987, p < 0.001; Fig. 2.2A), showed a positive relationship between leadership score and solo route efficiency, though this relationship did not hold unless one outlier (verified as an outlier with “Cook’s D”; Kim and Storer 1996) was removed from the dataset (with outlier – LM: DF = 7, t = 2.012, p = 0.084; outlier removed – LM: DF = 6, t = 2.631, p = 0.039; Fig. 2.3A). Group 2 (released from an Easterly bearing; Fig. 2.2) also had significantly lower airspeeds than group 1 (released from a Northerly bearing; Fig. 2.2) (t – test: DF = 168.85, t = 16.071, p < 0.001; see Chapter 2). Individuals which flew more often at the front of the flock (higher cranio-caudal distances) had higher leadership scores (LM; DF = 14, t =

1.978, p = 0.070). An individual's peak route fidelity had no impact on leadership (LM; DF = 13, t = -0.717, p = 0.486).

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 found them to not be predictive (LM: DF = 14, t = 0.121, p = 0.905; Fig. 2.3B).

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. 2.3D). Thus, the consistent and repeatable differences in individual preferred speed in solo familiar flights (R = 0.346 ± 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.

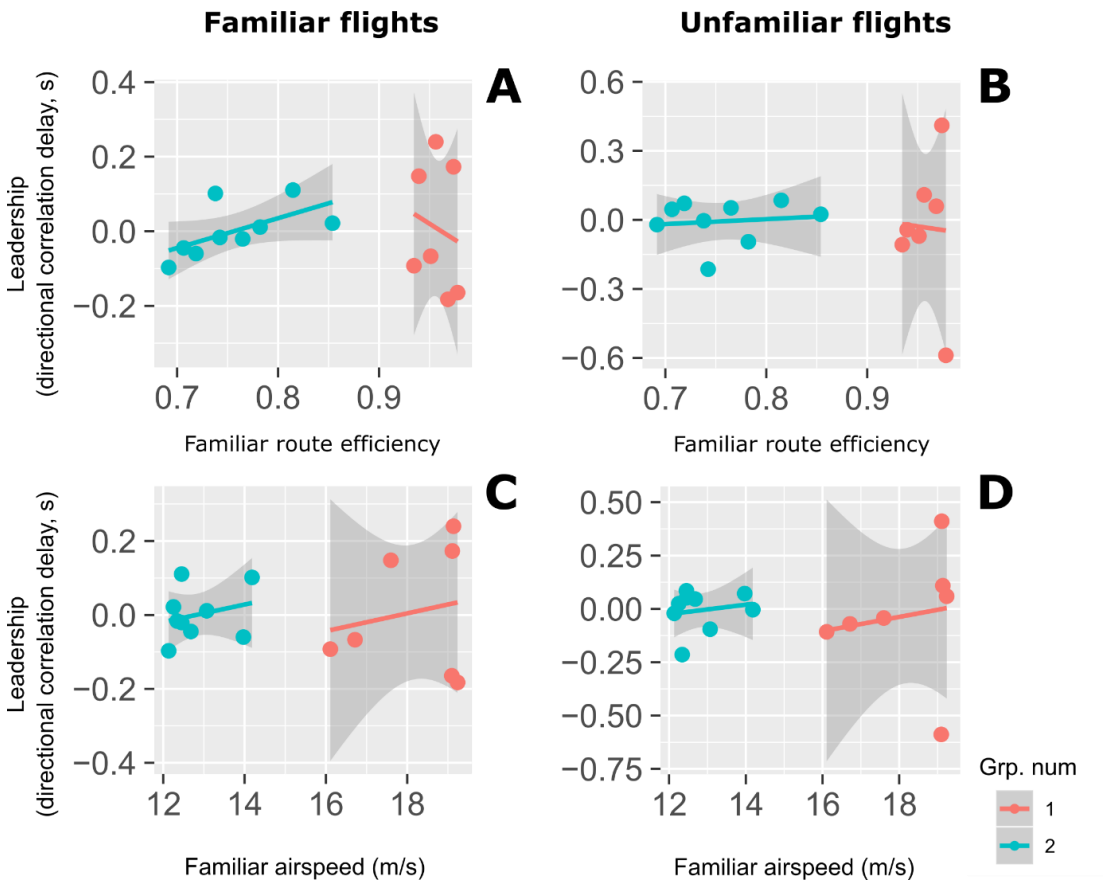

Figure 2. 3. Leadership, speed and route efficiency: results following predictions

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 (Table S2.1). Plots were generated in ggplot2 with 95% confidence intervals around a predicted linear model per group.

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), were significantly positively correlated (LM: DF = 14, t = 2.607, p = 0.021; Fig. 2.4), 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. Behavioural PC2 – corresponding mostly to the inverse of exploration (PCA loading = -0.94795, maximum range = -1 to 1) – was the greatest predictor of the behavioural components on leadership (Table S2.4). Nevertheless, exploration was not predictive of leadership in either "familiar" (LM: DF = 14, t = 1.03, p = -0.321; Fig. 2.4) or "unfamiliar" flights (LM: DF = 14, t = -0.744, p = 0.469; Fig. 2.4).

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. 2.4), 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. 2.4), whereas boldness was not (LM: DF = 14, t = 1.389, p = 0.186). This indicates that individuals more willing to investigate novel objects took up higher dominance ranks, but not those with decreased latency to leave the box.

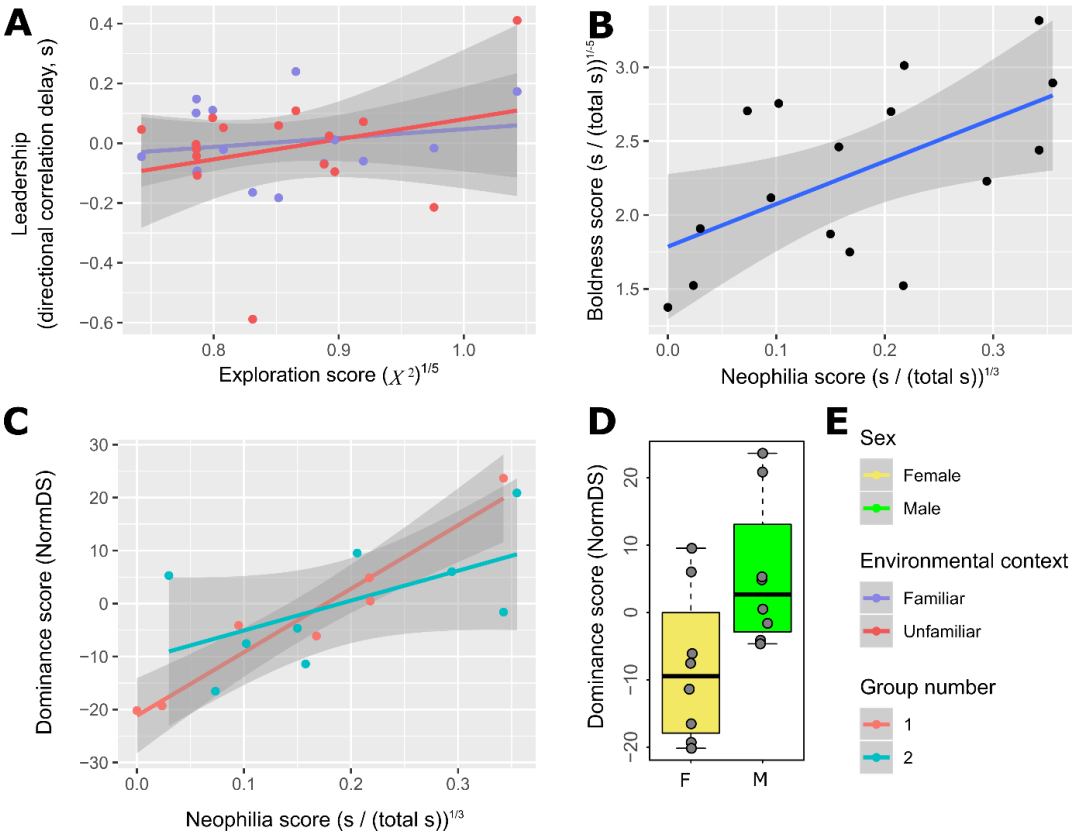

Figure 2. 4. Pigeon "personality" results

(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 normalised 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 (grey) illustrating dominance score (NormDS) against bird sex (yellow = female; green = male). **(E)** Legends for previous plots.

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; Table S2.3) 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. 2.5) 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. 2.5), and was not present in group 2 (LM; DF = 7, t = -0.474, p = 0.650; Fig. 2.5). 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; see Chapter 3), 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. 2.5) but not in “unfamiliar” flights (LM; DF = 14, t = 1.481, p = 0.161; Fig. 2.5).

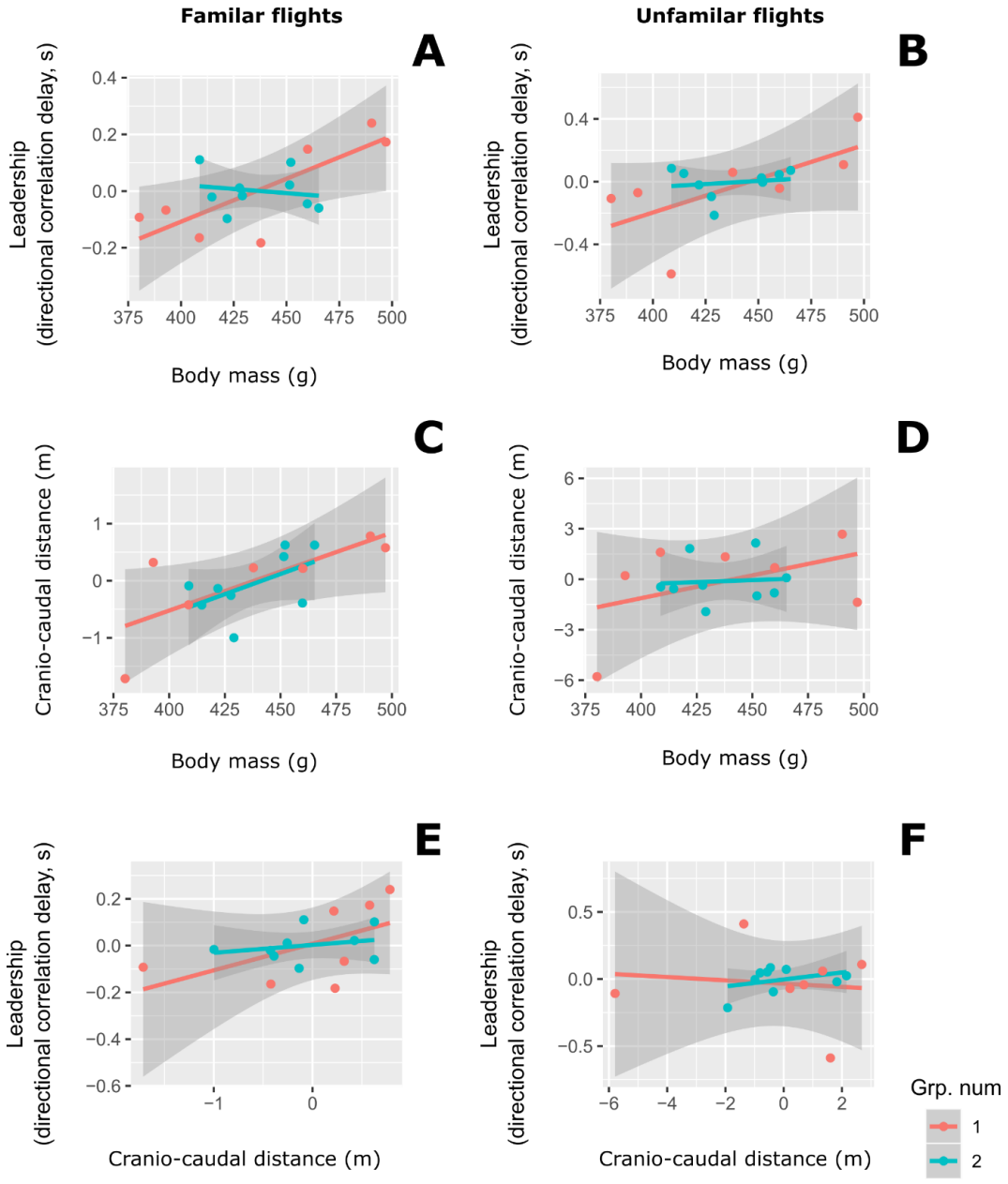

Figure 2. 5. Body mass, airspeed, and cranio-caudal distance in “familiar” and “unfamiliar” flights

(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 (see *Results*), though this may be due to their much smaller range in body mass (see *Discussion*). **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 (see *Results*). The effect of body mass (g) on **C)** cranio-caudal distance (m), and **D)** airspeed (m/s), was positive and significant (See *Results*).

Discussion

We did not find any evidence for context-dependent leadership hierarchies across environmental context (i.e. flights from "unfamiliar" and "familiar" terrain). Leadership across the two conditions was consistent across all data, though not when considering each group separately (see below). Additionally, 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 (see *Introduction*), 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 "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 (Schmidt-Nielsen 1972; Pettit et al. 2015; Sankey et al. 2019; Chapter 3), why should body mass predict leadership while solo flight speed did not? We expect that inter-individual differences in preferred solo flight speed (correlated with body mass, but not with leadership) could actually be predictive of leadership, but due to methodological imprecision, may not be observable in our dataset. At present, despite the "big data" provided by biologgers, our field, more often than not, uses an *averaging* approach to study individual *phenotype* (Freeman et al. 2011; Flack et al. 2012; Nagy et al. 2013; Pettit et al. 2015). Yet, speed, and all other variables, actually have high variance, both with and between flights (Pettit et al. 2013b). An approach to studying this variance has been utilised recently in the field of "animal personality" (Dingemanse et al. 2010, 2012; Webster and Ward 2011). We suggest such a method – incorporating variance within and across flights – could be beneficial in future work bridging the fields of leadership and "personality". Additionally, measurements of wind speed could – and perhaps need to be – improved to get measures of speed with enough precision to tease apart fine scale differences in leadership. Williams et al. (2018) have demonstrated that small, 2 mm diameter, "Pitot tubes", and barometric pressure sensors can be combined to measure airspeed, as experienced by soaring vultures, at high frequencies (40 Hz). These data, if utilised in pigeon leadership studies, could provide a better understanding of the relationship between body mass, flight speed, and concurrent leadership. An alternative explanation, that body mass

corresponds to dominance, which (in turn) predicts leadership, was not probable given no relationship between dominance and mass or leadership in *i*) our data, and *ii*) the results of Nagy et al. (2013) which found, likewise, no correlation between dominance and leadership.

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 stabilising. 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.

We argue that future research into the predictive power of route efficiency on leadership is highly important, because current hypotheses of collective motion implicitly assume that some degree of route efficiency will enhance an individual's influence in flocks. A major hypothesis explaining effective leadership posits that moving flocks enhance navigational accuracy via 1) a "sharing" (averaging) of directional preferences at low degrees of compromise (Couzin et al. 2005), and then 2) either follow one path or split (Biro et al. 2006; Sueur et al. 2011) when compromise is high (Couzin et al. 2005; Strandburg-Peshkin et al. 2015). In pigeons, which demonstrate unshared consensus over directional decisions (Nagy et al. 2010), this "sharing" may be skewed (unshared), favouring the directional decisions of individuals at the front (Nagy et al. 2010; Pettit et al. 2015; Yomosa et al. 2015). This might explain why route efficiency is less important in a "familiar" (low compromise) context (Flack et al. 2013) than when differences between route familiarity were greater (Flack et al. 2012). There is empirical evidence for the second part of this hypothesis in pigeons also. Biro et al. (2006) showed, using pairs of pigeons in a "familiar" context, but with highly conflicting idiosyncratic routes, that one individual would follow the other, or the pair would split and each go in

their preferred direction (Biro et al. 2006). Nevertheless, given that groups take more efficient routes than solo fliers (Dell'Ariccia et al. 2008; Taylor et al. 2019), the natural parsimony of the efficient individuals' routes would be thought to govern enhanced leadership through the following: 1) Following behaviour will emerge in individuals which temporarily attempt their own preferred direction before being drawn back into alignment with the "efficient" group. 2) Efficiency will confer greater speed – relative to the direction of travel. Finding no influence of route efficiencies in pigeons from "familiar" flights either suggests that 1) unshared consensus is heavily skewed (which would not explain why pigeons navigate more effectively in groups), or 2) individual route stereotypies are mostly ignored in pigeon flocks larger than pairs, perhaps in favour of balancing other environmental cues (e.g. "sun compass", magnetic field detection or olfactory cues; reviewed in Wallraff 2005), with social information (Guttal and Couzin 2010). Also see Chapter 7 for a novel third explanation involving individual decisions to balance "risk" and "compromise".

We observed a suggestive relationship between route efficiency and leadership score in "familiar" flights for group 2, which had lower overall route efficiencies than group 1. No such relationship was found in group 1 with high route efficiencies. (See Chapter 3 for further discussion on speed and efficiency differences between the two groups, thought to be linked to wind direction differences between the groups). Together, these data provide preliminary evidence of a plateauing effect of route efficiency on leadership (see Fig. 2.1; Fig. 2.3A). Firstly, in group 1, it is possible that the naturally high solo efficiencies reduced the route-conflict below a particular threshold, which diminished the

impact any further gains in efficiency could have on leadership (Fig. 2.1; Chapter 7). Second, in group 2, with lower overall efficiencies (and hence route-conflict), inter-individual differences in route efficiency may have a positive impact on leadership (See *Introduction*, Fig. 2.1; Watts et al. 2016; also see Chapter 7).

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. 2017b) and 2) the *costs* of route compromise (i.e. going in an undesirable direction; Conradt and Roper 2005; Sueur et al. 2011) (see Chapter 7). 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 behavioural ecology, which can explain how differences in fitness payoff can be maintained (Eberhard 1982; Dominey 1984; Emlen 1996; Davies et al. 2012). For example, male dung beetles (*Podischnus agenor*) of low body mass (due to ontogenetic conditions; Eberhard 1982; Dominey 1984) always demonstrate lower fitness than heavy individuals (Eberhard 1982; Davies et al. 2012). To mitigate this disadvantaged position, lighter dung beetles do not invest in horns, as heavier individuals do (despite being capable of doing so). In this way they do not risk further fitness losses, and therefore exhibit an optimal strategy given their phenotype (Emlen 1996). Alternatively there may be additional predation costs of leadership (Ioannou et al. 2019). Ioannou et al. (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 and remain evolutionarily stable via frequency dependent benefits (Johnstone and Manica 2011; Chapter 1).

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.

Our data suggest that ground-based dominance hierarchies may be more predictable than leadership hierarchies. Neophilia was consistently repeatable across individual, and predicted dominance rank. At present we cannot accurately assess whether dominance governs neophilia, or neophilia governs dominance, or that a completely different trait governs both (Kurvers et al. 2009). It was not our aim to disentangle such relationships, nevertheless, this finding highlights how little we still understand about the interaction between personality, and the hierarchical networks of dominance and leadership in pigeons (Nagy et al. 2013), geese (Kurvers et al. 2009), baboons (King et al. 2008) and many other species (Strandburg-Peshkin et al. 2018). It seems that two hierarchies (leadership and dominance), which are thought to confer benefit to high ranking individuals (Nagy et al. 2013), should relate to one another somehow, because benefits accrued in one interaction could be expected to "pass over" into favourable conditions for another. Perhaps there could a frequency dependent ratio of "dominant" types and "leader" types. Alternatively, the fitness benefits of leadership could be smaller than currently assumed (see Ioannou et al. 2019 and above for support of this point), and the magnitude of dominance benefits (Landau 1953) belie any gains from leadership influence. While the answers to such questions are likely to show species specific differences (Strandburg-Peshkin et al. 2018), these hypotheses remain untested in any system. As such, we argue that more focus on the interaction of stable hierarchies could be critical to understanding how hierarchical structures evolve and remain stable in animal populations.

Supplemental material

Flights

Flight training

To assess solo and flight differences in solo and group responses to unfamiliarity, we performed all training flights within 1 km of the home loft. Each bird was released 10 times from a mixed variety of locations within this 1 km radius around the loft.

Biologger attachment

We attached Velcro (hook side) to trimmed feathers on to the backs of the pigeons with epoxy glue (Araldite Rapid Adhesive, Araldite, Basel, Switzerland). The feathers were trimmed to increase the stability of the biologger attachment (following: Pettit et al. 2013b; Sasaki et al. 2018), as Velcro strips grip more closely to shorter feathers. Epoxy was prepared and applied following manufacturer instructions.

The GPS (5 Hz, QStarz BT-Q1300ST, Düsseldorf, Germany) circuit board and battery were removed from the outer casing to reduce mass (12.5 g after removal). Furthermore, the GPS were placed into small clear zip-lock bags and sealed with additional clear tape to prevent water damage to the loggers. Accelerometer loggers (Axivity AX3, Axivity Ltd, Newcastle upon Tyne, U.K.; 200 Hz; 8 g) were not placed in bags due to their plastic external casing. The Velcro (hoop side) was

attached to the zip-lock bags, or the outer casing for GPS and accelerometers respectively. The total logger mass was 20.5 g, which, given the mass distribution of the birds (380 g – 497 g) represents 4.1% - 5.4% of their total body mass. Although this violates a commonly cited "5% rule" (Portugal and White 2018), in some individuals (*N* = 4), the birds had unlimited access to food upon return, and thus semi-captive species, in this way, may be less vulnerable to greater mass loadings (Portugal and White 2018). For this study, and Chapters 3 and 4, Accelerometers and GPS were switched on and attached before transit, and data for the journey removed post-hoc.

Release protocol

For each flight release, we first checked that no rain was forecast, and that cloud coverage was less than 50%. If these conditions were met, one group of pigeons (either of the two groups; see *Methods*) were gathered from their respective loft, only one group at a time, and biologgers were switched on and attached (above) before transferring the birds into wicker boxes (80cm x 40 cm x 22cm). The birds were then driven to the intended release site (with the vehicle window open) for a maximum transit time of 25 mins. For solo flights, individuals were released, by hand in the order they were randomly selected from the wicker transport box. For group flights, all birds were released at the same time, by opening the side hatch of the wicker basket.

Treatment of biologging data

Cleaning and trimming GPS trajectories

We removed erroneous duplications of timestamps from the GPS data, and created additional rows (labelled "NA") for any missing timestamps. We further removed any erroneous coordinates from logger error; this was estimated at timestamps which would have required the pigeon to move at over 50 m/s. Trajectories were trimmed between 1000 m from release site and 500 m from home (see Taylor et al. 2017 and Chapter 3 for further validation); 9 km trajectories were trimmed between 500 m from release site and ~5 km+500 m from home (~5 km but depending on release site; see *Methods* and Table S2.1).We omitted ~5 km of the flight trajectory from 9 km flights as this was the same terrain as the shorter flight from this bearing (see trimmed trajectories in Fig. 2.2). The exact distance omitted was equal to an accurate distance from home to the 5 km site (see Table S2.1) calculated by the distance between the site coordinates and using a spherical projection of the earth (see Chapter 3 for detailed methods).

Removal of paired flights from solo GPS trajectories.

To determine solo flight speed, route efficiency, and route fidelity (Freeman et al. 2011), it was imperative that birds did not fly in pairs. Although solo releases of each individual were staggered, inevitably some birds did pair up between the release site and home. By calculating the distance between each of the bird's trajectories, we were able to determine how close and for how long pigeons flew

together if they did pair up. Our criteria for exclusion was that the birds were together (< 50 m; Pettit et al. 2015) for more than 50% of the journey home; if the criteria were met, that flight was removed from subsequent analyses

Centroid position and heading calculation

The centroid of a flying group was given by the mean of all pigeons' latitude and longitude at each timestamp, following the removal of any individuals which had split from the group. The furthest pigeons were removed from the centroid calculation one-by-one from the group if their distance to the centroid was over 50 m in a jack-knife fashion (see Chapter 3 and Portugal et al. 2014 for detailed methods). Centroid heading (or group-average heading, as referred to in *Methods*) was given by the angular difference between two successive locations with respect to north.

Leadership

We used directional correlation (r) over time-shifted (s) movement trajectories for pair-wise combination of birds to assess leadership. Essentially, one individual was "leading" another if their movement trajectories (latitude/longitude combined) needed to be shifted back in time to achieve the maximum correlation between the two trajectories. Data were only considered if the birds remained cohesive (50 m; Pettit et al. 2015) for over half the flight (as above). The average correlation across all group members and cohesive time-steps (mean) provides an individual's

"leadership score" (directional correlation delay, s). Because data are only provided in time-intervals of 0.2 s, we used a quadratic interpretation of the time-shifted correlation curves (as used by Pettit et al. 2015) to provide a less coarse estimate of leadership score. Leadership scores (s) from each bird and in each flight were weighted equally, and a mean value given for each context, i.e. a leadership score (s) was provided for both "familiar" and "unfamiliar" contexts for each individual.

Route fidelity

Following the methods of Freeman et al. (2011) we calculated route fidelity via analysis of the variance in solo, "familiar" flight paths. After removing paired pigeon trajectories, we set a sequential path of 500 points from home to the release site. Then, for each bin (N = 500) we took an average of the latitude and longitude in each bin per solo flight, and further calculated the mean route path (following the iterative approach described in Freeman et al. (2011). The variance of actual flight paths around this mean path was our measure of route fidelity.

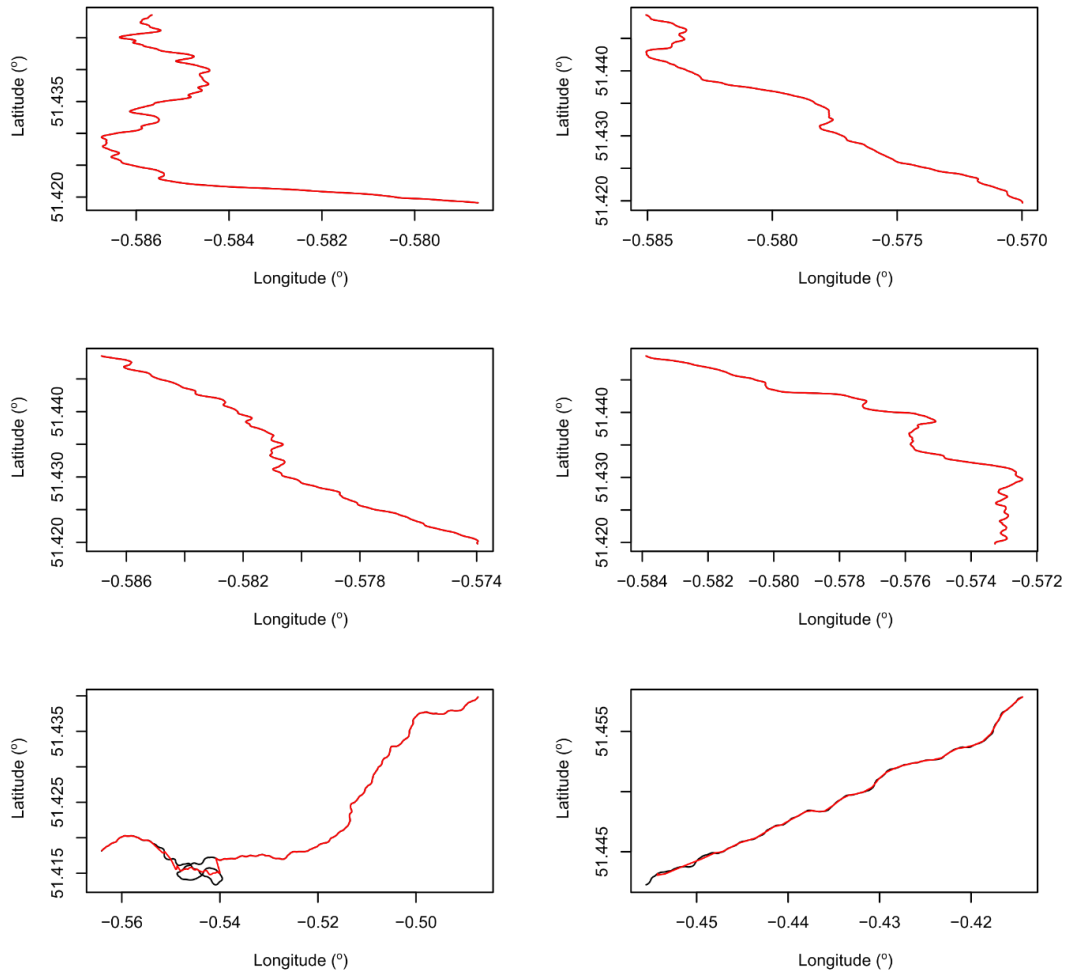

Figure S2. 1. Averaging trajectories into 500 bins for route fidelity calculations

Latitude (°) and longitude (°) was averaged or each subsequent bin (*N* = 500) from "home" to "site". The binned trajectory (red) is plotted over the original trajectory (black). The figure demonstrates the similarity of the two trajectories, but also demonstrates how looping movements (bottom left) are simplified into a mean path. The data are from the first familiar flights of six pigeons (in a randomised order).

Behaviour assays

Dominance protocol

Dominance followed the same protocols as (Portugal et al. 2017a, b). The first stage of each dominance trial was to remove food from the lofts 17 to 20 hours before the trial to increase food motivation. Immediately before the start of a trial, all pigeons were caught and had stickers with large numbers attached to their backs for identification from video footage. Birds were then held in a wicker basket prior to commencement of the trial. At the start of the trial, a small container of food was placed in the corner of an empty loft. The food container was small enough that only one to two birds could eat at one time, encouraging agonistic interactions, and enabling quantification individuals which initiate ("winners") and those which receive ("losers") more aggressive interactions (see *Methods: Dominance*). Following this, the camera was switched on (see *Methods: Personality*) and the birds were released into the loft, and filmed for 30 mins. After completion of the trial, pigeons were returned to a loft with full food troughs. This was to avoid food deprivation. For the same reason, we avoided conducting dominance trials within 24-hours (including removal of the food at the start of each trial) of each other. See *Methods: Dominance* for data treatment

Additional "personality" protocol

To measure "boldness" (time to leave shelter), "neophilia" (time spent in sector with novel object) and "exploration" (evenness of time spent in each sector) we

used a standard "personality" protocol (e.g. see Siviter et al. 2016; Portugal et al. 2017a). Individual pigeons were placed in a carrying box (1 m long x 60cm wide) – used to transport a pigeon from its home loft – and placed in the top left corner of the assessment arena. The individual was left for a short period of time to acclimatise. After this period, a camera (GoPro Hero4 or Akaso EK7000) fixed centrally to the ceiling was then turned on and the front of the carrying box opened. The observer immediately left the arena, allowing the pigeon to move freely for 20 mins. After 20 mins, the observer returned and retrieved the camera. The pigeon was recaptured and promptly returned to its flock. After a trial, the individual would not be used for another trial for at least 24 hours to avoid habituation (e.g. Schuett et al. 2011). See further details on trial types and calculation of key variables in *Methods: Personality*.

Transforming "personality" data

Raw data for "boldness" (proportion of time before leaving box), "neophilia" (proportion of time spent in sector with novel object) and "exploration" (evenness of time period in each of the sectors using chi-squared distribution; X^2) were all heavily left-skewed (Fig. S2.2). To minimise skew, we ran a series of transformations (using $x^{1/m}$. where m = -5 to 5, in segments of 1, but excluding 0), and chose the transformation with the greatest *W*-value, from Shapiro-Wilks test (measure of skewedness). The optimal transformation for "boldness" was m = -5 ($x^{-0.2}$), for "neophilia" was m = 3 ($x^{0.33}$), and for "exploration" was m = 5 ($x^{0.2}$) (see transformed

data in Fig. S2.2). Transformed data were further used in main analyses and data plots (see *Results*).

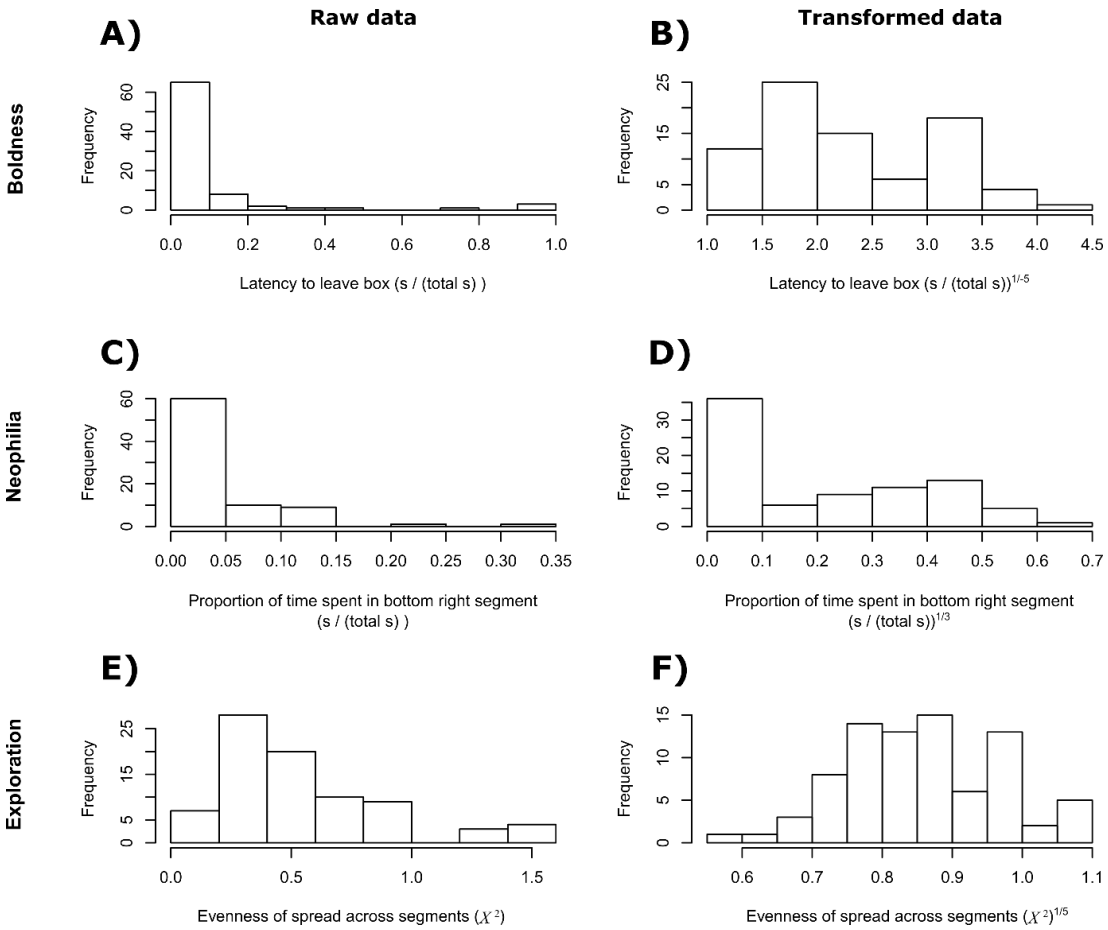

Figure S2. 2. Transforming "personality" data

Histograms provide "personality" scores from all individuals (*N* = 16). The first column of panels provides the raw observations; and the second column provides the transformed variables. **(A-B)** "Boldness", latency to leave box (s / (total s)); **(C–D)** "Neophilia", proportion spent in bottom-right segment with the novel object (s / (total s)); and **(E–F)** "Exploration", evenness of spread across the segments (X^2).

Repeatability of phenotype

Behavioural

All our measures of personality were significantly repeatable across individuals. Exploration score, evenness of distribution across testing arena (R = 0.357 ± 0.118 (SE), 95% CI: 0.126-0.564, $p < 0.001$); Boldness/shyness, the latency to leave box (R = 0.354 ± 0.125 (SE), 95% CI: 0.086-0.560, $p < 0.001$); Neophilia, time spent in the bottom right square (of 9 zones) in novel object trials (R = 0.304 ± 0.112 (SE), 95% CI: 0.078-0.555, p = 0.002). There was no observable habituation; neither exploration, boldness, nor neophilia changed significantly across successive trials (LME; Exploration – DF = 62, t = 0.921, p = 0.361; Boldness – DF = 62, t = 0.527, p = 0.600; Neophilia– DF = 62, t = -0.076, p = 0.939). Dominance hierarchies were transitive and linear for both flocks (group 1: transitivity (T) = 0.754, p = 0.001, group 2: t = 0.862, p =0.001) (De Vries et al. 2006).

In-flight

Route efficiency and speed were both significantly repeatable in "familiar" flights (N = 144 observations, after removal of N = 30 flights due to pairing of trajectories and/or data loss from N = 16 individuals) (route efficiency: R = 0.401 ± 0.107 (SE), 95% CI = 0.168-0.588, $p < 0.001$; speed: R = 0.346 ± 0.104 (SE), 95% CI = 0.139-0.531, p < 0.001). In "unfamiliar" flights, contrary to our expectations, route efficiency had low and non-significant repeatability (N = 71; R = <0.001, ± 0.058 (SE), 95% CI = 0-0.019, p = 0.516). Peak route fidelity, despite only having two

observations per individual (one from each "familiar" site), was significantly repeatable (R = 0.529 ± 0.177 (SE), 95% CI = 0.174-0.812, p = 0.021. Mean fidelity was close to, but not, significantly repeatable (R = 0.346 ± 0.220 (SE), 95% CI = 0-0.735, p = 0.085).

Table S2. 1. Release site information

Coordinates (longitude and latitude), site names, approximate distance (km), approximate bearing (N/E/S/W etc.), accurate bearing (rad) and accurate distance (m) are given from left to right for the home loft and all release sites used in the study. Accurate bearings and distances have quite a lot of variance, due to the non-trivial nature of finding release locations in open spaces away from traffic in the local area in Surrey, U.K. (*D. Sankey Pers. Obs.*).

Latitude	Longitude	Site name	Approx. distance (km)	Approx. bearing (N/E/S/W)	Accurate bearing (rad)	Accurate distance (m)
51.41537	-0.57262	Home	0	NA	NA	0
51.45755	-0.5884	N5	5	N	-0.14	4740
51.49697	-0.58891	N9	9	N	-0.07	9098
51.44844	-0.48017	E5	5	E	0.79	5464
51.46375	-0.39574	E9	9	E	0.87	9299
51.40179	-0.46796	SE5	5	SE	1.83	5057
51.39775	-0.39217	SE9	9	SE	1.72	8584
51.35934	-0.53085	S5	5	S	2.81	6547
51.32179	-0.49641	S9	9	S	2.76	11079
51.37103	-0.606	SW5	5	SW	-2.81	5180
51.3187	-0.64038	SW9	9	SW	-2.80	11270
51.40513	-0.65285	W5	5	W	-1.83	3859
51.38254	-0.77279	W9	9	W	-1.85	10103
51.43949	-0.64861	NW5	5	NW	-0.86	4298
51.46861	-0.6908	NW9	9	NW	-0.65	7772

Table S2. 2. Flight protocol

Columns from left to right describe: number of flights for each condition, group number, solo or group flight condition (see *Methods*), whether the site was "familiar" (F) or "unfamiliar", and the approximate distance and bearing to release site. Flights are in date order (last column; all dates recorded were in 2017).

Number of flights	Group number	Solo/ group	Familiar/ unfamiliar	Approx. distance (km)	Approx. bearing (N/E/S/W)	Date (day/ month)
12	1 & 2	Sol	F	5	N & E	1/6 - 30/6
6	1 & 2	Gro	F	5	N & E	1/7 - 7/7
12	1 & 2	Sol	F	9	N & E	7/7 - 17/7
6	1 & 2	Gro	F	9	N & E	17/7 - 25/7
1	1	Gro	U	5	E	26/7
1	2	Gro	U	5	SW	28/7
1	1	Gro	U	5	S	30/7
1	2	Gro	U	5	NW	30/7
1	1	Gro	U	5	W	31/7
1	2	Sol	U	5	S	31/7
1	1	Sol	U	5	SE	31/7
1	2	Sol	U	5	W	1/8
1	1	Sol	U	5	SW	1/8
1	1	Sol	U	9	E	1/8
1	2	Sol	U	5	N	2/8
1	1	Sol	U	9	S	3/8
1	2	Sol	U	9	SW	4/8
1	1	Sol	U	9	W	4/8
1	2	Sol	U	9	NW	6/8
1	2	Gro	U	9	S	7/8
1	1	Gro	U	9	SE	7/8
1	2	Gro	U	9	W	10/8
1	1	Gro	U	9	SW	10/8
1	2	Gro	U	9	N	10/8
3	1 & 2	Sol	F	5	N & E	11/8 - 13/8
3	1 & 2	Gro	F	5	N & E	14/8 - 17/8
3	1 & 2	Sol	F	9	N & E	18/8 - 20/8
3	1 & 2	Gro	F	9	N & E	23/8 - 25/8

Table S2. 3. PCA loadings and summary statistics

Phenotypes were categorised by category (i.e. “flight”, “morphological” and “behavioural”; left column. The summary statistic labels (grey shaded), and specific phenotypes for the PCA are described in the second column. The third to fifth columns represent either the influence of PC1 – PC3 on summary statistics (grey), or the loadings of each individual phenotype on each principal component.

Phenotype (category)	Phenotype (specific)/ Summary statistics	PC1	PC2	PC3
Flight	Familiar airspeed	-0.656	0.127	-0.223
	Familiar route efficiency	-0.651	-0.023	-0.307
	Peak fidelity	0.347	0.566	-0.747
	Cranio-caudal distance	-0.158	0.814	0.546
	Standard deviation	1.440	1.054	0.839
	Proportion of variance	0.518	0.278	0.176
	Cumulative proportion	0.518	0.796	0.972
Morphological	Toe length	-0.412	-0.213	-0.005
	Tarsometatarsus	-0.427	0.471	0.285
	Wing length	-0.063	0.072	-0.910
	Body width	-0.195	-0.652	0.178
	Body mass	-0.535	0.022	-0.219
	Root chord	-0.395	0.389	0.092
	Wing area	-0.404	-0.388	-0.040
	Standard deviation	1.680	1.171	1.050
	Proportion of variance	0.403	0.196	0.158
	Cumulative proportion	0.403	0.599	0.757
Behavioural (personality)	Dominance	-0.589	-0.069	0.507
	Boldness	-0.458	-0.311	-0.811
	Exploration	0.194	-0.948	0.229
	Neophilia	-0.637	-0.002	0.183
	Standard deviation	1.509	0.989	0.804
	Proportion of variance	0.569	0.245	0.162
	Cumulative proportion	0.569	0.814	0.975

Table S2. 4. Standard output from the "dredge" function in R package MuMIn

Tables are provided for analyses of "Familiar" flights and "Unfamiliar" flights (top and bottom tables respectively). Covariates analysed represent the first three principal components from each of our three domains of phenotyping ("flight" – e.g. FLIGpc1; "morphological" – e.g. MORPpc1 and "personality" or behavioural – e.g. PERSpc1). The best model is that with the lowest AICc score (three columns from the right). PC1 from the morphological PCA (MORPpc1) was the covariate with the lowest AICc of all models including covariates, and was investigated further. The behavioural ("personality") phenotype with the lowest AICc was PERSpc2, which was also investigated further. Flight phenotypes were already investigated extensively (see *Results*).

"Familiar" flights															
Model	(Intercept)	FLIGpc1	FLIGpc2	FLIGpc3	MORPpc1	MORPpc2	MORPpc3	PERSpc1	PERSpc2	PERSpc3	df	logLik	AICc	delta	weight
1	0.005	NA	NA	NA	NA	NA	NA	NA	NA	NA	3	7.831	-7.481	0.000	0.744
9	0.005	NA	NA	NA	-0.046	NA	NA	NA	NA	NA	4	8.300	-4.600	2.881	0.176
3	0.005	NA	0.046	NA	NA	NA	NA	NA	NA	NA	4	6.332	-0.664	6.817	0.025
129	0.005	NA	NA	NA	NA	NA	NA	NA	-0.027	NA	4	5.685	0.631	8.112	0.013
5	0.005	NA	NA	-0.022	NA	NA	NA	NA	NA	NA	4	5.646	0.707	8.188	0.012
257	0.005	NA	NA	NA	NA	NA	NA	NA	NA	-0.013	4	5.608	0.783	8.264	0.012
33	0.005	NA	NA	NA	NA	NA	0.010	NA	NA	NA	4	5.344	1.311	8.792	0.009
17	0.005	NA	NA	NA	NA	-0.012	NA	NA	NA	NA	4	5.275	1.450	8.931	0.008

"Unfamiliar" flights															
Model	(Intercept)	FLIGpc1	FLIGpc2	FLIGpc3	MORPpc1	MORPpc2	MORPpc3	PERSpc1	PERSpc2	PERSpc3	df	logLik	AICc	delta	weight
1	-0.022	NA	NA	NA	NA	NA	NA	NA	NA	NA	3	0.696	6.790	0.000	0.734
9	-0.022	NA	NA	NA	-0.063	NA	NA	NA	NA	NA	4	0.265	11.470	4.680	0.071
17	-0.022	NA	NA	NA	NA	-0.080	NA	NA	NA	NA	4	0.117	11.765	4.975	0.061
5	-0.022	NA	NA	-0.091	NA	NA	NA	NA	NA	NA	4	-0.076	12.153	5.363	0.050
33	-0.022	NA	NA	NA	NA	NA	-0.063	NA	NA	NA	4	-0.601	13.202	6.412	0.030
129	-0.022	NA	NA	NA	NA	NA	NA	NA	-0.045	NA	4	-0.958	13.915	7.125	0.021
257	-0.022	NA	NA	NA	NA	NA	NA	NA	NA	0.006	4	-1.065	14.130	7.340	0.019
3	-0.022	NA	0.009	NA	NA	NA	NA	NA	NA	NA	4	-1.275	14.551	7.761	0.015

Chapter 3: Speed consensus and the "Goldilocks principle" in flocking birds (*Columba livia*)

Daniel W. E. Sankey[1], Emily L. C. Shepard[2], Dora Biro[3] and Steven J. Portugal[1]

Sankey, D. W.E., Shepard, E. L. C., Biro, D., & Portugal, S. J. (2019). Speed consensus and the "Goldilocks principle" in flocking birds (*Columba livia*). *Animal Behaviour* (accepted: In Press)

Author affiliations:

[1] *School of Biological Sciences, Royal Holloway University of London, Egham, TW20 0EX, U.K.*

[2] *Swansea Laboratory for Animal Movement, Biosciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, Wales, U.K.*

[3] *Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, U.K.*

Abstract

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 thus forms 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 preferred solo speed were made to reach consensus in flocks. These data match theory which suggests that groups fly at an intermediate of solo speeds, which suggests speed-averaging. By virtue of minimising extreme compromises – speed-averaging can maximise selective benefits across the group, suggesting shared consensus for group speed could be ubiquitous across taxa. Nonetheless, despite group-wide advantages, contemporary flight models suggested unequal energetic costs in favour of individuals with intermediate body-mass/preferred-speed (hence the “Goldilocks principle”).

Introduction

The evolution of social behaviour was a major step in the evolution of complex animal life on earth (Maynard Smith and Szathmáry 1997; Sumpter 2010; Bourke 2014) conferring many selective benefits to animals which achieved sociality (e.g. increased predator avoidance (Kenward 1978; Krause and Ruxton 2002; Sumpter 2010; Handegard et al. 2012); energy conservation (Weimerskirch et al. 2001; Portugal et al. 2014); social information acquisition (Simons 2004; Biro et al. 2006)). Yet, achieving these advantages brought with it many challenges, such as how to coordinate movements and, therefore, remain spatially cohesive (Conradt and Roper 2003, 2005, 2009). Coordination is widely discussed in terms of consensus building (Seeley 2003; Conradt and Roper 2005; 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) (Strandburg-Peshkin et al. 2015; Gall et al. 2017), groups which achieve coordination essentially make unanimous movement decisions (i.e. they come to a shared/unshared consensus), or risk losing cohesion (Conradt and Roper 2005; Couzin et al. 2005; Ioannou et al. 2015). The dynamics of shared-unshared consensuses 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). Nonetheless, despite our

increasingly comprehensive understanding of collective decision making, thus far the field has largely focussed on direction ("where to go?") and timing ("when to leave?") of movements (Conradt and Roper 2005; Couzin et al. 2005; Sueur and 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, 2017a; 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 amongst group members (Biro et al. 2006; King et al. 2008). While convergence of preferences can lead to beneficial (accurate) group decisions (Conradt and Roper 2003; Simons 2004; Strandburg-Peshkin et al. 2015), decisions are in many cases dictated by particular individuals, such as those more

experienced (Prins 1996; McComb et al. 2011), 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 (Rands et al. 2003; Fischhoff et al. 2007; Conradt et al. 2009), or personality differences (Sih et al. 2012; Mcdonald et al. 2016). Here, decisions may be governed by signalling mechanisms which can build a shared consensus for departure time (Walker et al. 2002; Ramseyer et al. 2009), or dictated by movement initiators (Rands et al. 2003; Fischhoff et al. 2007).

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. 3.1A) (Pennycuick 1968; Tobalske et al. 2003; Hedenström 2009). 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, both on an intra- and an inter- specific level (Fig. 3.1A) (Norberg 1995; Winter 1999; Tobalske et al. 2003; Tobalske 2007; McFarlane et al. 2016). Flying faster in active flight necessarily costs more (Tobalske et al. 2003; Hedenström 2009); increased work-rate of muscles is required to increase flap frequency or wingbeat amplitude to achieve faster speeds (Hedenström 2009; Butler 2016). 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 (Schmidt-Nielsen 1972; Hedenström and Alerstam 1996; Tobalske et al. 2003).

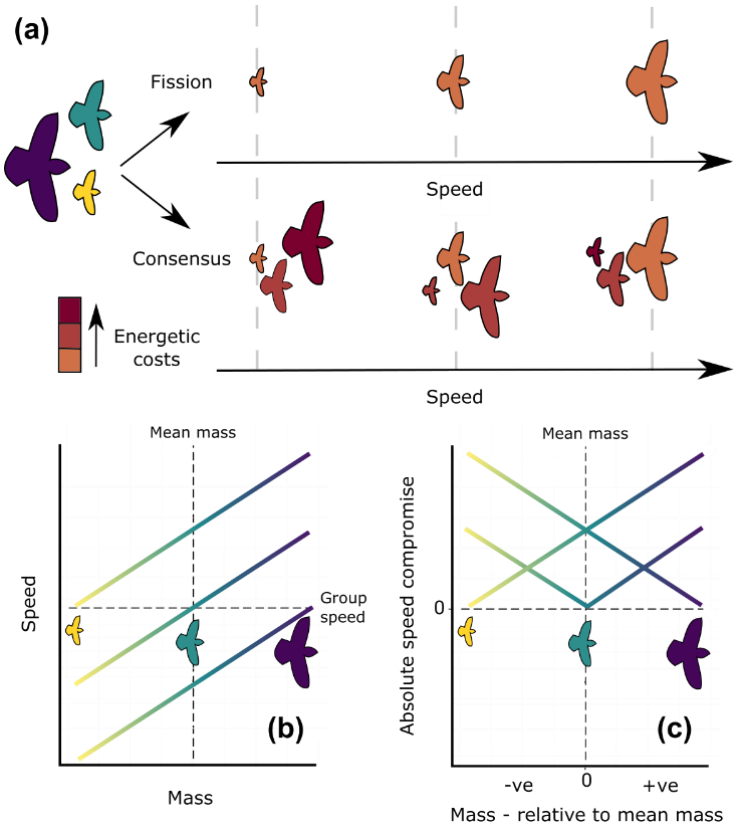

Figure 3. 1. Concept and hypotheses

(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; upper component of figure), 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; bottom component of panel), and benefit from decreased risk of predation and enhanced navigational efficiency associated with grouping (Krause and Ruxton 2002). Within a consensus context, we provide scenarios where the group travels at preferred speed of the small, the medium and the large bird (from left to right respectively). Energetic cost increases as the

deviation from an individual's optimum speed increases, whether flying faster or slower (Tobalske et al. 2003; Hedenström 2009). Therefore, both large and small individuals would likely pay a large cost to fly at one another's preferred speed (coloured deep red for energetic costs), Flying at 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. Predictions of our study are given in (b-c), hypothesis lines are coloured on colour scale corresponding to mass (Garnier 2017), **(b)** We predicted a positive influence of body mass (x-axis) on speed (y-axis) regardless of the group travelling speed (the first hypothesis; see *Introduction*). **(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 greater or lesser) 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 taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

Given that *i*) an aligned and coordinated flock can only fly at one speed without fragmenting, and *ii*) flying at any speed other than individually variable energetic optima is costly, conflicts of preference regarding group-speed will likely arise in bird flocks. Presumably, if the costs of resolving the conflicts are too large, this will result in group fission (Fig. 3.1A). On the other hand, if conflicts are resolved and a consensus is

reached, individuals may fare differently energetically (Fig. 3.1A). These costs of compromise ("consensus costs") (Conradt and 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 been frequently 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 (Usherwood et al. 2011; Taylor et al. 2017) and wind tunnels (Butler et al. 1977; Rothe et al. 1987a; Butler and Woakes 1990; Butler 2016). The hypotheses tested were, firstly, that body mass predicts solo flight speed in pigeons (Fig. 3.1B; McFarlane et al. 2016; Norberg 1995; Tobalske 2007; Tobalske et al. 2003; Winter 1999), and secondly that – in group flights – the birds will not split (following: Nagy et al. 2010, 2013; Watts et al. 2016), and compromise on speed. This second hypothesis is actually a set of three alternative hypotheses, depending on which birds compromise the most (see Fig. 3.1C).

Methods

Subjects and morphological measurements

Homing pigeons (*N* = 18), all aged between 1-1.5 years, were used in the experiments. They were housed in two separate groups of nine, in purpose-built lofts (7ft x 6ft) at Royal Holloway University of London (see Portugal et al. 2017b, a; 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 *Supplemental Material*).

Biologgers

Each bird was tagged with commercially available GPS loggers (QStarz BT-Q1300ST, Düsseldorf, Germany) which recorded latitude, longitude and time (GMT), five times per second (5 Hz). The outer casing was replaced with re-sealable bags and additional clear tape to reduce mass while retaining water proofing. Logger loading totalled 21 g which was 4.2-5.6% as a relative value of the pigeon's masses (mean = 4.8%). The loggers were attached by to the bird firstly by trimming feathers on the back of the

birds, 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 to 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.

Flight plan

Pigeons were released from a northerly bearing (only group 1; *N* = 9 birds – 5 male and 4 female, randomly chosen) or an easterly bearing (only group 2; *N* = 9 birds – 5 female and 4 male, randomly chosen), from two sites per group away from traffic at 5 km and 9 km by road (*Supplemental Material*). Sites were named N5, N9, E5 and E9 accordingly, retaining information about flight bearing (e.g. N or E) and distance (e.g. 5 km or 9 km) (Fig. S3.1). Each individual flew solo (*N* = 15 flights per site) and in their respective groups (*N* = 9 flights per site) (Table 3.1).

Table 3. 1. Release order, and number of flights from each of the homing pigeon release sites

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 – either solo or group – refers to whether the birds were released alone or in their respective groups. Dates of each phase of the study are provided also.

Site	Condition	No. 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

Solo/group condition was staggered to control for temporal variation in wind speed and direction (Table 3.1). Additionally, the solo stage was extended for the first set of releases from each site (see Table 3.1 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 previously 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. The results from an alternative analysis, omitting data before the seventh flight from each site (where unfamiliarity could play a larger role) was also conducted (see results in Table S3.2).

Missing data

Two birds, both from group 1, a male and a female, did not return home following a scheduled release. Both individuals went missing following releases from site N5. The first individual was lost following its fourth release, and the second individual was lost on its seventh release from this site. Neither individual had participated in any group flights, so both individuals were removed from the data set. For more information on missing data, and data processing see *Supplemental Material*. The final number of flights per individual is documented in Table S3.1.

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. 3.2A). 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. 3.2A). Then all theoretical speed estimates were converted into % values relative to $S_{\text{flock theor.}}$ (Fig. 3.2B). Minimum power speeds in free-flying pigeons are likely to be much greater 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 intra-group energetic increase as a result of speed compromise; importantly, theoretical estimated speed was not used in any of the tests of our main hypotheses.

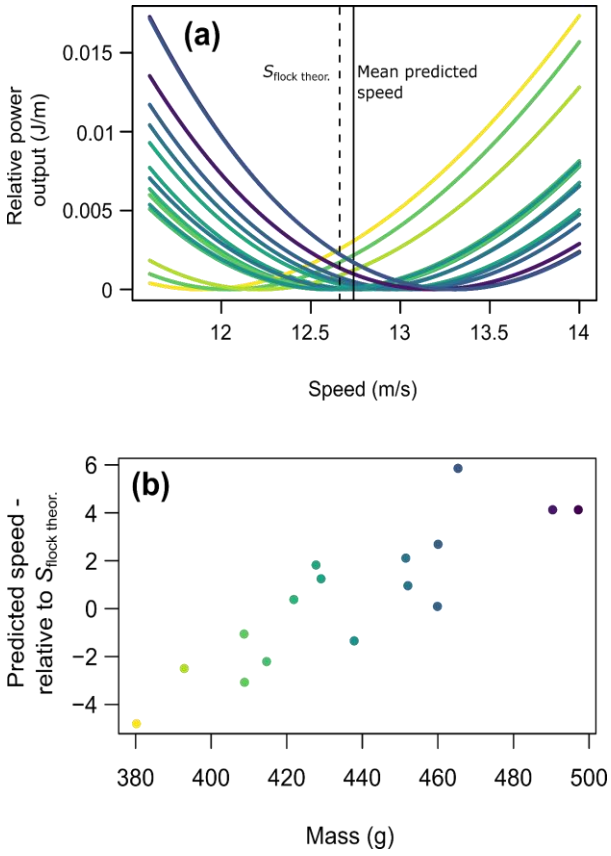

Figure 3. 2. Theoretical predictions and observed speeds

(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, non-optimal 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 $S_{\text{flock theor.}}$. 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 – speed of minimum power (see *Discussion*) – relative to $S_{\text{flock theor.}}$ is plotted against the bird's masses (g). Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

Speed

Ground speed from *solo flights* was calculated using the distance between locations at each GPS time-step (5 Hz) using GPS data (*Supplemental Material*). Ground speed of *group flights* was given by the speed between locations of group's centroid (after individuals which split from the group had been removed; see *Supplemental Material*). See Table S3.2 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. 3.3A-F). Means of airspeed per flight were

collated, and a median of these airspeeds was used as an individual's preferred speed (Fig. 3.3E). A mean was used for the intra-flight (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 and 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 likely 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 Table S3.2).The median of inter-flight 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 *Supplemental Material* 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 (*Supplemental Material*) were stronger for group flights (Fig. S3.2A). This further justifies our use of airspeed – a measure which 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 *Supplemental Material*).

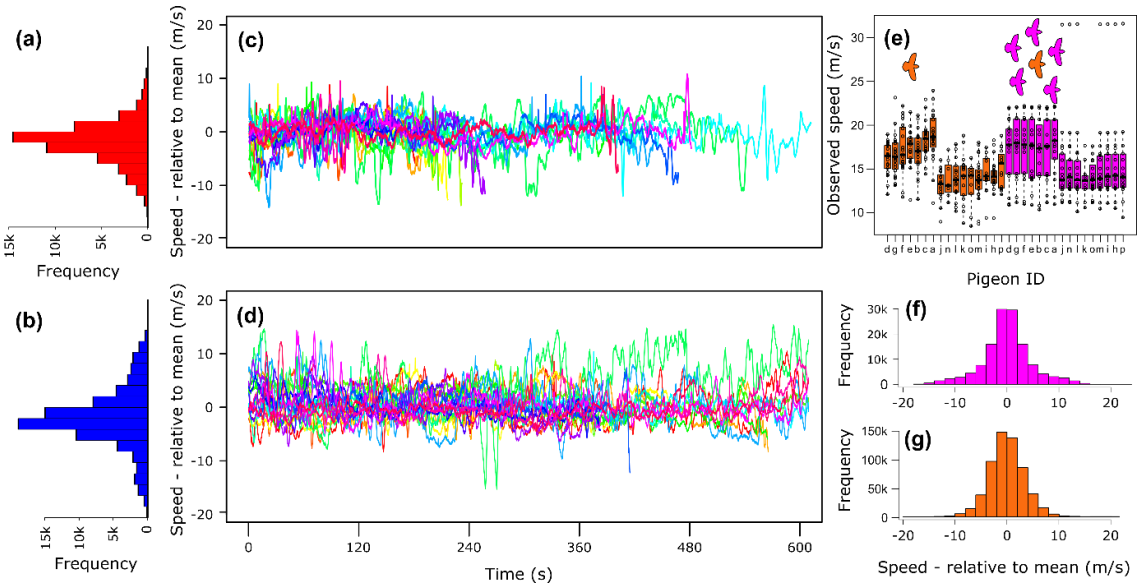

Figure 3. 3. Speed data

Centroid airspeeds (relative to mean value of speed per flight) (m/s) are represented as frequency histograms **(a-b)** and as speed traces for each group flight (up to a maximum of 600 s flight durations) **(c-d)** for groups 1 and 2 respectively. **(e)** Individual airspeeds in solo (orange) and group (purple) contexts, given as box and whisker plots for observed airspeed for pigeons A-P in both solo (orange) and group (purple) context. Pigeons A-G were in group 1 and pigeons H-P were in group 2. Panel **(e)** highlights both *i*) the similarity of speeds in a group flight context, (similar box and whiskers in purple), and *ii*) intergroup differences in speed (group 2 have lower speeds than group 1; see *Discussion*). Birds are ordered firstly by group, and second by increasing mass. **(f)** Combined frequency histogram of group airspeed (from centroid) from (a) and (b). **(g)** Combined frequency histogram for solo airspeeds, following methods used to generate **(f)**. Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

Statistics

For our statistical analysis we firstly we needed to account for the differences in airspeed across the two groups (Fig. 3.3E; Fig. S3.3), likely caused by the differences in support-wind commensurate with each release direction (see Discussion in *Supplemental Material*). 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. 3.3E) held significant influence over the direction of the predicted linear model: Cook's-D = 1.11, which is over the generally accepted thresholds *i*) 3* mean of Cook's-D: 0.38, and *ii*) a score of over 1.00 (Kim and Storer 1996). Following the removal of this individual, we found no difference between the gradient of the two groups' slopes for individual speed (ANCOVA; $N = 2$, $F_1 = 0.070$, $P = 0.800$); as expected significant differences were found between the intercepts (ANOVA; $N = 2$, $F_1 = 491.5$, $p < 0.001$). Had this individual not been removed from the data, the direction or significance values of the ANOVA slope and intercept did not change (see: Table S3.2 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. 3.1).

First, whether mass predicts speed was run both as a linear model (on median of airspeeds for each individual) (*N* = 16 individuals) but also 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-wind component and cross-wind component, 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 wind and crosswind – both used in the airspeed calculation – are present in the model. The resulting model had normally distributed residuals (Fig. S3.4).

To test the second set of predictions (see Fig. 3.1C; 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 a linear model with an anchor at zero (mean mass; Fig. 3.1C). If a linear fit predicted speed compromise, this would suggest that heavy or light individuals were compromising the least (if the slope of the model is negative or positive respectively; Fig. 3.1C). If, however, a linear model 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. 3.1C). This conclusion can only be reached if the two slopes on the anchor model are negative and positive respectively, forming a "V" shape (Fig. 3.1C); showing that greater deviance from mean mass necessitates larger compromises to remain cohesive. We also ran a linear model on speed compromise against absolute divergence from mean mass, post-hoc, as this may be more intuitive given our

eventual findings (see *Results*). Linear mixed models 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 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.

Results

The observed relationship between individual body mass and preferred solo speed was positive and linear (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, CI = [0.006, 0.024]; Fig. 3.4A-D), which is consistent with our predictions (Fig. 3.1B), and follows the same pattern predicted by our theoretical estimates

(Heerenbrink et al. 2015) (LM; N = 15, t_{13} = 5.46, p < 0.001; Fig. 3.2B). 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 = 3.001, 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 = 0.130; 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]).

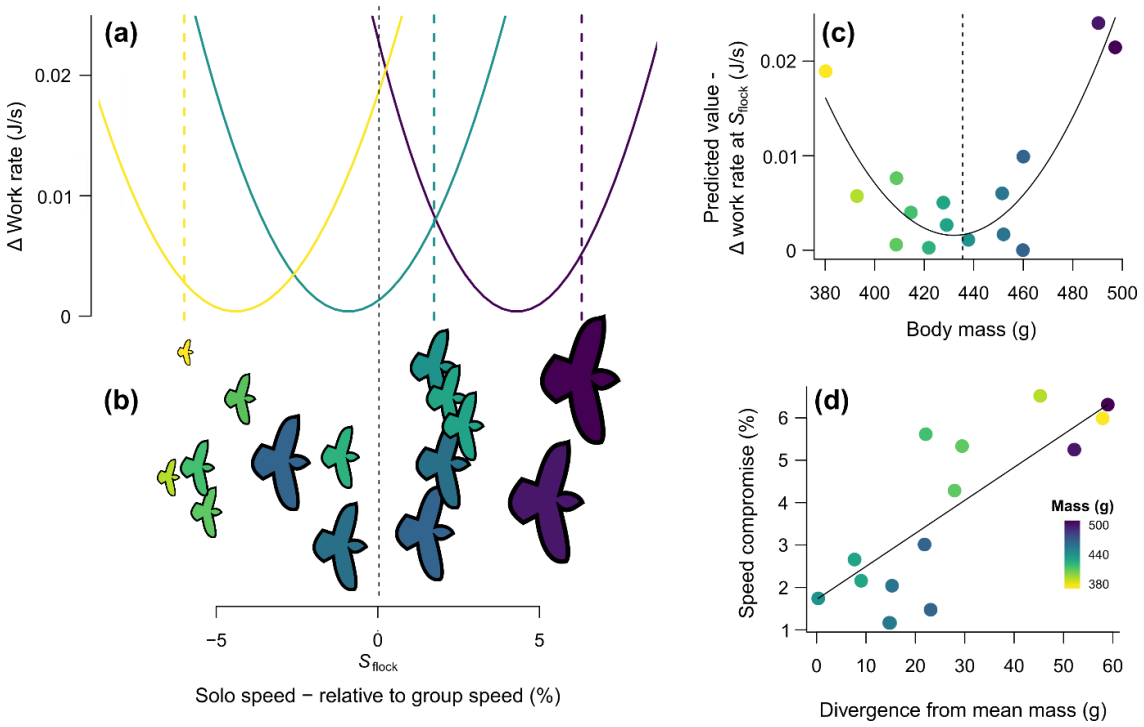

Figure 3. 4. The "Goldilocks" principle in pigeon flocks

All figure panels identify individuals by mass using colour scale (bottom right; colour scale provided by (Garnier 2017)). Bird images (bottom left) are both coloured and scaled (using bird mass (g) minus 350, divided by 150) according to mass. **(a)** Theoretical predictions (solid lines; R package "afpt"; Heerenbrink et al. 2015) showing predicted relative work rate (Δ J/s) across a range of flight speeds (%) in the heaviest (purple; *N* = 23 flights), the lightest (yellow; *N* = 22 flights) and the closest-to-the-mean body mass (purple/yellow blend; *N* = 21 flights) individuals. Observed solo speeds, relative to observed flock speed (%) are given as dashed lines (data as in **(c)**). **(b)** Median observed speed in solo flights (for *N* flights per individual, see Table S3.1), expressed as relative (%) to the average observed speed of the flock ($S_{flock\ obs.}$; segmented black line, *N* = 36 group flights) for each individual bird used in the analysis. **(c)** Theoretical relative power output at S_{flock} (Δ J/s) against body mass (g) for each pigeon (*N* = 15). This is the intersection of curves and $S_{flock\ theor.}$ from (a)). The solid

black line is a fitted polynomial regression line. The segmented black line is the mean mass of the birds. **(d)** Speed compromise (absolute value of solo speed, relative to group speed, %) vs the divergence from mean mass (absolute difference of an individual's mass from the mean mass of its respective group, g) for each individual (*N* = 15). The solid black line is a fitted linear model. Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

Heavier individuals (~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 (~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. 3.3E for full range of flying speeds). The closer an individual pigeon was to the mean body mass of the group, the closer they flew to their usual preferred solo speed (LM: $N = 15$, $f_{2, 12} = 13.49$; $R^2 = 0.64$, $p < 0.001$; Fig. 3.5A; see Table S3.2 for output statistics with modified analysis methods). The slope of the model for values below the mean mass was negative ($t = -5.09$, $p < 0.001$), and was positive for values above the mean mass ($t = 4.959$, $p < 0.001$), which creates the characteristic "V" shape (Fig. 3.5A). This matches the prediction that intermediate individuals compromise on speed the least (Fig. 3.1C). Table S3.3 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 which weigh at around 430 g (second order polynomial regression; $N = 15$, $t_{12} = 6.93$, $p < 0.001$; Fig. 3.4C). Birds which are heavier or lighter than this minimum are thus likely to expend more energy per unit time at the group's observed speeds.

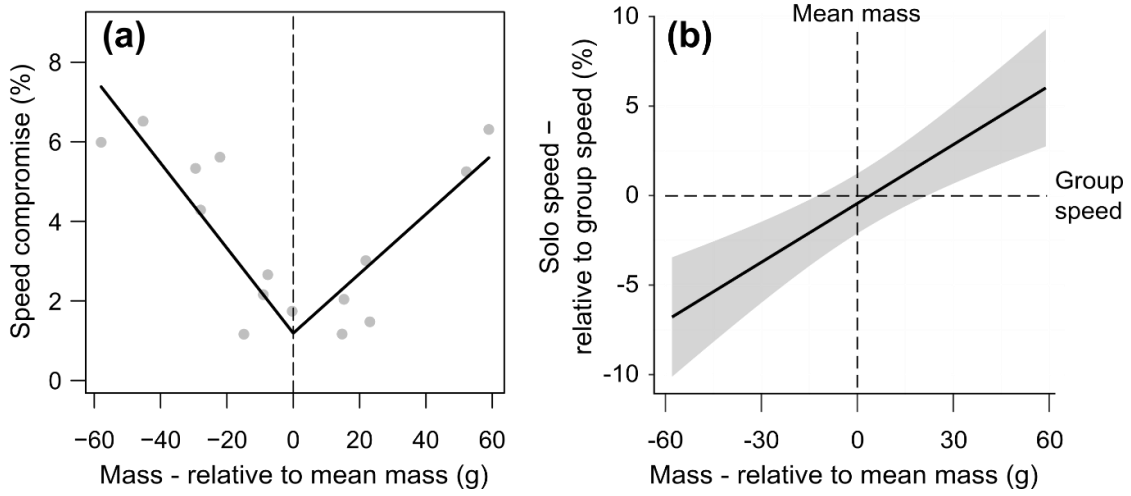

Figure 3. 5. Matching predictions to data

(a) Absolute speed compromise (%) against body mass (g), relative to the mean mass of the birds' respective groups (grey points). Following the rejection of the hypotheses that either heavier or lighter individuals were compromising least (LM: $N = 15$, $F_{2, 12} = -0.92$; $R^2 = 0.06$, $p = 0.37$), a linear model with two slopes and one intercept (see Figure 3.1C and *Methods*) was fitted to the data (LM: $N = 15$, $F_{2, 12} = 13.49$; $R^2 = 0.64$, $p < 0.001$), and is provided here (solid line). **(b)** Solo speed – given as (%) relative to observed group speed against mass (relative to mean mass). Linear model is fitted to data with 95% confidence intervals using ggplot2 (Kahle and Wickham 2013). The actual statistical test was a linear mixed model (LMM: $N = 299$, $t = 3.25$, $CI = [0.006, 0.024]$). To keep consistency with our predictions (panel Fig. 3.1B), we have not

included individual data points here. Instead, this variation can be found in Fig. 3.3E. Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

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 (Hedenström and Alerstam 1996; Alerstam et al. 2007). 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 character's food and sleeping arrangements to be "just right" at intermediate and not extreme ends of a spectrum (Zalasiewicz and Williams 2012)) has been used as an analogy in various fields of science to highlight the benefits of intermediate qualities (Kagan 1990; Zalasiewicz and Williams 2012). For example, in astrophysics, it is used to quantify habitable areas that are neither too far from and nor too close to the sun to support life (Zalasiewicz and Williams 2012); 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 minimise extreme speed compromises, and hence large increases in work rate associated with large speed adjustments (Fig. 3.1, 4C). This strategy may, therefore, reduce the likelihood of group fission (particularly by individuals with extreme values for preferred speed who 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 and Roper 2003) and homing accuracy (Biro et al. 2006; Dell'Ariccia et al. 2008), though 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 and 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. 3.5A). Thus, although speed compromise increases linearly for larger/smaller individuals (Fig. 3.5A), the energetic cost of compromise may follow a superlinear pattern (Fig. 3.4C). 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 which migrate in groups, this could have significant impacts on the costs of flight, and the fitness of the individuals which pay this cost of compromise (Hedenström and Åkesson 2017a; Flack et al. 2018).

The models which predict U-shaped power curves, while the best supported (Pennycuick 1968; Tobalske et al. 2003; Heerenbrink et al. 2015), 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 (Torre-Bueno and Larochelle 1978; Johansson et al. 2018). Nevertheless, most studies demonstrating flat power output only measure a speed range of ~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 which are orders of magnitude larger, e.g. some species of shark and pilot fish travel together for mutual benefit (Magnuson and 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 there is *i*) likely an energetic

cost (albeit potentially small) to pigeons which compromise on speed to fly in a flock, and *ii*) 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 multi-variate 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. 3.2A), which are similar to estimates from multiple wind tunnel experiments (approximately 11 m/s) (reviewed in Butler, 2016). However, two field studies which 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 greater 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 50). 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 and Alerstam 1996).

To further consider how group speed is governed and maintained, i.e. 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, greater group speeds were found in larger groups in three species of migrating birds (Eurasian oystercatcher, *Haematopus ostralegus*, red knots, *Calidris canutus*, and dunlins, *Calidris alpina*) (Hedenström and Åkesson 2017a). This suggests that in these species, larger and/or heavier (and therefore possibly faster) individuals were setting the pace (Hedenström and Åkesson

2017b). 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 phenotypic composition, specifically modifying the group's mass/speed distribution. Moving forward, teasing apart whether apparently "shared" decisions actually 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 hypothesised to respond to neighbours according to their absolute or relative distance by either *i*) moving closer to (at further distances), *ii*) moving away from (at close distances), or *iii*) aligning with (at intermediate distances) them (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; Katz et al. 2011; Jolles et al. 2017). 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 environments (Usherwood et al. 2011), or need greater control to avoid collisions and stay cohesive (Usherwood et al. 2011; Taylor et al. 2019). It seems likely that the effects of speed compromise and flying in a flock are additive, i.e. compromising comes at a cost, as does flying in a flock, and these costs are summed. Nonetheless, 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 which has arisen is how speed compromise plays out on a moment-to-moment basis. Our work looks at the average speed of individuals and groups, which gives us a broad understanding of the overall costs speed consensus, though the phenomenon is dynamic. It is actually possible for individuals to have the same average speed but nevertheless split due to individual differences in intra-flight 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 which 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 minimising overall time to reach a given destination rather than moment-by-moment optimisation 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 intra-specific 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.

Supplemental material

Morphological measurements

Body mass measurements (total = 12 per bird) were taken biweekly throughout the study period (three months – June-August 2017), using scales (CoffeeHit: Coffee Gear Digital Bench Scale – 2 kg/0.1 g limit/accuracy). A mean of all body mass measurements were used for analysis. Mean body mass (g) was likely 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% confidence intervals 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 tarso-metatarsus, and all subsequent morphological measures were taken on the 22nd of August 2017. A permanent marker was used to draw a dot at the intertarsal joint and the top of the metatarsal pad. Then, using flexible tape measure, the length between the two dots was measured. Using A4 graph paper (0.5cm squares), the outline of the right wing of each was drawn with pencil. 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 was given as 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 25 mins) in a wicker pigeon racing box (80cm x 40 cm x 22cm). Upon returning to the loft, the loggers were retrieved from the birds, and data 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. Nonetheless, despite this latter criterion, some greater 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 6:00AM and as late as 2 hours before sunset (date-depending). 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 seven-minute 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 timestamp (*t* Hz) is as follows:

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

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

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 in metres: 63710000 (Bullard 1948) and Hz is number of GPS fixes per second. 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 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 was 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^{o}, Latitude = 51.4154^{o}; height = 7.84 metres 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 period. For each flight, the first reading of the individual's timestamp 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 using the following steps: Firstly, the difference between *i*) the wind direction (above) and *ii*) the heading from the bird's track (Nagy et al. 2010) was calculated. Then, by integrating wind speed, a cross-wind, and support-wind could be estimated for each time-step. Finally, combining estimates for cross-wind and support-wind with ground speed (for ground speed see Eq.1 and 2 in *Supplemental Material*) 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 air speeds 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) (Pennycuick 1968; Rothe et al. 1987b; 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 in Fig. 3.3C). For group 1 and 2 respectively, the median of centroid airspeeds were 13.91 m/s (SD = 4.66) and 17.56 m/s (SD = 3.35) (*N* = 16 and *N* =16) and the median from all individual flights in a group context were 13.90 m/s (SD = 3.10) and 17.74 m/s (SD = 1.92) (*N* =117 and *N* = 150; Fig. 3.3C). 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; *Supplemental Material*).

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 re-introduced back into the group, and the study. In the case of 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, respectively. The final number of flights per individual is documented in Table S3.1. There was also the drop out of GPS data from individual timestamps, 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 release site and 500 m from the home loft. This process removes unwanted speeds from both climbing and descent at the start and end of the flight respectively (following Taylor et al. 2017).

Release site distance

Release sites at two different distances (5 km and 9 km) allowed an investigation into any potential impact of site distance on flight speed, and potentially avoided over-familiarising 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), though this result was not statistically significant (*t*-test; *N* =566; $t = 1.69$, DF = 559.61, $p = 0.09$). As the flight release treatment was the same across both groups (Table 3.1) 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 3.1) there was a statistically significant deviation in the support-wind component (for calculation and methods. See *Methods: Airspeed* in main text)

between solo and group flights (solo N = 267, group N = 384, t = 3.38, DF = 443.43, p < 0.001; Fig. S3.2A), with groups, on average, experiencing a greater 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 = -17.42, DF = 531, p < 0.001; Fig. S3.2B), we took the median value of support-wind for each condition (i.e. group or solo) and used the linear model to interpret what the extent of this deviation in support-wind would be, in terms of m/s (0.344 m/s; Fig. S3.2B). We added this value to all solo flight speeds and re-performed the main analysis. As the effect size of the deviation in wind-support component was small, the resulting re-analysis of speed compromise and mass deviation (from Fig. 3.2D) was similar (LM; N = 15, t = 2.68, DF = 13, p = 0.019). Therefore, we have not included this speed modification in our final regression. See Table S3.2 for all resulting statistics if we had not.

Centroid and fission analysis

Fission

In order to identify fission events, the centroid of the group was identified through a multi-step process. Firstly, 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 owing to the case of fission, whereby the centroid of the initial "group", could actually lie outside of the group itself. For example, if one individual in a group of five splits 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 re-calculate the centroid, in a jack-knife fashion (Portugal et al. 2014). Fission was comparatively rare (median proportion 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 inter-individual consistent differences in fission propensity (group 1: N = 118, DF = 115; F = 2.08; p = 0.15; group 2: N = 145, DF = 142, F = 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 = 10.53, DF = 507.39, 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, may 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 (*t*-test, group 1: N = 276; group 2: N = 257; t = 10.53, DF = 507.39, $p < 0.001$; Fig. 3.3C).

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. Firstly, using all individuals, but also using just lighter individuals (LM: N = 9, DF = 7, t = 4.10, R^2 = 0.66, $p < 0.01$) and just heavier individuals (LM: N = 6, DF = 4, t = 6.75, R^2 = 0.90, $p < 0.01$) as confirmatory analyses.

We treated the other morphological covariates (tarso-metatarsus, length and wing span) in the same fashion and found no interaction with group number (ANCOVA; tarso-metatarsus length: F = 0.84, DF = 1, p = 0.38; wing span: F = 0.46, DF = 1, p = 0.51). Thus, intergroup comparison was also possible with these morphological covariates.

Supplemental tables

Table S3. 1. Total usable flights for solo flights and group flights per individual

Total number of flights was 30 solo and 18 group, though data are missing due to any of the following reasons: 1) First flights not recorded with biologgers, 2) logger failure, 3) temporary disease, 4) paired flight, 5) flight took longer than battery length.

Pigeon	Group Number	number of usable Solo flights	number 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

Table S3. 2. Statistical outcomes from changes to the analytical methods

R^2, *t*-values (or *F*-values if given in brackets) and *p*-values [or CI if given in square 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 *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 which exceed the chosen parameter – 3 * mean Cook's distance. Note here that this is one of the only two methodological changes which changed the significance of any model (here the Anchor model), where the *p*-value rises to $p = 0.082$ (see Fig. S3.5 for diagnostics and validation for the removal of this individual). "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 (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 pseudo-replication is why a change in one summary statistic (for 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 ANOVA); 2) Intercept of ANOVA (Int. ANOVA); 3) Linear model: speed vs mass (lm: sp. vs mass); 4) Linear model: speed compromise vs mass residual (lm: sp. comp. vs mass resid.); 5) 2nd order polynomial – work-rate vs mass (2nd order poly. work vs mass); 6) Linear mixed model: speed vs mass (lmm: sp. vs mass). Linear model between speed compromise and mass residual are given in 7) Anchor model – where an anchor was specified at x = 0 (mean mass), and 8) Linear model of the same data (see Fig. 3.5A and Fig 3.5B respectively). For all models See Methods.

	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-value [or CI]	R^2	T or (F)	p-value [or CI]	R^2	T or (F)	p-value [or CI]	R^2	T or (F)	p-value [or CI]	R^2	T or (F)	p-value [or CI]	R^2	T or (F)	p-value [or CI]
Slope ANO	0.147	(0.269)	0.614	0.147	(0.269)	0.614	0.147	(0.498)	0.494	0.139	(0.065)	0.803	0.147	(0.269)	0.614	0.117	(0.25)	0.627
Int. ANO	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: sp. vs mass	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: sp. comp. vs mass. resid	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
2nd order poly. work vs mass	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: sp. vs mass	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 model	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
Linear model	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

Table S3. 3. Anchor model output

Linear model output from each change to the analysis methods (see Fig. 3.5A) All slopes for mass values below the mean have negative slopes; all slopes for values above the mean have positive slopes, indicating that each model shows a characteristic "V" shape as seen in Fig. 3.1 (main text). All significant *p*-values are **highlighted in bold**, the only *p*-values which did not reach significance were for when the individual was not removed due to the extreme Cook's distance (see Fig. S3.5).

		Estimate	Std.Error	*t*-value	*p*-value
Standard methods	intercept	1.03	0.85	2.64	**0.02**
	x.minus	-0.08	0.03	-5.09	**0.00**
	x.plus	0.16	0.05	4.96	**0.00**
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	**0.00**
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	**0.00**
	x.plus	0.20	0.04	4.54	**0.00**
Median instead of mean	intercept	1.57	0.80	1.97	0.07
	x.minus	-0.11	0.03	-3.81	**0.00**
	x.plus	0.15	0.05	3.02	**0.01**

Supplemental figures

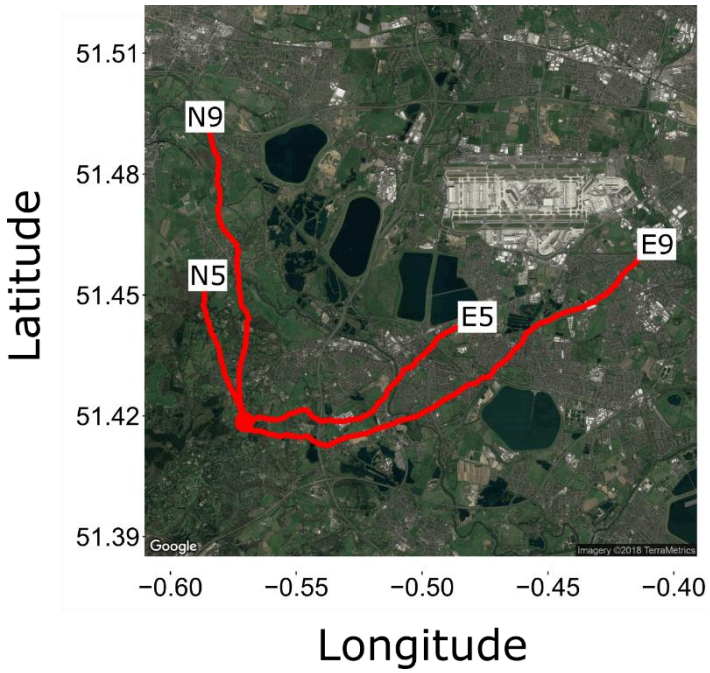

Figure S3. 1. Google Maps™ satellite image depicting the four release sites

Sites (N5, N9, E5, and E9) are indicated by the letter (N = north; E = east) and the number indicates approximate distance from home loft (i.e. 5, or 9, in km; accurate distances and more information in 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 confounding impact of terrain; different distances were chosen to investigate possible impact of distance on flight speed. Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

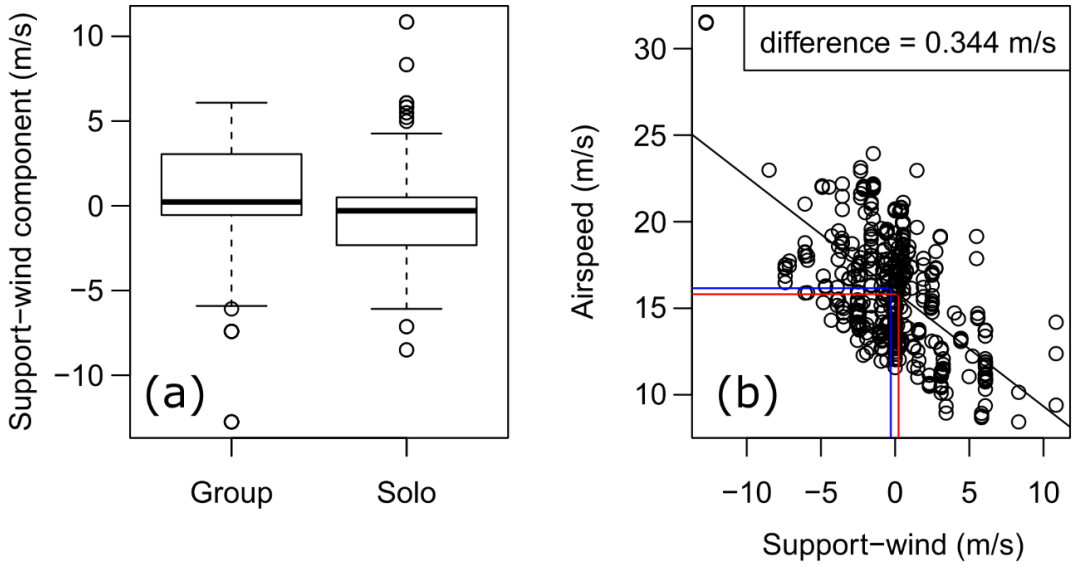

Figure S3. 2. Support wind and airspeed

(a) Box and whisker plot 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 greater associated support winds, despite attempts to control for seasonal and temporal differences in weather in the methods **(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 greater 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 re-conducted. Removal had no effect on the main statistics and thus conclusions and this analysis was removed from the main models. Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

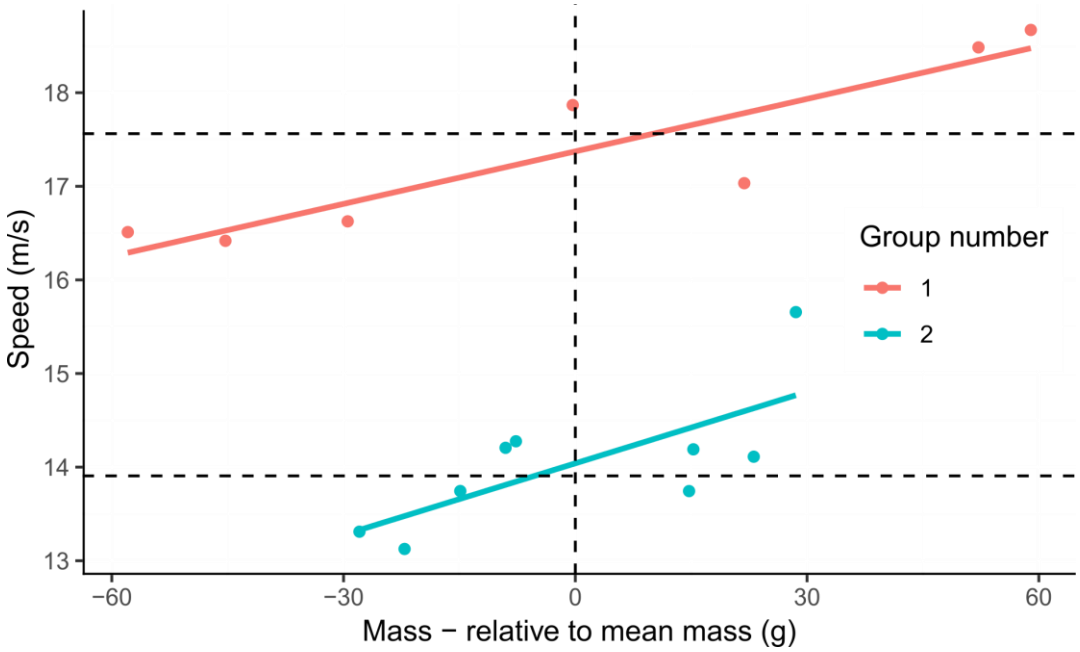

Figure S3. 3. Airspeed (m/s) and mass (g)

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 fit using ggplot2 (Wickham and Wickham 2007). Data points and models are colour coded by group (see legend). Upper and lower horizontal segmented lines represent average flock speed for group 1 and group 2 respectively. Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

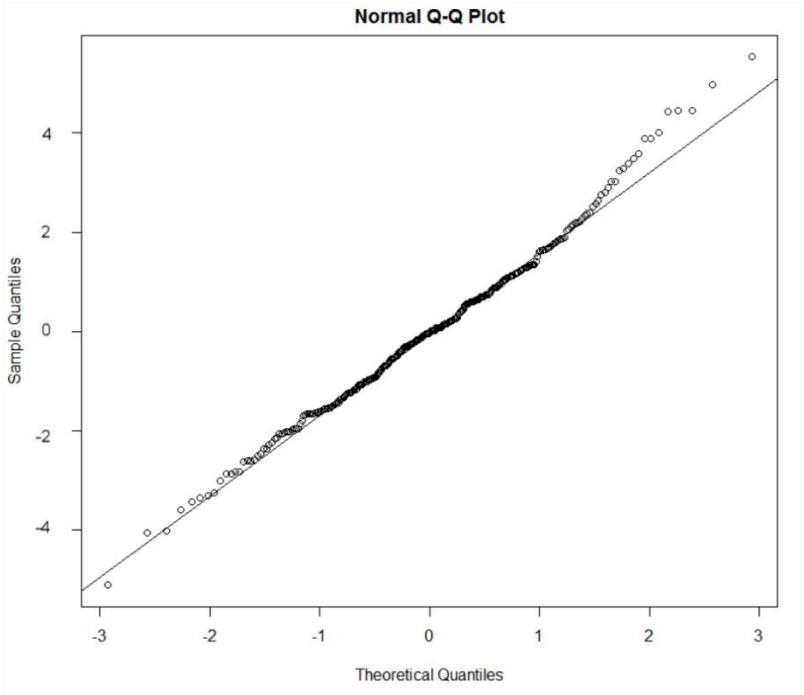

Figure S3. 4. Normal Quantile-Quantile plot for the linear mixed model

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 (*c*. < 2.5% of total flights). Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

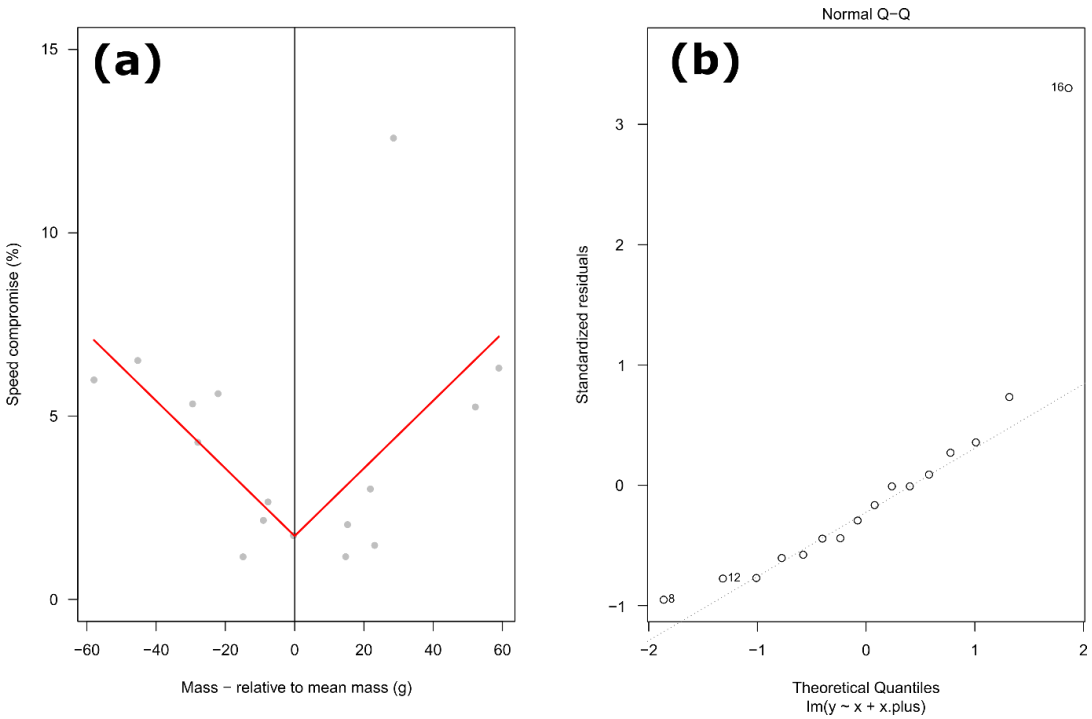

Figure S3. 5. Not removing individual due to extreme Cook's distance

Output statistics show the linear model for speed compromise (%) over body mass (relative to mean mass), here shown as a red line in **(a)** was not significantly different from a null distribution. This was likely 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 *i*) 3* mean of Cook's-D: 0.38, and *ii*) a value greater than 1.00 (Kim and Storer 1996). This causes the qq-plot **(b)** to skew, notice arced shape, with few values below the qq-normal line (dotted line). This means that the assumption of normally distributed residuals (an explicit assumption of linear models) has been violated, and therefore is not an accurate representation of the data. Figure taken from (Sankey et al. 2019) and formatted as per the accepted version in *Animal Behaviour.*

Chapter 4: When flocking is costly: reduced cluster-flock density over long-duration flight in pigeons

Daniel W. E. Sankey[1] and Steven J. Portugal[1]

Sankey, D. W.E., & Portugal, S. J. (2019). When flocking is costly: reduced cluster-flock density over long-duration flight in pigeons. *The Science of Nature*, *106*(7-8), 47.

Author affiliations:

[1] School of Biological Sciences, Royal Holloway University of London, Egham, TW20 0EX, U.K.

Abstract

Birds which fly in coordinated cluster-flocks can benefit through the formation of group-level structures and patterns which can deter predators by visual confusion. Though, unlike V-formation flight, cluster-flocking increases the energetic cost of flight, particularly in denser flocks. Cluster-formations therefore provide a unique opportunity to investigate trade-offs between increased work-rate (e.g. higher flap frequency) and other benefits of flocking. As part of a routine 9 km training flight release, a flock of six homing pigeons (*Columba livia*) with 5 Hz GPS and 200 Hz accelerometer biologgers attached flew an alternative trajectory totalling 177 km and 256 mins of flight. We provide the first evidence that during a long-duration flight, pigeons' pairwise and group-level distances increased (i.e. group structure changed), while flap frequency decreased over time. This implies that as birds tire during long-duration flight, the ultimate functions of cluster flocking – primarily anti-predator benefits– are overridden by the proximate costs of flying close to conspecifics.

Introduction

The benefits for animals living in groups can include enhanced vigilance and predator detection (Elgar 1989; Parrish and Edelstein-Keshet 1999), increased foraging efficiency (Pitcher et al. 1982; Brown 1988), and the sharing of information about resources or efficient routes (Biro et al. 2006). In addition, for animals that travel in groups, potential energetic savings can be achieved through positive aero- or hydro- dynamic interactions that enhance the locomotor performance of individuals in the assemblage (Portugal et al. 2014; Voelkl et al. 2015). It has been demonstrated that for birds flying in a V-formation, for example, positive aerodynamic interactions between members of the flock allow individuals to maximise the capture of beneficial upwash (Portugal et al. 2014). However, this aerodynamic power reduction due to group flight (for example, measured as a reduction in heart rate in flying white pelicans, *Pelecanus onocrotalus*; Weimerskirch et al. 2001) is not found in all bird groupings, with homing pigeons (*Columba livia*) flying in a cluster flock having increased flap frequencies when flying near other birds (Usherwood et al. 2011). This increase in work rate is exacerbated for birds flying either at the back of the flock, or in denser formations, thus suggesting that the other aforementioned benefits of being in a group must outweigh the immediate energetic costs of cluster-flocking. Whether individuals in a flock will take measures to try and reduce the costs of flight in tight clusters –

potentially by spreading out more – over long-duration flights, is not currently known.

Flight is the most energetically costly form of aerobic locomotion in vertebrates, although it may be less costly in terms of energy expended per metre (i.e. the cost of transport) compared with walking or running due to the speed of travel (Alexander 2002). Nevertheless, long-duration flight is costly, and birds typically experience extensive changes in body composition before- during- and after long flights (Wikelski et al. 2003). During long-duration flapping flight, it has been observed that heart rate can decrease as a function of flight time (Butler et al. 1998), assumed to be in response to the decrease in body mass that is observed in many species (Klaassen et al. 2000). For example, heart rate in migrating barnacle geese (*Branta leucopsis*) decreased by approximately 30% over the course of migration (Butler et al. 1998), while thrush nightingales (*Luscinia luscinia*) lost, on average 3.82 g (13%) of their body mass during a 12-hour flight in a wind tunnel (Klaassen et al. 2000). Thus, continuously measuring physiological and flight parameters in birds free-flying in a cluster has the potential to elucidate how individuals react to the changes in their physiology during long-duration flight, to establish if they attempt to reduce flight costs by spreading out from the cluster.

We analysed intra-group distances and flap frequency in a flock of six homing pigeons flying for 256 mins over a 177 km journey that occurred for unknown reasons during a routine 9 km training flight. We aimed to investigate whether (1) individuals begin to spread out (increased distances to nearest neighbour and the

group centroid) as flight duration increases, potentially to reduce the reported effects of flying in denser flocks, and (2) whether flap frequency decreases over time, to coincide with any increases in nearest neighbour distances.

Methods

Six homing pigeons of unknown sex, all aged between 12- 18 months (see *Supplemental Material* for housing and husbandry) were transported to, and released as a group from, a release site 9.10 km from the home loft, in an easterly bearing (Fig. 4.1; coordinates 51.4637^{o}, -0.3957^{o}). The birds were in transit for 20 mins in a wicker pigeon racing box (80cm x 40 cm x 22cm). Flight release protocol and husbandry conditions were approved by the Royal Holloway Ethical Review Board.

Each bird was tagged with both 1) a commercially available GPS logger (QStarz BT-Q1300ST, Düsseldorf, Germany; logger mass 12 g) used to measure latitude, longitude and time (GMT), five times per second (5 Hz), and 2) Axivity AX3 accelerometer (Axivity Ltd, Newcastle upon Tyne, U.K.) loggers (mass 8 g) were used to measure three-dimensional acceleration at 200 Hz (Taylor et al. 2017). See *Supplemental Material* for attachment protocols. The GPS units were programmed to "sports" mode, which is designed for use in fast activities involving high accelerations (up to 515 ms-1 speed, and up to 4g acceleration). For full calibration procedure and accuracy testing of the GPS loggers, see Brighton et al. (2017).

The birds had been released 12 times solo and three times as a group from the site, prior to the release in question. Each bird was equipped with GPS. The birds typically returned in 15.02 ± 41.93 mins (median±SD) for both solo and group flights combined, with an average group route efficiency of 0.43 ± 0.2 (median±SD), where 1 is the beeline distance, for the three group flights. The flight data for the extraordinary long flight presented took place on the 18th July 2017, and the cause of the severe extended flight duration and deviation from a homeward heading is unknown. The birds were released at 13:30 BST. Upon evaluation of the GPS traces, additional weather parameters were gathered from three locations (see *Supplemental Material* for full details) and assessed for repeatability to ensure dramatic changes in weather conditions were not responsible for the observed results. All parameters (wind direction, wind speed and gusts) were found to be consistent between locations (*Supplemental Material*).

Speed and neighbour-neighbour distance were both given by distance from one GPS position to another, using a spherical projection of the earth with radius = 63710 km (Chapter 3). Speed, between an individual's successive locations, and neighbour-neighbour distance between two individuals at the same timestamp. Flap frequency was identified from dorsal acceleration using the upper reversal point; dorsal body amplitude by integrating dorsal acceleration twice, and applying a Butterworth filter. More metrics, and more detailed descriptions of our calculations and equations are provided in the *Supplemental Material*.

We ran three models on each of our metrics over time, 1) linear models (LM), 2) linear mixed effects models, with individual as random intercept (LME-RI), and 3) linear mixed effects models with individual as random intercept and slope (LME-RIS) (*Supplemental Material*). Each model was run over 1000 bootstrap iterations to calculate average AIC values for model selection. Each iteration used AEPs (autocorrelation end points; *Supplemental Material*) as a sampling frequency to account for autocorrelation. The model structure with the lowest mean average AIC value was chosen as the best fit for the data. 1000 iterations of the chosen model were used to estimate R^2, T value and lower and upper confidence intervals (CI; using the estimate for the fixed effect ± 1.96*Standard error).

Results and discussion

The pigeon flock split after 97.62 mins of flight. The average accuracy (the length of the trajectory divided by the beeline distance) of the group was 0.03, taking an average of 213 ± 27 min (median ±SD) to return home. During the cohesive period (before the split) the nearest neighbour distance increased significantly over time (linear mixed effects model – LME; with random intercepts and slopes - RIS; CI = 0.14, 0.57; R^2 = 0.34; Fig. 4.2A, D). Similarly, individuals spread out with respect to the group centroid, in both the cranio-caudal (LME-RIS; CI = 0.30, 0.76; R^2 = 0.51) and lateral (LME-RIS; CI = 0.21, 0.59; R^2 = 0.39) axes (Fig. 4.1D-F). Flap frequency decreased significantly over the duration of the group flight (linear model LM; CI = -

0.23, -0.03; p = 0.031, R^2 = 0.02; Fig. 4.2B, *Supplemental Material*). The low R^2 in this model is likely to be explained by the high variability in flap frequency (see *Supplemental Material*), though not because of interspersed flapping/gliding phases, as no gliding phases over a second long were recorded (Fig. 4.1C). Dorsal body amplitude did not significantly change over the duration of the cohesive flight (LME with random intercepts - RI; CI = -0.02, 0.17; R^2 = 0.14; Fig. 4.2C). Group speed fell over the course of the cohesive period (LM; CI = -0.53, -0.32, R^2 = 0.18). It is possible that the reduction in wingbeat frequency over time was due to the birds slowing down as the flight progressed (see *Supplemental Material* for full discussion on speed). Once the flock had changed their trajectory and began heading south (Fig. 4.1A), it is conceivable that the birds switched from a maximum-range speed strategy to that of a minimum-power speed (Alexander 2002). Modulation of wingbeat characteristics has previously been demonstrated to occur in response to navigational knowledge (Taylor et al. 2017), and when some appreciation of the total length of the journey is known (Lilienthal 2001). That the pigeons gradually increase their nearest neighbour distance as the flight duration increases, suggests that the ultimate causes for cluster-flocking flight, such as predator confusion and increased vigilance becomes outweighed by the proximate costs involved with flying close to other birds in a cluster.

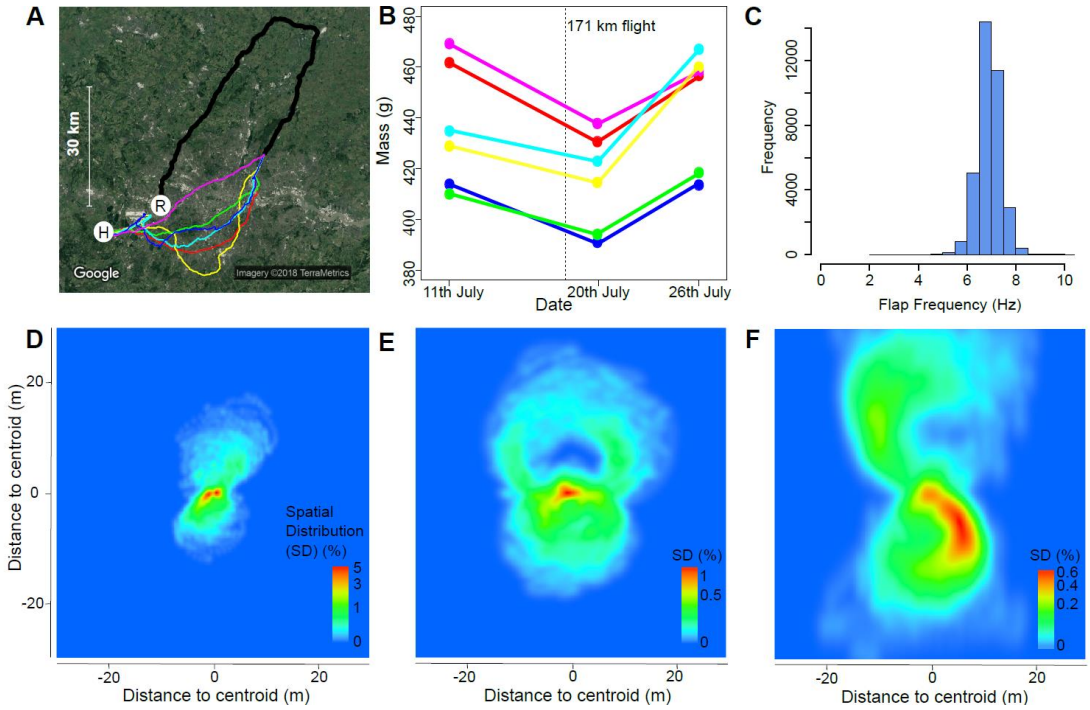

Figure 4. 1. The impact of long-duration flight on pigeons

(A) Route of 177 km light in homing pigeons (*Columba livia*; *n* = 6), plotted as black (group flight phase) and coloured (solo flight phase) lines, released from a 9.10 km beeline distance, north-east of their home loft (white circles labelled R and H respectively), and measured via GPS data loggers. **(B)** Body mass (g) of the six pigeons (coloured points/lines) on 11th July, 20th July, and 26th July 2017, respectively. There was a significant change in body mass from before to after the flight (*Paired t-test*: t_5= 6.78, $p < 0.01$). The 177 km flight was recorded on the 18th July (segmented line). **(C)** Frequency histogram showing accelerometer recorded flaps-per-second for all individuals (*N* = 6) for group phase of the flight (97.6 mins). **(D-F)** Frequency histogram of the group flight (*N* = 6, prior to when the birds separated) for time periods (D) 1-32.5 mins, (E) 32.5-65.0 mins, (F) 65.0-97.6 mins, respectively. Spatial distribution (SD) (%) (D-F) is the estimated probability density (x100) (using a 300x300 grid from function "stat_density2d" from package: "ggplot2" in R). All plots were generated in R (R Core Team. 2017). Figure taken from Sankey and Portugal (2019) and formatted as per the published version in *The Science of Nature.*

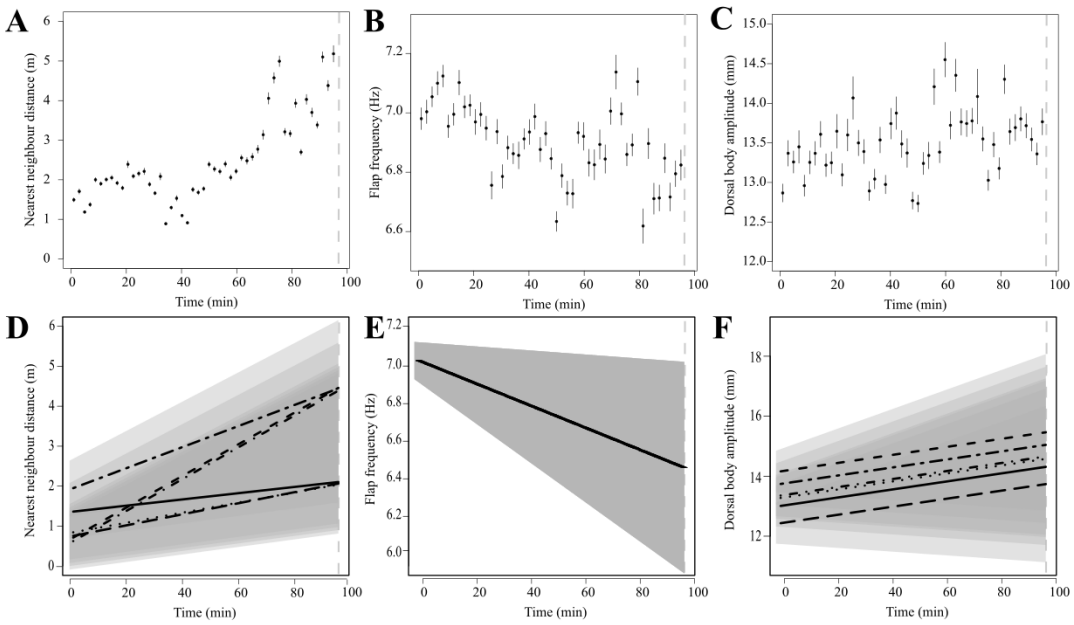

Figure 4. 2. Flight metrics and models

Nearest neighbour distance (m), flap frequency (Hz) and dorsal body amplitude (m) over long duration flight in homing pigeons (*Columba livia*; *n* = 6). These three variables are plotted respectively against time, as binned means (50 bins –points; bars = mean±SE) **(A-C)**, and average parameters from bootstrap estimates of the best (lowest AIC) model **(D-E)**. Dashed grey line represents where the group split (Fig. 4.1A). Wherever linear mixed models (LME) with individual birds as random intercepts (LME-RI) or intercept and slopes (LME-RIS) were the appropriate models, estimates for the intercepts and/or slopes per individual are plotted as segmented lines (**D**; LME-RIS, *CI* = 0.14, 0.57) (**F**; LME-RI, *CI* = -0.02, 0.17). Fixed effects are plotted as a thick black line **(D-F)**, and where mixed models did not yield the minimum for AIC scores, only fixed effects are plotted (plot **E**; LM, *DF* = 246, *p* = 0.031). Dorsal body amplitude **(F)** did not significantly change over time (using 95% confidence intervals). All plots were generated in R (R Core Team. 2017). Figure taken from Sankey and Portugal (2019) and formatted as per the published version in *The Science of Nature.*

As the flock began to spread out further, flap frequency decreased by approximately 0.3 Hz. Usherwood et al. (2011) demonstrated that a tenfold increase in the spatial density of a pigeon flock were observed to be associated with a 0.1 Hz increase in wingbeat frequency. Similar effects have been observed more recently in flocking corvids, where flying in a group resulted in a 0.7 Hz increase in flap frequency versus flying solo (Ling et al. 2018). Recent work studying paired flight in homing pigeons found that individual spacing has a significant effect on wingbeat frequency over an extended range of distances, such that birds flying 50 m apart has an expected wingbeat frequency 0.54 Hz lower than birds flying at 0 m spacing (Taylor et al. 2019), confirming firstly the importance of distances between individuals, but also confirming that the ~0.3 Hz flap frequency difference identified in the present study can be considered functionally significant.

The body mass loss after the long-duration flight was 22.23 ± 8.03 g (mean±SD) for the six pigeons, with the respective measurements taken seven days before and two days after the extended flight (Fig. 4.1B). We ran a linear mixed model with body mass as a dependent variable, and the date after the long flight as a different category than other data. Pigeon ID and Date were included as random intercepts. The long-flight category significantly predicted a drop-in mass by an average of 32 g ± 7.5 g (SE) (LMM: DF = 53, t = -4.30, p < 0.001). It is possible the reduction in flap frequency was a response to the expected loss in body mass. However, if body mass loss was the primary driver for the observed decline in flap frequency (Fig. 4.2B, D), we would expect flap frequency to continue to decrease over the solo

flight period following the split, which was not the case. This strongly suggests that it is the absence of close neighbours that prompted the reduction in flap frequency, rather than the decrease in body mass. The two components, however, do not necessarily need to be mutually exclusive.

Supplemental material

Supplemental methods

Birds/husbandry

The homing pigeons (*Columba livia*) were housed in purpose-built lofts (7ft x 6ft) at Royal Holloway (University of London; 51.415820, -0.572350). Food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, U.K.), grit (Versele-Laga - Colombine Grit and Redstone, Deinze, Belgium), and water were available *ad libitum*, and birds were weighed weekly (CoffeeHit: Coffee Gear Digital Bench Scale – 2 kg/0.1 g limit/accuracy).

Biologgers

The casing was removed from the standard GPS (QStarz BT-Q1300ST, Düsseldorf, Germany) units to reduce mass (final mass = 12 g), and the loggers were then

encased in small re-sealable bags held together with additional clear tape to prevent potential water damage.

The total mass of loggers was 20 g; 4.2-5.6% of the pigeon's masses (mean = 4.8%). A Velcro strip was attached to both GPS and ACC loggers. The Velcro, in turn, was attached to the pigeons using Araldite epoxy glue (Biro et al. 2006; Taylor et al. 2017) applied to trimmed feathers on their backs.

Wind recordings

We used a weather station (Aercus Instruments WS2083 Pro Wireless Weather Station; Greenfrog Scientific, Doncaster, U.K; wind direction: accuracy ± 22.5 degrees; wind speed: accuracy ± 0.1 m/s) to estimate wind speed/direction every half an hour. We have four recordings of wind speed/direction during the timeframe of the investigated flight: 3.6 km/h NE (at 13:19), 9.7 km/h NW (at 13:49), 9.7 km/h NW again (at 14:19), and finally 8.6 km/h NNE (at 14:49). The device was located on top of a building (7.84 metres height) at the pigeons' home loft (Longitude = -0.5726, Latitude = 51.4154).

Trimming GPS

In order to remove erroneous speeds/heading from a pigeon's climbing (circling) at the start of each flight, and their descent at the end, the trajectories were trimmed

from a 1000 m radius from the release site, to 500 m from the home loft. These distances were chosen based on the larger observed amount of circling at the start of the flights than at the end, and following Taylor et al. (2017).

Distance to centroid

Instantaneous individual distance to centroid (m) (see Chapter 3: *Supplemental Material: Centroid and fission analysis* for centroid calculation), was calculated at every time-step (5 Hz) for each individual, for the duration of the flight. The calculation uses the same two equations as speed calculation (Eqn 1,2), though, here x2 = longitude of individual, x1 = longitude of centroid, y2 = latitude of individual, y1 = latitude of centroid and Hz = 1.

For relative distances in-front/behind (cranio-caudal) and to the left/right (lateral) with respect to the flock centroid, we first found individual's angle relative to the heading of the centroid (following: Nagy et al. 2010). The cosine and sine of this angle was then multiplied by the distance to centroid, to provide the relative cranio-caudal and lateral distances respectively.

Nearest neighbour distance

Substituting Eqn. 1 and 2 (from Chapter 3: *Supplemental Material: Ground speed calculation*) for each pair of individuals' positions at each time-step (5 Hz) calculates

distance between each bird pair. For each individual, at each time-step, the minimum of these neighbour distances is assigned at the nearest neighbour distance.

Flap frequency and dorsal body amplitude

To detect wing flaps and thus calculate flap frequency, we used smoothed (0.025 s; five data points) dorsal (Z-axis) dynamic acceleration signal and found peaks in the data by identifying the upper reversal point (see: Portugal et al. 2014; Taylor et al. 2017). Static acceleration was removed by averaging acceleration over 15 wingbeat-cycles to remove error associated with half cycles. Timestamps attached to data from accelerometer loggers were used to calculate flap frequency (per second) at the moment of each flap (i.e. 1/ the time between flaps). For each second, a mean of all estimated frequencies was used as flaps per second (flap frequency).

Dorsal body amplitude (mm) was calculated by a double integration of smoothed dynamic dorsal acceleration (as above) (following: Usherwood et al. 2011; Taylor et al. 2017). After each integration, a 1 Hz (and subsequently 2.5 Hz cut-off frequencies) fourth-order, high pass Butterworth filters were used to filter data (see: Portugal et al. 2014).

Autocorrelation

To account for temporal autocorrelation, we first aimed to incorporate the autocorrelation structure into our linear mixed effects models (LME). However, the datasets were too large for conventional R software (which was used throughout analyses in the present Chapter; R Core Team., 2017; version 3.4.3). Instead we estimated the boundary (or, autocorrelation end points AEPs) from plots of the autocorrelation using base R function "acf()" (Fig. S4.1). AEP was used as a sampling frequency, such that random samples of our dataset were taken so that the data for further analysis on average comprised only one point every AEP estimate (Portugal et al. 2014).

Scaling data

Data for both the dependent and independent variables were scaled for our reported statistical analyses, because the model fails to converge completely with the gradient and models have very large eigenvalues (in both LME and LM models that were performed). However, scaled data were not used in plots or the statistics used in plotting model fits (Fig. 4.2A-F). To ascertain whether or not this had an impact on the direction of the statistics, we ran all analyses on both scaled and unscaled data (Table S4.1). We found that there was no difference in the direction or significance (and hence the interpretation) of the statistics.

Bootstrap estimates of statistics

Median value of each statistic was reported if the distribution of the bootstrapped statistics was significantly different from a normal approximation (Shapiro – Wilk test; accepted value $p < 0.05$). Vice-versa, a mean was used in the case where the distribution of sample estimates was not significantly different from a normal approximation (Table S4.1).

Weather data covering all sections of the long flight

To test whether significant differences in the local wind and other environmental conditions were impacting flock structure, nearest-neighbour distance and flap frequency, we collated data from three U.K. airports (Table S4.2), all of which encompassed a component of the long-duration flight, or came within 20 miles of doing so. The purpose of this was to check that variables: wind direction and wind speed did not differ across the spatial range of the flight. Both variables were found to be similar across different airports using ANOVA tests for differences in mean and variance (Wind direction: DF = [2, 39], $F = 1.23$, $p = 0.303$; Wind speed: DF = [2, 39], $F = 0.564$, $p = 0.573$). Recordings for gusts were 0 m/s for every location/time.

Supplemental discussion

Alternative hypotheses - duration

Duration of flight alone does not seem to be the cause of a decrease in flap frequency. If time was driving the phenomenon, we would expect frequency to continue to decrease after the eventual split (after 98 mins of flock flight). However, following an initial decrease at the time of fission, flap frequency increased (though not significantly) during the subsequent solo phase of the flight following the group split (LME-RI; CI = -0.02, 0.17; R^2 = 0.14). This is not, however, a full dataset. The shortest running accelerometer (each was programmed to run for a fixed period) stopped running at 49.12 mins into the solo flight period. All accelerometer loggers were trimmed at this point to avoid a disproportionate influence of any individual/logger. Total time to get home following the split was 117 ± 25.16 min (mean±SD).

Alternative hypotheses – stamina, speed preferences, physiology

The observed decrease in group density could be governed by factors other than a need to reduce energetic costs. For example, differences in stamina, individual speed preferences, and physiological state could drive the decrease in group density. Regardless, while experiencing decreased group densities and while flapping less, the birds are likely to have experienced decreased energetic output

(Usherwood et al. 2011) as well as an increased risk of predation (Kenward 1978). Whether or not these components are directly connected in a cause/effect relationship, the potential for a trade-off exists, nonetheless.

Alternative hypotheses - fission

Further evidence that the pigeon group reduced their cohesiveness to save energy is the eventual split from each other at 98 mins into the flight. Although, of course, this split may have been caused by several factors, including potentially a navigational conflict between flock members. Homing pigeon pairs are known to split when there is navigational conflict between two birds (Biro et al. 2006). This 'pigeon divorce', however, generally only occurs when two individuals have distinct homing routes they regularly recapitulate (Biro et al. 2006), and when the averaging of two idiosyncratic routes as a pair generates a conflict that becomes too great to remain cohesive. The group in the present study did split, but they all proceeded to follow the same heading. More importantly, they were not recapitulating a known route, thus, there was no opportunity to have a preconception, at the individual level, of route recapitulation that could cause conflict between members of the flock. This does not mean, *per se*, that there were not navigational conflicts, but the continuation of all individuals in the same heading suggest another cause for the group split.

Flap frequency variation

The decrease in flap frequency during the group phase of the flight was a key result, important as a test of our hypothesis. Given that the R^2 value was low (Scaled data: R^2 = 0.013; unscaled data: R^2 = 0.012; Table S4.1) and the *p*-values were both close to the threshold value of 0.05 (Scaled data: p = 0.031; Unscaled data: p = 0.044), this model warranted further investigation, to elucidate its validity. There were no clear patterns in the residuals of our model (Fig. S4.2). Our results therefore suggest that flap frequency is highly variable measure, intrinsically generating low R^2 values, and thus requires large amounts of data to establish statistical relationships with covariates. For this reason, it seems, we found a significant relationship between nearest-neighbour distance and flap frequency (LM: t = -7.62, p = < 0.001), though not after accounting for the high degree of autocorrelation in the GPS data (leaving 89 seconds of data across all individuals) for each permutation (1000 permutations: LM: t = -0.38, p = 0.435). Usherwood *et al.* (2011) found a relationship between flap frequency and flock density, though the authors registered over 9 hours of group flight across multiple flights, compared with our 97.6 mins in one flight.

We investigated whether gliding phases caused variation in flap frequency. However, interestingly, there were no gliding phases in any bird throughout the duration of the group-flight when we define gliding as the cessation of flapping for over one second (each second of flight is accounted for in our dataset and there were no seconds with no flaps; Fig. 4.1C). We reason that gliding phases would have to be synchronised in order to remain cohesive and coordinated in a flock, as

gliding causes temporary decreases in both speed and altitude. Synchronisation of gliding phases could be difficult to achieve, given that high flapping frequencies are thought to be required to increase flight precision to the level necessary for cohesive flocking clusters.

An investigation of speed

Although ground speed decreased during the course of the group-flight (Fig. S4.3), an accurate analysis of flight speed changes should ideally incorporate wind parameters, to estimate the birds' airspeeds (the vector difference between the *ground-speed/bird-heading* and the wind-*speed/direction)*. The wind speed/direction recordings (see *Methods*) were inconsistent, and measurements were taken at the home loft – many kilometres from the majority of the flight trajectory – and therefore of limited usefulness in such an analysis (but see *Section: Weather data covering all sections of the long flight* above). Therefore, a quantitative analysis of speed differences between the solo and group flight components in this study has been left out (though see Fig S4.4 for each individual's change in ground speed prior to and after the moment of fission). Nevertheless, we have reported the speed decrease during the group component of flight in our statistics, given that our overall focus is on how various flight parameters changed during the cohesive component of flight, and our finding of a decrease in ground speed could be an important pilot result.

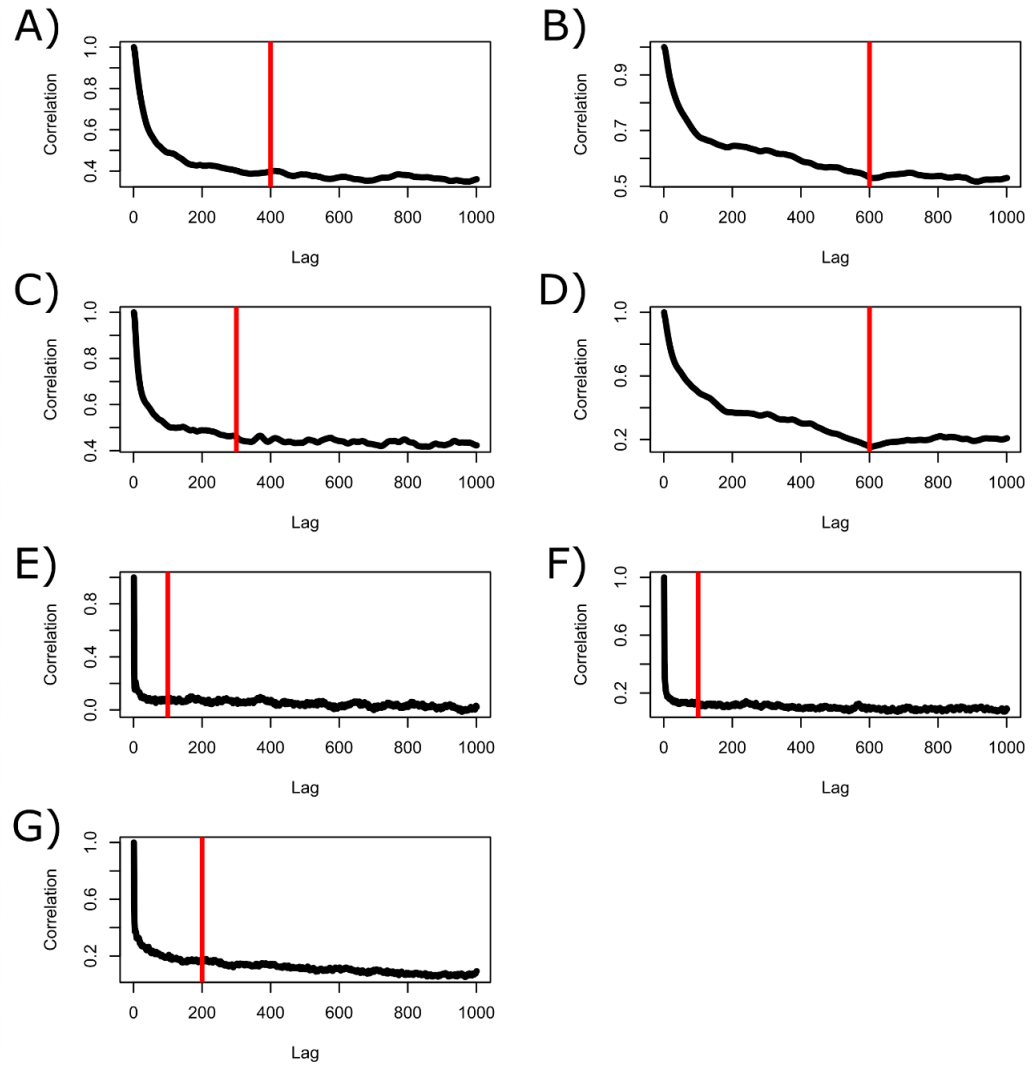

Figure S4. 1. Autocorrelation line plots

Autocorrelation (lag n=1000) of each variable used in the analysis. Red lines indicate the estimated autocorrelation end points (AEPs). **(A)** Nearest neighbour distance, **(B)** cranio-caudal distance to centroid, **(C)** lateral distance to centroid, **(D)** group speed, **(E)** flap frequency, **(F)** dorsal body amplitude, **(G)** flap frequency for solo flight, following fission. Figure taken from Sankey and Portugal (2019) and formatted as per the published version in *The Science of Nature.*

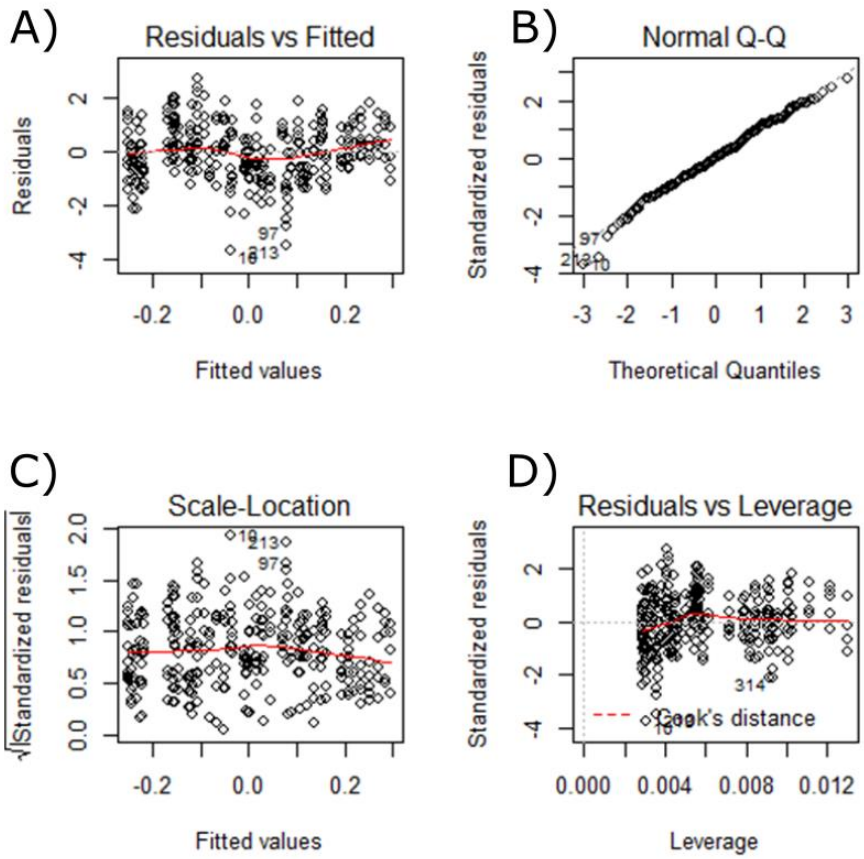

Figure S4. 2. Diagnostic plots

Diagnostics for linear model for flap frequency over time. *N* = 348 data points, after sub-sampling to account for autocorrelation. Typical diagnostic plot for a linear model using function "plot()" in base R (R Core Team. 2017). **(A)** Residuals vs Fitted plot shows no great deviation from zero, suggesting a linear model is appropriate. **(B)** Normal Q-Q plot Values of standardised values closely fit theoretical quantities, suggesting the residuals are normally distributed. **(C)** Scale-Location plots are to investigate the assumption of homoscedasticity. The relatively straight estimated line between square standardised residuals and fitted values suggest this assumption is valid. **(D)** Residuals vs leverage plot indicates that, in our present case, that no individual values are having a disproportionate influence on the slope estimate for the model. Figure taken from Sankey and Portugal (2019) and formatted as per the published version in *The Science of Nature*.

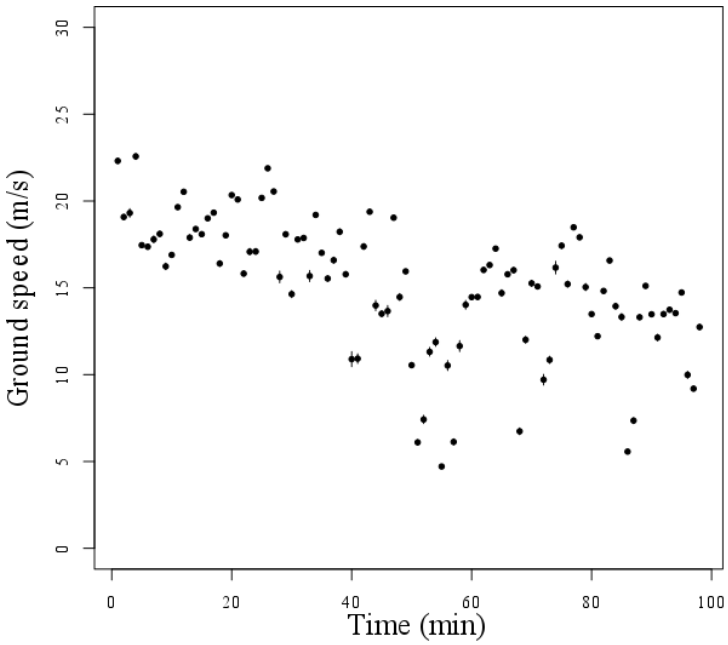

Figure S4. 3. Speed decrease over time

Ground speed (m/s) of all individuals (measured at 5 Hz) is plotted as means (points) with standard errors (bars) per minute over the course of the period of cohesive flight (97.6 mins) (see *Supplemental discussion: An investigation of speed*). Figure taken from Sankey and Portugal (2019) and formatted as per the published version in *The Science of Nature.*

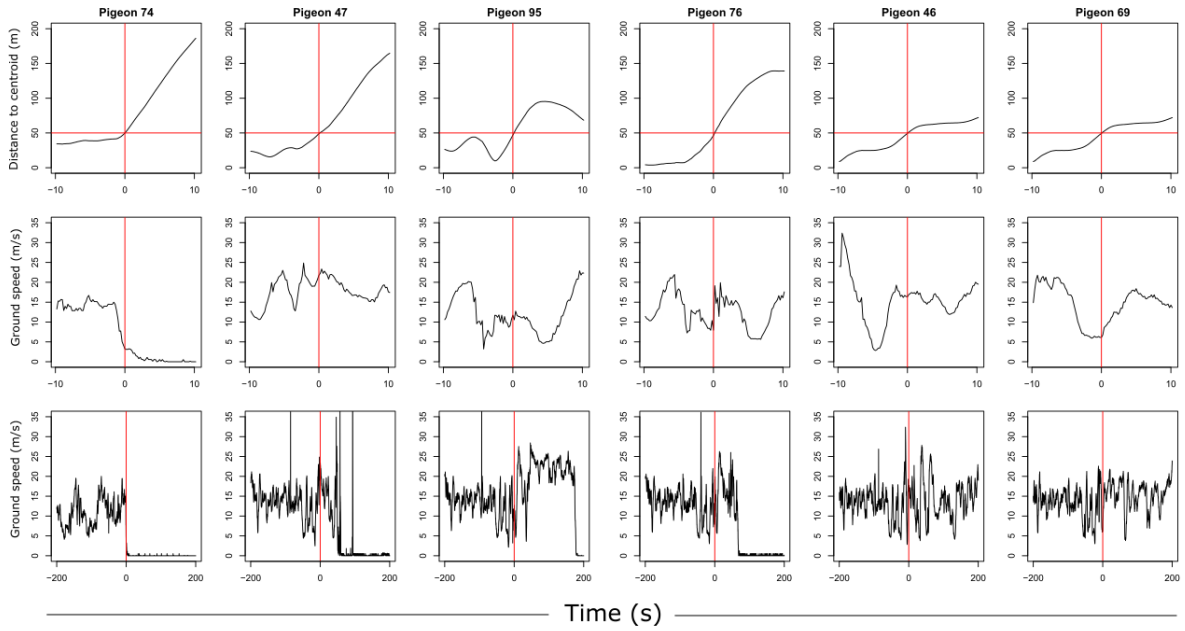

Figure S4. 4. Distance to centroid and ground speed at different timescales

All figures (columns) have same legend, and differ by individual pigeon (number in title of each figure). Additionally time zero (0) on the different figures (from left to right) differs, and is as follows: 0 s, 2419 s, 2424 s, 2436 s, 2468 s 2468 s, with respect to the furthermost left figure. (Top) Distance to centroid vs time. A lag of 10 seconds is used. When an individual reaches 50 m from the group's centroid this individual is considered to have split from the group (red lines x and y axis), and a new centroid is assigned to the remaining individuals. This was repeated until the remaining two individuals (furthermost right two figures) split at the same time. Ground speed over time is also given with a time lag of (middle) 10 seconds, and

(bottom) 200 seconds. See *Supplemental discussion: an investigation of speed.* Figure taken from Sankey and Portugal (2019) and formatted as per the published version in *The Science of Nature.*

Table S4. 1. Statistics

Results of statistical tests for each of the variables used in analyses. nn – nearest neighbour distance; cc – cranio-caudal distance to centroid; la – lateral distance to centroid; sp – ground speed; ff – flap frequency (during the 98 mins of group flight); dba – dorsal body amplitude; ffs – flap frequency solo (taken from 49 mins of solo flight following group fission). The table includes the best model (model with lowest AIC score) from a comparison between: linear model (LM), linear mixed effects model with individual as random intercept (LME-RI), and linear mixed effects model with individual as random intercept and slope (LME-RIS). Fixed-effects-R^2 (R^2 (f)) score is given for linear model, and conditional R^2 (accounting for fixed and random effects – R^2 (f+r)) given for linear mixed effects models. Lower (2.5%) and upper (97.5%) confidence intervals (CI). For LME tests, whether CI values cross zero determines if the data are significantly different from a null interpretation (Sig*); for LM tests, the *p*-value is provided and signature (*) given for values $p < 0.05$. All statistics were taken as either a median or mean of 1000 bootstrap estimates of the model statistic. Median value is reported if the distribution of the samples was significantly different from a normal approximation (Shapiro – Wilk test; base R; accepted value $p < 0.05$). Vice-versa, a mean was used in the case where the distribution of sample estimates was not significantly different from normal. All statistics were replicated across both a scaled data and unscaled data condition. Data are presented to the nearest three decimal places.

Variable	Best model			Scaled					Unscaled		
		R^2 (f)	R^2 (f+r)	CI (2.5%)	CI (97.5%)	Sig* (Y/N/p)	R^2 (f)	R^2 (f+r)	CI (2.5%)	CI (97.5%)	Sig* (Y/N/p)
nn	LME-RIS	NA	0.337	0.144	0.572	Y	NA	0.342	0.012	0.049	Y
cc	LME-RIS	NA	0.512	0.306	0.759	Y	NA	0.512	0.068	0.169	Y
la	LME-RIS	NA	0.396	0.207	0.589	Y	NA	0.391	0.024	0.07	Y
sp	LM	0.207	NA	-0.547	-0.341	<0.001*	0.167	NA	-0.094	-0.056	<0.001*
ff	LM	0.013	NA	-0.215	-0.006	0.031*	0.012	NA	-0.02	-0.001	0.044*
dba	LME-RI	NA	0.148	-0.024	0.174	N	NA	0.158	-0.002	0.059	N
ffs	LME-RI	NA	0.274	-0.041	0.333	N	NA	0.296	-0.018	0.108	N

Table S4. 2. Airport wind data

Location of U.K. airports where weather data was collected. Weather data was collated from the following website: https://www.weather.org/weather-history/. All three airports were encompassed or within 20 miles of part of the long flight. Full weather data is available as a separate document ('Sankey and Portugal Weather Data.xls')

Airport	Longitude/Latitude	U.K. Post Code
London Heathrow	51.4696° N, 0.4496° W	TW6 1EW
Southend	51.7700° N, 0.6939° E	SS2 6YF
Stansted	51.8860° N, 0.2389° E	CM24 1RW

Chapter 5: Flock stasis drives flight speed in pigeons, while artificial mass additions do not.

Daniel W. E. Sankey[1] and Steven J. Portugal[1]

Author affiliations:

[1] *School of Biological Sciences, Royal Holloway University of London, Egham, TW20 0EX, U.K.*

Abstract

Animals are characterised, in part, by their use of voluntary movement, which is used to explore and exploit resources from their surrounding environment. Movement can therefore benefit animals, but will cost them their energetic reserves. Thus, adaptations for faster movements with negligible increases in energy expenditure will likely evolve. Individual and social-level mechanisms have been shown to optimise this speed/energetic trade-off. Nevertheless, studies of social-level traits typically ignore individual variation, which is a cornerstone principle in evolutionary ecology. Furthermore, how individual phenotype interacts with the phenotypic composition of the group to govern the cost of transport may have been entirely overlooked. We investigate speed and the energetic consequences of individual-level phenotypic differences in body mass (both natural and artificially manipulated with additional weights) of homing pigeons (*Columba livia*) (*N* =16 birds; *N* = 193 useable flight trajectories). We then turn to social level phenomena, and manipulate the composition of pigeon groups by "natural" body mass in four treatments mixing 'heavy' and 'light' birds (*N* = 12 birds; *N* = 192 useable flight trajectories) and leadership rank to form groups of 'followers' and groups of 'leaders' (*N* = 30 birds in six groups of *N* = 5, *N* = 286 useable flight trajectories), with leadership being determined in earlier flights (*N* = 33 birds, *N* = 306 useable flight trajectories). "Natural" body mass was predictive of flying speed in solo flights, but not in groups of greater mass by composition; "artificial" mass loading had no impact on speed in solo fliers, and was not tested in groups. Groups

of *leader phenotypes*, showed faster speeds, and greater cohesion than *follower phenotype* groups, both in terms of flock spread, but also in consistency of positioning within the flock ("flock stasis") across the flight. Flock stasis was further analysed across all other group flights. Its positive impact on speed was found to be consistent across all experimental treatments. Therefore, predicting flock stasis may be critical to understanding optimal phenotypic compositions of birds, and thus the social evolution of birds which fly together. We provide evidence that greater stasis may be driven by phenotypic compositions (i.e. groups of leaders, and homogeneous mass groups) and also discuss the implications of stasis for different flocking structures (e.g. V-formations) and human crowd control.

Introduction

Voluntary movement is not unique to animals, but is a defining characteristic (Biewener and Patek 2018) that likely evolved to allow exploration and exploitation of the environment (Perry and Pianka 1997; Giuggioli and Bartumeus 2010). Expanding the range or speed of movements may enhance the benefits of exploration through increasing the rate of resource acquisition and/or by reaching farther away foraging or mating grounds (Pyke 1984; Brown et al. 1991), though this is likely to come at a greater energetic cost (Heglund and Taylor 1988; Alerstam et al. 2007). Accordingly, optimal foraging theory predicts that individuals that can move faster will increase their success of resource acquisition via an increased

encounter rate, with a major assumption being that the energetic cost movement will increase concurrently (Gendron and Staddon 1983; Pyke 1984). Nevertheless, this assumption might not always hold true as both individual and social-level strategies can offset the costs of movement (Tucker 1998; Hedenström and Liechti 2001; Dayton et al. 2005; McHenry and Lauder 2006; Wilson et al. 2012; Shepard et al. 2013).

At the individual level, physical adaptations can reduce the cost of travel. For example, body streamlining can reduce drag (and thus energetic cost) in aquatic (Dayton et al. 2005; McHenry and Lauder 2006) and aerial animals (Tucker 1990; Hedenström and Liechti 2001). Also, individual-level behavioural strategies may have evolved to optimise travel through the optimal use of their "energy landscape". For example, birds that make use of predictable rising air (e.g. thermals – columns of rising air) (Wilson et al. 2012; Shepard et al. 2013), or adaptive combinations of active and passive dispersal through water currents in juvenile fish (Dingle 2014). At the social level, behavioural interactions with conspecifics have evolved to optimise travel costs (Bill and Herrnkind 1976; Portugal et al. 2014; Voelkl et al. 2015). For example, in V-formation flights, vortices produced from the wingtips of leading individuals (Portugal et al. 2014; Voelkl et al. 2015) may explain decreased energetic output of trailing individuals (Weimerskirch et al. 2001), when relative body position and the timing of their flaps are spatially and temporally "in-phase" (Portugal et al. 2014). Similarly, fish have been shown to decrease muscle activity in artificial vortices (Liao et al. 2003), and these mechanics are suggested to

also be utilised in response to vortices of conspecifics (Liao et al. 2003). Additionally, lobsters walking in a line reduce drag and subsequently the energetic costs of movement (Bill and Herrnkind 1976). However, current studies of social-level energy-saving strategies still implicitly ignore individual phenotypic variation, which is a foundational principle in evolutionary ecology (Wade et al. 2006; but see Ling et al. 2019). Furthermore, for social species, an individual's success is intrinsically tied not only to its own phenotype, but also to the phenotypic composition of the surrounding group (Farine et al. 2015). Overall, how individual phenotype and group phenotypic composition interact to govern the speed and costs of travel is an important, but hitherto unknown, aspect of the life history of animals which travel in groups.

Homing pigeons (*Columba livia*) are well suited to answer questions about speed and the costs of movement, and the interaction of individual-level phenotype and group phenotypic composition, for a number of reasons. Pigeons, like most birds, use flight (a costly form of locomotion; Schmidt-Nielsen 1972) to navigate home, and can do so alone (Meade et al. 2005; Biro et al. 2006; Pettit et al. 2015), or in groups (Nagy et al. 2010, 2013; Watts et al. 2016). Group composition and group size are easy to manipulate in pigeons, by releasing birds in groups of predetermined phenotype. Pigeons also exhibit high robustness to the application of animal attached biologgers, which can be used to measure speed (using GPS; e.g. Pettit et al. 2013b, 2015) and energetic proxies (using accelerometers; e.g. Taylor et al. 2017, 2019). Through the application of biologging technology, measures of

morphological and behavioural phenotypes are easily attainable in pigeons, including repeatable “in-flight” phenotyping (which is rare in biologging studies; Chmura et al. 2018). For example, repeatable measures of speed (solo and group) and leadership (group) are easily measured with GPS loggers, due to the reliability of pigeons to return home (Nagy et al. 2010, 2013; Pettit et al. 2015; Chapter 2), and the consistent transient leadership hierarchies shown to be transitive in pigeon flocks (Nagy et al. 2010, 2013; Flack et al. 2012; Santos et al. 2014; Watts et al. 2016; Chapter 2). Biologging also has less welfare impact on captive animals, due to the relatively short-term attachment (<1 day; Portugal and White 2018), and the provision of surplus food to restore their energy levels after deployment (Chapter 3).

In Chapter 3, we found an example of how energetic costs may relate to individual phenotype and the phenotypic composition of pigeon groups. In birds, energetic output may be optimised (or minimised) by flying at an individually specific optimum speed (Tobalske et al. 2003), which we found may be characterised by morphological phenotype (i.e. body mass; Chapter 3). Flying any faster than this optimum preferred solo flight speed will require additional energy output, through increased chemical energy required to power flight muscles (Tobalske 2007); as will flying slower, via a reduction in lift produced by momentum (Tobalske et al. 2003). Birds were found to compromise from their preferred speed to fly with the group (Chapter 3), which highlights that the benefits of grouping, e.g. anti-predator benefits (Kenward 1978; Carere et al. 2009) or enhanced decision making accuracy

(Biro et al. 2006; Dell'Ariccia et al. 2008) may outweigh these costly compromises. Heavier and lighter pigeons – which are thought to optimise their energetic profile by flying faster and slower, respectively – may, therefore, have to increase their relative energetic output to fly (and stay) together in a group (Sankey et al. 2019; Chapter 3). Therefore, an individual of a given body mass (individual phenotype) would benefit energetically by flying in groups of similar mass (homogeneous group phenotypic composition) as the group may fly closer to the individual's preferred speed, which would require less of an *energetically costly* compromise. This highlights the potential of individual-level and social-level behavioural and morphological traits that may result in more effective travel. In this Chapter, we explore how individual-level phenotype and group phenotypic compositions may interact to govern speed and the energetic costs of bird flight, via experimental manipulations.

Individual-level phenotype: body mass and artificial mass manipulations

It is widely demonstrated that morphological phenotypes have a close relationship to flight speed and its associated costs (Tobalske et al. 2003; Alerstam et al. 2007; Heerenbrink et al. 2015). In particular, body mass and wing-loading (wing area divided by mass) have been shown to be predictive of solo flight speed in birds across multiple species (Alerstam et al. 2007). Moreover, intra-species differences in body mass have also been shown to predict greater flight speeds in heavier

pigeons (Pettit et al. 2015; Chapter 3). Furthermore, faster travel in powered flight is thought to be associated with greater energetic costs in birds (Tobalske et al. 2003; Hedenström 2009); heavier birds will require a faster air flow to produce the same amount of lift (Tobalske et al. 2003). A concurrent increase in energetic output is expected for heavier birds, because of the higher weight-per-area for each flap (wing loading) (Tobalske et al. 2003). Additionally, in barn swallows (*Hirundo rustica*), heavier birds demonstrated faster flapping frequencies, and their larger mass was associated with larger energetic output beyond the effect of frequency alone (Schmidt-Wellenburg et al. 2007), supporting a hypothesis that both increased flapping frequency and greater wing loading have an additive effect on energetic output in birds. Nevertheless, heavier individuals may mitigate the additional energetic costs through either greater food dominance (Portugal et al. 2017b) (acquiring more energy resources in non-flight periods) or efficient flight kinematics, as has been shown for birds carrying additional mass loads (Hambly et al. 2004; Lapsansky et al. 2019). For example, firstly, cockatiels (*Nyphicus hollandicus*) have been shown to slow down while retaining their flapping frequency in response to additional mass loading (Hambly et al. 2004). Strikingly, the birds were not found to increase energetic output across a range of artificial mass loadings as high as 20% of their body mass perhaps owing to consistency in the wingbeat kinematics (Hambly et al. 2004). Second, zebra finches (*Taeniopygia guttata*) have been shown to increase flapping and decrease wing amplitude in response to artificial mass loadings (Lapsansky et al. 2019). Owing to a reduction in their usual, and costly, “bounding” flight dynamics, increasing flapping may actually

lead to more efficient flight (Lapsansky et al. 2019). However this latter study, conducted in a wind tunnel, enforced a speed of 10 m/s, and therefore the zebra finches were not capable of responding by slowing down (Lapsansky et al. 2019). Neither mechanism is likely in heavier pigeons, which do not use bounding flight (Usherwood 2016; Sankey and Portugal 2019; Chapter 4), and where heavier individuals are faster (not slower). Instead, heavier pigeons may mitigate energetic costs by switching from high frequency to high amplitude flight, as greater flapping frequencies are thought to be highly costly in pigeon flight, compared with relatively uncostly wingbeat amplitudes (Usherwood et al. 2011; Taylor et al. 2019). We ask the question as to whether larger birds naturally employ this strategy (high amplitude/ low frequency). Additionally we ask whether we can induce these same tactics – or those employed by cockatiels (Hambly et al. 2004) or zebra finches (Lapsansky et al. 2019) – by manipulating the mass of individuals artificially during solo homing flights.

Social-level behavioural traits: flock leadership manipulations

Studies of collective movement suggest that consistent individual behavioural phenotypes are likely to play a role in inter-group differences in optimising the trade-off between the speed of travel and energetic costs. This may be particularly pertinent in bird flocks. For example, Usherwood et al. (2011) found that flying in a cluster flock comes at an energetic cost for pigeons, with individuals in denser

flocks exhibiting greater flapping frequencies, even after accounting for speed. Furthermore, over long-duration flight in cluster flocks, pigeons have been found to reduce spatial density, providing further support for a proximate cost of flying close to conspecifics (Sankey and Portugal 2019; Chapter 4). Therefore, any experimental treatment which can manipulate the dynamics of cluster flocks to reduce the *density* could provide a method to reduce the *energetic cost* without concurrent reductions in speed (or vice versa, increases in speed without concurrent increases in energetic cost). Johnstone and Manica (2011) provide a potential solution to this methodological problem in their evolutionary model of group leadership dynamics. They demonstrated that populations of leader phenotypes – owing to their goal-oriented nature – suffer reduced coordination/cohesion as a result of all individuals attempting to dominate movement decisions (Johnstone and Manica 2011). Together, the studies of Johnstone and Manica (2011) and Usherwood et al. (2011) suggest that groups of individuals with an *on-average* greater leadership composition could form less dense flocks (Johnstone and Manica 2011), and further, owing to this reduction in density, will fly further/faster per unit energy (Usherwood et al. 2011). Here, we ask the question as to whether a behavioural phenotype (leadership) can manifest in more effective flight when alterations are made to the group phenotypic composition of a flock.

Social-level morphological traits: group mass composition manipulations

Given that heavier birds fly faster both across (Alerstam et al. 2007) and within species (Schmidt-Wellenburg et al. 2007; Pettit et al. 2015; Sankey et al. 2019; Chapter 3), manipulations of the group composition via instantaneous artificial additions to body mass provides a novel way to test the impact of group phenotypic composition on the relationship between group flight speed and energetic costs or travel. As discussed previously, individuals of a similar body mass are likely to have similar preferred optimal flight speeds, and thus a homogeneous group comprising birds of a similar body mass may reduce the speed compromise between individuals (Hedenström and Åkesson 2017b; Sankey et al. 2019; Chapter 3), which may be highly costly in birds (Tobalske et al. 2003). Such a reduction in compromise (and hence flight costs) would highlight a benefit individuals can achieve at the social level, via optimal choice of group membership via selective joining of a group or eviction/allowance of other members (Farine et al. 2015). The resulting energetic benefits for an individual travelling in a group could, therefore, be specific to their own phenotype, and the phenotypic composition of their associated group (Farine et al. 2015). Nevertheless, this question remains unstudied at present. Here we ask whether manipulations of the *body mass* composition within a group can influence speed and energetic proxies across the social context (i.e. phenotypic composition).

Alternative social-level strategies: flock stasis

Inferring benefit from more efficient use of speed and/or energetic expenditure in less dense flocks (see *Social level behavioural traits*, above) is problematic, as birds which form dense clusters will do so for adaptive benefit, for example for protection against predators (Kenward 1978; Carere et al. 2009). Therefore we expanded our search for optimal strategies beyond *flock density*, and into *flock stability* (or, stasis). Specifically, by flock stasis, we are referring to the potential for differing degrees of consistency in the spatial positioning of individuals in certain flocks over others, the difference of which may be based upon their phenotypic composition. Flying in a cluster flock has been shown to increase the energetic expenditure of birds compared to flying solo (Taylor et al. 2019), which is thought, in part, to be attributable to the unpredictability and/or inconsistency (i.e. heterogeneity) of airflows left in the wake of birds in front (Usherwood et al. 2011; Taylor et al. 2019). Stasis in flock positioning could, therefore, make the air environment more predictable and/or homogenous. We expect individuals of a similar mass to exhibit greater stasis, due to their comparatively lower levels of speed compromise, which may manifest in accelerations (by lighter, slower birds) or decelerations (by heavier, larger birds), which retain cohesion but may modify the air environment negatively compared with birds which fly at a consistent speed. Given the expected stability of the air environment as a result of greater stasis, we expected higher flock stasis to be predictive of flock speed; i.e. the flock will fly fastest when stasis is greatest. Additionally, we expect that groups of leader

phenotypes will exhibit lower stasis than groups of follower phenotypes, due to a reduction of "attempted leadership initiations" in the follower phenotypes via reduced route conflict (King 2010; Johnstone and Manica 2011). Therefore how group phenotypic composition influences flock stasis, and whether flock stasis is predictive of optimisation of the speed to energetic cost trade-off, was another question approached in the present study.

Methodology and predictions

We experimentally manipulated individual body mass (artificially), group leadership composition, and the group body-mass composition of homing pigeon flocks to test *a priori* predictions (in brackets) through experimental manipulations over three separate experiments. Furthermore we conducted a comparative analysis of all group flights to investigate flock stasis (described above). **In experiment one**, by artificially increasing the mass of pigeons, we predicted (***1***) reductions in solo flight speed while energetic costs remain stable – following the results of experiments which allowed speed changes in response to artificial mass loadings (Hambly et al. 2004). We also predict (***2***) that body mass will positively covary with speed and flap frequency (following (Schmidt-Wellenburg et al. 2007)), regardless of treatment. **In experiment two**, by predetermining leadership hierarchies, we first separated birds into groups of leaders and followers. We predicted that (***3***) groups of leaders would show reduced density (following (Johnstone and Manica 2011)), and with this, (***4***) a

reduction in speed and/or energy expenditure proxies in less dense flocks (following (Usherwood et al. 2011)). **In experiment three**, if body mass predicted solo speed in individuals, we predicted (***5***) that group flights comprising more heavy individuals would exhibit greater flock speeds. We also predicted (***6***) that heterogeneous groups (i.e. those with a mixture of heavy and light individuals) would experience greater costs of group flight relative to flying in homogenous groups (see above, and Chapter 3). Following this, we then combined all group flights for **our comparative analysis** to look for evidence of flock stasis, which we predicted would (***7***) positively correlate with flock speed and/or decrease energetic proxies. Additionally we predicted greater stasis in (***8***) in groups of "followers" over groups of "leaders", and (***9***) homogeneous body-mass groups over heterogeneous compositions. For all predictions see Table 5.1.

Table 5. 1. Predictions, rationale and results

Columns from left to right represent: (from *Introduction*) prediction number, predictions and supporting evidence and/or rationale; (from *Results*) Finding and Figure reference, and whether the prediction was observed (Yes or No) as well as, in some cases, brief discussion. "Inc." and "Dec." are shorthand for observed increases and decreases respectively; FF and DBA are shorthand for flap frequency and dorsal body amplitude respectively.

Prediction	Prediction	Supporting evidence and/or rationale	Finding (and Figure)	Prediction match?
1.	Artificially mass manipulations will induce reduced solo flight speed, with no difference in energetic proxies	Cockatiels show these dynamics (Hambly et al. 2004) when not constrained to fly at artificial flight speeds in wind tunnels (as in Lapsansky et al. 2019)	Speed: ND FF: Inc. DBA: Dec. (Fig. 5.2)	Speed: No FF: No DBA: No
2.	Natural body mass will be predictive of solo flight speed, and flap frequency	Naturally heavier barn swallows demonstrate faster speeds and higher flapping frequencies (Schmidt-Wellenburg et al. 2007)	Speed: Inc. FF: Inc. (Fig. 5.3)	Speed: Yes FF: Yes
3.	Groups of leaders would show decreased flock density	Reduced coordination in groups of leaders in an evolutionary model, via too many leaders attempting to dominate movement decisions (Johnstone and Manica 2011).	F-spread: ND DV-spread: Inc. CC-spread: ND	No, measures mostly had opposite trend
4.	Denser flocks will demonstrate decreases in speed and/or increases in energy expenditure proxies	Pigeons in denser flocks have been shown to have increased energy expenditure after accounting for speed (Usherwood et al. 2011).	Speed: Inc. FF: ND DBA: ND	No, the opposite trend was observed for speed
5.	Groups comprising more heavy individuals will exhibit greater flock speeds	Body mass predicts pigeon speed in solo flights (Pettit et al. 2015; Sankey et al. 2019; Chapter 3)	Speed: ND (Fig. 5.2)	No
6.	Heterogeneous mass groups would experience greater costs of flight relative to homogeneous groups	As groups need to reach speed consensus ((Sankey et al. 2019; Chapter 3), which involves – potentially costly – speed compromise	FF: ND DBA: ND (Fig. 5.2)	No, but heterogeneous mass groups were slower
7.	Greater flock stasis will enhance flock speed and/or decrease energetic proxies	Predictability and homogeneity in the air environment of a cluster flock (Usherwood et al. 2011) likely to increase in static flocks.	Speed: Inc. FF: ND DBA: ND (Fig. 5.4)	Yes
8.	Groups of “followers” will exhibit greater flock stasis than groups of “leaders”	Reduced coordination in groups of leaders (Johnstone and Manica 2011), as above in prediction (3), may impact stasis as well as density.	Stasis: Dec. (Fig. 5.5)	No, conversely leaders demonstrated greater stasis
9.	Homogeneous mass group compositions will exhibit greater flock stasis than heterogeneous compositions	Reduced acceleration/deceleration response of homogenous mass groups reaching speed compromise (Chapter 3) may increase stasis	Stasis: Inc. (Fig. 5.5)	Yes

Methods

Homing pigeons (*N* = 49) were kept in purpose-built lofts at Royal Holloway University of London (Surrey, U.K.; latitude = 51.416, longitude = -0.572), and provided with food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, U.K.), water, and grit (Versele-Laga - Colombine Grit and Redstone, Deinze, Belgium) *ad libitum* throughout the course of the study period (April—September 2018).

Experiments and general protocol

All birds were weighed (CoffeeHit: Coffee Gear Digital Bench Scale – 2 kg/0.1 g limit/accuracy) weekly, providing a key morphological covariate ("natural" bird mass), while simultaneously monitoring welfare (Angelier et al. 2016). Repeatability of body mass (g) was deduced using likelihood ratio tests, with 95% confidence intervals estimated using 10,000 parametric bootstrap iterations.

The study comprised three experimental flocks. Experiment (1), the *artificial mass manipulations of birds flying solo* (*N* = 16 birds, age = 2.5 years old), the dates of experiment (1) were April—May 2018, with all birds having had previous experience from the release site (see below). Experiment (2) was the *group leadership composition manipulations* (*N* = 33 birds, age = 9 months), conducted between July—September 2018. Here birds had no experience of the release site at the beginning of the study (see Training protocol however in *Supplemental*

Material). Finally, experiment (3) *Group body mass composition manipulations*, consisted of (*N* = 12 birds, age = 9 months), assorted by body mass into categories of either 'heavy' or 'light', using the same birds as in *Group leadership composition manipulations*. This study was conducted throughout September 2018.

Our key parameters of interest across the experiments were flight speed (m/s), and energetic proxies *i*) flap frequency (Hz), and *ii*) dorsal body amplitude (mm) (Usherwood et al. 2011; Taylor et al. 2017, 2019; Sankey and Portugal 2019; Chapter 4). To record these variables we adopted a biologging approach, using GPS (speed; 5 Hz, QStarz BT-Q1300ST, Düsseldorf, Germany; mass = 12.5 g) and accelerometers (flap frequency and dorsal body amplitude; 200 Hz; AX3, Axivity Ltd, Newcastle upon Tyne, U.K.; 8 g). See *Supplemental Material* for further information on logger treatment and attachment.

Each flight experiment comprised releasing the homing pigeons from a site between Windsor Castle and Eton (coordinates: latitude = 51.497^{o}, longitude = -0.589^{o}) away from their home lofts at Royal Holloway (coordinates: Latitude = 51.415^{o}, Longitude = -0.573^{o}). Firstly, birds were gathered from their home loft and placed into wicker carrying baskets (dimensions = 80cm x 40cm x 22cm) for transportation to release site. Following this, the birds were driven 8.90 km north (exact bearing = -0.07rad) to the release site. The birds were typically in transit for 15-25 mins. Older birds (experiment one) had experience from the Windsor-Eton release site, for training protocol on younger birds (experiments two and three) see *Supplemental Material*. At the release site, both GPS and the accelerometers were

switched on and attached to the back of each bird. GPS loggers were switched on at least five mins before deployment to ensure an accurate signal was being received from the satellites. The birds were released either *i*) solo (experiment one), in the order they were randomly selected from the box, and following a minimum of 10 mins delay from the release of the previous bird, or *ii*) as groups (experiments two and three) by opening the side hatch on the wicker basket following at least a 15-min delay from the release of a previous group. This time-delay ensured birds were not subsequently meeting up en-route from the release site to the home lofts.

Experiment one: solo flight mass manipulations

For experiment one (solo mass manipulations), the purpose was to manipulate the body mass of individuals to determine the impact of this mass manipulation on solo flight speed (*sensu*, Pettit et al. 2015; Sankey et al. 2019; Chapter 3) and flight kinematics (*sensu* Hambly et al. 2004; Lapsansky et al. 2019). Individuals either flew without any mass manipulation, as a control condition (~0 g, Velcro strip), or with 5 g or 10 g additional mass added to their backs using tin wheel-balancing bicycle weights (Abba ME, Essex, U.K.). The self-adhesive weights were attached to the accelerometer loggers (on the cranial end of the pigeons' backs) to ensure the additional artificial mass was close to the centre of the pigeon's body mass, which is located towards the head (Rutz and Troscianko 2013).

Given the initial mass of the birds (range 409.6 g – 533.1 g), the mass load as a proportion of body mass (logger mass plus additional mass load by bird mass) ranged from 3.8% for heaviest birds in the 0 g artificial mass treatment, to 7.4% for the lightest birds in the 10 g artificial mass treatment. This means that a commonly cited 5% rule was surpassed in some cases in the present study (Portugal and White 2018); however as mentioned, impact of biologging may be mitigated in captive animals relative to wild species (see *Introduction* and Portugal and White 2018). Additionally, we were able to provide data on the response of pigeons to the additional mass, which could inform ethical decision making in future work.

Each flight release event contained a mix of the three mass loading treatments between flocks (i.e. control, 5 g and 10 g), to regulate for temporal differences in weather conditions – which may perturb speed, despite us controlling for wind conditions in the analyses (see *Speed, Tortuosity and Wind parameters*, below; also see *Supplemental Material* and Table S5.1 for randomisation procedures). Before the termination of the study, we explored the data for any evidence of pigeons "pairing up" (see *Computational methods* below), to, firstly, remove the data from the analysis, and second, to ensure that each individual had completed at least three solo flights per mass condition. Determination of whether birds flown under solo treatments did subsequently pair up was defined as: less than 50 m from a neighbour (following: Pettit et al. 2015) for over 50% of the flight was stated as being a pair. Following removal of paired flights, the number of solo flights per mass

condition were 0 g (N = 60 flights); 5 g (N = 66 flights); 10 g (N = 67 flights) (see Table S5.4).

Experiment two: group leadership composition manipulations

For experiment two (group leadership composition manipulations), we firstly randomly allocated 33 pigeons into three separate groups. Following a training phase (see *Supplemental Material* for details on training), each of the three pigeon groups (N = 11, N = 11, N = 10 for each group respectively, following one loss in training flights) were released ten times from the standard Windsor-Eton release site to establish leadership hierarchies (Nagy et al. 2010, 2013; Flack et al. 2013; Pettit et al. 2015; Watts et al. 2016). These flights are subsequently referred to as "leadership identification flights".

Following the allocation of leadership ranks (following: Nagy et al. 2010; also see below), each group was subdivided into leaders (top 5 leadership scores) and followers (bottom 5 scores). In the groups of 11 (*N* = 2 groups) the individual with the middle score (at leadership rank 6) was left-out of further study. The new groups (*N* = 6 groups; three groups of leaders and three groups of followers) were released a further 10-11 times (Table S5.3) to assess differences in group dynamics between groups of leaders and groups of followers (subsequently referred to as "leadership manipulation flights"). Bird losses (i.e. birds which did not return from a particular flight; *N* = 3), as well as all logger failures (*N* = 6), and flights where one or

more groups did not participate. A maximum of one flight was missed per group, due to individuals undergoing routine procedures; all flights are documented in Table S5.3. Groups were not changed as a result of losses but instead group size (which was thus diminished in some cases) was treated as a categorical variable with fixed effects in our models (see *Statistics*).

Experiment three: group mass composition manipulations

For experiment three ("mass manipulation flights"), we took 27 pigeons with body mass distribution approximately normal (Shapiro Wilks test; $W = 0.962$, $p = 0.392$), and formed two subsequent groups: 'light' and 'heavy'. Six light individuals and six heavy individuals (randomly selected from the bottom/top eight of the 27 birds, respectively) were selected, leaving a difference of 46.9 g between the heaviest bird from the light group (mean = 374.3 g; SD = 19.3 g) and lightest bird from the heavy group (mean = 455.3 g; SD = 15.4 g). On a given flight/day the groups were either flown as complete but separate heavy/light groups (homogeneous mass groups), or with two individuals swapped into the other group (heterogeneous mass groups) before flight. See *Supplemental Material* and Table S5.2 for randomisation of group compositions. Therefore we utilised four distinct mass compositions, 1) "all light" (N = 6 'light' birds), 2) "predominantly light" (N = 4 'light' birds; N = 2 'heavy' birds), 3) "predominantly heavy" (N = 4 'heavy' birds; N = 2 'light' birds), and 4) "all heavy" (N = 6 'heavy' birds). We flew each composition

eight times, totalling 192 trajectories, with no missing data or birds. We express these conditions as the proportion of heavy individuals in the flock, therefore we had eight group flights with each [0], [0.33], [0.67] and [1], as a proportion heavy birds [square brackets are used to denote the proportion of heavy birds in this study throughout].

Computational methods

Fission, cohesion and sensitivity algorithms

We removed all GPS timestamps for the first 1000 m and last 500 m of the flights (see Chapters 2, 3 and 4) to compare only relatively steady sections of the return flight home. Further, in group flights, we removed individual data where the distance of an individual was over 50 m to the centroid (mean of latitude and longitude across group at each timestamp; see *Supplemental Material*). We also ran statistics on centroid distances of 25 m and 75 m to test the sensitivity of the statistics to our arbitrary choices of parameters. Fission – the proportion of flight an individual is separated from the group – was then calculated by dividing the total number of timestamps removed by the total number of steps.

We only recorded further metrics for each flight if a group remained stable in their composition. This was defined as *unchanged group membership* for a proportion of over 0.1 (10%) of the flight, and is subsequently referred to as “minimum flight

proportion". This allowed us to reduce erroneous readings, which may be caused by different group sizes or different group compositions, which come about by fission and/or fusion of birds. However, it was therefore possible to record multiple readings of a single metric in one flight (i.e. a reading for each of the different group compositions which remained stable for over 10% of the flight). Therefore we recorded the date and unique flight ID, to use as random intercepts (see *Statistics*), to deal with pseudoreplication (Davies and Gray 2015). We tested the sensitivity our subsequent analyses to our arbitrary choice of "minimum flight proportion", by testing "minimum flight proportion" values of 0.05 and 0.25, as well as 0.1 (see *Supplemental Material*).

Leadership

To assess leadership, we used pairwise correlations analysis on the merged trajectories (see methods in Chapter 2: *Supplemental Material: Treatment of biologging data: Leadership* and Nagy et al. 2010), whereby time-lags of similar movements are used to quantify the directional correlation delay of their turns (and hence the leadership). For example, if one individual turns (on average) 0.2 s before the rest of the flock, it will be considered a leader; whereas another individual which turns 0.2 s after the rest of the flock, it will be considered a follower. Leadership analysis was not considered if individuals did not remain cohesive (<50 m; following: Pettit et al. 2015) for over 50% of the flight. If the resulting

"leadership" matrix from all flights demonstrates significant transitive hierarchy (following: Nagy et al. 2010, 2013; Flack et al. 2012, 2013; Pettit et al. 2015; Watts et al. 2016), we can separate flocks by leadership rank to test our hypotheses, i.e. to test the relationship between leadership, flock composition and flock density and the efficiency of travel (see *Predictions* and Table 5.1).

Speed, tortuosity, and wind variables

We measured ground speed using point-to-point distance travelled between GPS coordinates at each time-step (5 Hz), for both individuals and groups ("flock speed", using centroid coordinates). Tortuosity – which is a key component to control for in models of speed (Safi et al. 2013) – was measured by the difference in heading between each time-step. We took a median of speed and tortuosity for the entire flight (solo flights), or for sections of flight with different, but stable, group compositions (group flights; see above). The efficiency of each flight was classically calculated as the perfect beeline (straight line between the site and the loft) divided by the total distance travelled (Biro et al. 2006; Freeman et al. 2011). This metric was calculated for each individual/group for each flight.

As speed can be influenced by wind speed and direction relative to the direction of travel (Safi et al. 2013), we recorded wind speed (accuracy ± 0.1 m/s) and direction (accuracy ± 22.5 degrees) every 0.5 hours at the home loft using a weather station (Aercus Instruments WS4083 Pro Wireless Weather Station; Greenfrog Scientific,

Doncaster, U.K). Using the nearest timestamp of wind data to the first timestamp of trimmed GPS pigeon data, we calculated wind currents parallel (support wind) and perpendicular (cross wind) to direction of travel (following: Safi et al. 2013). A mean of support and cross wind components were calculated across the whole flight (solo), or for periods of flight with stable group composition as above (group).

Energetic proxies: accelerometer measures

Data were downloaded from the accelerometry loggers as .svg files, and then processed to .csv files in OMGUI (https:// github.com/ digitalinteraction/ open / movement/ wiki/ AX3-GUI), before exporting to R (R Core Team. 2017). We then trimmed accelerometer data to match the start and end of the timestamps from the trimmed GPS (see above). Following this, we calculated flap frequency and dorsal body amplitude for each pigeon, for each flight. Flapping frequency was calculated using smoothed dorsal acceleration (z-axis of accelerometer; smoothed over 0.025 s), and removing static acceleration (over 15 wingbeat cycles, >2 s, see Taylor et al. 2017), before estimating upper reversal point (see Portugal et al. 2014) as a measure of each flap cycle. This measure was calculated at each wingbeat (i.e. time between one flap and the next, in flaps per second, Hz). The amplitude (mm) of the dorsal body acceleration ("dorsal body amplitude") was estimated via double integration of the acceleration curve, before passing through a Butterworth filter with cut-off frequency 2.5 Hz (see Usherwood et al. 2011; Taylor et al. 2017 and

Chapter 4 for further information). Again, this measure was calculated at each wingbeat. Medians of accelerometer measures were taken per bird, per flight, in all experimental treatments.

Flock density and stasis

In group flights, we calculated a further series of covariates describing the flock density. Across the flock, all neighbour-to-neighbour distances (in metres) were collated and averaged (mean average) at each time-step distance (Fig. 5.1). Flock spread was defined as the median value of these per-time-step values across sections of flight where group composition remained stable (as in speed, tortuosity and wind parameters; see above). Dorso-ventral and cranio-caudal spread were defined as the distance (in metres) between the furthest individuals to the left/right or front/back, respectively, with regard to the heading of the centroid (Sankey and Portugal 2019; Chapter 4). Consistent with flock spread this was recorded at each time-step, and then further reduced to a median value across cohesive sections of flight to provide measures of dorso-ventral spread and cranio-caudal spread for further analysis.

Additionally, following our rationale and predictions for social-level strategies which may confer optimal use of the aerodynamic environment, we measured flock stasis, a novel measure which estimates the variability in inter-individual positioning across the flock. Flock stasis was calculated by using flock spread data, but using the

inverse of the standard deviation instead of a *median* of the data from all time-steps (Fig. 5.1). Therefore we present flock stasis with units (-*std*(m)), reflecting the input variable (distance, m) and the statistic (standard deviation, *std*) used to derive the measure.

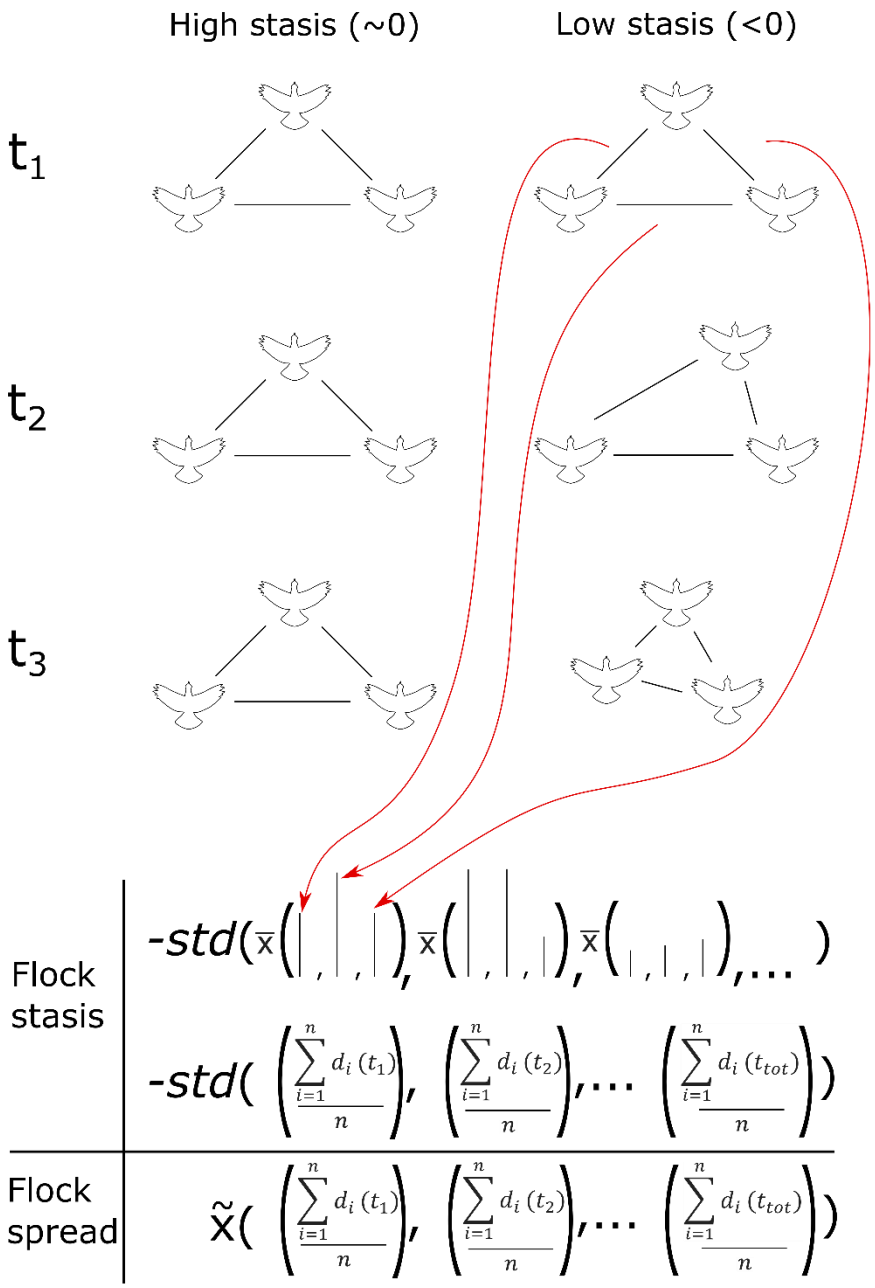

Figure 5. 1. Flock stasis and flock spread calculation schematic

Distances (m) between each individual (black lines) are calculated between each bird and for each time-step (t_1, t_2, etc.). These are then compiled (red arrows), summed and divided by the total number of distances (mean average, $\bar{x}$) at each

time-step. Our measure of flock stasis is the inverse of the standard deviation (*std*) of these data (units = -*std*(m)). Our measure of flock spread is a median value ($\tilde{x}$) of the same data (units = m). Birds in the left column represent a highly static flock, with values for flock stasis close to zero; birds in the right column represent a flock with low (more negative) stasis, due to individual's moving around more.

Statistics

We used linear mixed models (R package "nlme"; Pinheiro et al. 2012) to estimate the explanatory power of various covariates on dependent variables; solo speed, flock speed, flap frequency, dorsal body amplitude, and flocking parameters (e.g. flock stasis; above). Fixed effects were as follows: experimental treatment (i.e. artificial mass load – solo flights, and group composition – group flights); group size (after fission and bird losses; see above); support-wind and cross-wind components; "natural" – non-manipulated – bird mass was a fixed variable in solo flights, and tested via group composition changes in group flights; finally, flocking parameters were used as fixed effects when they were not treated as dependent variables (e.g. in models of flock speed). Our random effects included: pigeon ID (in solo flights and group flights without group level measures); group number (in experiment two; as the same treatment was conducted across three separate groups); unique flight ID and date (unique flight ID and date picking up smaller and larger scale local perturbations in temporal environmental conditions respectively); finally, when we compared all data from experiments two and three (cf. our comparative analysis;

see *Predictions*); experimental treatment was also included as a random intercept (i.e. “leadership Identification flights”, “leadership manipulation flights”, and “mass manipulation flights”). All model fits were tested to for a fit to the assumption of parametric residuals, and, depending on the greatest visual coherence of model residuals with a fitted qq-norm plot (R Core Team. 2017) were treated with either *i*) no transformation, *ii*) Box-Cox transformations (Sakia 1992), or *iii*) log transformations.

In our model estimating flock speed, collinearity of flocking parameters (e.g. flock spread, flock stasis) was dealt with by removal of less statistically significant parameters over a threshold value of correlation coefficients ($|r|>0.5$), following Dormann et al. (2013) (see Fig. S5.1 for a schematic and detailed description of this process).

Results

Experiment 1: Solo flights with artificial mass manipulations

Artificial mass manipulations.

Following prediction (1), that artificially mass manipulated birds would slow down, while keeping energetic proxies – flap frequency and dorsal body amplitude – constant, was not supported (see all predictions, and whether they were supported in Table 5.1). There was no evidence that manipulating mass loading (5 g weights,

10 g weights) decreased ground speed in pigeons (N = 16 birds; maximum N = 15 flights per bird: five flights in each of the three conditions) either as a numeric variable (LME; DF = 64, t = -0.766, p = 0.447) or as a categorical variable (LME with Tukey's pairwise post-hoc test; DF = 63; comparisons: 0 g - 5 g – *t.ratio* = 0.380, p = 0.924; 0 g - 10 g – *t.ratio* = 0.772, p = 0.721; 5 g - 10 g – *t.ratio* = -0.425, p = 0.905; see Table S5.4 for all statistics; Fig. 5.2A). Additionally, flap frequency did not remain stable, it showed significant increases when artificial mass load was treated as a numeric variable (LME; DF = 64, t = 2.067, p = 0.043; Fig. 5.2B), however, not when treated as categorical variables (Table S5.3). The increase in flap frequency was only slight, with an increase of approximately 0.02 Hz per gram of added artificial mass. Dorsal body amplitude also changed across mass load, the observed amplitude was significantly lower when treated as a numeric variable (LME; DF = 64, t = -4.682, p < 0.001) and across categorical group (10 g condition) when compared with 0 g and 5 g treatments (LME with Tukey's pairwise post-hoc test; DF = 63; comparisons: 0 g - 10 g – *t.ratio* = 4.760, p < 0.001; 5 g - 10 g – *t.ratio* = 3.712, p = 0.001; Fig. 5.2C). Decreases in amplitude were more marked than differences in flap frequency, with an estimated decrease of approximately 0.17 mm per additional gram of artificial mass. In additional analyses, we found that support wind component and cross wind components had a significant impact on ground speed (positive and negative respectively; support wind – t = 2.680, p = 0.009; cross wind – t = -3.432, p = 0.001).

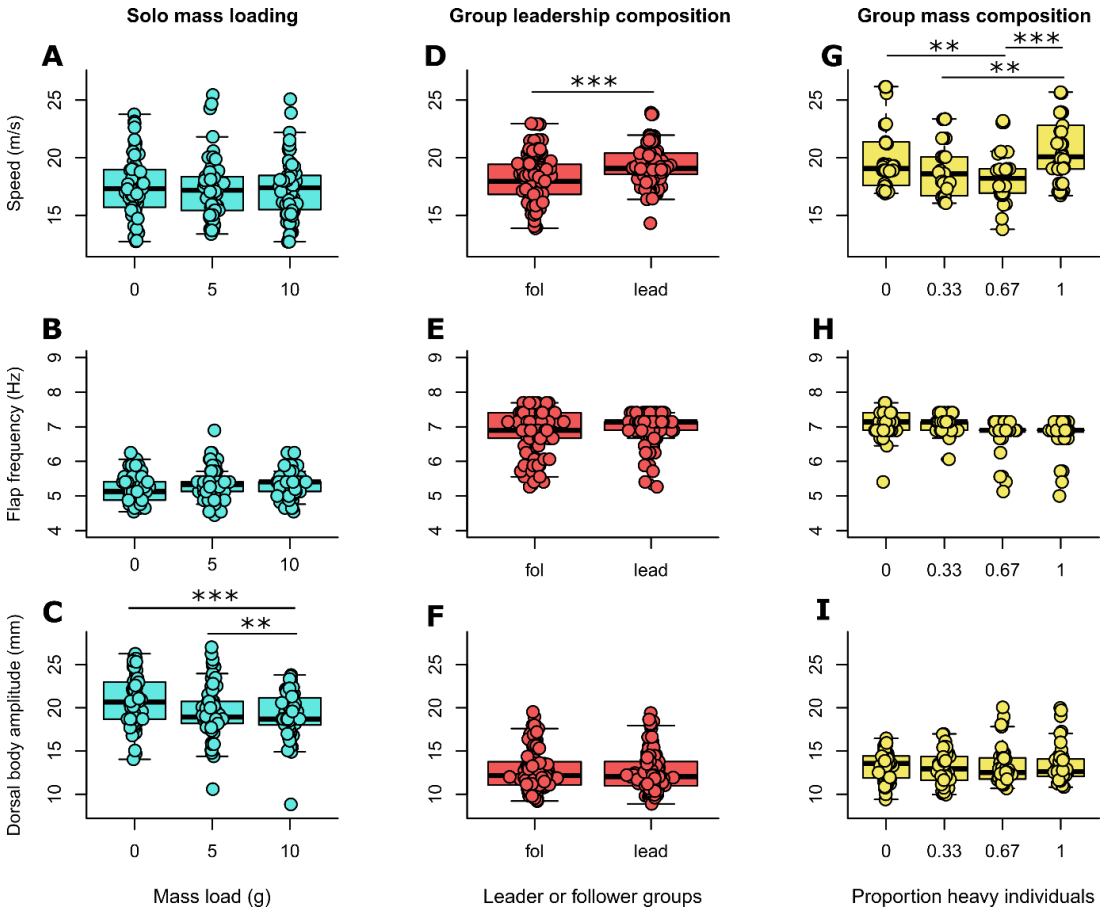

Figure 5. 2. Individual level flight metrics from all three experiments

Median flight speeds (m/s; top row), flapping frequencies (Hz; middle row) and dorsal body acceleration values (mm; bottom row) are given as points with box and whisker plots for each experiment as follows: **(A-C)** Solo mass loading (turquoise): flights with additional artificial mass loadings attached to the accelerometer logger either 0 g (Velcro strip), 5 g or 10 g (see *Methods*). **(D-F)** Group leadership composition (orange-red): metrics for individuals in groups of followers (fol) or leaders (lead) (see *Methods*). **(G-I)** Group mass composition (yellow): group flights with different proportions of heavy individuals; either 0 (six light individuals), 0.33 (four light and two heavy individuals), 0.67 (two light and four heavy individuals), or 1 (six heavy individuals). Statistically significantly different responses between

groups are provided from a Tukey posthoc test of a linear mixed effects model (see *Methods*), where *p*-value is either < 0.05 (*), < 0.01 (**), or < 0.001 (***).

Solo speeds and accelerometer metrics.

As expected from prediction (2), "natural" (non-manipulated) bird body mass was a predictor of flight speed, regardless of artificial mass treatment, with an estimated increase in speed of 0.1 m/s per gram of additional "natural" body mass (LME; DF = 168, t = 5.564, p < 0.001; Fig. 5.3A). As predicted, higher body mass was also associated with higher flap frequencies (LME: DF = 167, t = 3.255, p = 0.001; Fig. 5.3B). Dorsal body amplitude was significantly lower (DF = 167, t = -2.503, p = 0.013; Fig. 5.3C), together indicating that the birds used faster, shallower wingbeats. Individual measurements of "natural" bird mass were also highly repeatable (repeatability analysis, using likelihood ratio tests, with 95% confidence intervals estimated using 10,000 parametric bootstrap iterations; R = 0.80 ± 0.03 (SE.), 95% CI: 0.73–0.85, p < 0.001).

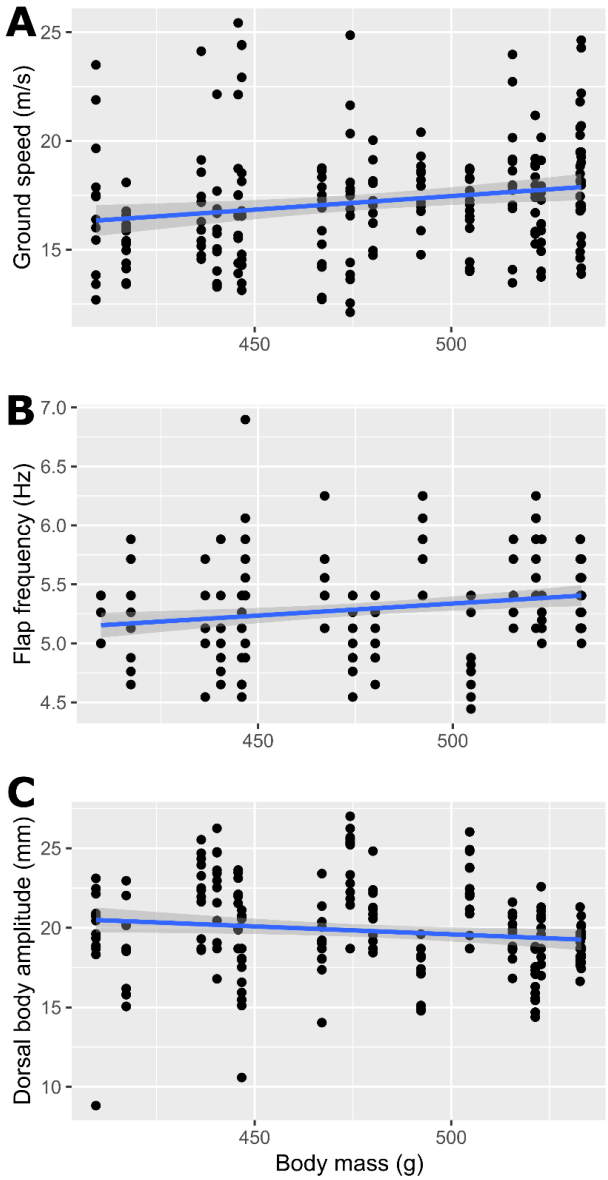

Figure 5. 3. The effect of "natural" bird mass on speed and energetic metrics

Bird mass (g) (x-axis) is plotted (points) with fitted linear model (blue line with grey shaded 95% confidence intervals, fitted in "ggplot"; Wickham and Wickham 2007), against **A)** Median ground speed (m/s), **B)** Median flap frequency (Hz), and **C)** Dorsal body amplitude (mm). All relationships were statistically significant – see above in *Results: Solo flights – speeds and accelerometer metrics*.

Experiment 2: group leadership composition manipulations

Leadership identification

All three groups exhibited significantly transitive leadership hierarchies (methods from (Nagy et al. 2013); T_1 = 1.000, T_1 = 1.000, T_1 = 0.890; $p < 0.001$ for all groups), and so were divided into groups with the five lowest and five highest leadership scores (directional correlation delay; see *Methods*) per group. Body mass was not predictive of leadership score in any of the three groups (LM; DF = 8; Group 1: t = -0.494, p = 0.635; Group 2: t = 0.334, p = 0.747; Group 3: t = 2.254, p = 0.054), nor was there any significant difference in the body mass of leaders and followers (mean mass of followers/leaders = 403.03 g/413.16 g respectively; T-test; DF = 26.624, t = 0.841, p = 0.408), thus suggesting body mass was not a significant factor in determining leadership. See also Chapter 2 for evidence that neither body mass, nor personality traits are predictive of leadership.

Effect of group phenotypic composition

Contrary to our expectations in prediction (3), leader flocks had increased density in two of our three measures of flock density, with decreased flock spread (LME with negative Box-Cox transformation; DF = 15, t = 1.975, p = 0.067), and significant decreases observed in dorso-ventral spread (LME with negative Box-Cox transformation; DF = 15, t = 2.376, p = 0.031), but with no observed difference in

cranio-caudal spread (LME with negative Box-Cox transformation; DF = 15, t = 0.743, p = 0.469). Further analyses of dorso-ventral spread found this to be the *flock-density* measure with the highest predictability of flock speed (see models from our comparative analysis below). Therefore, dorso-ventral spread is arguably the most important density measure we recorded, given the major thesis of our present work (cf. speed and the costs of transport).

Prediction (4) was also not supported, as the leader flocks, which were more dense (dorso-ventrally), demonstrated greater speeds than follower flocks (LME: DF = 28, t = -6.087, p < 0.001; Fig. 5.2D), with an estimated speed increase of approximately 1.19 m/s for leader groups, from 18.11 m/s (± 1.98 (SD)) to 19.30 m/s (± 1.53 (SD)). Flock speeds for training flights were closer to the speed of followers – 18.13 m/s (± 1.53 (SD)). We found no effect of leadership composition on energetic proxies flap frequency (LME: DF = 27, t = 0.9607, p = 0.345) or dorsal body amplitude (LME; DF = 27, t = 0.212, p = 0.833).

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

Experiment three: group mass composition manipulations

We found no support for prediction (5); that flocks with a greater number of heavy individuals by proportion would fly faster. When treated as a numeric variable, the proportion of heavy birds was not predictive of flight speed (LME; DF = 136, t = 1.000, p = 0.319). However we did find that certain group mass compositions were predictive of speed over others (LME with Tukey's pairwise post-hoc test; DF = 134; comparisons, given as proportion of heavy individuals in group [in square brackets] are as follows: [0 - 0.67] – *t.ratio* = 3.287, p = 0.007; [0.33 – 1] – *t.ratio* = -3.341, p = 0.006; [0.67 – 1] – *t.ratio* = -4.402, p < 0.001, see Table S5.4 for all statistics; Fig. 5.2G). The most significant differences were observed between homogeneous groups ([0] and [1]) and heterogeneous groups ([0.33] and [0.67]) where the homogeneous mass groups flew an estimated 1.56 m/s faster (using mean values).

We also found no support for prediction (6), that energetic proxies (flap frequency and dorsal body amplitude) would be reduced in groups of homogeneous composition. There was no difference in either flap frequency, or dorsal body amplitude in homogenous groups (flap frequency: LME; DF = 28, t = 0.396, p = 0.694; dorsal body amplitude: LME; DF = 28, t = 0.396, p = 0.480), When treated as a categorical or numeric variable (Fig. 5.3H, I; see Table S5.4 for statistics), the closest value to significance for energetic proxies across groups was flap frequency between [0] and [0.67] (Tukey corrected p value DF = 161, *t.ratio* – 2.353, Tukey corrected p-value = 0.090). For dorsal body amplitude, despite heavier groups

[0.67] and [1] showing some of the highest values (20.05 mm and 19.98 mm), the medians were lower (13.56 mm, 12.94 mm for lighter groups [0] and [0.33] respectively; vs. 12.50 mm and 12.60 mm for heavier groups [0.67] and [1] respectively), and there was no difference across the groups (greatest difference was between [0.33] and [1]; DF = 161, *t.ratio* = -0.409, *p* = 0.974).

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

Comparative analysis: density, stasis and speed across group-flight treatments

Flock speed models

In support of prediction (7), the selected model predicting flock speed (See *Methods* and Fig. S5.1) across all group flight experiments, showed that flock stasis had significant positive impact on group flight speed (LME; DF = 100, Flock stasis – *t* = 5.590, *p* < 0.001;Table 5.2; Fig. 5.4; for diagnostics see Fig. S5.2). Flock stasis, as a predictor, was robust to a sensitivity analysis on chosen parameters “Fission

distance" and "Minimum flight proportion" (see *Methods* and Table S5.6), and as a predictor of flight speed across each experiment (Table 5.2). Simultaneously there were no significant changes in the mean group flap frequency or mean dorsal body amplitude in more static flock flights. This was only performed on the experimental conditions ("leadership manipulation flights", and "mass manipulation flights"), however, and not the "leadership identification flights", as the accelerometer data were not analysed (flap frequency: LME; DF = 48; t = 0.576, p = 0.567; dorsal body amplitude: LME; DF = 48, t =0.176, p = 0.861). Experimental treatment "Leadership composition" as a factor, was still a significant predictor of speed in a model with flock stasis added (LME; DF = 14, t = 3.96, p = 0.001). Conversely, group mass composition was not predictive of speed in models including flock stasis (homogeneous vs. heterogeneous: LME; DF = 14, t = -1.130, p = 0.270). This implies that flock stasis does not fully describe the variation in group speed in leader vs. follower flocks but may describe the differences in the groups of different mass composition, i.e. whether homogeneous or not.

In additional analyses, the impact of group size, when treated as a numerical covariate, was close to significant as a predictor of speed, with a negative relationship between the two variables (LME with negative Box-Cox transformation; DF = 111, t = 1.807, p = 0.074), it is therefore unlikely that the larger group sizes in leader flocks (due to greater losses in follower groups, see Table S5.3) explain the speed differences between the groups.

Table 5. 2. Selected model for flock speed

Significance scores (*p*-values; if applicable) are reported for the impact of flocking variables ("Flock stasis" and "Dorso-ventral spread") on speed, and the model with the lowest AIC score ("Best model", either one flocking variable "1var", both flocking variables in an additive model "sum" or as an interaction "int"; See detailed methods in *Supplemental Material* and Fig. S5.1). Values are reported for each series of flights as well as a combination of all flights (columns: leadership composition manipulations – "Lead comp.", mass composition manipulations "Mass comp.", leadership identification flights "Lead. Identify", and all flights combined "All").

	Lead comp.	Mass comp.	Lead. Identify	All
Flock stasis	<0.001	0.0453	0.035	<0.001
Dorso-ventral spread	NA	NA	NA	0.007
Best model	"1var"	"1var"	"1var"	"sum"

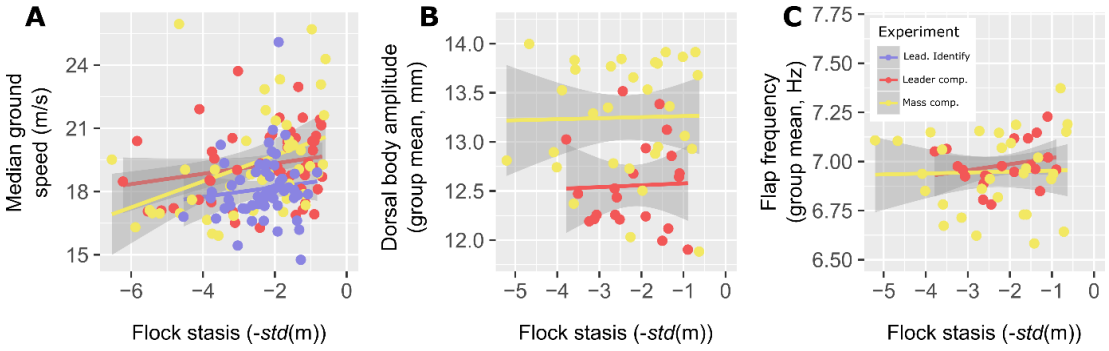

Figure 5. 4. Flock stasis is predictive of greater speed, without increases in energetic proxies

Flock stasis (-*std*(m)) is plotted against **(A)** Median flock speeds (ground speed (m/s); points) for sections of flight where group composition remained stable (more than 10 % of a flight), **B)** Dorsal body amplitude (mm; mean of values across whole group/flight) and **C)** Flap frequency (Hz, mean values across whole group/flight). Linear models with 95% confidence intervals are fitted using R-package "ggplot2" (Wickham and Wickham 2007). Colours of lines and points correspond to leadership identification flights (purple), leadership composition manipulations (orange-red) and mass composition manipulations (yellow) (see legend in **(C)**). Accelerometer data used in the generation of **(B)** and **(C)** were not analysed for leadership identification flights.

Flock stasis and flock density models

Contrary to prediction (8), groups of leader phenotype had a positive influence on flock stasis in group leadership manipulation experiments (LME: DF = 15, t = 2.237, p = 0.041; Fig. 5.5*A*; Table S5.6). This result held for 4 out of 5 trials testing for sensitivity of parameters "Fission distance" and "Minimum flight proportion" (see Table S5.6). Prediction (9), otherwise, was supported, as homogeneity of mass was predictive of flock stasis (LME: DF = 14, t = -2.261, p = 0.040; Fig.5A). Homogeneity of masses held as significant in 3/5 of the sensitivity iterations (Table S5.6).

In additional analyses, homogeneous flocks, across all experiments, showed greater flock stasis (where leader flocks, follower flocks, and similar sized mass groups were treated as homogeneous; and leadership identification flights, and mixed mass groups were considered as heterogeneous). However this increase was not statistically significant unless flights from follower groups were taken out (with followers included – LME: DF = 35, t = 1.649, p = 0.108, Fig. 5.5B; with followers excluded – LME: DF = 35, t = 2.080, p = 0.045, Fig. 5.5C). Sensitivity analyses showed statistical significance for 1/5 iterations with followers included and 4/5 without (Table S5.6). Additionally, flight order was found to have negative impact on flock stasis, which was close to significance (LME; DF = 103, t = -1.927, p = 0.057), meaning more experienced flocks exhibited less stability in their positioning. Flock

size, after accounting for individuals which split from the group, had no relationship with flock stasis (LME; DF = 111, t = -1.388, p = 0.168).

Dorso-ventral spread (m), as reported above, was decreased in leader flocks compared with follower flocks (LME; DF = 15, t = 2.376, p = 0.031), and the result held for 3/5 of the sensitivity analysis iterations (Table S5.6), from a mean lateral flock spread of 5.12 m in followers to 4.71 m in leaders. This is despite leader flocks having a biased starting size due to greater pigeon losses in follower groups (Table S5.3), and flock size having a strong positive impact on dorso-ventral spread (LME with negative Box-Cox transformation; DF =110, t = -9.939, p < 0.001). Mass compositions were not predictive of dorso-ventral spread, in any condition, nor was homogeneity of flock composition across experiments (see Table S5.6). Flight order, additionally, had no impact on dorso-ventral spread (LME; DF = 102, t = 1.585, p = 0.116).

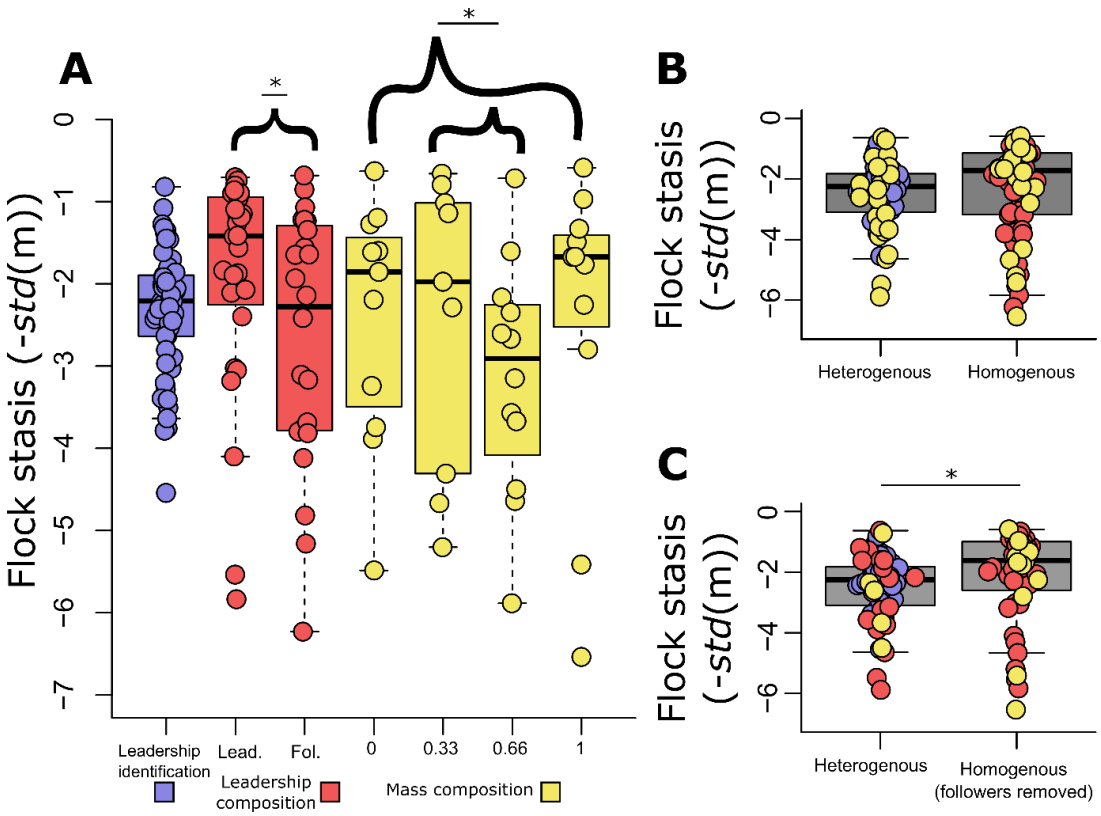

Figure 5. 5. Flock stasis for groups of different phenotypic composition

Flock stasis (-*std*(m)) is plotted (points; box and whisker plots), against phenotypic composition. **(A)** (From left to right) leadership identification flights (*N* = 10-11), groups of leaders (*N* = 4-5; Table S5.3), groups of followers (*N* = 3-5; Table S5.3), mass manipulated groups (*N* = 6) with proportions of heavy individuals either [0], [0.33], [0.67], [1] respectively. Statistically significantly different responses between groups are drawn for *p*-values of either < 0.05 (*), < 0.01 (**), or < 0.001 (***). The curly brackets above the mass manipulation experiments represent a statistical comparison between homogeneous groups ([0] and [1] proportions of heavy individuals) and heterogeneous groups ([0.33] and [0.67] proportion of heavy individuals). **(B-C)** show a comparison of homogeneous groups and heterogeneous groups across all experiments, where heterogeneous groups are defined as: heterogeneous mass groups, and leadership identification flights; and

homogeneous groups are defined as homogeneous mass groups, leader groups and follower groups, **(B)** or with follower groups omitted **(C)**. Colours correspond to leadership identification flights (purple), leadership composition manipulations (orange-red) and mass composition manipulations (yellow) (see colours in boxes below **A)**). Overall this figure highlights that group phenotypic composition can impact flock stasis, with homogenous mass groups, leader groups, and homogenous groups across all experiments (bar followers) having significantly greater stasis.

Discussion

We have identified mechanisms which can facilitate speed increases in animal groups. Specifically, groups which can remain highly static in their positioning (i.e. high flock stasis) travel faster at no extra energetic cost, even when accounting for differences in the tortuosity of flight movements (Safi et al. 2013). This suggests that group compositions which manage to keep stable flock structures can benefit energetically, while also flying in a denser cluster (i.e. on the dorso-ventral axis), which may confer additional anti-predator benefits (Couzin et al. 2011; Hogan et al. 2017a). Although the most highly cited function of flying in groups is that of energetic saving (Weimerskirch et al. 2001; Bajec and Heppner 2009; Portugal et al. 2014; Taylor et al. 2019), cluster-flocking has been shown to actually impose additional energetic cost over solo flight (Taylor et al. 2019), especially in tighter clusters (Usherwood et al. 2011; Ling et al. 2019; Taylor et al. 2019). Flock stasis may function to mitigate these additional costs. Such costs are thought to be produced by *i*) the increased control over movements to avoid collisions

(Usherwood et al. 2011; Taylor et al. 2019), and *ii*) the production and arrangement of inconsistent airflow which is likely to be a heterogeneous mix of upwash and downwash currents, which will also be highly unpredictable and dependent on local and wider-scale wind conditions (Usherwood et al. 2011). Consistency in the positioning of individuals will likely increase either (or both) of the above, as the predictability of neighbours' movements may reduce the risk of collisions (increasing the confidence of movement decisions, Fruin 1993), and also the predictability and general homogeneity in the airflow left in the wake of other pigeons. Thus, combined, stasis allows birds to fly faster, and in more tightly compact groups, without necessitating concurrent increases in energetic output (Usherwood et al. 2011; Taylor et al. 2019), which will likely be adaptive when energetic constraints represent a substantial selective pressure (Pyke 1984; Tobalske 2007; Wilson et al. 2012).

We suggest that certain configurations of group phenotypic composition are predictive of high levels of stasis in flight, and furthermore that greater stasis allows faster flying speeds. Nevertheless, a valid alternative interpretation is that group phenotypic composition governs speed, and speed itself is what determines flock stasis. However, if phenotypic composition primarily governed speed, we would expect groups with a greater proportion of heavy individuals to fly faster, as individual body mass and solo speed were highly correlated in experiment one (and observed in Pettit et al. 2015; and Chapter 3; Sankey et al. 2019). However, this was not the case; instead, we observed that homogeneous mass groups travel faster

than heterogeneous mass groups, regardless of group mass by proportion. This suggests homogeneity in mass composition facilitated speed increases through increases in flock stasis. (See more discussion of group mass composition below, in section subtitled: *Social-level morphological traits: group mass composition manipulations*).

Individual-level phenotype: body mass and artificial mass manipulations

While groups of greater mass composition were not predictive of greater flight speeds, body mass in solo flights was, and this held regardless of artificial mass load treatment. However, body mass – while predictive of speed – showed conflicting results in terms of energetic output, with greater flapping frequencies and lower dorsal body amplitude observed in heavier individuals. Nevertheless, despite this conflict, the energetic cost of steady, horizontal flight is thought to be proportional to the cube of flap frequency, while only to the square of wingbeat amplitude (Greenewalt 1962; Lilienthal 2001). Additionally, empirical work has suggested that wingbeat cycles with high frequency, low amplitude are necessary for (more costly) powered turning flight (Usherwood et al. 2011). Therefore it is likely that heavier individuals are likely to pay a higher cost for their faster speeds, via their increases in flap frequency.

In artificially mass manipulated flight, our observed decrease in dorsal body amplitude had a greater effect size than the observed increase in flapping

frequency. However it is highly unlikely that pigeons *save energy* while maintaining speed in artificially mass manipulated flight. To use an analogy of airplanes, one would be unlikely to power an Airbus A380 (560,000 kg maximum take-off weight; EADS N.V. 2008) on the engine of an Airbus A320 (68,000 kg maximum take-off weight; Department of Transportation 2007) (Tennekes 2009). Instead, it seems, as demonstrated theoretically (Lilienthal 2001) and empirically (Usherwood et al. 2011), increases in flap frequency may be much more costly than decreases in wingbeat amplitude, and our work further supports this point. Overall, we suggest that pigeons are robust to the application of moderate mass loadings (3.8%–7.4% of total body mass) because they have the capacity to adjust flight kinematics to retain their usual flying speed. This suggests either that *i*) speed is under high selection pressure (Tobalske 2007), or that *ii*) the result of slowing down would reduce momentum induced lift to unsustainable levels (Tobalske et al. 2003).

Further increasing the additional artificial mass load might reveal a critical point in pigeons at which speed can no longer be maintained, and reduces. Alternatively, this critical point may result in flight stopping altogether, and thus such studies would be more suited to wind tunnel experiments, due to ethical considerations of undertaking such work in free-flying birds (Vandenabeele 2013). Further *decreases* in logger mass might, on the other hand, prove more useful in free-flying pigeons for estimation of both *i*) the impact of biologgers, and *ii*) natural unloaded movement kinematics of birds and flight (see Wilson and McMahon 2006 for how to use regression to estimate these parameters).

Our prediction was that, in mass loaded pigeons, flight kinematics would remain stable (following Hambly et al. 2004), and this was not supported. However we also suggested, in the *Introduction*, that a similar flight kinematic response could be seen in mass loaded birds as observed in "naturally" heavier birds. This was indeed the case, whereby heavier individuals (either "artificially" or "naturally") demonstrated both increased flap frequency and decreased dorsal body amplitude. Nevertheless, "naturally" heavier birds also increased speed, which the "artificially" loaded individuals did not. This suggests that *speed enhancement* concurrent with additional "natural" body mass is more than just a result of increased wing loading (Alerstam et al. 2007). The pectoralis muscle is thought to be the major driver of wing suppression and the supracoracoideus muscle with elevation (Tobalske 2007). Our work suggests that the aforementioned muscles could be larger, by proportion, in heavier pigeons, with a concurrent increase – or "scaling up" – of the metabolic supply of chemical energy necessary to power these relatively larger muscles (Taylor et al. 1982; Tobalske 2007).

Social-level behavioural traits: flock leadership manipulations

We found that "leader groups" demonstrated higher density and flock stasis than "follower groups", despite our predictions to the contrary. We initially reasoned that leaders would attempt more initiations (Johnstone and Manica 2011; Ramos et al. 2015), and that this in turn would result in reduced flock density and stasis.

However, our predictions were not supported, with leaders exhibiting significantly greater cohesion, and stasis. As our birds were all flown from the same site, this may have reduced the conflict in navigational decision making (Conradt and Roper 2003; Biro et al. 2006). Further, as leaders have been shown to learn routes better than followers (see Pettit et al. 2015), this conflict may have actually *reduced* in leader flocks which all know the route better than follower flocks. Therefore, we suggest that with reduced conflict in route direction, the "leader groups" were able to *optimise their flock dynamics*, rather than *attempt initiations* toward their preferred direction of travel.

Leader pigeons may also exhibit a more goal-oriented individual-level phenotype (Freeman et al. 2011; Sasaki et al. 2018). Pigeons with greater "peak-fidelity" – a measure of their coherence (or, "goal-orientedness") in their solo flight routes – predicted leadership in pigeon pairs (Freeman et al. 2011). Goal-orientedness was also shown to have a positive impact on leadership in fish, however, only when balanced with moderate levels of social tendency, as fish which were highly goal-oriented would split from the group, reducing their influence (Ioannou et al. 2015). As goal-orientedness is thought to represent a trade-off between propensity to risk isolation and the safety of the group (Ioannou et al. 2008), such a behaviour may correlate with individual differences in boldness (Ioannou et al. 2008; Jolles et al. 2017). Indeed boldness has been found to predict leadership propensity in fish (Jolles et al. 2017) and pigeons (Sasaki et al. 2018; but see Chapter 2 for evidence to the contrary). Additionally, faster pigeons have been shown to lead movements

(Pettit et al. 2015; but see Chapter 2 for evidence to the contrary). This might explain why "leadership composition" as a factorial variable had predictive power on flock speed in the models in the present study – above the predictive power from the stasis variable alone.

Our methods were designed to decrease flock density, and hence modify the speed/energetic trade-off, by forming groups with high conflict through increases in their natural goal-orientedness (see *Introduction* and Johnstone and Manica 2011). Our attempted density manipulations may have not been successful, due to the potential *decreases* in conflict through enhanced route learning (as mentioned above). To increase route conflict, future work should potentially *i*) train individuals from different sites (before releasing in groups), or *ii*) fly the leaders of one group with the leaders from another group (each group may have conflict in their "preferred" path). Both these concerns were taken into consideration in the present study: nevertheless, firstly, our employed comparative analyses required consistency in the experimental set-up (release site); second, by chance alone, intrinsic "leader phenotypes" could be unevenly distributed across experimental groups, and mixing across groups could introduce unaccountable bias.

Social-level morphological traits: group mass composition manipulations

Increased flock stasis in homogeneous mass groups was expected, nevertheless our results suggest a different mechanism than the one proposed. We expected that 1)

in groups of a similar mass, we would find an intrinsic reduction in speed compromise between the birds (*sensu* Chapter 3). Further, 2) acceleration/deceleration responses would be less common (or indeed necessary), and thus, via moving around less, would result in greater levels of stasis. Following our results, this now seems unlikely, as groups of heavy birds did not fly faster than groups of slower birds, so speed compromise may not be the governing force we expected it to be (Chapter 3). Instead we hypothesise the following: that *i*) the general morphological profile of individuals (e.g. wingspan, structural size; which has been shown to correlate with body mass in birds; Alerstam et al. 2007; Sullivan et al. 2019), will affect the flow rate and magnitude of air currents left in their wake and *ii*) individuals can achieve a more optimal trade-off between downwash avoidance and upwash exploitation in the wake of similar sized individuals. This is highly speculative, as no present evidence can confirm or reject this claim. However, a recent study suggests that a previous dichotomy between cluster-flocking and V-formation flight mechanisms (Bajec and Heppner 2009) might not be as straightforward as first thought, with observations of "compound V" flock shapes within the cluster formations of shorebirds (Corcoran and Hedrick 2019). We know that flying in a flock comes at a cost in pigeons (Usherwood et al. 2011; Taylor et al. 2019), but this does not rule out the possibility for *relative* savings when individuals are matched in size and/or gait.

Comparative analyses

In an attempt to identify the mechanism underpinning how some flocks are able to reach higher stasis, we also investigated whether homogeneous groups, more broadly, were indicative of greater stasis. To test this "post-hoc prediction", we added the leadership identification flights (a heterogeneous mix of birds) to the analysis. However our results were that homogenous groups did not show significantly increased stasis, unless homogeneous "follower" phenotypes were removed from the analysis. It seems reasonable that a category as broad as "homogeneity" will not explain the nuances of stability in flock positioning. Our work thus draws into question the value of being a "follower". Recent work has suggested that leaders could be exposed to greater risk (Ioannou et al. 2019). Here, by measuring predation events of "virtual prey" (pre-defined in their leadership behaviour) by real fish predators, Ioannou et al. (2019) revealed that individuals on the leading edge suffer greater predation. Additionally, a "follower personality" could be maintained by frequency-dependence (Johnstone and Manica 2011). Here, follower phenotypes were beneficial in populations with a majority of leader phenotypes in evolutionary simulations, owing to their social-tendency, which kept groups cohesive and thus safer from assumed "threat" (Johnstone and Manica 2011). Alternatively, there could be no benefit to followership (see Chapter 2), with followers making the "best of a bad job" (Davies et al. 2012), owing to their intrinsic handicap in either genetics or ontogeny.

Optimal phenotypic compositions

A question arises that, if flock stasis is so beneficial, why would all individuals/groups not exhibit similar and high levels of stasis? Firstly more experienced individuals may have superior knowledge of a particular route (McComb et al. 2011; Flack et al. 2013; Biro et al. 2016), which may allow for less conflict and thus greater stasis. Conversely, if their "preferred routes" are in conflict, groups of experienced and unexperienced individuals may be less likely to achieve high stasis. Linked to experience is age, whereby developmental progress may be necessary to flock optimally also (Biro et al. 2016). Juvenile white ibis (*Eudocimus albus*) and northern bald ibis (*Geronticus eremita*) have both been shown to increase their time participating in optimal V-formation flocking (Weimerskirch et al. 2001; Portugal et al. 2014) over ontogeny (Petit and Bildstein 1986; Biro et al. 2016). Whether physiological development and/or cognitive development drives the juveniles' increase in optimal group-level behaviour, is still unknown (Biro et al. 2016). Flock stasis in pigeons could prove a useful model system, owing to the simplicity of experimental manipulations.

We provide the first evidence for optimal group compositions in flight, which suggests benefit for individuals which may choose when to leave or join groups adaptively (Farine et al. 2015). This would require individuals to assess the phenotypic composition of the group before making a decision, based upon the

individuals which comprise the group (Farine et al. 2015). Such dynamics have been verified experimentally in mixed species flocks, where the removal of a "nuclear" species will dramatically reduce the likelihood of "satellite" species to join groups in foraging activities (Dolby and Grubb 1999). There is also evidence that individuals within species can choose to join groups with particular phenotypic compositions. Pruitt and Goodnight (2014) found that groups of social spiders *Anelosimus studiosus* re-formed previously optimal phenotypic compositions when experimentally perturbed. This could be explained by simple "emergence", with individual actions in response to the environment alone resulting in the formation of these groups. Yet this explanation seems less likely than an internal "choice" mechanism, because the composition of *reformed groups* resembled compositions *at their native site*, not the site to which they were experimentally translocated (Pruitt and Goodnight 2014). In light of evidence of "choice" in less cognitively adept spiders (Pruitt and Goodnight 2014; Thorndike 2017), it seems plausible that birds could "choose" social partners to benefit from optimal group phenotypic compositions. It is well established that birds can assess mate quality by recognition of phenotype (Orians 1969; Hunt 1980). Whether the energetic costs of flight exert a strong enough selective pressure to favour the evolution of phenotypic recognition related to optimal group composition is likely to be debated, but see (Tobalske 2007) for a discussion on how the costs of flight has been – and continues to be – a strong selective pressure, shaping the evolution of birds.

It is possible that optimal compositions will be depend on the ecological context (referred to as context dependent optimal compositions, or CDOCs in Chapter 1). Perhaps an individual's membership of certain (mostly homogeneous) groups, can provide benefit, and this may reflect the optimal compositions in our experimental context. Specifically, the environmental context here was "familiar", and hence relatively predictable. As an example, "leader" phenotypes in our study may have come to a consensus on travelling route through enhanced learning (Pettit et al. 2015), which enhanced flock stasis and flying speed (see above). In a less predictable context, such groups may experience more conflict (Johnstone and Manica 2011) and split from one another an attempt to satisfy individually variable differences in resource requirements or preferences (Sueur et al. 2011), potentially decreasing fitness (Conradt and Roper 2003). In such contexts with reduced predictability, the optimal composition may be a more heterogeneous mix. Heterogeneity has been shown to have important benefits whereby individuals in mixed phenotype groups can utilise a larger pool of different preferences or abilities (Dyer et al. 2009). Perhaps "leader" phenotypes should assemble for *known flight routes* but mix with followers for *unknown exploratory flights*, to retain the CDOC. Though this leaves a situation where individuals must either reorganise the hierarchy, or share leadership (Couzin et al. 2005; Strandburg-Peshkin et al. 2015) in known routes. Researchers may categorise such a group into "leaders" and "followers" erroneously (given the broader population-level dynamics), thus stressing the importance of data collection across multiple animal groups. Currently there is little or no work investigating changes in optimal compositions across

ecological context. This could be a productive area of research, as changes in ecological factors (e.g. seasonality in temperate species) could provide a selective pressure for a reorganisation of group structure.

Broader implications

Greater flock stasis is likely beneficial across multiple bird species and flock types, including both cluster flocks and V-formations. Birds which fly in V-formation are – conversely to cluster flocking birds – famous for achieving positive aerodynamic interactions via the wake left behind other birds (Weimerskirch et al. 2001; Bajec and Heppner 2009), which is thought to be a property of both the birds' spatial positioning (Voelkl et al. 2015) and phasing of their wing flaps (Portugal et al. 2014). Flock stasis relates directly to spatial positioning, and as an easily measurable metric, could be useful in the further study of V-formations. We know that V-formations are rarely optimal in their structure at any given moment in time (Portugal et al. 2014; Voelkl et al. 2015), and that the stability of V-formations can improve through learning (Biro et al. 2016). Flock stasis can also be modified for use in V-formations, by, for example, separating the dorso-ventral, and cranio-caudal components of stasis, where both components are known to be of crucial importance (Portugal et al. 2014). Therefore, in birds which travel in groups, especially when group flight represents a large component of a species' life history,

achieving greater flock stasis through learning or choice of social partners could be adaptive.

It is also important to note that the fitness of individuals will rarely be driven by one facet (e.g. speed/energy optimisation) alone. Instead, the benefits conferred to different individuals/phenotypes will likely be context dependent (Dyer et al. 2009; Nagy et al. 2013; Ioannou et al. 2019). Demonstrating the benefits of an optimal phenotype (or phenotypic composition) in one context could not provide a genuine inference of fitness in the tested animals, whether wild or captive/semi-captive. Nevertheless, in captive animal systems, we can identify a known evolutionary pressure in birds (here, the costs of flight (Schmidt-Nielsen 1972)), and test, via manipulations, the influence of individual phenotype, and group phenotypic composition (e.g. Dyer et al. 2009). Therefore, we can learn about one important component of life history in isolation, and derive conclusions about individual and group-level success (Farine et al. 2015).

Effective use of space can be important in terrestrial animals too, including humans. In human crowd disasters, for example, movement pathways and space use have been identified to influence the chances of stampede (Fruin 1993). Additionally, turning movements can cause trampling and stampede in humans (Chertkoff and Kushigian 1999), and ants (Shiwakoti et al. 2011). Ants are deemed useful in evacuation dynamics due to their evolutionary history of travelling *en-masse* in the same direction (Couzin and Franks 2003; Shiwakoti et al. 2011). As (Shiwakoti et al. 2011) phrased the idea in their empirical work on turning movements and

stampede in ants: “humans have been dealing with traffic congestion for only a few hundreds of years, while ants have been dealing with congestion during millions of years of evolution.” This is also true of birds, where effective collision avoidance could potentially be difference between life and death (Usherwood et al. 2011; Taylor et al. 2019). Of course, the major caveat to the usefulness of our work in human crowd disasters is that we were looking at relatively “steady” travel. Nevertheless, a holistic framework of effective group travel, identifying differences between non-panicked and panicked groups across taxa could be fruitful.

Conclusion

Flock stasis is a novel metric, which was a consistent predictor of flight speed across all group flights in the study, and robust to a sensitivity analysis of arbitrary parameters. Nevertheless our understanding of how individual phenotype and group phenotypic composition interact to predict flock stasis is not yet conclusive. This inconclusiveness is due to “leader groups” and “homogeneous mass groups”, which, while significant predictors of stasis in initial models, were not entirely robust to sensitivity analyses on arbitrary parameters. Regardless, we introduce a metric, predictive of flight speed at no observable energetic cost, to the combined fields of aerodynamics and group movement worthy of further exploration.

Our conclusions can be applied to wild animal systems and towards a broader understanding of animal ecology. A major current challenge in behavioural biology

is to understand how changing environments (e.g. human-driven reduction in naturally occurring resources) may impact social groupings (Mathieson and Wall 1982) and animal movement ecology (Fahrig 2007). We have evidence that group composition can impact the cost of group flight. If groups need to fly further to reach new resources in the future, are we likely to see a movement towards particular phenotypic compositions, or are the relative benefits of heterogeneity (e.g. Dyer et al. 2009) still more powerful? This is a question, which we provide some foundational principles toward, but which will require a collective effort by empiricists (both wild and captive behaviourists) and theoreticians to address.

Supplemental material

Logger treatment and attachment

The outer casing of the GPS (QStarz BT-Q1300ST, Düsseldorf, Germany) was first removed to reduce mass. The device was then painted top-to-bottom (excluding the electrical port) with liquid electrical tape (Performix, Liquid Tape – Electrical, Minnesota, U.S.A.) to waterproof the circuit board. The GPS weighed 12.5 g after treatment. Accelerometers (200 Hz; AX3, Axivity Ltd, Newcastle upon Tyne) were not treated in this way due to their relatively lighter starting mass (8 g).

Velcro strips, attached via epoxy glue (Araldite Rapid Adhesive, Araldite, Basel, Switzerland), were used to attach the biologgers to trimmed feathers on the birds'

backs (Portugal et al. 2017a; Taylor et al. 2017). Accelerometers were placed on the cranial end of the Velcro strip based upon a practical assumption that the tag will move and pick up less noise closer to the head region, and therefore to maximise sensitivity/noise ratio when measuring dorsal body displacements. GPS were attached to the caudal end of the strip.

Experiment one: solo flight mass manipulations

Randomising the trial conditions.

Each full replicate of the study (of which we performed five) would require each bird to fly with each mass treatment (0 g, 5 g and 10 g). We did not assume a bird's treatment masses should follow in this ascending order. For each replicate, instead, 0 g, 5 g and 10 g were randomly allocated to "treatment 1", "treatment 2" and "treatment 3". Bird IDs (N = 16) were also shuffled at the beginning of each replicate. In trial one, the first six birds (resulting from this shuffling of IDs) were allocated mass treatment "treatment 1", the next five birds with "treatment 2", and the final five birds with "treatment 3". In trials two and three, birds which flew with "treatment 1" in the previous flight would fly with "treatment 2"; likewise "treatment 2" birds would fly with "treatment 3"; and "treatment 3" with "treatment 1". The reason we released six, five and five birds with the respective treatments was to reduce any confounding effects temporal weather changes (wind

in particular can strongly influence speed in birds; Safi et al. 2013). See an example of a replicate matrix in Table S5.1.

Table S5. 1. Replicate matrix

Bird IDs as well as treatment ID were shuffled randomly and used to generate matrices such as the table below. Here “treatment 1” was 10 g, “treatment 2” was 0 g and “treatment 3” was 5 g. We performed five complete replicates this protocol in the present study.

Pigeon ID	flight 1	flight 2	flight 3
58	10	0	5
78	10	0	5
85	10	0	5
47	10	0	5
81	10	0	5
76	0	5	10
39	0	5	10
95	0	5	10
67	0	5	10
53	0	5	10
69	5	10	0
74	5	10	0
46	5	10	0
55	5	10	0
32	5	10	0
59	10	0	5

Table S5. 2. Paired and solo flight counts across all individual and additional mass loads

Totals of each column are provided in italics and number of solo flights per condition in bold.

Pigeon ID	Additional mass load					
	0 g		5 g		10 g	
	paired	solo	paired	solo	paired	solo
32	0	4	1	6	0	5
39	0	5	0	4	0	5
46	0	4	0	5	0	4
47	2	3	1	3	0	5
53	0	4	1	4	4	4
55	2	5	2	4	0	4
58	1	4	0	4	0	4
59	1	4	0	5	0	4
67	0	4	0	4	1	4
69	1	5	2	4	0	4
74	0	4	1	4	0	5
76	6	3	0	4	2	4
78	0	4	0	5	0	5
81	1	3	0	5	0	5
85	1	4	1	5	1	5
95	1	4	1	4	1	4
Total	*15*	***60***	*9*	***66***	*8*	***67***

Experiment two: group leadership composition manipulations

Training flights

All 33 birds used in experiments two and three were trained using the same protocol as follows. Firstly, they were trained to enter the loft via a hatch on the front side, using a small cardboard box (roughly ten times the volume of a pigeon)

with windows cut out (to see the surrounding area) and a flap leading from the box to the hatch. This protocol was carried out many times throughout the course of three-four weeks. Following this, all birds were released (following protocol for group flights; see *Main text*) from the locations at the following distances from the loft, all in the direction of the release site (all distances are approximate; 0 m, 500 m, 2100 m, 4700 m, 6000 m, 7200 m and finally the release site at 8900 m). Releases from each successive location were repeated until all individuals returned home. Losses from the first two release sites totalled nine birds (these are not included in the 33). Following this, there was only one more loss, at the 6000 m site.

Experiment three: group mass composition manipulations

Randomising the trial conditions.

Small individuals (*N* = 6) and large individuals (*N* = 6), were allocated a number and randomly shuffled. The first two randomly selected from each group would be the first two to join the individuals from the opposite mass group (in the first mixed mass flight). Then, in the second mixed mass flight, the second selected individual would leave their mass group along with the third randomly selected individual, then third with fourth thereupon. After the sixth randomly selected bird flies with the first (to complete the loop), the first then flies with the third (not the second as

before). This successfully stopped any repeats of pairs of birds leaving their mass group.

Figure S5. 1. Model selection for predicting flock speed

Flocking variables are treated individually as covariates (**A** – "Speed vs. Flock variables (*p-value*)"), we report *p*-values of the estimate for each variable (see rows in **(A)**), using data from four sources (see columns in **(A)**) as follows: *i*) Leadership composition manipulations, *ii*) Mass composition manipulations, *iii*) Training flights, and *iv*) all flights combined. Then, following red arrows (and numbers) we conducted the following adjustments to account for co-linearity of covariates (following an "absolute value of correlation coefficients" method from (Dormann et al. 2013)): (1.) The minimum *p*-value (in this case "Flock stasis") is taken as the first variable in each of the three models given in **(B)** ("m.sum" – sum of flocking co-variates; "m.int" – interaction of covariates; "m.1var" – only the first covariate). (2.) We then took the flocking covariate with the second lowest *p*-value (here, "Dorso-ventral spread"), and, given that this was beneath a critical *p*-value ($p < 0.05$), which it was ($p < 0.001$), we then (3.) checked the correlation tables **(C)** "Flock variables correlation matrix (*r*)" for the correlation between the first and second covariate, with a critical threshold for exclusion ($|r| < 0.5$; following (Dormann et al. 2013)). (4.) Given that the score ($r = -0.1846$) was lower than the critical threshold, the covariate was included in the models "m.sum" and "m.int". (5.) The covariate with the next lowest *p*-value, "Flock spread", was also below the critical threshold, and thus we checked for correlation between this and both of the first co-variates (6.) and (7.). (8.) The correlation coefficient between "Dorso-ventral spread" and "Flock spread" was above the accepted correlation value ($r = 0.8718$), and so was not added to the models. (9.) Finally all three models (from **(C)**) were compared for each of the four conditions (*i-iv*) in **(D)** "Model selection". In both experiments (*i, ii*), and in training flights (*iii*), the single-variable model "m.1var" had the lowest AIC score, and was selected as the best model. Over all flights, "m.sum" the additive model, had a lower AIC, suggesting a better fit when including "Dorso-ventral spread".

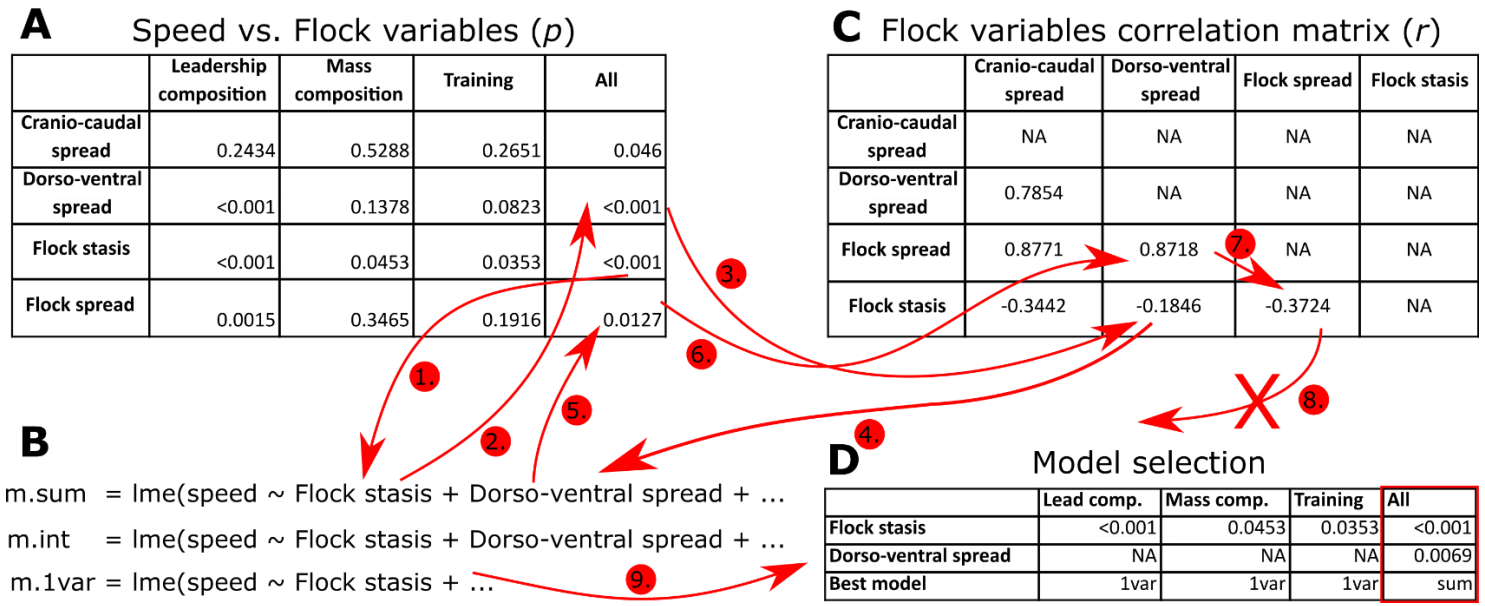
A
Speed vs. Flock variables (p)
Leadership composition
Mass composition
Training
All
Cranio-caudal spread
0.2434
0.5288
0.2651
0.046
Dorso-ventral spread
<0.001
0.1378
0.0823
<0.001
Flock stasis
<0.001
0.0453
0.0353
<0.001
Flock spread
0.0015
0.3465
0.1916
0.0127
C
Flock variables correlation matrix (r)
Cranio-caudal spread
Dorso-ventral spread
Flock spread
Flock stasis
Cranio-caudal spread
NA
NA
NA
NA
Dorso-ventral spread
0.7854
NA
NA
NA
Flock spread
0.8771
0.8718
NA
NA
Flock stasis
-0.3442
-0.1846
-0.3724
NA
1.
2.
3.
4.
5.
6.
7.
8.
9.
B
m.sum = lme(speed ~ Flock stasis + Dorso-ventral spread + ...
m.int = lme(speed ~ Flock stasis + Dorso-ventral spread + ...
m.1var = lme(speed ~ Flock stasis + ...
D
Model selection
Lead comp.
Mass comp.
Training
All
Flock stasis
<0.001
0.0453
0.0353
<0.001
Dorso-ventral spread
NA
NA
NA
0.0069
Best model
1var
1var
1var
sum

Table S5. 3. Leader/follower groups, flight participation table

Pigeon trajectories presence/absence are denoted by 1 or 0 respectively. Groups 1 to 3 are subdivided into groups of leaders/followers from 10 previous baseline flights (see *Methods*). Each row represents an individual flight. Different shading on the zeros denote different reasons for our lack of data in further analysis: red shaded zeros show when a pigeon failed to return from the previous flight, green shaded zeros denote flights where pigeons were undergoing routine procedures and could not be used in the present study, yellow shading represents when individuals were unable to fly as they were outdoors when the experimenter was collecting the birds, and finally blue shaded zeros show data that was lost due to logger failure.

	Group 1										Group 2					Group 3														
	Followers					Leaders					Followers					Leaders					Followers					Leaders				
Flight \	2	6	7	8	9	2	2	4	4	6	3	4	6	7	9	2	4	5	8	9	30	5	6	7	8	3	4	6	8	9
ID	9	1	9	0	1	4	8	5	8	4	7	3	5	2	2	7	0	7	4	4		1	2	5	8	1	2	3	2	8
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4	1	1	0	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
5	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
6	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
8	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
9	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
10	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
11	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1

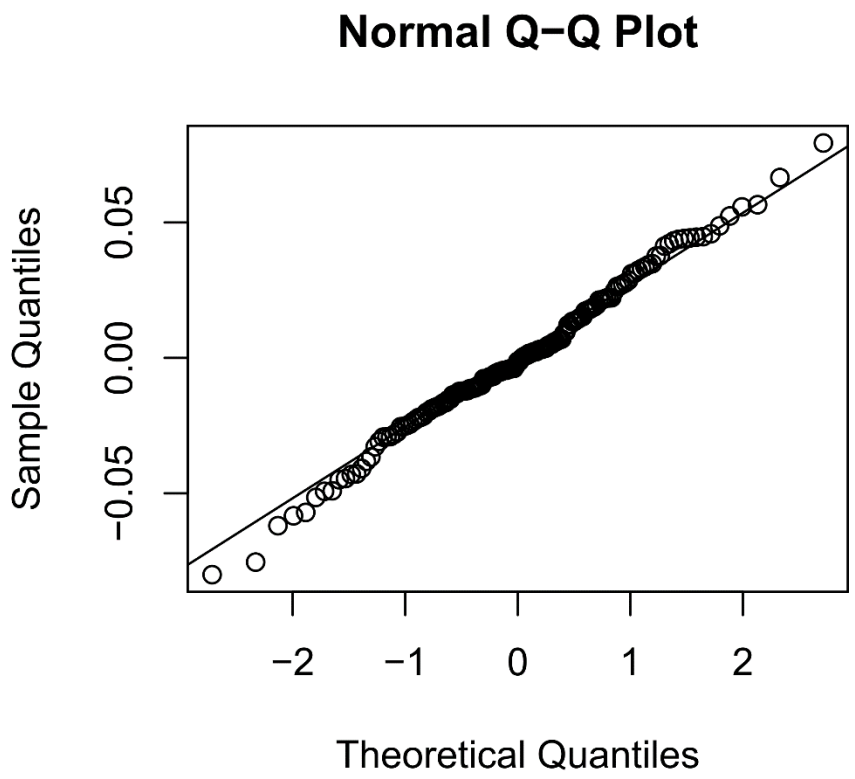

Figure S5. 2. QQ norm with QQ line for final "flock speed" model

The normalised residuals (QQ-norm) closely fit the predicted values (QQ-line) indicating a good fit, which does not violate the assumptions (i.e. normally distributed residuals that are not heteroscedastic) for the chosen final model predicting speed across all experiments. The dependent variable was log transformed, due to the better fit to the assumptions, than was possible with Box-Cox transformations, see *Methods: Statistics.*

Table S5. 4. Individual-level flight parameter statistics

Dependent and independent variables, and summary statistics (see *Methods: Statistics*) for experiments one, two and three (see *Methods*).

Data	Dep. var	Indep. var	Value	SE	df	t-rat./val.	p-val.	Sig.
Experiment 1: Solo flights with artificial mass loadings	speed	0 g - 10 g	0.2448	0.317	63	0.772	0.7214	NS
	speed	0 g - 5 g	0.1133	0.2979	63	0.3801	0.9235	NS
	speed	10 g - 5 g	-0.1315	0.3091	63	-0.4254	0.9052	NS
	ff	0 g - 10 g	-0.1815	0.0884	63	-2.0534	0.108	NS
	ff	0 g - 5 g	-0.1037	0.0829	63	-1.2503	0.4285	NS
	ff	10 g - 5 g	0.0778	0.0861	63	0.903	0.6404	NS
	amp	0 g - 10 g	1.7182	0.361	63	4.7597	<0.001	***
	amp	0 g - 5 g	1.3455	0.3625	63	3.712	0.0013	**
	amp	10 g - 5 g	-0.3726	0.3503	63	-1.0637	0.54	NS
	speed	support.wind	0.3754	0.1401	63	2.6795	0.0094	**
	speed	cross.wind	-0.4624	0.1347	63	-3.4318	0.0011	**
	speed	Exp. cond., as num.	-0.0241	0.0315	64	-0.766	0.4465	NS
	ff	Exp. cond., as num.	0.0182	0.0088	64	2.0672	0.0428	*
	amp	Exp. cond., as num.	-0.1696	0.0362	64	-4.6827	<0.001	***
Experiment 2: Group leadership composition	speed	fol - lead	-1.1883	0.1952	28	-6.0871	<0.001	***
	ff	fol - lead	-0.12	0.1249	27	-0.9607	0.3452	NS
	amp	fol - lead	0.1289	0.6059	27	0.2127	0.8332	NS
	speed	support.wind	0.2732	0.0487	231	5.607	<0.001	***
	speed	cross.wind	-0.1435	0.051	231	-2.8118	0.0053	**
Experiment 3: Group mass composition	speed	0 - 0.33	1.6868	0.7537	134	2.2381	0.1183	NS
	speed	0 - 0.67	2.5045	0.7621	134	3.2865	0.007	**
	speed	0 - 1	-0.8001	0.63	134	-1.27	0.5836	NS
	speed	0.33 - 0.67	0.8177	0.7856	134	1.0408	0.7258	NS
	speed	0.33 - 1	-2.4869	0.7444	134	-3.3407	0.0059	**
	speed	0.67 - 1	-3.3045	0.7506	134	-4.4023	1.00E-04	***
	ff	0 - 0.33	0.0291	0.0754	161	0.3854	0.9805	NS
	ff	0 - 0.67	0.3691	0.1569	161	2.3525	0.0907	NS
	ff	0 - 1	0.3021	0.1525	161	1.9809	0.1995	NS
	ff	0.33 - 0.67	0.34	0.1544	161	2.2016	0.1272	NS
	ff	0.33 - 1	0.273	0.1549	161	1.7629	0.2951	NS
	ff	0.67 - 1	-0.067	0.0765	161	-0.8751	0.8177	NS
	amp	0 - 0.33	0.2793	0.32	161	0.8728	0.8189	NS
	amp	0 - 0.67	-0.1252	0.9951	161	-0.1258	0.9993	NS
	amp	0 - 1	-0.1369	0.9827	161	-0.1393	0.999	NS
	amp	0.33 - 0.67	-0.4044	0.9882	161	-0.4093	0.9768	NS

	amp	0.33 - 1	-0.4162	0.9894	161	-0.4207	0.9749	NS
	amp	0.67 - 1	-0.0118	0.3247	161	-0.0362	1	NS
	speed	support.wind	0.0742	0.0907	134	0.8181	0.4148	NS
	speed	cross.wind	-0.6024	0.1618	134	-3.7229	3.00E-04	***
	speed	Exp. cond., as num.	0.6473	0.6474	136	0.9997	0.3192	NS
	ff	Exp. cond., as num.	-0.1002	0.1272	163	-0.788	0.4318	NS
	amp	Exp. cond., as num.	-0.2641	0.581	163	-0.4545	0.6501	NS

Table S5. 5. Sensitivity of speed model statistics to the changing of arbitrary parameters

The impact of changing parameters on model selection (Fig. S5.1) and the resulting statistics (Table 5.1). Parameters changed were *i*) Fission distance (first column (metres); distance from the flock before an individual is considered to be separated from the group, and *ii*) Minimum flight proportion (second column; proportion of flight at any given flock size before statistics are collected on any flight). Changes include as follows: in the third row, where Dorso-ventral spread was selected as the first model covariate (see Fig. S5.1); in the fifth row, Flock spread was selected as the second model covariate; also in this row, the best model was not with summed covariates, but instead with one variable – Flock stasis. The grey shaded area represents the statistics for the chosen parameters, and is reported in the main text (see *Results*).

Fission distance (m)	Minimum flight proportion	Best model tables	Lead comp.	Mass comp.	Training	All
50	0.1	*Flock stasis*	0.0002	0.0453	0.0353	<0.001
		Dorso-ventral spread	NA	NA	NA	0.0069
		Best model	***1var***	***1var***	***1var***	***sum***
50	0.05	*Flock stasis*	0.0000	0.0335	0.0307	<0.001
		Dorso-ventral spread	NA	NA	NA	<0.001
		Best model	***1var***	***1var***	***1var***	***sum***
50	0.25	*Dorso-ventral spread*	0.0043	0.0426	0.3128	0.0029
		Flock stasis	NA	NA	NA	<0.001
		Best model	***1var***	***1var***	***1var***	***sum***
75	0.1	*Flock stasis*	0.0002	0.0201	0.0370	<0.001
		Dorso-ventral spread	NA	NA	NA	0.0048
		Best model	***1var***	***1var***	***1var***	***sum***
25	0.1	*Flock stasis*	0.0002	0.0063	0.0046	<0.001
		Flock spread	NA	NA	NA	NA
		Best model	***1var***	***1var***	***1var***	***1var***

Table S5. 6. Sensitivity of parameters on prediction of flocking variables

The impact of condition on flocking variables (first column) “Flock stasis” and “Dorso-ventral spread”, under different choices of fission distance “Fis. dist.” (second column) and minimum flight proportion “Min. flight prop.” (third column; see *Methods* for a description of both parameters). Comparison (fourth column) represents the condition that was the covariate in question for all remaining statistics: this is either differences in leader groups against follower groups; differences between groups of different mass composition (“l.all” is all light individuals, “l.mixed” is majority light individuals, “h.mixed” is majority heavy individuals, and “h.all” is all heavy individuals); homogenous vs. heterogeneous mass conditions (i.e. “all” vs “mixed” groups) are given with the results reported as the impact of heterogeneous groups against homogenous groups (this is consistent throughout). Finally homogeneity is considered across all experiments, with training flights considered heterogeneous, and either i) both leadership compositions considered as homogenous, or ii) with followers completely omitted from the analysis (sub followers). The subsequent columns are the model output from function “lme” in R-package “nlme” (Pinheiro et al. 2012). Grey shaded cells represent the statistics for the chosen parameters, some of which are reported in the main text (see *Results*).

Flocking variable	Fis. dist.	Min. flight prop.	comparison	Box-Cox trans.	Value	Std.Err	DF	t.value	p.value
Flock stasis	25	0.1	Leadership comp. (leaders)	0.1	0.0370	0.0154	16	2.3936	**0.0293**
			l.all - l.mixed	1	0.3554	0.1699	18	2.0917	0.1934
			l.all - h.mixed	1	0.5575	0.1701	18	3.2771	0.0199
			l.all - h.all	1	0.1499	0.1585	18	0.9458	0.7809
			l.mixed - h.mixed	1	0.2021	0.1429	18	1.4143	0.5070
			l.mixed - h.all	1	-0.2055	0.1649	18	-1.2464	0.6068
			h.mixed - h.all	1	-0.4077	0.1669	18	-2.4426	0.1044
			Mass comp. homogeneity (heterogeneous)	0.8	0.3755	0.1314	14	2.8584	**0.0126**

			Homogeneity (heterogeneous)	1.2	0.0397	0.0253	35	1.5651	0.1265
			Homogeneity, sub followers (heterogeneous)	1.2	0.0518	0.0232	35	2.2306	**0.0322**
	50	0.05	Leadership comp. (leaders)	-0.2	-0.0840	0.0334	23	-2.5118	**0.0195**
			l.all - l.mixed	1	0.0326	0.0313	21	1.0405	0.7280
			l.all - h.mixed	1	0.0743	0.0312	21	2.3770	0.1127
			l.all - h.all	1	0.0166	0.0300	21	0.5515	0.9451
			l.mixed - h.mixed	1	0.0417	0.0277	21	1.5021	0.4540
			l.mixed - h.all	1	-0.0160	0.0319	21	-0.5031	0.9574
			h.mixed - h.all	1	-0.0577	0.0319	21	-1.8070	0.2980
			Mass comp. homogeneity (heterogeneous)	0.1	0.0455	0.0243	14	1.8759	0.0817
			Homogeneity (heterogeneous)	0.4	0.0048	0.0058	35	0.8246	0.4152
			Homogeneity, sub followers (heterogeneous)	0.2	0.0038	0.0028	35	1.3656	0.1808
	50	0.1	Leadership comp. (leaders)	-0.2	-0.0801	0.0358	15	-2.2369	**0.0409**
			l.all - l.mixed	1	0.0579	0.0340	18	1.6997	0.3525
			l.all - h.mixed	1	0.0905	0.0340	18	2.6619	0.0690
			l.all - h.all	1	0.0271	0.0302	18	0.8953	0.8074
			l.mixed - h.mixed	1	0.0326	0.0271	18	1.2023	0.6333
			l.mixed - h.all	1	-0.0308	0.0314	18	-0.9802	0.7623
			h.mixed - h.all	1	-0.0634	0.0316	18	-2.0064	0.2223
			Mass comp. homogeneity (heterogeneous)	0.1	0.0581	0.0257	14	2.2609	**0.0402**
			Homogeneity (heterogeneous)	0.5	0.0122	0.0074	35	1.6487	0.1082
			Homogeneity, sub followers (heterogeneous)	0.1	0.0029	0.0014	35	2.0796	**0.0450**
	50	0.25	Leadership comp. (leaders)	-0.5	-0.1645	0.0771	9	-2.1332	0.0617
			l.all - l.mixed	1	0.0513	0.0378	12	1.3569	0.5472
			l.all - h.mixed	1	0.0904	0.0365	12	2.4800	0.1141
			l.all - h.all	1	0.0063	0.0344	12	0.1823	0.9977
			l.mixed - h.mixed	1	0.0391	0.0316	12	1.2389	0.6156
			l.mixed - h.all	1	-0.0450	0.0368	12	-1.2244	0.6241
			h.mixed - h.all	1	-0.0841	0.0357	12	-2.3581	0.1391
			Mass comp. homogeneity (heterogeneous)	0.1	0.0693	0.0281	14	2.4703	**0.0270**
			Homogeneity (heterogeneous)	0.1	-0.0037	0.0016	35	-2.2785	**0.0289**
			Homogeneity, sub followers (heterogeneous)	0.3	-0.0130	0.0045	35	-2.8669	**0.0070**
	75	0.1	Leadership comp. (leaders)	-0.5	-0.2132	0.0827	14	-2.5778	**0.0219**
			l.all - l.mixed	1	-0.0566	0.0381	17	-1.4857	0.4670
			l.all - h.mixed	1	-0.0812	0.0379	17	-2.1414	0.1800
			l.all - h.all	1	-0.0309	0.0338	17	-0.9142	0.7977

			l.mixed - h.mixed	1	-0.0246	0.0313	17	-0.7867	0.8595
			l.mixed - h.all	1	0.0257	0.0357	17	0.7203	0.8876
			h.mixed - h.all	1	0.0503	0.0352	17	1.4298	0.4989
			Mass comp. homogeneity (heterogeneous)	-0.1	-0.0512	0.0283	14	-1.8124	0.0914
			Homogeneity (heterogeneous)	0.5	-0.0179	0.0082	35	-2.1820	**0.0359**
			Homogeneity, sub followers (heterogeneous)	0.4	-0.0172	0.0065	35	-2.6423	**0.0122**
Dorso-ventral spread	25	0.1	Leadership comp. (leaders)	-0.8	0.0618	0.0260	16	2.3764	**0.0303**
			l.all - l.mixed	1	-0.0055	0.0140	18	-0.3947	0.9785
			l.all - h.mixed	1	-0.0185	0.0140	18	-1.3195	0.5630
			l.all - h.all	1	-0.0153	0.0123	18	-1.2409	0.6101
			l.mixed - h.mixed	1	-0.0129	0.0112	18	-1.1527	0.6629
			l.mixed - h.all	1	-0.0098	0.0136	18	-0.7182	0.8886
			h.mixed - h.all	1	0.0031	0.0138	18	0.2289	0.9956
			Mass comp. homogeneity (heterogeneous)	0.2	-0.0093	0.0259	14	-0.3568	0.7266
			Homogeneity (heterogeneous)	1	0.0142	0.0204	35	0.6974	0.4902
			Homogeneity, sub followers (heterogeneous)	0.9	0.0175	0.0194	35	0.9041	0.3721
	50	0.05	Leadership comp. (leaders)	-0.8	0.0618	0.0262	23	2.3554	**0.0274**
			l.all - l.mixed	1	-0.0051	0.0380	21	-0.1350	0.9991
			l.all - h.mixed	1	0.0298	0.0378	21	0.7878	0.8592
			l.all - h.all	1	0.0359	0.0305	21	1.1779	0.6469
			l.mixed - h.mixed	1	0.0349	0.0284	21	1.2279	0.6167
			l.mixed - h.all	1	0.0410	0.0379	21	1.0805	0.7048
			h.mixed - h.all	1	0.0061	0.0379	21	0.1615	0.9985
			Mass comp. homogeneity (heterogeneous)	-0.6	-0.0063	0.0305	14	-0.2058	0.8399
			Homogeneity (heterogeneous)	0.9	-0.0135	0.0218	35	-0.6177	0.5408
			Homogeneity, sub followers (heterogeneous)	1	-0.0110	0.0224	35	-0.4906	0.6268
	50	0.1	Leadership comp. (leaders)	-0.7	0.0706	0.0297	15	2.3760	**0.0313**
			l.all - l.mixed	1	0.0265	0.0336	18	0.7867	0.8595
			l.all - h.mixed	1	0.0499	0.0335	18	1.4882	0.4646
			l.all - h.all	1	0.0416	0.0290	18	1.4322	0.4965
			l.mixed - h.mixed	1	0.0234	0.0262	18	0.8923	0.8089
			l.mixed - h.all	1	0.0151	0.0312	18	0.4854	0.9614
			h.mixed - h.all	1	-0.0083	0.0313	18	-0.2640	0.9933
			Mass comp. homogeneity (heterogeneous)	-0.6	0.0137	0.0258	14	0.5312	0.6036
			Homogeneity (heterogeneous)	1.1	-0.0018	0.0215	35	-0.0837	0.9338
			Homogeneity, sub followers	0.9	0.0017	0.0213	35	0.0807	0.9361

			(heterogeneous)						
	50	0.25	Leadership comp. (leaders)	-0.8	0.0479	0.0318	9	1.5080	0.1658
			l.all - l.mixed	1	0.0195	0.0291	12	0.6693	0.9066
			l.all - h.mixed	1	0.0279	0.0280	12	0.9959	0.7545
			l.all - h.all	1	0.0254	0.0264	12	0.9618	0.7729
			l.mixed - h.mixed	1	0.0085	0.0243	12	0.3484	0.9848
			l.mixed - h.all	1	0.0060	0.0283	12	0.2105	0.9965
			h.mixed - h.all	1	-0.0025	0.0274	12	-0.0912	0.9997
			Mass comp. homogeneity (heterogeneous)	-1	0.0114	0.0220	14	0.5157	0.6141
			Homogeneity (heterogeneous)	1	0.0026	0.0221	35	0.1192	0.9058
			Homogeneity, sub followers (heterogeneous)	1	0.0076	0.0222	35	0.3409	0.7352
	75	0.1	Leadership comp. (leaders)	-0.7	0.0549	0.0291	14	1.8875	0.0800
			l.all - l.mixed	1	0.0294	0.0279	17	1.0526	0.7217
			l.all - h.mixed	1	0.0412	0.0278	17	1.4825	0.4689
			l.all - h.all	1	0.0316	0.0226	17	1.4021	0.5150
			l.mixed - h.mixed	1	0.0118	0.0211	17	0.5599	0.9425
			l.mixed - h.all	1	0.0022	0.0266	17	0.0839	0.9998
			h.mixed - h.all	1	-0.0096	0.0263	17	-0.3651	0.9828
			Mass comp. homogeneity (heterogeneous)	-0.9	0.0172	0.0220	14	0.7832	0.4466
			Homogeneity (heterogeneous)	1.1	-0.0185	0.0112	35	-1.6529	0.1073
			Homogeneity, sub followers (heterogeneous)	1	-0.0145	0.0110	35	-1.3174	0.1962

Table S5. 7. Fission and route efficiency models

Statistics for both group manipulation experiments (experiments two and three; first column) in models predicting fission and route efficiency (second column; see *Methods*). Contrast (third column) refers to the statistical comparison, either between groups of different mass composition (referred to in terms of the proportion of heavy individuals in the group, i.e. either [0], [0.33], [0.67], or [1]), these same proportions as a numeric variable "Mass comp. as num.", homogeneous mass groups (i.e. proportions [0] and [1]) vs. heterogeneous groups (i.e. proportions [0.33] and [0.66]) "Hom. vs. Het.", or finally between groups of leaders and groups of followers "Lead vs. Fol.". Where comparisons between mass groups have been made (e.g. when "Contrast" is [0] – [0.33]), Tukey posthoc tests provided statistics (Lenth 2018), otherwise output is provided by R-package "nlme" (Pinheiro et al. 2012), columns for both sets of statistical output are equivalent.

Experiment	Dependent var.	Contrast	estimate	SE	df	t.ratio	p.value
Group mass comp.	Fission	0 - 0.33	3.96969	5.205365	13	0.762615	0.869699
		0 - 0.67	9.952144	5.280794	13	1.884592	0.281087
		0 - 1	4.173806	3.348494	13	1.246472	0.610202
		0.33 - 0.67	5.982454	3.332289	13	1.795299	0.318664
		0.33 - 1	0.204116	5.128759	13	0.039798	0.999976
		0.67 - 1	-5.77834	5.193105	13	-1.11269	0.688415
		Mass comp. as num.	-5.41158	3.329035	15	-1.62557	0.124862
		Hom. vs. Het.	4.277996	4.579853	14	0.93409	0.366089
	Route efficiency	0 - 0.33	0.009934	0.044991	13	0.220808	0.996006
		0 - 0.67	0.038631	0.045569	13	0.847757	0.830899
		0 - 1	-0.00174	0.025038	13	-0.06948	0.999873
		0.33 - 0.67	0.028697	0.02501	13	1.147407	0.668272
		0.33 - 1	-0.01167	0.04447	13	-0.26251	0.993349
		0.67 - 1	-0.04037	0.044972	13	-0.8977	0.806225
Leader comp.	Fission	Lead. vs. Fol.	2.293789	1.46894	50	1.561526	0.124707
	Route efficiency	Lead. vs. Fol.	0.057356	0.047809	50	1.199687	0.235915

Chapter 6: Cooperation and defection in bird flocks under threat

Daniel W. E. Sankey[1], Rolf. F. Storms[2], Robert. J. Musters[2], Timothy. W. Russell[1], Charlotte. K. Hemelrijk[2] and Steven J. Portugal[1]

Author affiliations:

[1]*School of Biological Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, U.K.*

[2]*Groningen Institute for Evolutionary Life Sciences, University of Groningen, Centre for Life Sciences, Nijenborgh 7, 9747AG Groningen, The Netherlands*

Abstract

Collective behaviour in biological systems can vary from mostly or entirely cooperative, to exhibiting significant trade-offs between mutualistic and selfish benefits (i.e. with more motivation to "defect"). Animals such as bird flocks and fish shoals which display collective motion are thought to be an example of systems with greater motivation to "defect". A "selfish-herd" mechanism, whereby individuals head to a central point in the flock (centroid attraction), has been shown to minimise individual risk at the expense of conspecifics when under threat, consistent with "defection" behaviour. Conversely, individuals could align with their neighbours' orientations (alignment) and confer enhanced group-level benefits such as collective escape, consistent with "cooperative" behaviour. We investigated these predictions using homing pigeons (*Columba livia*) and a remote-controlled model peregrine falcon (*Falco peregrinus*). The RobotFalcon and each pigeon were tagged with 5 Hz GPS loggers. Pigeons were either chased by the RobotFalcon (*N* = 27 flights) or not (control; *N* = 16 flights), and were part of small (*N* = 8-10 birds) or large (*N* = 27-34 birds) flocks. Despite responding strongly to the proximity and orientation of the RobotFalcon, cohesively moving flocks demonstrated no increased centroid attraction. Our results suggest, therefore, that mutualistic benefits of alignment may outweigh the selfish benefits of centroid attraction. Thus we provide tentative evidence for a new hypothesis that "selfish-herd" dynamics

could be rare or even absent in birds, or even, more broadly, species which elicit collective motion. Altogether our results challenge a current hypothesis that collective motion is more vulnerable to defection than collective systems with more genetically related actors (e.g. body cells and eusocial insects), and instead argue for a more nuanced hypothesis which incorporates the magnitude of the mutualistic benefit. Throughout, we highlight an important link between collective behaviour and evolutionary game theory, shedding light on the evolution of collective phenomena.

Introduction

Collective behaviour can be defined as coordinated actions across multiple actors which create adaptive group-level properties (Sumpter 2006, 2010). Such examples as the oscillating and bending forms of European starling (*Sturnus vulgaris*) murmurations (Ballerini et al. 2008; Hildenbrandt et al. 2010), the orderly lane formations of army ants (*Eciton burchelli*) (Couzin and Franks 2003) and humans (*Homo sapiens*) (Helbing et al. 2005) and perhaps even the emergence of human consciousness from brain cells (Crick and Koch 2003), are thought to arise from only the most basic of interactions between the individual animals or cells (e.g. neurons) (Sumpter 2006, 2010; Vicsek and Zafeiris 2010). Benefits of these emergent phenomena are mutualistic (Maynard Smith and Szathmáry 1997; Sumpter 2006, 2010; Hölldobler and Wilson 2009), i.e. each actor profiting concurrently with their

neighbours, not at their neighbours' expense. It is owing to the scope of these mutualistic benefits – which are often ratchetting with increasing group sizes (Sumpter 2010; Cornforth et al. 2012) – that collective phenomena have evolved in many biological contexts (Bonabeau et al. 1998; Couzin and Franks 2003; Crick and Koch 2003; Helbing et al. 2005; Ballerini et al. 2008). Nevertheless, in the evolution of cooperative behaviour, a significant individual motivation to behave selfishly has extensive support from mathematical game theory (Trivers 1971; Axelrod and Hamilton 1981; Ghoul et al. 2014), and empirical observations of animal behaviour (Bourke 1988; Magrath and Yezerinac 1997; Riehl and Frederickson 2016). Only when mutualistic fitness benefits (including those accrued in genetically related actors) fully outweigh selfish benefits across any context, do we expect to see complete stability in collective behaviour (Maynard Smith and Szathmáry 1997; Corning and Szathmáry 2015). Thus, it is generally believed that collective behaviour in highly related systems would be less vulnerable to defection than those in systems comprising less related individuals (Couzin 2009; Hölldobler and Wilson 2009; Ioannou 2017). However, this argument ignores the magnitude of the mutualistic benefits, which, if large enough in unrelated actors, would be expected to exhibit high stability.

Perhaps the most widely known selfish benefits in group movement, are those conferred by "selfish-herd" behaviour. Hamilton (1971) explained that individuals who stay close to others will be at a selective advantage, when individuals in less dense regions of a group (with a larger "domain of danger") are disproportionately

subject to predation, known as “marginal predation”. The “selfish herd” hypothesis has been extended more recently to include the possibility that individuals may actively track – and head towards – a locally perceived group centre (henceforth, centroid attraction) (Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Morrell and James 2007; Wood and Ackland 2007; King et al. 2012; Demšar et al. 2016), to increase their own relative safety, while increasing the relative danger for their neighbours’ by leaving them more exposed (Wood and Ackland 2007). There is growing empirical evidence that individuals use locally (or even globally) perceived centroid attraction rules, noted in domestic mammals (*Ovis aries*) (King et al. 2012), fish (*Poecilia reticulata*) (Kimbell and Morrell 2015), and invertebrates (*Uca pugilator*) (Viscido and Wethey 2002). “Selfish herd” dynamics are potentially harder to study in free-flying birds (with a three-dimensional spread in spatial composition), than captive or terrestrial animals such as fish (Kimbell and Morrell 2015), sheep (King et al. 2012) and crabs (Viscido and Wethey 2002), and mechanistic evidence of “selfish-herd” dynamics in bird flocks still lacking (but see Caro 2005; Quinn and Cresswell 2006 for evidence of “marginal predation”). Nevertheless, this may be due to the difficulty in studying the positioning of birds in flight (Quinn and Cresswell 2006), rather than absence of “selfish-herd” dynamics, given the strong support for this hypothesis in other taxa (Stankowich 2003; Caro 2005; Quinn and Cresswell 2006), including collectively moving fish (Kimbell and Morrell 2015). Altogether, if marginal predation exerted even weak selective pressure in bird flocks, simple mechanisms such as “attraction” to a locally-

perceived centroid would be expected to evolve in the absence of benefits from alternative mechanisms.

The mechanics of collective motion can provide alternative mutualistic benefits which may outcompete the benefits of "selfish herd" dynamics. Collective motion is thought to operate via simple movement rules, which each group member employs in response to the positions and orientations of their local neighbours (Couzin et al. 2002; Vicsek and Zafeiris 2010). These "rules", such as *attracting towards* and *aligning with* locally perceived neighbours, create complex swarming phenomena in simulations (Couzin et al. 2002; Vicsek and Zafeiris 2010) and there is empirical evidence for the use of such rules in fish (Herbert-Read et al. 2011; Katz et al. 2011) and birds (Pettit et al. 2013b). These "rules of interaction" are thought to have evolved in animals, at least in part, due to the predator-risk diminishing properties of the emergent group-level patterns (Wood and Ackland 2007; Ioannou et al. 2012; Herbert-Read et al. 2017). While both "attraction" (to a locally perceived centroid) and "alignment" rules are necessary for collective motion, it is likely that individuals in a group which bias their movements towards a locally perceived centroid (centroid attraction), would be relatively less vulnerable to predation than other group members. However, the group as a whole will likely slow down (Wood and Ackland 2007; Ioannou et al. 2012), and decrease conformity in their movements (Herbert-Read et al. 2013), diminishing mutualistic benefits (see Sumpter et al. 2018). Therefore, to the best of our current knowledge, "centroid attraction" can be thought of as a "defection" response. Conversely, aligning with

neighbours (alignment) may result in faster groups with an enhanced collective escape response (Wood and Ackland 2007; Ioannou et al. 2012), which share mutualistic information (Wood and Ackland 2007; Herbert-Read et al. 2015; Sumpter et al. 2018), and could elicit greater visual confusion in a predator (Procaccini et al. 2011). Therefore, alignment may be considered a "cooperative" behaviour. Linking mechanism to function in this way was identified by Sumpter et al. (2018), and has highlighted the potential for individuals in a collective to trade-off mutualistic movement rules (alignment) with selfish rules (centroid attraction). Evolutionary models which support this have shown that groups of either high centroid attraction or high alignment can evolve to stability in response to predation, just by the fine-tuning of these two simple behaviours (Wood and Ackland 2007).

Another context where "selfish" decisions may be favoured is at close proximity to a predator, when faced with the decision to either 1) *stay with the group* (henceforth, group cohesion) or 2) *avoid the predator* (henceforth, predator avoidance). If there is no conflict between group cohesion and predator avoidance ("no conflict") we expect individuals to move in accordance with these matching angles (Fig. 6.1). However, in "conflict scenarios", i.e. where individuals need to choose between *predator avoidance* or *group cohesion*, splitting may be favoured, though only at extremely close predator approaches (Fig. 6.1). Splitting, here, may have *relative benefit* for the individual, because choosing *not to avoid the predator* would result in capture ("altruistic", because capture may allow other group

members to escape). While avoiding capture, such splitting movements may confer a relative cost to the other group members, as the decision may result in a decline in group size (Krause and Ruxton 2002; Conradt and Roper 2003), or in another individual being targeted (Fig. 6.1). Hence we describe splitting at *extremely close* distances to the predator – when capture becomes near inevitable – as "selfish" (relative benefit for actor and relative cost for neighbours). We pose that such "selfish" decisions are at the expense of "altruism" (Fig. 6.1), and thus cannot be considered "defection", which relies on a conflict between "cooperative" and "selfish" decisions (Axelrod and Hamilton 1981). We would expect "selfish" and not "altruistic" decisions to emerge at this critical point where staying with the group would lead to likely capture (following: Davies et al. 2012; Bourke 2014).

Still in "conflict scenarios", but now considering intermediate to large predator-prey distances, staying with the group would be thought to be beneficial for all individuals (i.e. "cooperative" benefits). The alternative – splitting – here may increase relative individual risk (Fig. 6.1), as predator attacks on singletons have been shown to have greater success in fish (Foster and Treherne 1981) and birds (Zoratto et al. 2010) (see Landeau and Terborgh 1986 for a review). This risk also applies to the context above (close predator approaches), however when the predator is further away, the immediate risk will be less, which will likely "tip the balance" of the relative benefit, in favour of remaining in the flock (Fig. 6.1). Whether this has a negative or positive relative impact on other group members likely depends on the number of predators chasing the group. A diminished group

size, caused by the split, may *increase* relative benefit for neighbouring individuals ("altruistic", if one predator is present and chases the singleton); though as the split reduces group size, this may also *reduce* relative benefit for other group members if more than one predator is present ("spite") (Fig. 6.1). Both "spite" and "altruism" are negative for the actor, and thus, this response would not expected in any scenario (following: Davies et al. 2012; Bourke 2014). Altogether, we suggest that individuals should split (fission) at close predator distances (in "conflict scenarios"), but re-join (fusion) if the immediate threat has passed. An example of fission/fusion dynamics which fit this hypothesis are the flash expansions exhibited by starlings, which represent an impressive, high speed, combination of the two processes above (Storms et al. 2019). 1) Flash expansions in starlings occur at close predator approaches. Then, only moments later, their predators, peregrine falcons (*Falco peregrinus*) may be at much greater relative distances to the flock, as peregrine falcons use high speed strike attacks (Storms et al. 2019). As such, 2) the contractions which follow the flash expansion may be a response to these greater predator distances.

We modified the predator context of both *i*) small (*N* = 8-10) and *ii*) large (*N* = 27-34) homing pigeon (*Columba livia*) flocks by introducing a remote-controlled robotic model of a male peregrine falcon, hereafter referred to as the RobotFalcon. Homing pigeons are a model species for collective motion (Biro et al. 2006; Sumpter et al. 2008; Nagy et al. 2010; Pettit et al. 2013b), which, despite domestication, remain suitable for studying prey responses to predation (See *Methods: Pigeons as a model*

species and Henderson et al. 2004). By manipulating the perceived risk of predation, we aimed to investigate the following predictions; 1) that pigeons under RobotFalcon treatment conditions will demonstrate observable increases in "centroid attraction", compared with control flights (i.e. flights with no RobotFalcon). This prediction is consistent with reducing the individual "domain of danger" from the "selfish herd" hypothesis (Hamilton 1971). 2) When *predator avoidance* and *group cohesion* conflict (cf. "conflict scenarios"), we predict that *predator avoidance* (avoidance of RobotFalcon) will override *group cohesion* (attraction/alignment), but only at closer predator approaches (Fig. 6.1). Thus, we are providing a formal test whether birds employ "altruistic" or "spiteful" behaviour as opposed to more well-supported "selfish" and "cooperative" movements (Fig. 6.1). 3) When there is "no conflict" between *predator avoidance* and *group cohesion*, we expect movements away from the group to be unlikely at all predator-prey distances. 4) If prediction (2) is supported (splitting in at close approaches), we predict such mechanics will result in larger scale fission/fusion phenomena governed by the distance to the RobotFalcon, as we have argued is the mechanism employed during "flash expansions" of starling murmurations (Storms et al. 2019).

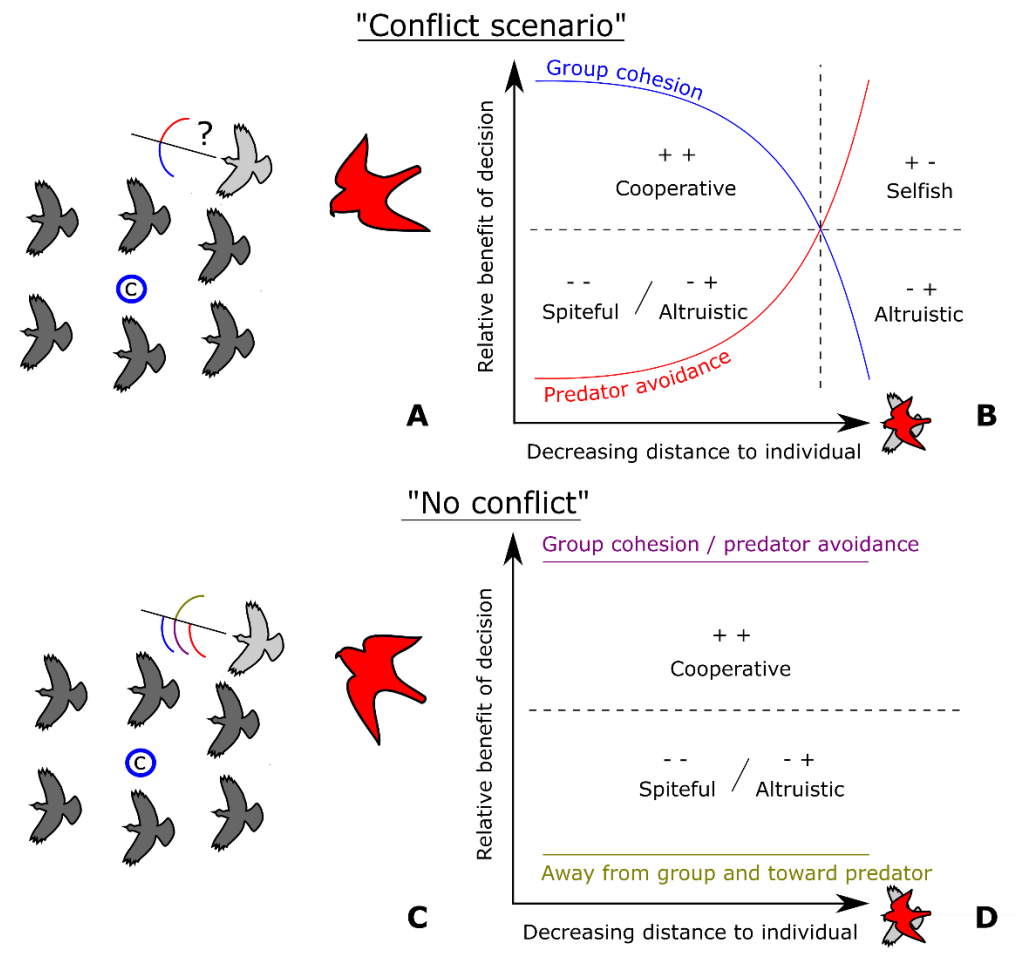

Figure 6. 1. Hypothesis and predictions

Following predictions 2) and 3), we expect individual decisions to enhance *predator avoidance* and/or *group cohesion* to be impacted by 1) whether these two decisions are conflicting **(A-B)** or not **(C-D)** and 2) the distance of the predator to a focal bird (**B** and **D**). We have applied game-theoretic principles to the behavioural decisions: *i*) avoidance a predator and *ii*) maintaining cohesion with a group. We discuss behavioural decisions in terms of their proposed outcomes in relative benefit or cost (as + and – respectively) for actors/recipients, in accordance with normal denotation in game theory (Davies et al. 2012). Hence, selfish actions are denoted with (+/–), cooperative actions as (+/+), altruistic (–/+) and spite (–/–) (**B** and **D**). **(A)**

A schematic of “conflict scenarios”. The focal bird (light grey) has to choose between avoidance of falcon (falcon image and turning angle to avoid the falcon in red), and cohesion with other flock members (dark grey) (group centroid and turning angle to align/attract with group in blue), as the two angles are in conflict (see *Methods: Conflict scenarios/ no conflict*). **(B)** In conflict scenarios, we predict diminishing fitness benefits (relative benefit of decision, y-axis) to *remaining in the group*, but only at extremely close predator-prey distances (slope decreases only near to the extreme end of predator-prey distance on the x-axis). Choosing not to avoid the predator, here, may result in capture and may therefore be seen as “altruistic” (–/+). Conversely, avoiding the predator and at close approaches, may confer relative benefit for the actor, but diminish the relative benefits for neighbouring individuals (a “selfish” decision (+/–)). At intermediate and large predator-prey distances, we expect *group cohesion* responses to be favoured (seen as “cooperative” (+/+)). Turning away from the group (resulting in splitting) at intermediate/large predator-prey distances will likely be negative for the actor (–), due to singleton flight being highly risky (Zoratto et al. 2010), and can be seen as either “altruistic” (–/+) or “spiteful” (–/–). **(C)** A schematic of scenarios with “no conflict”. Here, *predator avoidance* (red), and *group cohesion* (blue), are in the same direction (purple). The turning angle away from both the group and toward the predator (olive) is provided. **(D)** In scenarios with “no conflict”, we expect the matching *predator avoidance* and *group cohesion* turning angle (purple) to be more beneficial than movements away from the group/ toward the predator (olive) at all distances to the predator.

Methods

Pigeons as a model species

Pigeons, which naturally form collectively moving groups (Nagy et al. 2010), must respond adaptively to ecological conditions to ensure they return home. In the past, pigeons that did not return home did not breed at the loft, and subsequently, successful homers make up lineages of homing pigeons that generally stretch over many generations (Shapiro and Domyan 2013). Henderson et al. (2004) provide strong evidence that racing pigeons are commonly predated by woodland-living Eurasian sparrowhawks and peregrine falcons which occupy coastal and inland areas, including cities (Henderson et al. 2004). This implies that anti-predator responses are still "selected for", despite domestication. Pigeons, therefore, may have retained naturally selected anti-predator traits, which we aimed to study.

Release protocol

Homing pigeons (*N* = 34) aged between 15 and 27 months were housed at Royal Holloway University of London in purpose-built lofts. Birds were provided were provided food, water and grit *ad libitum*. All birds had experience of flying multiple times from sites away from the present study site (Chobham Common, CC; see *Supplemental Material*); no birds had experience of homing from CC. For more

information on the housing and husbandry of our pigeons, and site permissions, see *Supplemental Material*.

Following a series of training flights (*N* = 10) from a nearby location (see *Supplemental Material*), four categories of flight were conducted in a randomised order, following two days of initial treatments of small pigeon groups (*N* = 8-10 birds) with "falcon present" for pilot training purposes (*Supplemental Material*). Thirty four pigeons split into four groups (*N* = 8, *N* = 8, *N* = 8, *N* = 10) were released either once or twice a day (morning and/or afternoon flights), either as small flocks (*N* = 8-10 birds; in their respective groups) or large flocks with all groups combined (*N* = 34 birds for morning flights; *N* = 27-31 in afternoon flights). These smaller numbers of birds in the afternoon flights for the large flocks were due to individuals which had not returned to their loft from the morning flight being excluded. Flocks were flown either with the robotic falcon ("RobotFalcon"; see below) chasing the pigeons, or absent (i.e. control flights). The total number of flights in each of the four categories were as follows: small groups with predator – 20 flights; large groups with predator – 7 flights; small groups with control conditions – 12 flights; and finally large groups with control conditions – 4 flights; providing *N* = 169, *N* = 229, *N* = 101 and *N* = 129 individual trajectories for each condition respectively (total pigeon trajectories *N* = 628; see *Supplemental Material* for more information on release protocol).

Biologgers

To determine the positioning, trajectory and speed of each individual within the group, we deployed GPS loggers (5 data points per second – 5 Hz; QStarz BT-Q1300ST, Düsseldorf, Germany; mass = 12.5 g) for each bird and for each flight throughout the duration of the study (see *Supplemental Material* for more details and attachment methods). Logger failures were rare (1.2%). Significantly, GPS never failed during a flight with the RobotFalcon present, and failed rarely on control flights (see *Release protocol* below). Total logger mass included accelerometers (AX3, Axivity Ltd, Newcastle upon Tyne, U.K.; 8 g; data not used in the present study), bringing total logger mass to was 20.5 g. See *Supplemental Material* and (Sasaki et al. 2017) for more detailed information regarding logger treatment and attachment.

Robotic falcon

The model, robotic falcon (or, "RobotFalcon") was developed by RJM, with key attention to copying the behaviour as well as morphological likeness of a male peregrine falcon. The mass of the RobotFalcon was 0.245 kg. The RobotFalcon had a First-Person View camera (Runcam micro swift 2), which transmitted images (600TVL, 30fps) in real time to a set of goggles worn by the pilot (Fig. 6.2). The RobotFalcon's direction and speed were controlled by the pilot, by commands sent

via remote control to each of two propellers on the RobotFalcon's wings. A GPS unit (5 Hz), as described above, was attached to the inside of the body of the RobotFalcon casing with Velcro strips. For more information about materials used and the operation of the RobotFalcon, please contact RJM by email at: info@roflight.com. We were granted informal permission from the U.K.'s civil aviation authority (CAA) to conduct the flights. We did not require formal permission, because of the low mass of the RobotFalcon and the non-commercial nature of our study.

Pilot and chase protocol

RJM who piloted the RobotFalcon (Fig. 6.2) has over 30 years' experience as a falconer, and over 40 years' experience as a model airplane flyer. The final chase protocol was based on repeatable methods, from findings from the literature (Ratcliffe 2010) as well as discussions amongst authors (DWES, RFS, RJM) as follows. Wherever possible, the RobotFalcon would gain height before stooping (Ratcliffe 2010). Also, as we intended to investigate the impact of attacks on bird groups – not individuals – the RobotFalcon would always chase the largest group. Indeed, individuals which split from the group, usually did so alone; split subgroups consisted mainly of singletons (76% in small flocks and 79% in large flocks; see *Supplemental Material*).

The RobotFalcon was launched by hand (as in Fig. 6.2), from a hill with good visibility of the release site (*Supplemental Material*), 500 m north-east of the release location (below). Just prior to this, we put a large dark mat over the wicker basket(s) which contained the birds, to prevent the pigeons getting an early visual on the RobotFalcon, and to minimise any differences between "control" and "predator" conditions before release. When the RobotFalcon was in a good position to stoop for an initial attack (defined as approximately 50 m behind the wicker basket and 5 m above), the mat was taken off and the birds were released. The RobotFalcon stooped approximately two to three seconds after the birds were released, when they had already gained sufficient altitude and speed to be a cohesive flying group (all birds out of the box and flying with approximately 3 m altitude or more).

Figure 6. 2. The "RobotFalcon" and the pilot

(A) The robotic falcon and **(B)** with designer/pilot Robert Musters (RM).

Computational methods

Grouping GPS data

After each flight, loggers were removed, recharged and the data downloaded. Erroneous GPS points were then removed, as well as duplicate timestamps, before trimming the dataset according to a defined site radius (see *Supplemental Material*; and Fig. S6.1). Following this, pairwise distances between all pigeons' GPS locations were calculated (following: Portugal et al. 2014) at each timestamp (5 Hz) for each flight. If a pigeon was less than ten metres from any neighbour, they were considered to be in the same group (Fig. 6.3; Fig. S6.2). Therefore there is a potential scenario whereby two neighbours which are further than ten metres could be considered part of the same group if another neighbour (or set of neighbours) connected them together (see Fig. S6.2 for a visual representation). We based our choice on the rarity of these observations, the wingspans of pigeons, and also on visual observations of flock fission under a range of "fission distances" (5 m, 7.5 m, 10 m and 12.5 m, respectively, see *Supplemental Material* and Fig. S6.4 for a detailed description of our choice).

Time spent separated from the largest group was recorded as a proportion of the total flight time, referred to as "proportion separated". The global group centroid (not "perceived centroid"; see *Supplemental Material*) was given by the mean of latitude and longitude for all remaining individuals, after outliers were removed

following the above protocol. For descriptive data on subgrouping (i.e. individuals not part of the largest group, as per the algorithm employed, but cohesive with neighbours nonetheless) see *Supplemental Material* and Fig. S6.3.

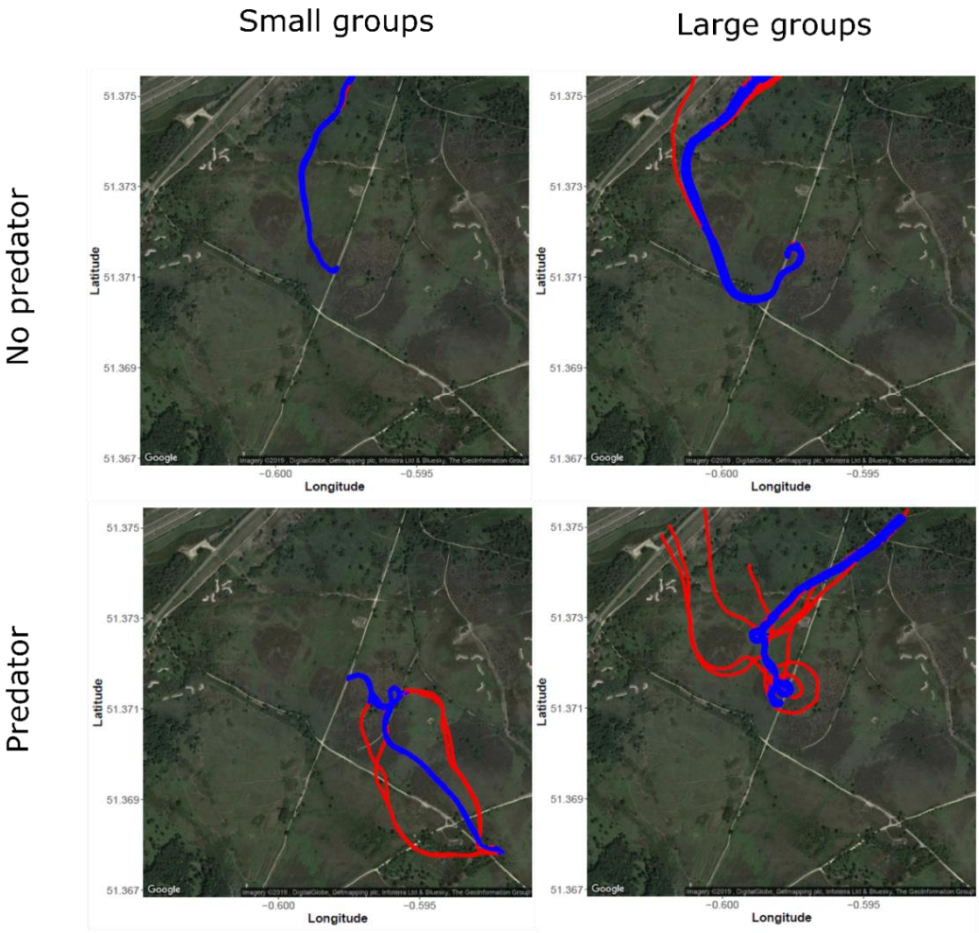

Figure 6. 3. Flock cohesion

Google Maps^{TM} plots of various flights. Images are centred on the release site coordinates at Chobham Common (see *Supplemental Material*; lon = -0.5979^{o}, lat = 51.371^{o}). For each time step, individual coordinates which are cohesive with the group (see *Methods: Grouping GPS data*) are coloured blue and non-cohesive individuals are coloured red. The top/bottom rows of figures show data for trajectories in the absence/presence of the RobotFalcon respectively. The first (left) column of figures shows data from the releases of the small flocks (*N* = 8-10 individuals); the second (right) column, for the releases of the large flocks (*N* = 27-34 individuals). Plots were created using "ggmap" (Kahle and Wickham 2013) in R (R Core Team. 2017).

Fission/fusion

Our grouping algorithm (above) also provided binary data on splitting (fission) and re-joining (fusion) events which were integral to the testing of our prediction (4) that close "predator" approaches would elicit fission, and likewise that fusion would be more common at greater pigeon-falcon distances. Specifically, the point at which an individual was not considered part of the largest group was considered as fission; and vice versa re-entry of the individual to the group was considered fusion. We made the criteria more stringent by including an "exclusion parameter", ignoring fission/fusion events which occurred within two seconds of the last event (but see our sensitivity analysis to this using one and three seconds in *Supplemental Material* and Table S1).

Polar variables

Polar covariates (Fig. 6.4A-E) were used to test predictions. Firstly, to test whether individuals were attracted to a central position in the flock, we derived the predictive effect of the angle toward a "locally perceived" centroid (centroid attraction, Θ_{ca}; Fig. 6.4C) on the instantaneous turn angle of the birds (Θ_t) (see *Supplemental Material* Fig. S6.5, measured at each time-step – 5 Hz). The optimal number of neighbours (*N*) to use in the Θ_{ca} calculation was established by the number of neighbours which had the largest predictive power over a focal

individual's movement (Θ_t) across all data (Fig S6.4; see *Supplemental Material*). Alignment (Θ_{ali}) was given by the turn angle necessary to align with the mean orientation of the optimal number (*N*) of nearest neighbours (Fig. 6.4D; Fig. S6.6; see *Supplemental Material*). Comparisons of Θ_t were made with values of $\Theta_{ali\text{-}n}$ $\Theta_{ca\text{-}n}$ from the previous time step, so that individuals had time to respond to the positions and/or orientations of their neighbours. The optimal number of neighbours for Θ_{ca} was $\Theta_{ca\text{-}7}$ (small groups) and $\Theta_{ca\text{-}33}$ (large groups); and for Θ_{ali} was $\Theta_{ali\text{-}1}$ (small groups) and $\Theta_{ali\text{-}5}$ (large groups) (see *Supplemental Material*). Therefore, our calculations estimate that (on average) pigeons were *attracted* to all individuals, while the topological range for *alignment* differs with group size. Interestingly, the optimal "locally perceived" centroid in small flocks (*N* = 7) and in large flocks (*N* = 33), is the same as, or close to, the global centroid in our case given group sizes of *N* = 8-10 and *N* = 34 (minus 1 for the focal individual making the decision).

Other polar variables measured were the angle (rad) toward the "RobotFalcon's position" (Fig. 6.4A), "RobotFalcon's orientation" (Fig. 6.4B) and "home" (Fig. 6.4E) with respect to the heading of a focal individual (Fig. 6.4). "RobotFalcon's position" and "home" were calculated in the same manner as centroid attraction (i.e. the turn necessary to attract to a given point), using RobotFalcon and home coordinates respectively. "RobotFalcon's orientation", on the other hand was calculated in the same manner as alignment (i.e. the turn necessary to align with a given orientation; or, heading) (see Fig. 6.4).

An individual's turning angle (Θ_t) towards the "locally perceived" centroid (Θ_{ca}), with respect to the alignment parameter (Θ_{ali}) was termed the "instantaneous centroid attraction" (Θ_{ica}; Fig. S6.5). Here, movement away from the flock centroid would give negative scores, and movement toward the centroid would be positive. "Instantaneous centroid attraction" is functionally equivalent to "centroid attraction" but reflects an actual turning angle, rather than the "pull" of a set of coordinates. "Instantaneous centroid attraction" was useful for *i*) visualisation, *ii*) some confirmatory statistics, and *iii*) to compare results to the output from a flocking agent-based model (methods from Couzin et al. 2002; see *Supplemental Material* and Table S2)

Conflict scenarios / no conflict

For 30.3% of all data within the site radius, movements toward the group (*group cohesion*), and movements away from the RobotFalcon (*predator avoidance*) would require opposite, *conflicting*, turning angles (cf. "conflict scenarios"; Fig. 6.1). *Group cohesion* was defined as the circular mean of the attraction and alignment components (above) weighted according to the effect size (of attraction/alignment) on turning angle Θ_t (for effect sizes see *Results*; "weighted circular mean" was calculated using algorithms in Pewsey et al. 2013). *Predator avoidance* was given by the turn necessary to align with the "RobotFalcon's orientation" as opposed to "RobotFalcon's position", as it had a stronger and negative effect on turning angle.

Interestingly “RobotFalcon’s position” was actually a positive predictor of turning angle (see Table S3*; Supplemental Material*, and Fig. S6.7). As both *group cohesion* and *predator avoidance* had a strong impact on movement decisions in the subsequent time step (see: *Results*), it is likely that the pigeons were often faced with a genuine conflict regarding directional preference in these situations. In these scenarios, whether the subsequent turning angle was biased away from the predator, or towards the group centre, was recorded as a binomial variable. Time steps with “no conflict” (69.7 % of all data) were subset as moments when *group cohesion* and *predator avoidance* required the same direction of movement.

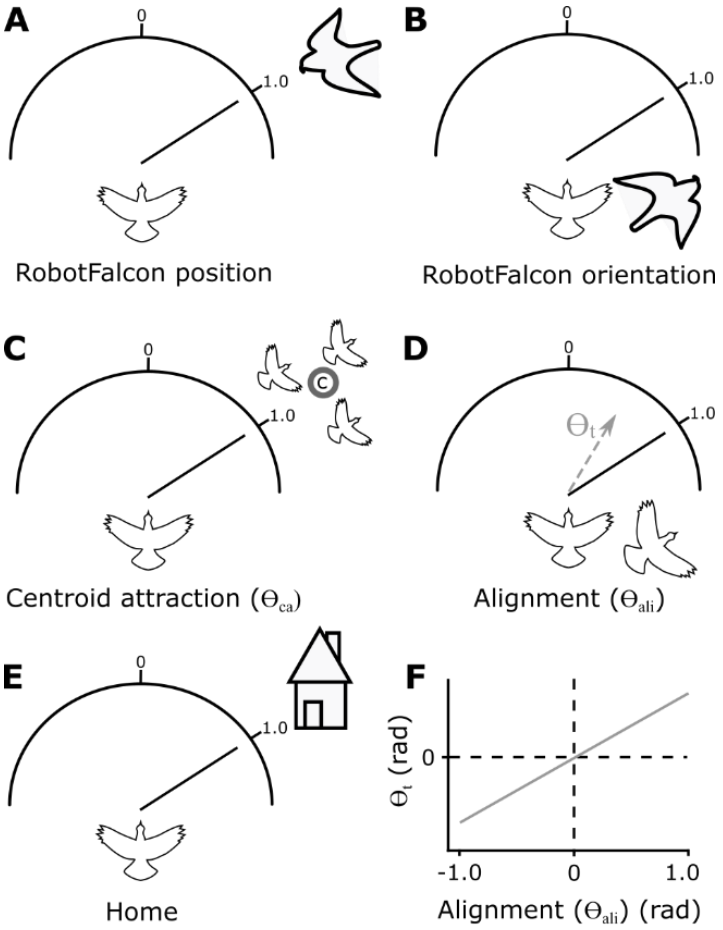

Figure 6. 4. The influence of polar variables on turning angle Θ_t

Polar variables which may influence turning angle Θ_t were defined as the angle between the focal individual's orientation and the following polar variables (using one radian as example for each, in line with what the statistical model effect sizes represent). The position **(A)** and **(B)** the orientation of the RobotFalcon respectively**; (C)** Centroid attraction Θ_{ca} – the position of the derived "locally perceived" centroid (see *Supplemental Material*); **(D)** alignment Θ_{ali} – the average orientation of the derived "optimum" number of nearest neighbours; and **(E)** Home – the position of the home loft. Panel **(F)** provides a potential relationship (grey) of alignment (Θ_{ali}) (black line in **(E)**) on turning angle (Θ_t) (grey arrow in **(E)**). This is only to provide a visual example of our dependent and independent variables used in statistical

models, and should not be taken as *a priori* prediction of the shape of the slope or magnitude of the effect. Hence there are no labels on the y-axis other than zero.

Statistics

Models including both control and predator treatment groups

We used linear mixed models (Pinheiro et al. 2012) to test the impact of the predator treatment on individual movement decisions Θ_t (Fig. 6.4) and Θ_{ica} (Fig. S6.5). Where Θ_t is the pigeon turning angle with respect to their previous heading (recorded at 5 Hz; Fig. S6.5), and Θ_{ica} is instantaneous centroid attraction: which is principally, turn angle Θ_t towards or away from the centroid, with respect to perfect alignment Θ_{ali} in the direction flock heading (Fig. S6.5). Further details can be found in the *Supplemental Material* for details on transformations, autocorrelation corrections and qq-plots (Fig. S6.8; Fig. S6.9) for these analyses – and all other – dependent variables.

Fixed variables were either a factor that could impact turning angles (Θ_t and Θ_{ica}), i.e. 1) other polar variables (Fig. 6.4A-E), or 2) factors which may interact with such variables. Firstly, this included two interactions, including non-polar variable absence or presence of the RobotFalcon and a polar variable: either, *i*) "angle to centroid" Θ_{ca}, which was expected to have a larger impact on dependent variable Θ_t in the presence of the RobotFalcon (prediction 1); or *ii*) "angle to alignment" Θ_{ali} (see Fig. 6.4F for an example regression). Also included as fixed variables were

"home" and cross-wind (strength of the wind in the lateral direction of the birds' orientation; see *Supplemental Material*). Support wind (cranio-caudal wind strength) was not used, as this would not be expected to influence turning angle, i.e. whether an individual turns left or right (logically following from Safi et al. 2013). Random variables were pigeon ID, group ID, unique flight number, and flock size (i.e. small or large flocks). The same model was repeated on data from cohesive flocks (i.e. datasets which had individuals removed once split (see *Methods: Grouping GPS data* and Fig. S6.2).

Models including only predator treatment groups

Using data from predator treatment flocks alone; it was possible to add predator covariates *i)* "RobotFalcon's position" and *ii*) "RobotFalcon's orientation" to the same linear mixed models (as above). The only contrast between the models was the addition of both predator covariates (above) and the hence the removal of experimental treatment (i.e. predator presence/absence).

We also constructed binomial models to analyse 1) *conflict scenarios*, where the binary variable is either turning towards the group, or turning away from the RobotFalcon, 2) *no conflict*, i.e. either towards group *and* away from predator *or* vice versa (Fig. 6.1). These models (GLMMs with binomial error family; Pinheiro et al. 2012) were constructed following prediction that individuals will split from the group at close RobotFalcon-pigeon distances, but only when the turning angles are

in conflict, following predictions (2) and (3) (Fig. 6.1). We also analysed binary 3) fission/fusion dynamics, i.e. splitting and re-joining events (Fig. 6.3; Fig. S6.4), following prediction (4) that splitting at closer predator distances will impact larger scale splitting and re-joining dynamics. The "distance to RobotFalcon" (m) was used in all binary models as a fixed variable in an interaction with flock size (i.e. large or small).

Results

As predicted by the "selfish-herd" hypothesis, the effect (or, pull) of the "locally perceived" centroid (cf. centroid attraction Θ_{ca}) on turning angle Θ_t was greater in the predator treatment over the control treatment (LMM: DF = 11563, t = 3.513, p < 0.001; Fig. 6.5A). However, this variation was not found in the spatially cohesive flocks (LMM: DF = 9356, t = -0.172, p = 0.892; Fig. 6.5A). Therefore there was no support for the selfish herd hypothesis in cohesive flocks (see maps/trajectories in Fig. 6.3). In cohesive bird flocks, regardless of treatment, *centroid attraction* remains around zero (Fig. 6.5B), until focal distances to centroid reach around 10 m (Fig. 6.5B). At greater distances than 10 m, differences emerge in the control group whereby individuals turn (and hence move) further away from the flock centroid, whereas in predator treatment groups, *centroid attraction* remains around zero (Fig. 6.5B). This is reflected in the statistics showing that "instantaneous centroid attraction" Θ_{ica} (see *Methods*) was significantly predicted by an interaction between

predator treatment and distance to centroid (LMM: DF = 7657, t = 2.69, p < 0.01; Fig. 6.5B). 10 m is more than four times larger than the median distance to centroid in cohesive flocks (2.34 m) and almost twice as large as the median from the entire dataset (5.33 m). Additionally, there were no inter-individual differences in Θ_{ica}; (removal of pigeon ID produces a better model fit; ΔAIC = -2). Therefore, despite pigeons responding strongly and negatively to the orientation of the RobotFalcon (Fig. 6.5A; LMM: DF = 7311, t = -14.006, p < 0.001), predator treatment groups did not exhibit greater *centroid attraction* than control groups until large (and rare) distances from the centroid.

Movements, more generally, across both predator treatments (i.e. presence or absence), were predicted strongly by flock alignment Θ_{ali} (LMM: DF = 11563, t = 9.124, p < 0.001; Fig. 6.5A; see *Supplemental Material* for derivation), and to a lesser extent, by centroid attraction Θ_{ca} (LMM: DF = 11563 t = 3.284, p < 0.01; Fig. 6.5A). Θ_{ali} and Θ_{ca} had additive impact on turning angle, while correlation between the variables was marginal (Pearson's correlation coefficient; r=0.071). "Turn angle to home" also had a significant impact on movement decisions, as would be expected from pigeons which all returned home (LMM: DF = 11563, t = 10.992, p < 0.001; Fig. 6.5A). Statistics reported in this paragraph, and the previous paragraph, are reproduced in Fig. 6.5A in the order reported (from top to bottom of the figure panel).

Although "selfish-herd" mechanics (i.e. net positive $\Theta_{ica;}$ Fig. 6.5B) were not observed in our data, a visual inspection of the agent-based model data indicates net positive Θ_{ica} across a range of distances to the centroid (Fig. 6.5B). This reveals that "selfish-herd" dynamics *can exist* in a cohesively group with strong "repulsion" dynamics (see *Supplemental Material: Agent-based model and instantaneous centroid attraction* and Couzin et al. 2002).

In conflict scenarios – where *i*) *predator avoidance* and *ii*) *group cohesion* were opposite turning angles – we found greater emphasis on avoiding the RobotFalcon than attracting toward the centroid in the subsequent time-step (GLMM binomial: DF = 2854, t = 4.767, p < 0.001; Fig. 6.5C). This bias towards avoiding the RobotFalcon is especially prevalent at close predator approaches (up to 73% vs 27% at distances of closer than 10 m to the RobotFalcon; Fig. 6.5C). Thus we find some support for our second prediction, however, *group cohesion* was only favoured at comparatively large distances (~50 m to the RobotFalcon), which was not as low as expected, and the shape of the curve was different than that predicted (Fig. 6.1). There were no differences here between two flock sizes (GLMM binomial: DF = 2854, t = 0.418, p = 0.676; Fig. 6.5C), nor was there any strong evidence for an interaction between "distance to RobotFalcon" and flock size (GLMM binomial: DF = 2854, t = 0.988, p = 0.323; Fig. 6.5C). When there was "no conflict" between *predator avoidance* and *group cohesion*, splitting was not favoured at any distance to the predator (Fig. 6.5C), as expected from our third prediction. Yet, the results show an increase in the likelihood splitting at larger RobotFalcon-pigeon distances,

which was not expected (GLMM binomial: DF = 3246, t = -5.121, p < 0.001; Fig. 6.5C) (see *Discussion*).

Coherent with prediction (4), we found that fission/fusion events could be explained by a logistic regression model against "distance to RobotFalcon", with closer RobotFalcon approaches predicting higher fission (splitting), and accordingly with fusion (re-joining) more common at greater distances (GLMM binomial: DF = 167, t = -4.331, p < 0.001; Fig. 6.5D; see *Supplemental Material* for a sensitivity analysis on the exclusion parameter defined in *Methods: Fission/fusion*). The "proportion separated" from the largest group (see *Methods: Grouping GPS data*) increased in the predator condition from a mean of 13.1% (± 26.4% S.D) of the flight to 20.6% (± 33.2% S.D) (LMM: DF = 592, t = 3.171, p < 0.01; Fig. S6.10, Table S3). Predator condition, however, had less of an impact on "proportion separated" than the flock size condition, with pigeons splitting from the main group 24.4% (± 34.0% S.D) of the flight in large flocks as opposed to 9.2% (± 24.0% S.D) in small flocks (LMM: DF = 592, t = -6.595, p < 0.001; Fig. S6.10).

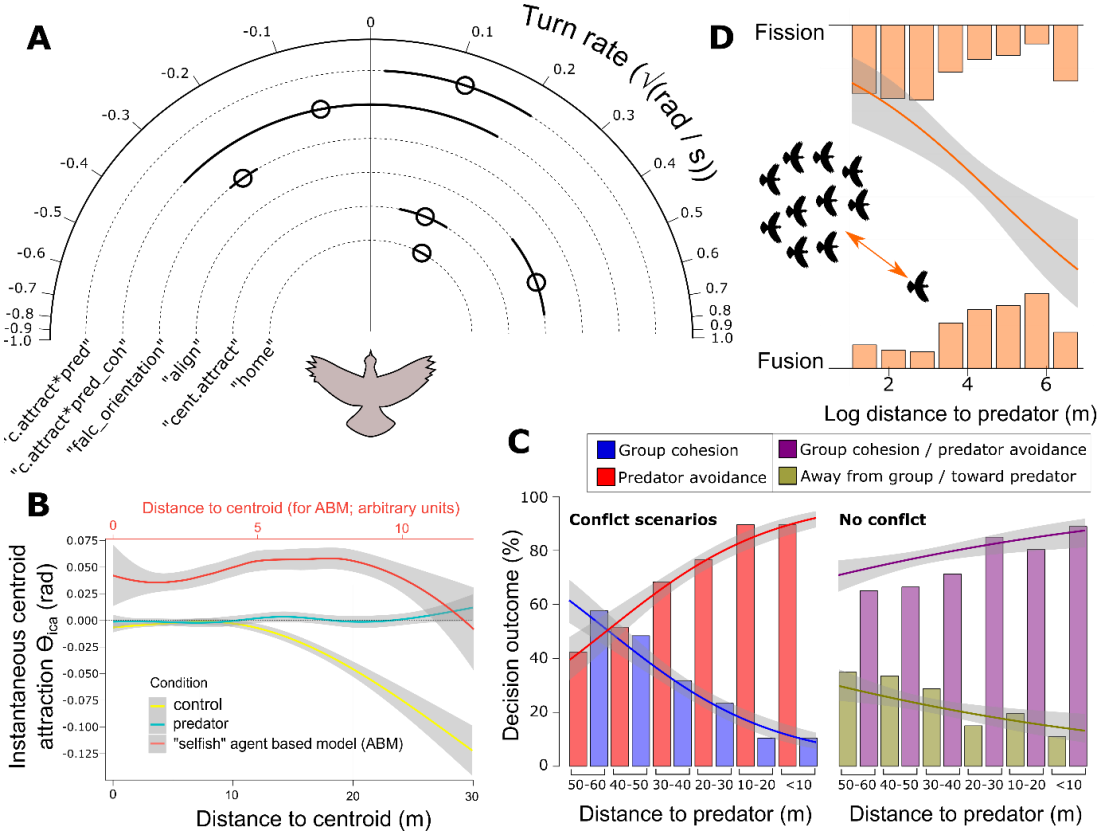

Figure 6. 5. "Cooperative" and "selfish" behaviour in pigeon flocks

Panels **(A-D)** are presented counter-clockwise. **(A)** Mean estimate (black circles) and 95% confidence intervals (bars) illustrate the impact of predictor variables on turning rate of a focal individual √(rad/s) (on square root scaled axis) (see Table S3 for all statistics). The illustrated effect size is the square root of the estimated turn rate when *i*) focal heading and *ii*) predictor variable, have a difference of one radian (~57°; see Fig. 6.4A-E). Predictor variables are given from left to right (bottom left of (**A**)); *i*) an interaction between Θ_{ca} and predator treatment; *ii*) the same interaction using only data from spatially cohesive flocks (see *Methods*); *iii*) the "RobotFalcon's orientation"; *iv*) "alignment" Θ_{ali}; *v*) "centroid attraction" Θ_{ca}; and finally *vi*) "home". The main prediction was that predator treatment groups would demonstrate greater attraction, which was confirmed ("c.attract*pred"), however, this effect fell

away in spatially cohesive flocks ("c.attract*pred_coh"), and so the difference between treatments was due to individuals which split from the group. **(B)** Treatment differences in "instantaneous centroid attraction" (Θ_{ica}) for "control" (yellow); "predator" (green) and modelled (orange/red) groups, with 95% confidence intervals. For all confidence intervals we use R-package "ggplot2" (Wickham and Wickham 2007) (smoothed by the least sum of squared residuals). Behavioural differences in Θ_{ica} between "control" and "predator" conditions are found only at greater distances to centroid (m) (see *Results*). This implies that when in a stable group, there is no extra attraction to the centroid. Results from the agent-based model demonstrate net positive Θ_{ca} is possible at a range of distances to centroid (arbitrary Euclidian units). This shows that "selfish-herd" dynamics *can exist* in cohesive, and moving groups. **(C)** "Conflict scenarios" (left) and "No conflict" (right) (see *Methods: Conflict scenarios/ no conflict* and Fig. 6.1). In "conflict scenarios" pigeons were observed to preferentially choose *predator avoidance* over *group cohesion* (decision outcome on y-axis), but only at RobotFalcon approaches closer than 50 m (x-axis). When there was "no conflict" *group cohesion / predator avoidance* was always preferred. **(D)** The fission/fusion dynamics (splitting from the group, vs re-joining, y-axis) are predictable by a logistic regression model (plotted using with 95% confidence intervals) against the log of "distance to RobotFalcon" (x-axis). Histograms "orange" reflect the relative quantities of observed fission (top) or fusion (bottom) in each bin. Splitting from the group at close predator approaches, and fusion at further distances potentially reflects a large-scale phenomenon produced from mechanisms observed in **C**).

Discussion

We have demonstrated an absence of a "selfish-herd" mechanism (cf. greater "attraction") in pigeon flocks when exposed to ecologically relevant conditions (i.e. our simulated predator attacks), which may favour the collapse of mutualistic benefits in favour of a mechanism enhancing selfish benefit. Therefore, we suggest that the anti-predator benefits of "centroid attraction" may be overshadowed by the *mutualistic* benefits of collective motion with high "alignment". Importantly, our results do not refute the "selfish-herd" hypothesis in organisms which *do not* use coordinated collective motion (e.g. fiddler crabs; Viscido and Wethey 2002), and sheep (King et al. 2012), but suggest that group-level benefits could outweigh selfish benefits in animals which *do*. Our study therefore provides the first tentative evidence for a new hypothesis that "selfish-herd" dynamics could be rare, or even absent, in cluster-flocking birds, or even, species which demonstrate adaptive collective motion patterns more broadly (including shoals of fish).

This first finding, i.e. the absence of "selfish-herd" dynamics in a collective animal system, leads to the question of why fish – which can move collectively and produce complex emergent phenomena – have been shown to behave accordingly with a "selfish-herd" mechanism (Krause and Tegeder 1994; Kimbell and Morrell 2015). Collision avoidance could explain such differences between birds, and fish, as collisions are potentially more costly for air-flying birds (Norberg 2012). However our results showing that *centroid attraction* was not favoured until centroid-to-

pigeon distances over four-times greater than the median distance to centroid, suggests the pigeons at the upper bounds of this distance (10 m) could have moved closer to the centroid without collision, had it been beneficial, as observed in the agent-based model. Alternatively, we suggest that previous findings of selfish-herd dynamics in fish (Krause and Tegeder 1994; Kimbell and Morrell 2015) could be caused by the testing environment of laboratory fish. The impermeable walls of fish tanks, often used in such studies, will intrinsically favour *centroid attraction* over *alignment* – which would be more likely to produce collisions with the tank walls. Therefore, we suggest that the findings (c.f. "selfish-herd"; Krause and Tegeder 1994; Kimbell and Morrell 2015) should be replicated in free-ranging environments, to validate claims of a "selfish-herd" mechanism in shoaling fish. This work is important, given that increased group speed (or, acceleration; Howland 1974) – one of the major mutualistic benefits of alignment behaviour (Ioannou et al. 2012; Sumpter et al. 2018) – is only possible in more wide-ranging, naturalistic spaces. Indeed such a test is important in mammals too, whereby current evidence suggestive of "selfish-herd" dynamics was conducted in relatively enclosed spaces (King et al. 2012). Also see *Supplemental Material* for a discussion on the absence individual differences in "selfish-herd" mechanics.

It has previously been argued that collective motion in animal groups is more subject to invasion by selfish behaviours than other, more genetically related, collective systems (Couzin 2009; Hölldobler and Wilson 2009; Ioannou 2017). This hypothesis does not provide a holistic understanding of when to cooperate/defect,

as the stability of cooperation will also depend on the magnitude of the benefit. Therefore, we argue for a more nuanced hypothesis incorporating the relative benefits of actions. Nevertheless, we did find behaviour consistent with "selfish" motivations. At close approaches from the RobotFalcon, we found that pigeons were more likely to split from the group, if remaining in the group put an individual in immediate danger. However, we argue that this "selfish" behaviour, was not at the expense of "cooperation"; instead, "selfish" behaviour was at the expense of "altruism", and thus does not characterise as "defection" (Axelrod and Hamilton 1981). Therefore, these data line with inclusive fitness theories (Bourke 2014), as was the rarity of splitting at greater RobotFalcon approaches, consistent with "cooperative" benefits over either "altruism" or "spite" (see *Introduction*).

This finding, following our second prediction that individuals will choose *predator avoidance* over *group cohesion* in moments of high perceived threat – for which we provide the ecologically relevant proxy of "distance to RobotFalcon" (Storms et al. 2019) was supported. Yet, the slope of the decision curve was shallower than that predicted. This may be because splitting, in pigeons, is not as costly as we had expected. While there is evidence that group size confers anti-predator benefit in a closely related species (woodpigeons *Columba palumbus*), there is also evidence that high flock density is also associated with greater energetic cost in homing pigeons (Usherwood et al. 2011; Sankey and Portugal 2019). Therefore, our results may be consistent with a trade-off between ultimate (predation) and proximate (energetic) costs, which are favoured towards avoiding ultimate costs (*predator*

avoidance) at closer approaches (Sankey and Portugal 2019; Chapter 4). Proximate costs may also explain why individuals demonstrated reduced *group cohesion* and *predator avoidance* at further distances to the RobotFalcon in moments of "no conflict" between the two decisions. Despite splitting never crossing 50% likelihood in moments of "no conflict", and thus consistent with our third prediction, the proximate component may have favoured movements to reduce flock density at greater RobotFalcon distances. Teasing apart proximate and ultimate costs of flocking will be challenging but necessary for a more holistic understanding of the costs/benefits of such groupings (see Sankey and Portugal 2019).

Given our support for splitting (fission) in "conflict scenarios" at close predator approaches, we predicted that such a mechanism may scale up to larger fission/fusion phenomena. Indeed, we found that larger scale fission and fusion events – at closer and farther distances to the RobotFalcon respectively – were consistent with our data. Re-joining the group once split (fusion), supports the hypothesis that singletons (or smaller groups) are at greater risk of predation (Carere et al. 2009; Zoratto et al. 2010; Handegard et al. 2012; Storms et al. 2019). Peregrine falcon attacks on singleton starlings have been shown to have a much greater (60.9%) success rate than attacks on groups (18.8%) (Zoratto et al. 2010). Additionally, in areas of greater predation threat, groups of starlings were observed to be larger and more compact (Carere et al. 2009). The oddity effect hypothesis stands as a potential mechanism governing this phenomenon, whereby individuals which stand out may be more easily tracked and hence targeted by predators

(Landeau and Terborgh 1986), and is thought to explain enhanced synchronicity of fish in high-risk conditions (Bode et al. 2010). While *any* observed fission seemingly refutes the oddity effect hypothesis (though we have argued, is predominantly only in high-risk conditions); the fusion response at greater distances supports the ecological relevance of oddity.

Our method of measuring attraction and alignment to a topological neighbour structure – although regularly used in the field of collective motion (e.g. Ballerini et al. 2008; Ward et al. 2017) – has come under criticism in recent years (Sumpter et al. 2018), and thus poses a potential limitation to our findings. This is likely due to studies which showed, firstly, using pairs of fish, that alignment can be more effectively explained as an interaction between repulsion and attraction zones, and mediated by changes in acceleration (Herbert-Read et al. 2011; Katz et al. 2011). Secondly, topological neighbour structure has been shown to be less explanatory on movement decisions than a sensory network of neighbours, i.e. only responding to neighbours that the focal individual can sense (Strandburg-Peshkin et al. 2013). We respond to these concerns in order. Firstly, despite fish interactions being governed by "attraction" and "repulsion" alone (Herbert-Read et al. 2011; Katz et al. 2011), the emergent movement patterns often take on high degrees of alignment, and this is subject to natural selection pressures (Sumpter et al. 2018). A recent principal component analysis of a large range of collective motion measurements revealed two key axes: sociability and activity, which were linked to greater levels of attraction and alignment respectively (Sumpter et al. 2018).

Additionally, in contrast to the findings that fish do not “align”, a recent study found distinct “alignment” interactions in fish (Calovi et al. 2018). Perhaps most importantly is that pigeons were found to use social “rules” consistent with “alignment” and “attraction”, validating this approach, at least in our system (Pettit et al. 2013b). Second, while sensory mechanisms present a more intuitive hypothesis, topological rules have been shown to explain the complex movements of starlings (Ballerini et al. 2008). Therefore topological rules present an appropriate heuristic for further questioning in the field of collective flight.

Our study has highlighted a trade-off between cooperative and selfish mechanisms in collective motion (centroid attraction vs. alignment), and thus synthesises this field with evolutionary game theory: a field which uses the Prisoner’s Dilemma game to investigate the interplay between cooperative and selfish actions (Trivers 1971; Axelrod and Hamilton 1981; Ghoul et al. 2014). Highlighting such a link between game theory and collective motion is surprisingly rare (although see: (Sumpter et al. 2008, 2018; Perc and Grigolini 2013; Voelkl et al. 2015)) given that collective behaviours function at the mutualistic (or, group) level (Sumpter 2006, 2010). The stability of collective behaviour is thought to rely on mechanisms which constrain defectors, for example through increased oddity (Krause and Ruxton 2002; Bode et al. 2010; Ioannou et al. 2019) (as discussed), reciprocity in information-sharing (Herbert-Read et al. 2015; Sumpter et al. 2018), or reciprocal exchanges of energetic benefits (Biro et al. 2006; Voelkl et al. 2015). However, the benefits conferred by mutualistic movement decisions could potentially exceed the

benefits of behaving selfishly – as we have discussed in detail in the present work – which would violates the conditions of the Prisoner's Dilemma (Trivers 1971; Axelrod and Hamilton 1981; Ghoul et al. 2014). If this is indeed the case, the evolution of cooperative collective behaviours could proceed without the need for a mechanism to constrain defectors. Altogether, how the constraints induced by oddity and information-sharing fit into a game-theoretical approach, and other fundamental questions such as how collective motion (with mutualistic benefits) evolves from non-coordinated (and selfish) individuals are still not well understood (Sumpter et al. 2018). A formal synthesis of collective motion with game theory, or more broadly, the evolution of cooperation (e.g. mechanisms such as kin selection and reciprocity (Nowak 2006)) could prove timely, and informative.

Supplemental material

Birds and husbandry

Housing and husbandry

Thirty-four homing pigeons were raised from the age of two months in lofts at Royal Holloway University of London (latitude = 51.4154°; longitude = -0.5726°). Birds were provided food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, U.K.), grit (Versele-Laga - Colombine Grit and Redstone, Deinze, Belgium) and

water, *ad libitum* throughout the duration of the study. At the time of the study, ten pigeons were aged between 27-32 months old, and formed the first group; the further 24 birds (all aged 14 months old) were assigned randomly into three groups of 8. Each group was housed separately. In the event of an individual going into a different group's loft, they were relocated back to their own group's loft within 24-hours.

Welfare measurements and ethics

Our data were also collected to inform part of another, ethically driven, tandem project, focussed on providing bird-deterrent solutions to airports, in the hope of reducing bird collisions with aircrafts. However we also took our responsibility to monitor the pigeons' welfare seriously, as we knew a model predator could produce a fear response in our pigeons. Body mass loss was used as a proxy for welfare (Hawkins et al. 2001; Jacquin et al. 2012). There is good evidence to suggest that this was appropriate, given that body mass and corticosterone levels can covary in pigeons (Angelier et al. 2016). We weighed the birds with electronic scales (CoffeeHit: Coffee Gear Digital Bench Scale – 2 kg/0.1 g limit/accuracy) each day after the birds were flown with the RobotFalcon (1/10/18 – 12/10/18 and 17/10/18), and most days after a control flight (except on 13/10/18, 18/10/18 and 22/10/18). Twelve mass measurements were taken per bird– three on days after control flights and nine on days after the predator treatment or mixed (i.e. when

the bird flew twice in a day). On each day of weighing, we checked a pigeon's mass against its first recorded mass, to check for significant reductions which may be indicative of stress (Cuthill 1991). We set this threshold at 90% of this first recorded mass, whereby if an individual was beneath this mass, it would be taken out of the study for a day, and would join if and when the mass returned to above this threshold. We chose this threshold based on our knowledge (from careful monitoring of pigeons masses throughout the year) that both seasonal fluctuations and flight days can reduce mass by even greater amounts that 10% over the space of two weeks (*D. Sankey, Pers. Obs.*). This did not occur throughout the duration of the study for any individual, and pigeons were hence not rested, except on a specific rest day for all individuals on 06/10/2018.

Differences in mass between treatments were analysed using a linear mixed model, with pigeon ID as a random variable, and the previous day's flight distance (sum of GPS distances from the previous day's flights) and predator treatment (i.e. control or in presence of the RobotFalcon) as fixed variables. Our analysis of these data revealed that, despite not crossing our predetermined threshold, there were significant reductions in mass in days following predator treatment (LMM: DF = 334, t = -4.810, p < 0.001). Distance flown the previous day also had a significant impact on mass loss (LMM*:* N = 370, DF = 334, t = -4.858, p < 0.001). This suggests that birds may have been stressed by the RobotFalcon, as mass and corticosterone have been shown to be correlated in pigeons (Angelier et al. 2016). We hope these data

will brought into consideration during ethical discussions regarding future work in this area.

Logger attachment

GPS loggers (QStarz BT-Q1300ST, Düsseldorf, Germany) had their outer casing removed, so that only the circuit board and battery remained. They were then wrapped in generic duct tape (one layer) before having gaps at the top and bottom painted and filled in with liquid electrical tape (Performix, Liquid Tape – Electrical, Minnesota, U.S.A.) for waterproofing. Velcro strips (hoop side) were then attached to the battery side of the logger for deployment. The GPS loggers weighed 12.5 g each after this treatment. Accelerometers (AX3, Axivity Ltd, Newcastle upon Tyne, U.K.; 8 g) did not need modification, except the Velcro strip (hoop side) on one side. For each flight, we attached one GPS logger, and one accelerometer logger, to another Velcro strip (hook side), which was attached to a trimmed 10 cm strip of feathers at the centre each of the pigeons' backs with epoxy glue (Araldite Rapid Adhesive, Araldite, Basel, Switzerland) (Biro et al. 2006; Taylor et al. 2017).

Flight methods

Release site and transit

Each flight in the present study was conducted from a release location in the southern area of Chobham Common (CC), England (latitude = 51.3712^{o}, longitude = -0.5979^{o}) 5066 m in a southerly direction (bearing = -2.91 radians) from the home loft at Royal Holloway University of London. Permissions were granted from the landowners (Surrey Wildlife Trust, England). The exact release location within CC was chosen based on the minimisation of potential obstructions (e.g. trees) and the centrality of the location within the common. Pigeons were transported to the release site by car in wicker boxes: either one box (dimensions = 80cm x 40 cm x 22 cm) for small flocks or two boxes (dimensions = 80cm x 40cm x 55cm) for large flocks (see *Supplemental release Protocol* below for definition of flock size). The total time in transit was 15 mins by car, and then a further five mins travel on foot to the release site.

Training

Each bird was trained from a site just outside Chobham Common (CC) for a total of 10 flights prior to the study (latitude = 51.3625, longitude = -0.5737) between 15/9/18 and 1/10/18. This was to familiarise the birds with the surrounding area; a number of studies suggest that routes are learned before the 10th flight, as route

efficiency improvements stabilise at this point (Biro et al. 2006; Taylor et al. 2017). The last two training flights were recorded with GPS, but given the large differences in topology (training site was at a lower altitude in a heavily wooded area) we do not compare the data from the two sites; only between control and predator treatments during the experimental phase at CC.

Supplemental release protocol

The predator treatment period ran for 11 days, from 02/10/2018, to 13/10/2018 with a rest day on 6/10/2018. Each small flock (total groups *N* = 4) had four predator treatment flights during the predator treatment period, and three control flights: one during the predator treatment period (one group per day selected at random after the first two days using treatment, for pilot training and methodological purposes; see below), and two following the RobotFalcon treatment period on 16/10/2018 and 19/10/2018. Large groups had seven predator flights, and four control flights: two flights towards the end of the predator treatment period (10/10/2018 and 12/10/2018), and two following, on 18/10/2018 and 22/10/2018. Methodological protocol during pilot training (the first two days) was consistent with the methods from all other days, except that the pilot was closer to the release site (~50 m), data from these days were analysed alongside other data.

Data treatment

Site radius

To compare predator and control treatments, we needed to define an appropriate site radius, i.e. the area in which the falcon could come close and potentially cause a proximate response in the pigeons. Firstly we defined our release site coordinates, by taking medians of the first recorded latitude and longitude (after release from the wicker box; see *Methods: Release protocol*) for each flight. Then we measured the distance from the predator to *i*) the release site coordinates and *ii*) the flock's centroid (see *Methods: Grouping GPS data*). This enabled us to investigate the potential impact of the falcon at different distances to the release site (or, different potential site radii), using falcon distance to flock centroid as a temporary proxy for the impact of the falcon (Fig. S6.1). Even at the RobotFalcon's furthest distances from release site coordinates (>400 m), predator-to-centroid distances as low as 46.1 m were still observed. We therefore included all falcon data (site radius = 451.7 m); further, we added an additional 50 m, as the pigeons may have responded beyond these limits (see Fig. 6.5C for evidence of responses up to 50 m). The site radius was, therefore, defined as 501.7 m, rounded down to 500 m, which captured the radius of Chobham Common (see: Fig. S6.1).

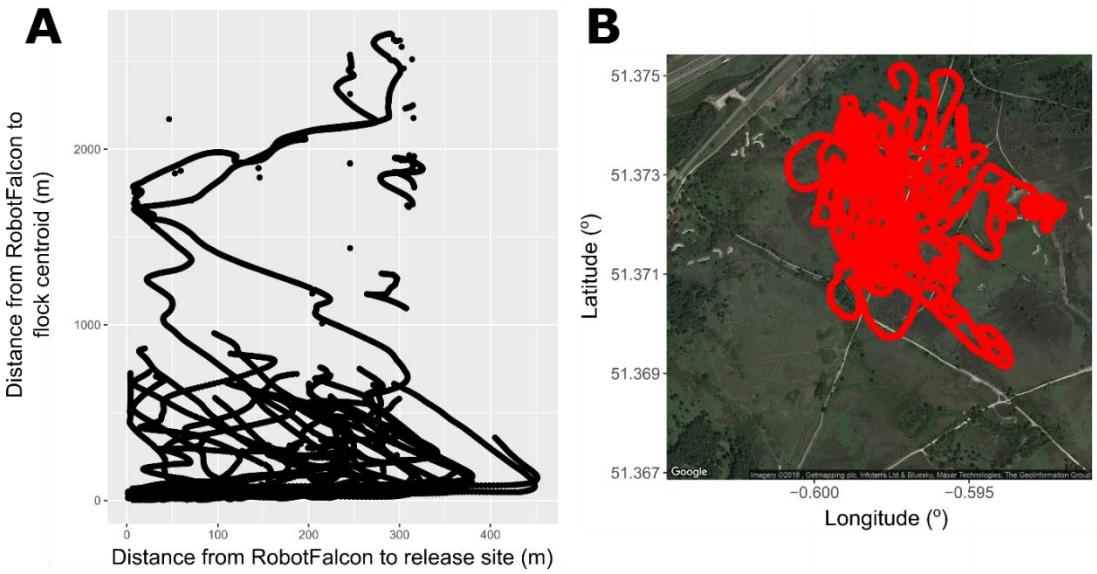

Figure S6. 1. Choosing minimum site radius

(A) Distance from the RobotFalcon to the centroid of the pigeon flock (m) is plotted over distance from the falcon to the release site coordinates (m). **(B)** Predator trajectory from all predation flights (N = 27). Even at larger predator distances to the release site (x-axis in **A**), the predator gets close to the flock centroid (see bottom right of **A**). Given that close encounters were still possible at these distances (as close as 46.1 m), we chose the site radius to be at least the maximum predator distance from the site (451.7 m) with an additional 50 m for to capture pigeon responses beyond this distance (rounded to 500 m).

Cleaning and grouping GPS trajectories per flight

GPS data (latitude, longitude, and time, all sampled at 5 Hz) with missing timestamps were labelled as NA (not applicable), while duplicated timestamps were removed. Erroneous coordinates, i.e. coordinates so far from the previous location

that the bird would have had to travel over 100 m/s to reach the location, were labelled NA also. Data were grouped per flight at the point that the last individual in the group reached a speed of over 10 m/s, for a duration of over 10 seconds, i.e. to signify the birds were in flight. Speed, here, was smoothed over ± 1 second, which is equal to 11 data points at 5 Hz. There was no flight where the last individual did not reach 10 m/s within two seconds of the first individual, and this matched observations: whereby the whole group would take flight concurrently (*D. Sankey Pers. Obs.*). The grouping algorithm, used to determine flock participation is described in the main text (and Fig. S6.2).

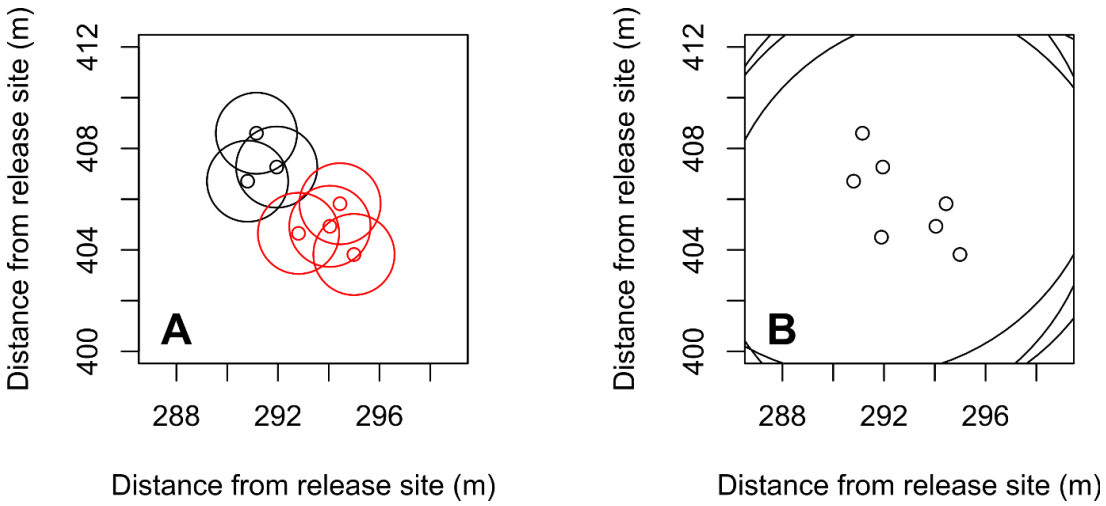

Figure S6. 2. Grouping algorithm

Individuals (points) were considered part of the "main flock", if they were connected to the largest group of connected birds with a minimum of 10 metres distance (circles) to at least one neighbour. **(A)** Uses a radius of 1.5 metres to demonstrate how an individual (see individual closest to the bottom right of the panel) could be connected to the largest group (red) by only one neighbour in its radius. **(B)** Shows the algorithm employed, with 10 metre radii.

Subgrouping

Proportion of total time separated from the main group after fission was generally rare compared with the data for cohesive movement with the main flock (11.2% of observations were outside of the main flock). In this 11.2%, most of the observations outside of the group were of singleton flight (76% in small flocks and 79% in large flocks; Fig. S6.3). Therefore, the comparatively rare occurrences of larger subgroups does not greatly conflict with our implicit assumptions of the risks of splitting from the group in our hypotheses (Fig. 6.1 and *Introduction*). Nevertheless a more detailed approach, involving analysis of responses given the subgroup size is worthy of further investigation in future work.

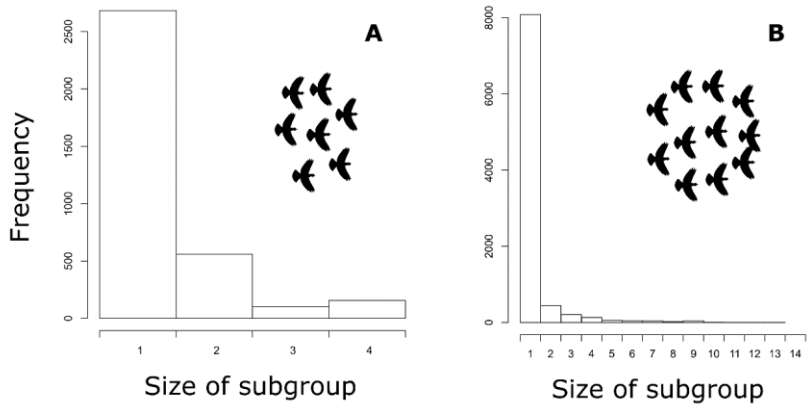

Figure S6. 3. Subgrouping

Frequency (y-axis) is plotted against the size of the subgroup for **(A)** Small flocks (*N* = 8-10 individuals) and **(B)** Large flocks (*N* = 27-34 individuals). Small flocks could have maximum subgroup size of four, and large groups as much as 16, as any larger sub-flock size would constitute half of the group, and therefore be considered the main group instead (see *Methods: Grouping GPS data*).

Choosing fission distance

We chose 10 m as a parameter, whereby if individuals were not connected to the main group by a neighbour *at most* this distance apart, they were considered as split from the group (see *Methods*). Ten metres was chosen for several reasons. Firstly, nearest neighbour distances of over 10 m were rare (between the 94th and 95th percentile of nearest neighbour distances: 9.73 m and 13.01 m). Second, given pigeon wingspans are roughly 62cm (Tobalske and Dial 1996), ten metres is more than ten times the birds' wingspans, which would suggest the birds could fly much closer to their closest neighbour in the largest sub-flock if it was intended (or indeed, was possible). Finally, we also used visual observations of flock fission under a range of "fission distances" (5 m, 7.5 m, 10 m and 12.5 m, see Fig. S6.4 below). Ten metres was chosen as it appeared to remove most of the erroneous splitting, while also not gathering too much data on birds which were in the process of leaving or joining a group (see Fig. S6.4 legend for further details).

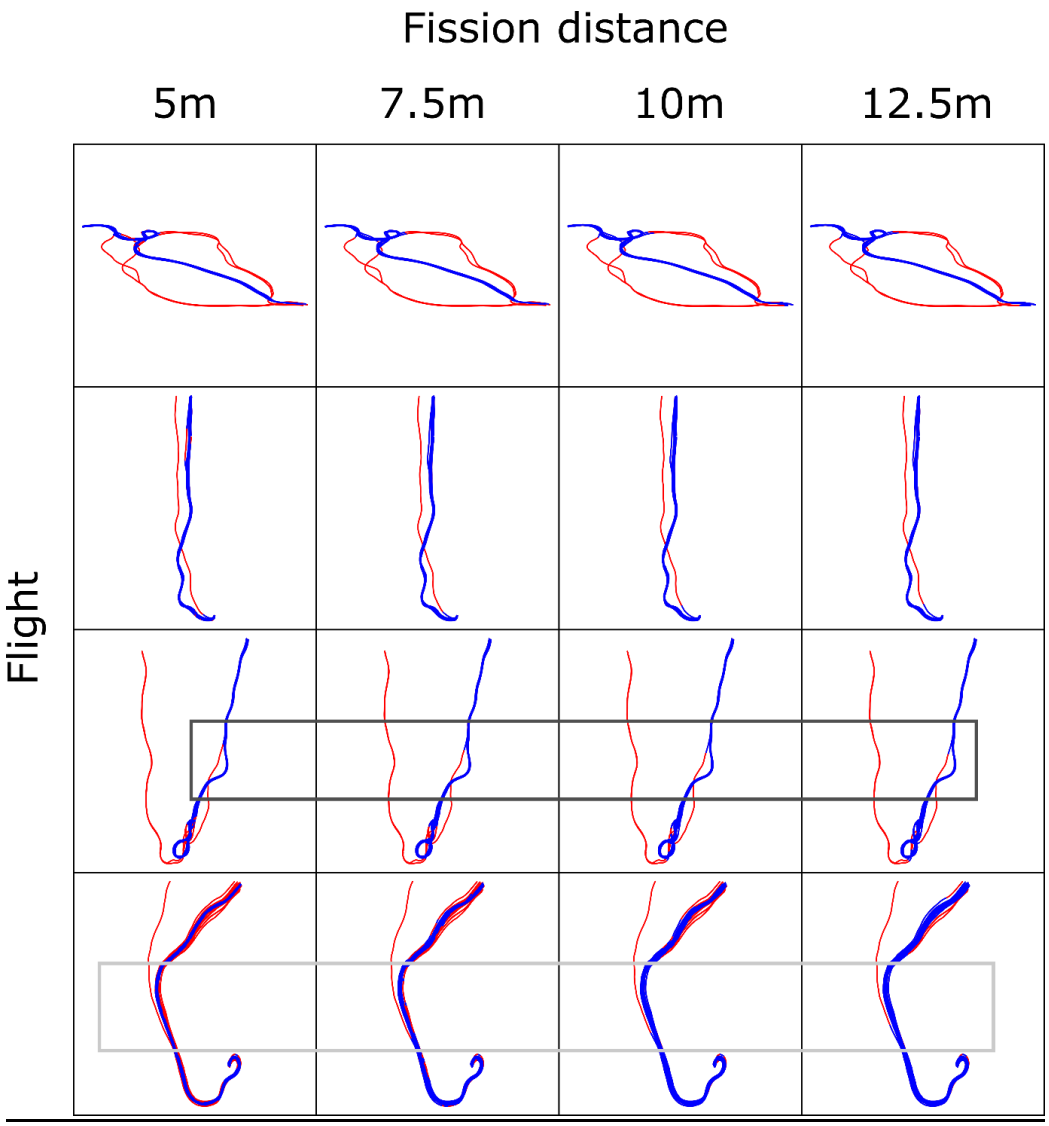

Figure S6. 4. Choosing fission distance

Four different grouped pigeon GPS flight trajectories (rows) are plotted against the "fission distance" used in the grouping algorithm. Split individuals/trajectories are in red, while cohesive individuals/trajectories are in blue. Ten metres was chosen as the final "fission distance" as it 1) removed data where pigeons appear to be cohesive but look as if they remained in the group. See for example, the light grey box in the bottom row. Here, only 10 m and 12.5 m fission distances seem to

include all “visually cohesive” individuals. 2) We aimed to minimise the amount of data from individuals either leaving or joining a group (because the trajectory may not be representative of the group’s centroid and/or heading). See for example, the dark grey box, where an individual is joining the group. Each successive fission distance records less data from the joining individual. Altogether, as 10 m seems to avoid erroneous splitting, and includes less data from joining/splitting individuals than 12.5 m, it was chosen as the fission distance moving forward with our analyses.

Instantaneous turning angle

We used the instantaneous turning angle Θ_t as our response variable – which ranges from sharp anticlockwise turns to sharp clockwise turns. This was given by the difference between the orientation of the bird at t_{-1} (0.2 seconds prior to measurement) and orientation at t_0 (Fig. S6.5). Orientation is the polar heading of an individual with respect to GPS coordinates in the next time step (Pettit et al. 2013b).

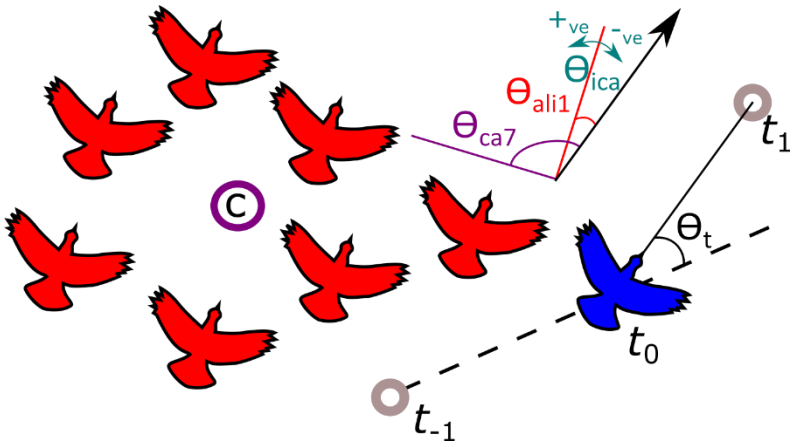

Figure S6. 5. Polar variables schematic

The focal bird (blue) is turning at angle (Θ_t) at time t_0, with respect to its previous orientation at t_{-1}, to reach the coordinates at t_1. Alignment parameter ($\Theta_{ali\text{-}n}$) and centroid attraction angle ($\Theta_{ca\text{-}n}$), here, n = 1 and 7 respectively, are provided. These variables are used to examine the predictive power of social neighbours (red birds) position/orientation on the focal individual's turning angle Θ_t in the next time-step. Alignment to the nearest neighbour (1NN) and attraction towards the centroid of seven nearest neighbours (7NN; circled letter C) had the greatest effect on subsequent movement choices in small groups (see Fig. S6.6 and *Supplemental Material*), and are pictured here. "Instantaneous centroid attraction" (turquoise; Θ_{ica}) is positive for movements biased to the centroid with respect to ($\Theta_{ali\text{-}n}$), here pictured as a two headed arrow demonstrating positive and negative values ($+_{ve}$/$-_{ve}$). It cannot be seen from this schematic whether the focal bird's turn (Θ_t) has positive or negative Θ_{ica} in this schematic, because the calculation is with respect to the centroid in the previous time-step (not pictured).

Topological range of interaction

To estimate how many neighbours our pigeons responded to, we found (for each successive neighbour iteratively (see Ballerini et al. 2008), *i*) the average orientation (*alignment*), and *ii*) flock centroid (*centroid attraction*). Here, each iteration adds another neighbour – in rank distance order – to the calculation. The relative difference between an individual's orientation and the orientation denoted by centroid attraction/alignment (Θ_{ali} and Θ_{ca}) from the *previous time step* (giving individuals an opportunity to respond) was recorded for each time step (5 Hz) across all flights within the earlier denoted site radius. To gauge which topological range had the greatest impact (effect size) on alignment and centroid attraction movements, we ran linear models between Θ_t and alignment/centroid attraction (for topological range: N = 1-7, or N = 1-33 for small and large flocks respectively) (Fig. S6.6). This was performed separately for the predator treatment condition (N = 27 flights), and the control condition (N = 16 flights), and for large flocks (N = 11 flights) and small flocks (N = 32 flights). The optimum number of neighbours (N) (alignment = 1 and 5; centroid attraction = 7 and 31, for small flocks and large flocks respectively) was given as the largest effect size after an equally weighted mean of predator and control conditions (i.e. mean not biased by the unequal lengths in the initial calculation) was taken (Fig. S6.6). In cases where group size was less than the chosen topological range, we took the value for the closest number of neighbours possible (which was the highest). This approach is justified in that it was only necessary for Θ_{ca}, where the slope for *t*-value for increasing topological structure is

mostly continuous and positive (Fig. S6.6). Thus, implying that the closest number of neighbours (to 7 or 31 neighbours; for small or large flocks) will reflect the strongest impact of Θ_{ca} on Θ_t.

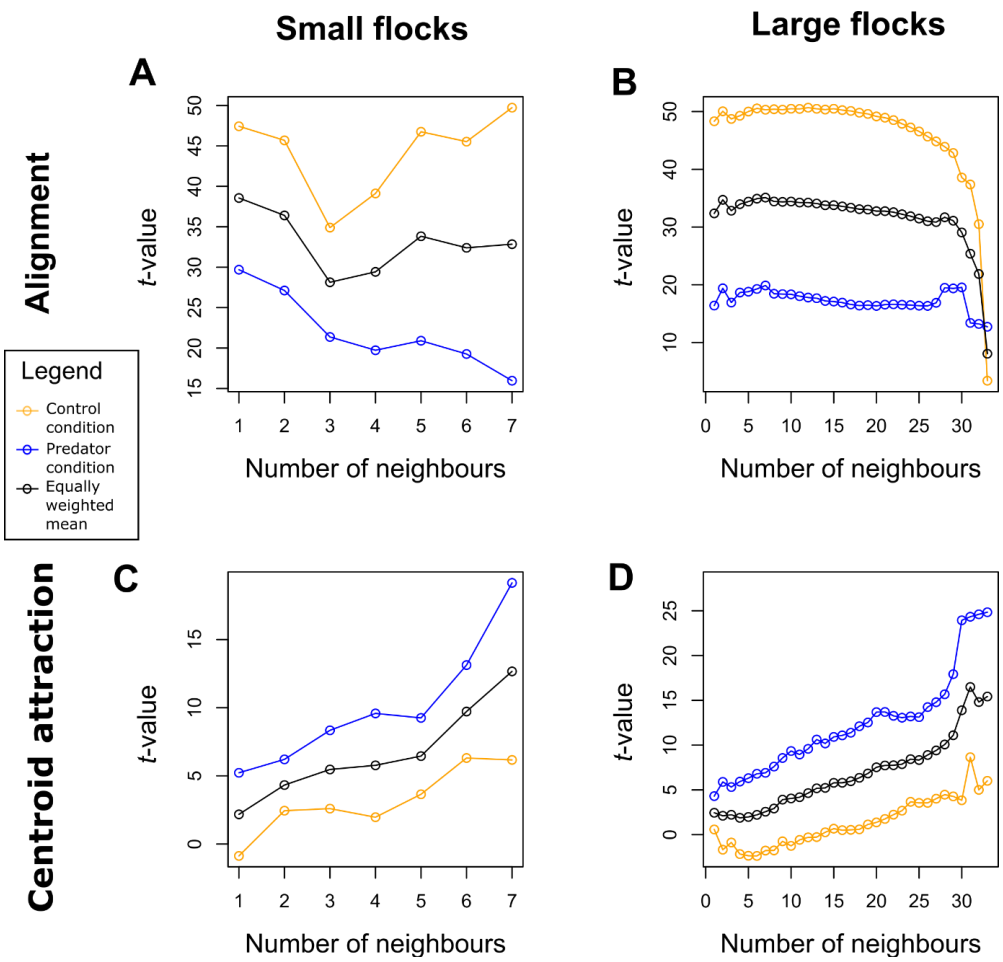

Figure S6. 6. The effects of topological range

Effect size (*t*-value) from linear models of Θ_t against alignment (top row) and centroid attraction (bottom row) against turning angles (or, movement decision). Effects are given for predator condition (blue), control condition (orange) and an equally weighted mean of both scores (black). The chosen topological range (where *t*-value is maximised) for latter statistical models was taken from the equally weighted mean (for consistency across treatment). This resulted in optimal topological structures as follows: for alignment, one for small flocks **(A)** and five for large flocks **(B)**; for centroid attraction, seven for small flocks **(C)** and 33 for large flocks **(D)**. This chosen range reflects the number of neighbours (used in the calculation) which had the strongest positive influence on centroid attraction and alignment decisions.

RobotFalcon position and orientation

We further investigated an interesting and unexpected result, that, while turning *away from* the RobotFalcon's orientation was supported, pigeons were additionally found to turn *toward* the RobotFalcon's position. With respect to the focal individual's heading, the position of the RobotFalcon had a positive impact on turning angle (LMM; DF = 5089, t = 15.471, $p < 0.001$), and the orientation of the falcon had a negative impact (LMM; DF = 5089, t = -14.077, $p < 0.001$). Therefore, there was more confidence (greater absolute t-value) in the finding that pigeons turned toward the RobotFalcon's position than away from the orientation; yet the estimated effect size was lower, 0.035 (rad/s) vs. -0.055 (rad/s) for position and orientation respectively.

While making movements to avoid aligning with a predator makes sense, it seems counter-intuitive that birds would turn *towards* the threat. However, the RobotFalcon was more often behind the birds (with respect to bird heading) as is clearly seen below in Fig. S6.7 (with RobotFalcon orientation occupying a broader range of angles). Here, movements towards the direction of the RobotFalcon's position may not result in collision, especially when there were many other variables that positively predicted turning angles (i.e. "home", "alignment", "centroid attraction"). This finding it is outside of the realm of the present paper's major thesis, but nevertheless is likely to have implications for the escape strategies of birds, and is worthy of further investigation.

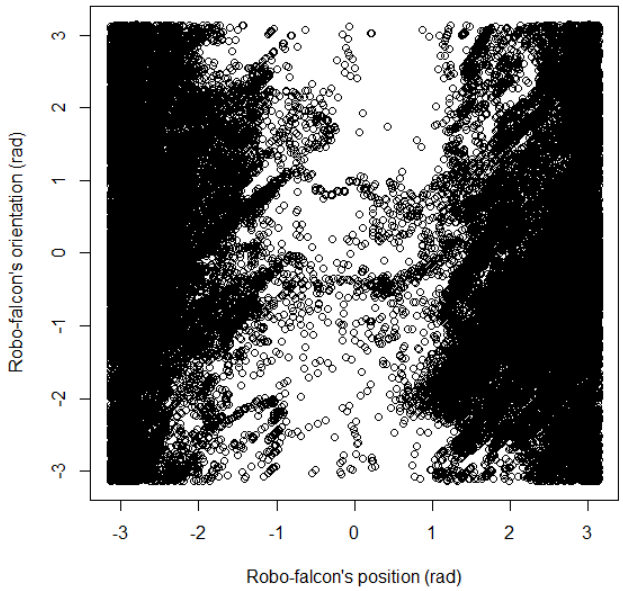

Figure S6. 7. RobotFalcon's orientation and position

All data (points) for "RobotFalcon's orientation" (rad) over "RobotFalcon's position" (rad) with respect to the focal individual's heading. The RobotFalcon's position was often behind the focal individuals (most data points are close to –pi and pi radians), whereas the RobotFalcon's orientation occupied a broader spread (data are spread between –pi and pi radians).

Statistics

Autocorrelation

We calculated temporal autocorrelation using "acf()" function in base R (R Core Team. 2017) for each of the following continuous variables: 1) turning angle, and hence also "instantaneous centroid attraction", which is essentially turning angle

with respect to neighbour orientation, 2) speed, 3) speed variance, 4) centripetal acceleration, 5) distance to the centroid, and 6) nearest neighbour distance for each unique trajectory (for each bird/flight). For each autocorrelation curve (i.e. one per unique trajectory), the point at which the curve passed below the 95% confidence interval was noted, and all such points collated. These data are displayed as histograms in Fig. S6.8. Median values were used instead of mean values when distributions were non-normal, due to greater accuracy at estimating central tendency in skewed distributions (Hubert and Van der Veeken 2008), as was the case in the first four of our autocorrelation estimation distributions but not in the last two (Shapiro-Wilks test; turning angle: $W = 0.808$, $p < 0.001$; speed: $W = 0.924$, $p < 0.001$; speed variance: $W = 0.180$, $p < 0.001$; centripetal acceleration: $W = 0.753$, $p < 0.001$; distance to centroid: $W = 0.940$, $p = 0.063$, nearest neighbour distance: $W = 0.955$, $p = 0.172$). Median/mean temporal autocorrelation estimates were 1.8 s, 4.8 s, 0.2 s, 1.2 s, 5.4 s and 5.2 s, for each dependent variable respectively (rounded to the nearest 0.2 s), and were used to subsample data (every *n* seconds) in the respective statistical models describing these variables.

Temporal autocorrelation in turning angle Θ_t for "conflict scenarios" (see *Methods: Conflict scenarios/ no conflict*) was treated differently to other larger models described above. As this variable is already staggered in time (subset according to conflict criteria). Here, all data were treated together for autocorrelation (not per flight and in variables described above). All together this gave an estimate of 1.8 seconds autocorrelation for both "conflict scenarios" and "no conflict".

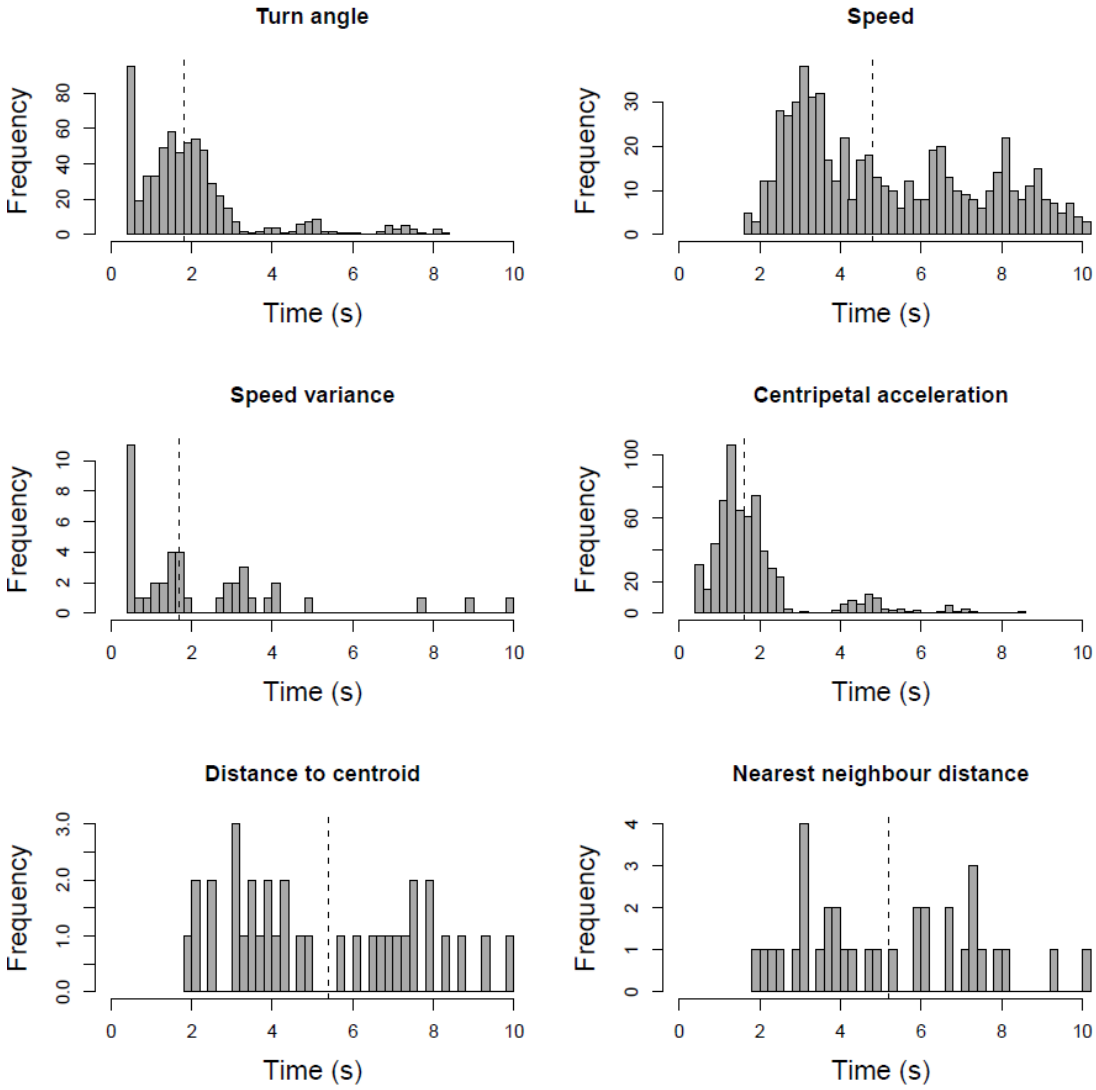

Figure S6. 8. Autocorrelation estimates

Histograms for temporal autocorrelation estimates for each unique trajectory, and median value (segmented vertical line), for dependent variables: **(A)** turn angle (rad), **(B)** speed (m/s), **(C)** speed variance (no units), **(D)** centripetal acceleration (m/s^2), **(E)** distance to centroid (m), and **(F)** nearest neighbour distance (m).

Transformations

Turning angle data Θ_t were first trimmed by removing turn rates of over 0.3 radians per second (both anticlockwise and clockwise), which were over the 99% quantile range (1% = -0.22 rad/s; 99% 0.294 rad/s), and likely reflects slight errors in the GPS coordinates (Brighton et al. 2017). We further trimmed turning angle to remove movement in a straight consistent heading (turning angle less than 0.02 rad/s). This was necessary to satisfy the assumptions of the model (Fig. S6.9), but removed 29.9% of the data representing flight in a relatively straight line. Our models, therefore, predict turning decisions of the pigeons, but cannot be interpreted to predict decisions to fly straight ahead. A model was run on all of the data, i.e. with straight line flight too, and the major statistics reported in the main text did not change in their direction or significance (Table S4), however, this model did not satisfy the assumption of normally distributed residuals. The removed 29.9% were at greater distances from the site coordinates (median distance was 258 m compared with 169 m from time steps in turning flight) and greater distances from the predator (107 m compared with 68 m), and therefore possibly less important to our conclusions.

Speed was trimmed at less than 5 m/s. This is in-between walking speed (1 m/s) (Fujita 2002) and slow flying speeds (9 m/s) (Rothe et al. 1987a). We also trimmed speed at values and greater than 36 m/s (above the 99% quantile at 35.5 m/s). Again we trimmed the top 1% to reduce error from GPS inaccuracies. Speed

variance was transformed to the power of -0.18, following a Box-Cox transformation procedure (Sakia 1992). Centripetal acceleration was also transformed using Box-Cox methods, to the power of 0.18, after being trimmed for values over 13 m/s (99% quantile) and lower than 0.01. This lower boundary was to remove straight line flight, where centripetal acceleration is negligible (the range of turning angles for the removed rows here was -0.0006, 0.0006 rad/s). Distance to centroid data best fit the model assumptions when transformed by the natural logarithm, and finally, nearest neighbour distance was best treated by transforming (to the power of 0.25) and then applying the natural logarithm.

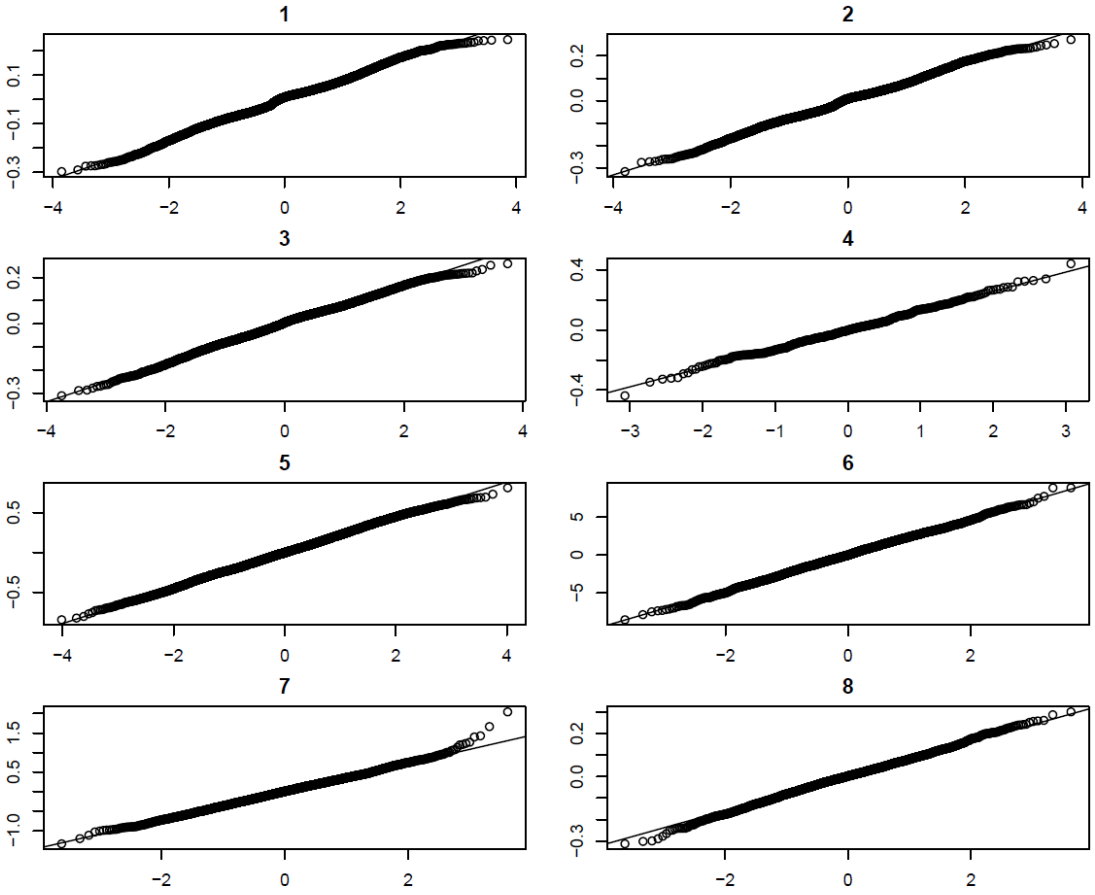

Figure S6. 9. Quantile-quantile plots

1) Turn angle, 2) turn angle for pigeons in cohesive flocks, 3) turn angle including predator variables, 4) speed variance, 5) centripetal acceleration, 6) speed, 7) distance to centroid, 8) nearest neighbour distance.

Flock cohesion

Methods and statistics

Nearest neighbour distance and distance to the centroid (see *Methods: Grouping GPS data*) were recorded at each time step (5 Hz). Fixed variables describing the variance in these "Flock cohesion" variables were: interaction between predator treatment and flock size (*n* individuals remaining in the largest group; see *Methods: Grouping GPS data*); absolute value of cross-wind component, and support wind component (not transformed) and also distance to the release site coordinates logged value. This last variable was used to understand the impact of distance from the transport/release box (where all individuals were together) on group cohesion. Random variables were, again (as in *Methods*), pigeon ID and unique flight identifier.

"Proportion separated", here defined as the proportion of time split from the group was recorded for each unique individual/flight trajectory (within the site radius; see above *Site radius*). "Proportion separated" was used as a dependent variable in a linear mixed effects model with condition and flock size as fixed effects, and pigeon ID as random intercepts.

Results and discussion

Some measures of flock cohesion decreased in predator treatment groups while others did not. Time spent split apart from the main group ("proportion separated"), for example, increased from a mean of 13.1% of the flight to 20.6% (LMM: DF = 592, t = 3.171, p = 0.002; Fig. S6.10). Predator condition, however, had less of an impact on "proportion separated" than flock size, with pigeons splitting from the main group 24.4% of the flight in large flocks as opposed to 9.2% in small flocks (LMM: DF = 592, t = -6.595, p < 0.001; Fig. S6.10A). Distance to centroid (in cohesive flocks) was not significantly different across treatments (LMM: DF = 571, t = 1.496, p = 0.135; Fig. S6.10B), however, nearest neighbour distances in cohesive flock data were impacted by treatment (LMM: DF = 575, t = 2.518, p = 0.012; Fig. S6.10C). "Instantaneous flock size", specifically, the number of individuals which made up the main group (see *Methods: Grouping GPS data*) was a stronger predictor of both these cohesion variables (distance to centroid – LMM: DF = 2744, t =-5.583, p < 0.001; nearest neighbour distance – LMM: DF = 2853, t = -4.514, p < 0.001; Fig. S6.10B, C). This measure of flock size, as an interaction term with predator condition, demonstrated a relationship suggesting that – when exposed to the predator treatment – flock cohesion was minimised in smaller flocks and increased in larger flocks, albeit not significantly for distance to centroid measures and thus only suggestive (distance to centroid – LMM: DF = 2744, t = -1.826, p = 0.068; nearest neighbour distance – LMM: DF = 2853, t = -3.261, p < 0.01; Fig. S6.10). There are problems, however, with the interpretation of two-dimensional

nearest neighbour distances, especially in larger flocks where more of the group spread will be in the third dimension. We could not use the third-dimension data for GPS data due to inconsistencies which were hard to predict. Kaplan and Hegarty (2005) state that the precision of height (third dimension) measurements, is considerably lower than for horizontal positions. It is suggested that this is because there are no satellites below the loggers, and that this geometry of the satellites causes a reduction in precision.

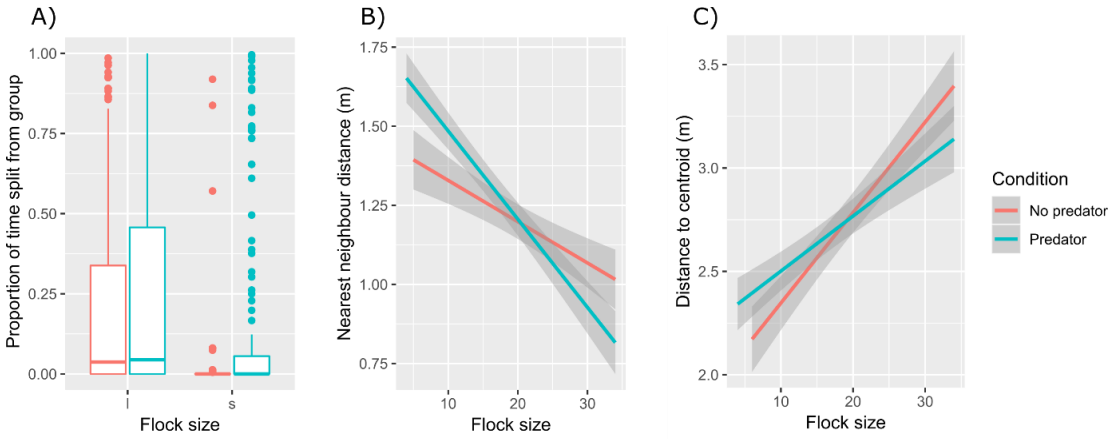

Figure S6. 10. Flock cohesion variables

The impact of predator condition ("no predator", or "predator"; red/blue; see legend) and flock size on flock cohesion variables. **(A)** "Proportion separated", proportion of time split from the group (relative to total flight length; see *Methods: Grouping GPS data*); **(B)** nearest neighbour distance (m), and **(C)** distance to the group centroid (m). Large or small flock sizes refer to either *i*) experimental treatment (**A**; *N* = 27-34, or *N* = 8-10 individuals respectively) or *ii*) number of individuals connected to the main group (**B-C**; see *Methods: Grouping GPS data*).

Aerodynamic variables

Methods

Speed (*s*) was calculated for each individual at each time-step within the earlier defined site-radius (Fig. S6.1), using the metric distance between each successive GPS point (m). Speed was then further divided by the rate of recordings per second (5 Hz), to give speed in m/s. The group's total speed variance was also recorded at each time step, for each flight in the study. Centripetal acceleration was calculated at each time step (5 Hz), for each bird, and for each flight (after the removal of data outside the site radius); a_c=*s*^2/r, where *s* = speed, and r = turning radius, and *r* = *s* / Θ_t (following methods in Wilson et al. 2013). Wind speed was recorded before each flight using a hand held anemometer (Windmaster2, Kaindl Electronics, Rohrbach, Germany). Wind direction was estimated with an approximate accuracy of ± 45 degrees. The wind vector (product of speed and direction) was combined with the pigeon's orientation (heading between GPS locations) to estimate the impact of cross winds and support wind on the pigeons' speed and turning angles (see methods in Safi et al. 2013). For some statistical models (specifically aerodynamic variables – see below; not turning angles), the cross-wind component was transformed to absolute values, where wind strength, but not directionality (i.e. left or right), was of potential importance (Safi et al. 2013).

Statistics

For each of our flight aerodynamic variables (centripetal acceleration, speed and speed-variance), we used linear mixed models with added autocorrelation structure (see above: *Autocorrelation*) to investigate the impact of the predator treatment. To test whether any differences in speed variance held across different flock sizes, flock size was included a fixed effect in an interaction with predator treatment, to establish *i*) whether the falcon treatment had different impact on flocks of different size, and *ii*) to establish whether speed variance differs between flock sizes more generally. Other fixed variables were absolute values of cross-wind component and support-wind component. Speed variance was square rooted to fit the assumptions of the model. Centripetal acceleration and speed were treated in the same way, except that being an individual- and not group-level measure, pigeon ID could was added as a random intercept.

Results and discussion

We found results suggestive of speed (*s*) decreases in the predator treatment, with mean speed in control groups at 18.74 m/s and in predator groups at 17.59 m/, though this relationship was not statistically significant (Fig. S6.11; LMM: DF = 542, t = -1.907, p = 0.057). Any effect present here was likely driven by the small flock flights (N = 8-10 individuals), as there was a significant interaction term between

condition and flock size (LMM: DF = 542, t = -3.603, p < 0.001; Fig. S6.11). Although speed decreased, it was not at the expense of centripetal acceleration (a_c), which was not different across condition (median = 0.95 m/s^2 vs 0.64 m/s^2 for control flocks; LMM: DF = 591, t = 0.755, p = 0.450). Again, there was a greater relationship in small flocks, suggested by a significant interaction between condition and flock size on centripetal acceleration (LMM: DF = 591, t = 7.812, p < 0.001; Fig. S6.11). This implies that speed decreases may have been necessary to increase centripetal acceleration, and that only small flocks exhibited this behaviour. Speed variance (coefficient of variation - CV) increased significantly in the predator condition, from a median of 0.03 to 0.06 (LMM with negative transformation term: DF = 40, t = -3.873, p < 0.001; Fig. S6.11).

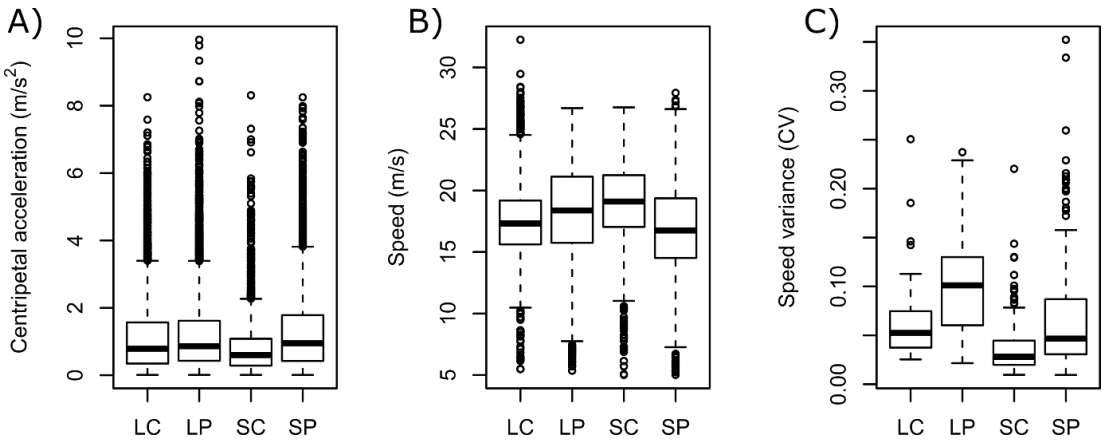

Figure S6. 11. Aerodynamic variables

The impact of flock size ("L" or "S"; large or small) and predator treatment ("P" or "C"; predator or control) on aerodynamic variables: **(A)** Centripetal acceleration (m/s^2); **(B)** speed (m/s), and **(C)** speed variance: coefficient of variation (CV); no units.

Fission/fusion events – Exclusion parameter sensitivity

We tested the sensitivity of the exclusion parameter, i.e. the threshold for fission/fusion events to be ignored, when occurring within *N* seconds of the last event. Having used two seconds in the main analysis (see *Methods* and *Results*), we then tested the effect of one and three seconds on the resulting statistics (Table S1; below). We found no differences in the direction or the significance of the statistics under any condition (Table S1).

Table S6. 1. Exclusion parameter sensitivity

Fission/fusion events which occur within *N* seconds of the last are excluded from the data (cf. "exclusion parameter" see *Methods: Fission/fusion*). The sensitivity of this parameter is described in the top row. The second row describes the type of statistic (i.e. degrees of freedom "DF", *t*-value or *p*-value). Further rows describe the effect on fission/fusion of the following predictor variables: "dist2pred" (log of the distance to the RobotFalcon); "flock-size" refers to either small or large flocks (see *Methods*); "interaction_fs_d2p" is an interaction term between the "flock-size" and "dist2pred"; Statistics for the chosen parameter are shaded grey.

Exclusion parameter sensitivity ->		One second			Two seconds			Three seconds		
Statistic ->		DF	*t*	*p*	DF	*t*	*p*	DF	*t*	*p*
Variable	dist2pred	278	-3.950	<0.001	168	-4.147	<0.001	120	-4.793	<0.001
	flock-size	276	1.370	0.172	166	1.303	0.194	118	0.129	0.897
	interaction_fs_d2p	276	-1.410	0.160	166	-1.301	0.195	118	-0.110	0.913

Agent-based model and instantaneous centroid attraction

Methods and results

It was, considered that net-positive "instantaneous centroid attraction" Θ_{ica} across a group might be an impossible outcome for cohesive flocks of animals (or indeed, agents). The reasoning here is that if all individuals in a group had positive scores for Θ_{ica}, then perhaps the group would collapse in on itself, and hence slow down to minimal speeds, and cease to fit the definition of a *moving* group. We employed an

agent-based model, mimicking Couzin et al.'s (2002) flocking model, with parameters set in the range tested in the original model (see Table S2). Each iteration of the model (*n* = 1000) ran for 1000 time-steps, but we removed the first 500-time steps to reduce any bias of initial conditions. We recorded data on distance to locally perceived centroid and Θ_{ica}, with locally perceived centroid defined as the central location of *all individuals* within a focal individual's zones of attraction, orientation and repulsion combined, and alignment defined as the turn angle necessary to align with all individuals in the zone of alignment. Alignment, as defined above, is the angle against which Θ_{ica} is based. All results were combined and plotted by the lowest sum of squared differences between the data (using package "ggplot2" in R with function, method = "loess"; Wickham and Wickham 2007; Fig. 6.5B).

Discussion

The agent-based simulation (following: Couzin et al. 2002) showed that "instantaneous centroid attraction" Θ_{ica} (attraction to perceived centroid, relative to alignment parameter Θ_{ali}) could, in fact, exist in collective systems. Why such "attracted" groups do not result in collapse could be because agents (like birds) are limited in their maximum turn angle per unit time (Couzin et al. 2002; Pettit et al. 2013b), and therefore it was possible for all individuals in the group to make more movements towards a locally perceived centroid than away from it, while

remaining mobile. Additionally the simulation data, combined with the pigeon data, refute “collision avoidance” as an alternative interpretation of the results (Yang and Schmickl 2019). Firstly net positive Θ_{ica} was found in modelled data, despite “repulsion” (collision avoidance) responses *always* outcompeting “attraction” or “alignment” responses in the agents’ movement decisions (methods from Couzin et al. 2002); second, from the empirical data, net-positive Θ_{ica} should be observable at least when the distance to centroid is greater than the median distance to centroid (the median was 2.34 m in cohesive flocks and 5.33 m across entire dataset, which was not found (Fig. 6.5B). James et al. (2004) have criticised studies that have looked for net-positive Θ_{ica}, because domains of danger (the angle of an animal’s body exposed to the outside, which is vulnerable to attack) cannot decrease “on average” when considering all individuals in a group (James et al. 2004). Instead, it is suggested that average Θ_{ica} would be zero, but, individuals could attempt to outcompete one another with differential success (i.e. some have positive Θ_{ica} and some have negative) (James et al. 2004). This valid criticism is answered by our finding that the Θ_{ica} model had a lower AIC value when pigeon ID (as a random intercept) was taken out, suggesting that Θ_{ica} was similar across all individuals. Together we have strong evidence that “selfish-herd” dynamics, while *possible* as a component of collective motion, were *not present* in our data at the group or individual level.

Additional tables

Table S6. 2. Agent-based model parameters

Following methods from Couzin et al. (2002) we constructed an agent-based model with the following parameters (present study values), which were all within the boundaries specified in the original paper (Couzin et. al. 2002 values).

Parameter (units)	**Couzin et. al. (2002) values**	**Present study values**
Number of individuals (none)	10-100	10
Zone of repulsion (units)	1	1
Zone of orientation (units)	0-15	7.5
Zone of attraction (units)	0-15	7.5
Field of perception (degrees)	200-360	300
Turning rate (degrees per second)	10-100	55
Speed (units per second)	1-5	3
Error (radians)	0-0.2	0.1
Time step increment (seconds)	0.1	0.1

Table S6. 3. Model output from linear mixed models

Using package "nlme" (Pinheiro et al. 2012) in R. Dependent variable, and brief description of data treatment is listed in the furthest left column. Turning angles, here, are turn rate per time step, not per second as is reported in the main text. The next column "X" describes independent variables: "conditionp" is predator treatment; "c.attract" is centroid attraction; "align" is alignment; "dist2cent" is distance to centroid; "cross.wind" and "support.wind" are cross- and support- wind components respectively; "turn2home" is the angle from current orientation to home; "turn2falchead" and "turn2falcpos" are angles between current orientation and falcon's orientation and position respectively; "small.bigs" is small flocks; "flock.size" is the number of individuals in the largest cohesive part of the flock; "dist2site" is distance to the release site coordinates. Colons ":" represent interactions between independent variables. Other columns provide slope estimate, standard error, degrees of freedom, *t*-value and *p*-value (two-tailed) respectively (see Pinheiro et al. 2012). Values appear different from those in Fig. 6.5A, as values reported here have been transformed differently (see above), and reflect values recorded at 5 Hz whereas values in Fig. 6.5A are values per second (and are square rooted).

Dependent variable - data treatment	X	Slope	Std.Error	DF	t-value	p-value
Turn angle - omitted < 0.02 rad	(Intercept)	0.025	0.002	7774	12.828	0.000
	conditionp	-0.008	0.002	593	-3.328	0.001
	c.attract	0.004	0.001	7774	4.016	0.000
	align	0.060	0.010	7774	6.038	0.000
	cross.wind	0.000	0.000	7774	0.361	0.718
	turn2home	0.007	0.001	7774	9.985	0.000
	conditionp:c.attract	0.003	0.001	7774	2.286	0.022
	conditionp:align	-0.047	0.011	7774	-4.442	0.000
Turn angle - only cohesive flock	(Intercept)	0.026	0.003	6323	8.905	0.000

	conditionp	-0.015	0.004	558	-4.155	0.000
	c.attract	0.005	0.001	6323	3.628	0.000
	align	0.041	0.014	6323	2.928	0.003
	cross.wind	0.000	0.000	6323	-0.300	0.764
	turn2home	0.008	0.001	6323	9.757	0.000
	conditionp:c.attract	-0.001	0.002	6323	-0.513	0.608
	conditionp:align	0.017	0.017	6323	1.038	0.299
Turn angle - with falcon data	(Intercept)	0.017	0.001	5089	12.955	0.000
	c.attract	0.004	0.001	5089	6.967	0.000
	align	0.016	0.004	5089	4.194	0.000
	turn2falchead	-0.011	0.001	5089	-14.077	0.000
	turn2falcpos	0.007	0.000	5089	15.471	0.000
	cross.wind	0.002	0.000	5089	4.775	0.000
	turn2home	0.006	0.001	5089	7.555	0.000
Speed variance	(Intercept)	1.278	0.061	423	20.978	0.000
	conditionp	-0.171	0.044	40	-3.873	0.000
	small.bigs	0.178	0.049	40	3.635	0.001
	abs(cross.wind)	0.007	0.006	423	1.194	0.233
	log(dist2site + 1)	0.082	0.006	423	13.154	0.000
	support.wind	-0.006	0.004	423	-1.613	0.108
Centripetal acceleration	(Intercept)	1.188	0.010	16160	116.001	0.000
	conditionp	0.006	0.008	591	0.755	0.450
	small.bigs	-0.074	0.009	591	-7.983	0.000
	abs(cross.wind)	0.011	0.001	16160	9.240	0.000
	support.wind	0.000	0.001	16160	-0.603	0.546
	log(dist2site + 1)	-0.051	0.002	16160	-32.559	0.000
	conditionp:small.bigs	0.089	0.011	591	7.812	0.000
Speed	(Intercept)	6.824	0.305	3095	22.397	0.000
	conditionp	-0.522	0.274	542	-1.907	0.057
	small.bigs	-0.092	0.315	542	-0.294	0.769
	abs(cross.wind)	0.045	0.035	3095	1.317	0.188
	log(dist2site + 1)	2.385	0.041	3095	58.618	0.000
	support.wind	-0.203	0.021	3095	-9.477	0.000
	conditionp:small.bigs	-1.427	0.396	542	-3.603	0.000
Distance to centroid	(Intercept)	1.048	0.039	2744	26.678	0.000
	flock.size	0.010	0.002	2744	5.583	0.000
	conditionp	0.073	0.049	571	1.496	0.135
	flock.size:conditionp	-0.004	0.002	2744	-1.826	0.068
Distance to nearest neighbour	(Intercept)	0.718	0.007	2853	96.243	0.000
	flock.size	-0.002	0.000	2853	-4.514	0.000
	conditionp	0.023	0.009	575	2.518	0.012

	flock.size:conditionp	-0.001	0.000	2853	-3.261	0.001
Conflict scenarios	(Intercept)	-0.335	0.065	3235	-5.153	0.000
	dist2pred	0.001	0.000	3235	4.047	0.000
	small.bigs	0.044	0.092	362	0.477	0.634
	dist2pred:small.bigs	0.000	0.000	3235	1.032	0.302
Proportion separated	(Intercept)	0.195	0.028	592	7.079	0.000
	conditionp	0.074	0.023	592	3.171	0.002
	flock.sizes	-0.150	0.023	592	-6.595	0.000
Instantaneous centroid attraction	(Intercept)	-0.008	0.006	7657	-1.408	0.159
	conditionp	0.004	0.005	623	0.775	0.439
	dist2cent	-0.001	0.000	7657	-2.973	0.003
	small.bigs	0.002	0.005	623	0.314	0.753
	cross.wind	0.000	0.000	7657	0.590	0.555
	conditionp:dist2cent	0.001	0.000	7657	2.639	0.008
	conditionp:small.bigs	0.001	0.007	623	0.090	0.928
Turn angle - all data	(Intercept)	0.016	0.001	11279	12.576	0.000
	conditionp	-0.003	0.002	593	-1.633	0.103
	c.attract	0.003	0.001	11279	3.977	0.000
	align	0.048	0.007	11279	6.704	0.000
	cross.wind	0.000	0.000	11279	0.699	0.485
	turn2home	0.006	0.001	11279	11.626	0.000
	conditionp:c.attract	0.002	0.001	11279	3.025	0.003
	conditionp:align	-0.036	0.008	11279	-4.704	0.000

Chapter 7: General Discussion

I proposed that individual-level responses to environmental and social stimuli govern the structure and function of bird flocks. Such that, while some species have evolved relatively fixed social interactions – emerging in distinct "flocking types" (Chapter 1) – interactions could also retain plasticity to cope with proximate challenges. With hypothesis driven rationale, my co-authors and I used pigeons as a model system to test the impact of experimental manipulations of proximate context – i.e. navigational, risk and social/aerodynamic contexts – on flocking dynamics. We found no response to changes in familiarity (navigational environment; Chapter 2), but strong responses to a model predator (risk environment; Chapter 6) and flock composition (social/aerodynamic environment; Chapter 5). Further, we found serendipitous evidence that individuals can adapt their behaviour in response to energetic fatigue, which resulted in modified flock structure across an unexpected long-duration flight (Chapter 4). Additionally an exploration of the data revealed more fundamental mechanisms to the evolution of group flight, namely that birds (and collectively moving animals more broadly) need to reach a speed consensus to travel together and retain the proposed benefits of group flight (Chapter 3).

Pigeon leadership is still an open question

As discussed in Chapter 2, current mechanistic hypotheses of leadership assume a positive covariance of route-efficiency on leadership in low-compromise situations "familiar" flights. To reiterate, this hypothesis asserts that of navigational preferences are "averaged" at low degrees of route compromise (Couzin et al. 2005; Fig. 7.1), and then when degree of compromise becomes too large, "leadership" or even "splitting" will occur (Biro et al. 2006; Strandburg-Peshkin et al. 2015). Averaging of movement preferences in low-compromise situations, however, would presumably elicit emergent "following" behaviour in less route-efficient individuals, via the following: 1) less route-efficient individuals would attempt to travel their own preferred direction, before being drawn back into alignment with the naturally parsimonious routes of individuals with high route-efficiency (given that groups of pigeons are more route-efficient than solo fliers; Biro et al. 2006; Dell'Ariccia et al. 2008; Taylor et al. 2019). Furthermore, 2) efficiency will confer greater speed relative to the direction of travel, which may enhance individual leadership rank, as speed is thought to govern leadership (Pettit et al. 2015; Jolles et al. 2017) . Thus the "averaging" component of the Couzin et al. (2005) hypothesis may not be matching well with empirical data (Freeman et al. 2011, Flack et al. 2013; but see Biro et al. 2006, Strandburg-Peshkin et al. 2015, and Fig. 7.1) .

Notwithstanding our negative results of speed as a predictor of leadership (Chapter 2; but see below for a *Critique of leadership consistency in pigeons*), I offer a new hypothesis consistent with a positive covariance of speed on leadership. Firstly if faster individuals do indeed travel to the front of collective groups (Couzin et al. 2002; Pettit et al. 2015; Jolles et al. 2017), and from there dominate movement decisions (Herbert-Read et al. 2011; Katz et al. 2011; Yomosa et al. 2015), it follows that trailing individuals can either *i*) compromise ("follow"), and travel in a direction which conflicts with their interest, or *ii*) take their own preferred route, and risk losing the benefits of grouping (Sueur et al. 2011). This is essentially the same hypothesis as proposed by Couzin et al. (2005), but without "averaging" at lower degrees of compromise. Hence I refer to the hypothesis as "binary choice". These trailing individuals may "weigh-up" both options based upon the *degree of compromise*, and the *costs of a potential split,* such as increased risk of predation; Zoratto et al. (2010). I discussed in Chapter 2 how such a trade-off of the *costs* of splitting vs the *costs* of route compromise suggests that "following" may never be as beneficial as leading, and suggested that trading-off these options *optimally* may represent the best possible strategy given their intrinsic handicap (Eberhard 1982; Davies et al. 2012).

Following a "binary choice" hypothesis, individuals with high route efficiencies are not likely to "follow" individuals with low route efficiencies, even if they were previously successful leaders (Watts et al. 2016), as here, the degree of compromise may be too high. Instead of following inefficient individuals, they may choose to

attempt initiations in the direction of their *own preferred route* (King 2010). After a certain degree of "familiarity" (and hence route efficiency; Chapter 2) has been established, however, compromise for both parties becomes minimal, and trailing individuals may "put up with" intermediate degrees of compromise to *avoid the costs of splitting*. Therefore "binary choice" may be more consistent with empirical data than "averaging" at low degrees of route compromise (Freeman et al. 2011; Flack et al. 2013; Watts et al. 2016).

The "binary choice" hypothesis, at first glance, does not work with well with observations of route "averaging" (Fig. 7.1), observed in baboons (Strandburg-Peshkin et al. 2015), and, indeed, pigeons (Biro et al. 2006). It may seem that when "binary choice" is the only option, the "winner takes all" every time, even at lower degrees of compromise. However this may not be the case. Route sharing may be an emergent property of shared leadership governed by "binary choice". Here, a follower would initiate a movement when the degree of compromise increases above a threshold. If the "leader" in this situation were to follow the initiator, it may lose its frontal position, and thus become a follower. This is supported by the work of Yomosa et al. (2015), who show that pigeon initiators are more likely to take frontal positions in subsequent movements, because of the relatively sooner time (directional correlation delay; leadership) which they made the movement in the new direction. The previous "leader" may become the new "follower" if and when its degree of compromise crosses the threshold, and the process could repeat itself. This may result in the emergence of "shared routes" which appear to be

"averaged" (Fig. 7.1). However, explaining previous empirical work with this hypothesis would require an extension. Specifically, that extreme degrees of compromise would reduce the likelihood of initiation. Pigeons and baboons are not seen to route share when compromise is large (Biro et al. 2006; Strandburg-Peshkin et al. 2015), instead the empirical and theoretical work points to leadership by one individual/party at larger compromises (Couzin et al. 2005; Biro et al. 2006; Strandburg-Peshkin et al. 2015). My extension to the original hypothesis would require that at a critical point, attempting to initiate towards a preferred route would make a journey longer (which has energetic consequences; see Chapter 4) or cross unknown terrain (which may carry additional risk; see Chapter 6), and here, "trusting a leader" may pay-off more than following a preferred route. This hypothesis is worthy of further exploration. I will aim to demonstrate in future work that an agent-based model with individuals following "binary choice rules", that the dynamics proposed are observed, and align well with empirical data.

This hypothesis provides an interesting alternative to classical models of collective behaviour with three interaction rules: "attraction", "alignment" and "repulsion" (Reynolds 1987; Couzin et al. 2002). Perhaps via a sequence of initiation and following movements, alignment may emerge without the need for specific "alignment rules". This is supported in pairs (and indeed groups) of fish, which showed no evidence of alignment, yet, via dynamic changes in acceleration, remained cohesive on the move (Herbert-Read et al. 2011; Katz et al. 2011). Indeed, it was already established that theoretical "swarms" could demonstrate

effective alignment through "attraction" rules alone (Strömbom 2011). Nevertheless, current evidence suggests that pigeon pairs use "alignment rules" (Pettit et al. 2013b). This may be a useful metric for quantifying changes in behaviour across context (Chapter 6). However, these empirical works measuring behavioural interactions, and fitting "interaction rules", do not test "interaction rules" as a hypothesis (see my *Critique of agent-based models and "interaction rules" hypothesis* below).

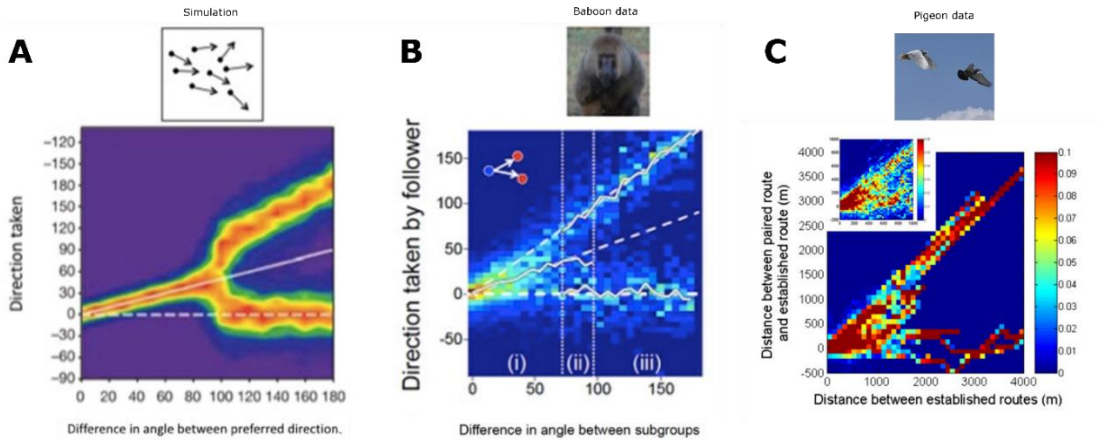

Figure 7. 1. "Averaging" hypothesis

Current simulation **(A)** and empirical **(B-C)** data suggest that route conflict governs a compromise and leadership dynamic (Couzin et al. 2005). Panels taken from **(A)** Couzin et al. (2005), **(B)** Strandburg-Peshkin et al. (2015), and **(C)** Biro et al. (2006). An "averaging of orientations" is supported at low degrees of conflict (low values on x and y axes), and leadership or splitting expected at larger conflict (larger x and y values). I have suggested that "binary choices" and "turn-taking" may produce similar data to the "averaging" component of the hypothesis.

Critique of leadership consistency in pigeons

The dominant paradigm utilised in pigeon leadership (Nagy et al. 2010; Flack et al. 2013; Pettit et al. 2015) may be providing researchers with unrealistic expectations regarding the consistency and repeatability of leadership in pigeons. Currently, pairwise time-lag leadership scores (fully described in Chapter 2) from every flight in a given study are combined into one matrix. The transitivity *T* of the hierarchy (i.e. if "A" leads "B", and "B" leads "C", then "A" leads "C") is seemingly very high, likewise the chance *p* that the observed transitivity were due to chance alone is seemingly low. There are problems here. For one thing, pairwise interactions should be independent of other group members, and this is not the case in leadership hierarchies. Just because individual "A", for example, turns 0.2 s after individual "B", this does not mean that "A" is following "B", it could be following "C". Nevertheless, the relationship is calculated as if dyads are independent (De Vries et al. 2006). In dominance matrices this approach is justifiable, for example, when individual "A" is seen to "wing slap" (Chapter 2) individual "B", no others are involved in this momentary instantaneous interaction. Of course social context could play a role in whether or when this behaviour occurs (Bernstein and Gordon 1980), but this can be captured in the data, i.e. whether individual "A" is more likely to "wing slap" individual "B" in the presence of individual "C" is testable.

More troubling for me was that a simple repeatability analysis of my own leadership data was showed a lack of repeatability in leadership. I assumed my

algorithms were wrong at first, as the original pigeon leadership paper quotes: “birds tended to copy consistently the directional behaviour of particular individuals, while being copied in their orientational choices by others” (Nagy et al. 2010). The term “consistently” here assumes at least some degree of repeatability. By analysing data I attained by reverse engineering plots from the original pigeon leadership paper (Nagy et al. 2010), I found the same inconsistencies as identified in my own data (Fig. 7.2; using data from Nagy et al. 2010, likelihood ratio tests with 1000 parametric bootstrap permutations to estimate 95% confidence intervals; R = 0.045, SE = 0.058, CI = [0, 0.188], p = 0.210). Fig. 7.2 was provided in the Supplemental Material of Nagy et al. (2010) to validate the repeatability of pigeon leadership, which seems peculiar, given that the statistics show that the individual data were not unlikely to be taken from the same (null) distribution.

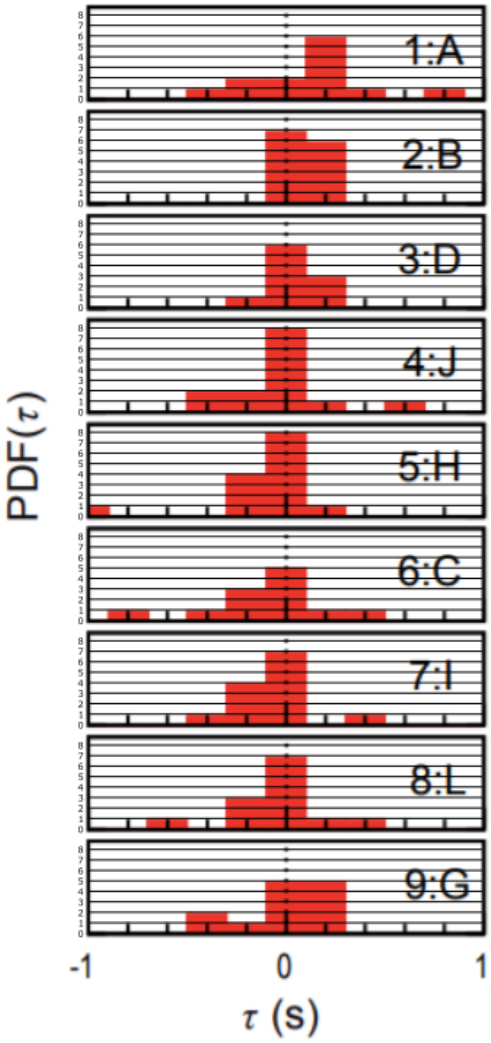

Figure 7. 2. Is pigeon leadership repeatable?

This plot was taken from Nagy et al. (2010) and modified with my own drawn horizontal lines and y-axis, to provide a count of data from each flight in each bin (correlation time lag, s). Leadership scores had to be multiples of 0.2, given the methods provided, using GPS loggers recording at 5 Hz (every 0.2 s), which made reverse engineering possible. Note no repeatability analyses were conducted in the original paper (Nagy et al. 2010).

Why did my data show that “leader flocks” have greater speed and stasis?

Individual leadership scores in my study were not repeatable, with similar scores observed in the retrospective analysis of Nagy et al.’s (2010) data above. Nevertheless, I found larger differences when the groups were separated out according to the top five mean leadership scores “leaders” and the bottom five leadership scores “followers” (Fig. 7.3). While “leadership” as a phenotype was not repeatable, differences may become clearer when separating into groups as “top five” and “bottom five”. Whether or not the “top five” would remain the same if I repeated the experiments from a different site, the simple detail remains that the “top five” in my study did lead more of the flock’s movements. This “leadership”, whether by coincidence or not, may have increased their learning of the homing route (as observed in Pettit et al. 2015), which we propose may have reduced conflict and enhanced flock stasis (Chapter 5).

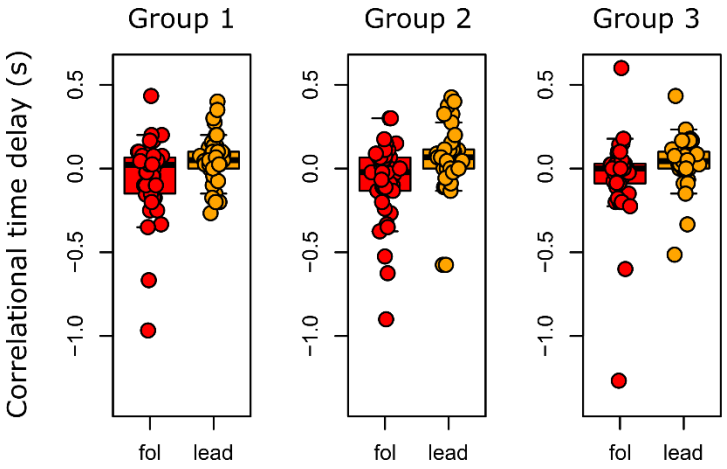

Figure 7. 3. Groups of leaders and followers

We separated the three groups (Group 1, 2, and 3) by top five (lead; orange) and bottom five (fol; red) mean leadership scores (correlational time delay, s). This separation demonstrated tangible difference between leader groups and follower groups on their flock dynamics, in terms of stability ("stasis") and speed (Chapter 5). Mean leadership score at the individual level (i.e. the work in Chapter 2) was not predicted by any phenotype (Chapter 2), which may be due to low repeatability at the individual level.

The future of leadership

Newer algorithms are under development which instead identify the influential individuals in flocks by the predictability of neighbour movements from the movements of "influencers" on a moment-by-moment time scale, i.e. not averaging

over an entire flight (Lecheval et al. 2017). Indeed, it seems this approach is being adopted in the field (see review in Strandburg-Peshkin et al. 2018). Nevertheless, inferring that the movement decisions of one individual influences the movements of another in a group of multiple individuals is still a challenge. Rosenthal et al. (2015) used "startle responses" in shoals of fish (Golden Shiners, *Notemigonus crysoleucas*), whereby "startling" only one individual can create emergent waves of collective motion, yet, as they reason (correctly), only the behaviour of first responder can be properly assessed. Once the second responding fish moves, was it because of the first responder, or a time-delayed response to the original "startled" fish? The answers to individual response "rules" to multiple actors may come from placing real fish in virtual reality systems (Stowers et al. 2017), where responses to neighbours can be controlled and manipulated (*I. Couzin Pers. comms*). A major criticism here is the assumption of *visual sensory information alone* governing "interaction rules". Mechanosensory information, for example, is likely crucial to the behaviour of collectives, given that is fish respond to vortices (Liao et al. 2003) and eliminating mechanosensory in saithe (*Pollachius virens*) was found to increased collisions with group members (Partridge and Pitcher 1980; alternative sensory modalities for collective behaviour are reviewed in Pita et al. 2016).

Do energetics impact the cluster-flock structure?

I was previously sceptical that a cluster-flocking system such as pigeons – which may have evolved to mitigate knowledge deficits and/or predator costs (Chapter 1) – would respond adaptively to their energetic environment. Although previous evidence had shown energetic increases in paired flight over solo flight (Taylor et al. 2019), and further increases in denser flocks (Usherwood et al. 2011), I would still ask whether the weight of these energetic increases had sufficient importance (relative to navigation and risk) to have a tangible impact on the flock dynamics. Although only one observation, the unexpected long-duration flight documented in Chapter 4 demonstrated that over time, the accumulation of energetic costs can have a strong impact on flock dynamics. Specifically we observed a reduction in flock-density, followed by a splitting of the entire group, which was the direction of events expected following an adaptive response to the costs of flock flight found in Usherwood et al. (2011) and Taylor et al. (2019). While Chapter 4 demonstrated that energetic constraints may have an increasing impact on collective dynamics; Chapter 5 showed that flocks of particular phenotypic compositions may have the ability to counteract these constraints through stability, or stasis in their movements. Indeed, even at closer densities, more static groups were able to increase speed without compromising energetic costs (contrary to the results of Usherwood et al. 2011). Taken together, these Chapters suggest that 1) energetics can impact flock dynamics (Chapter 4), and 2) phenotypic differences in effective

coordination could lead to preferential survival of successful collaborators (Chapter 5). One might ask how a successful collaborator (or, cooperator) might have preferential survival over selfish individuals which cheat and free-ride on the behaviour of others. This question is addressed with regards to flock stasis below, respect to anti-predator benefits both below, and in Chapter 6.

The evolution of collective behaviour – personal insights from investigations of flocking

When we study behaviour, we are studying nature's solutions to problems imposed by the present or ancestral environment. Indeed, when these problems align with our own issues, learning nature's solutions can help inform our own decision making on matters such as technological and scientific progress (e.g. "ant colony optimisation" algorithms are used in computer science; Dorigo and Birattari 2010), as well as ethics (Harlow 1958; McLeod 2009). As an example in ethics, the abandonment of an unhelpful "classical conditioning" paradigm for childcare is often attributed to a study by Harlow (1958) in rhesus macaques (*Macaca mulatta*), where infants preferred to cling to artificial "mothers" made of cloth (with no food), than wire "mothers" with food (McLeod 2009). We know that behaviour, designed to tackle ecological challenges can exist at the level of the individual, where an individual can respond more-or-less optimally to a present set of circumstances

(Davies et al. 2012). However, outside of self-replicating organisms, behaviour independent of social context is rare. More often, behavioural patterns are developed and performed in response to the behaviour of others, both in their past experiences (e.g. learning and parental care; Mutzel 2013), and present context (e.g. social interactions and sexual reproduction; Emlen and Oring 1977). The social context matters, because some of nature's "problems" require collaboration from multiple individuals to find effective "solutions".

Although it has long been known that groups can employ effective solutions such as collective problem solving (Costa and Hertz 1997), decision making (Prins 1996), defence (Ims 1990) and predation (Packer and Ruttan 1988), the incorporation of such phenomena into individual level selection has been rare (but see, e.g. Wolf et al. 1999; Farine et al. 2015), due to methodological and/or conceptual constraints. Today, behavioural research is undergoing a transition, whereby adaptive group-level solutions (which emerge from behavioural coordination) can be studied with increasing precision (Berdahl et al. 2018). However, at this historical "turning-point" also lies a classical "trap": that we must not wrongly interpret selection at the level of groups (Bourke 2014). Although collective phenomena are built on mutualisms (Sumpter 2006; 2010), defection may still occur as animal groups often consist of unrelated individuals (Couzin 2009). Thus, the evolutionarily stable strategy (ESS) may be non-optimal for the group (Davies et al. 2012). Implicit in my approach throughout the thesis is that collective phenomena need to be based upon an understanding of motivations from the perspective of individuals (individual-level

selection) and their optimal choices. As we have shown, these optimal choices may vary given *i*) their own phenotype (Chapter 3), *ii*) the phenotypic composition of the group (Chapter 5) and *iii*) the proximate context (Chapter 6).

There is a key problem with such reasoning. If collective behaviour requires "multiple agents performing the same behaviours in unity" (paraphrased from Sumpter 2006, 2010), how can evolution provide the necessary two, three, or more individuals with the *same behaviour* at the *same time*? This would seemingly be necessary for the evolution of collective behaviour, and is an unanswered question. Nevertheless, the more mutualistic (emergent) benefits may have precursors in the simpler individual motivations.

Take, for example, the results of Chapter 3. Here we saw that the effective collective response to the problem of "coordinating speed to maximise grouping benefit, while mitigating energetic cost" may be best achieved by a shared speed consensus. This solution may be effective at the individual level, achieved by speed compromise to avoid the costs of splitting from the group. Speed compromise may therefore be adaptive, and does not require any individual to "sacrifice themselves for the group" or indeed any effective "cooperation". Nevertheless, once a "selfish" group unite, opportunities to behave for cooperative benefit will emerge. As we saw in Chapter 5, individuals which remain "static" in their positioning may ease the energetic requirements of cluster-flocking. Remaining stable, therefore, could have cooperative benefits: not only is it good for the individual with low variability in its

movements, but such stable flight could have a positive outcome on their neighbours too. Selection favours beneficial behaviour, whether behaviour is selfish or cooperative (Bourke 2011), so stable movements might be expected to evolve irrespective of their benefits to neighbouring individuals (but see below).

Our work on flock stasis (Chapter 5) may, therefore, suggest another answer to a question explored more deeply in Chapter 6 (where mutualistic "alignment" was assumed to be a function of predation pressure) but is not necessarily more valid. The arguments can equally be applied to an individual which aligns movements with another, and receives anti-predator benefit (not energetic benefit) in the process. To reiterate in the context of predation: an individual which aligns its movements with another may receive anti-predator benefits in the form of enhanced information (Herbert-Read et al. 2015), collective escape (Ioannou et al. 2012), or predator confusion (Procaccini et al. 2011) through conformity (Herbert-Read et al. 2013) (see Chapter 6). This *aligning* individual may well enhance the fitness of its neighbour through mutualistic anti-predator benefits, but the neighbour's benefit may only have minimal impact (through increased resource competition; Bourke 2011) on this focal, *aligning* individual.

Agent-based models and the evolution of collective motion

Future work could employ a semi-artificial system, combining *virtual* pairs of "random walkers" with "aligning" or "attracting" individuals in response to *real* predators (following the methods of Ioannou et al. 2012, 2019). If "aligning" individuals have enhanced survival, irrespective of benefits to "random walkers", we will finally have a rational hypothesis of how collective motion can evolve without an implicit assumption that multiple individuals evolve interactions in tandem.

A limitation of this proposed study system is that virtual "prey" cannot respond to the real predators, and we know that individuals in a collective do indeed respond to predators (Storms et al. 2019; Chapter 6). A present alternative is to use virtual prey and modelled predators (Wood and Ackland 2007), which has its own limitations, namely, assumptions need to be made on the individual's responses to the predator, and one another (see below for my *Critique of agent-based models and "interaction rules" hypothesis*). Nevertheless this latter approach may have value toward understanding the evolution of cooperation in collective motion, as such models could provide theoretical support or refutation for our hypotheses of "selfish", "altruistic", "cooperative", and "spiteful" decisions by individuals in flocks (Chapter 6). By simulating alternative responses to social and/or predator cues, and measuring capture/escape of the focal individuals/neighbours, we may be able to quantify the individual and group-level fitness impact of focal decisions on the flock.

Critique of agent-based models and "interaction rules" hypothesis

Notwithstanding the successes of an "interaction rules" approach to simulate qualitatively similar flocks on a computer screen (Reynolds 1987; Couzin et al. 2002), and descriptive accounts of the coordinated swarming movements of, for example, starlings (Ballerini et al. 2008), the hypothesis is at risk of self-perpetuating. The problem emerges when 1) investigators successfully simulate a group of particles resembling a flock with simple "rules of interaction" (Reynolds 1987) and others conclude that animals must respond to neighbours according to simple "rules" (e.g. Bajec and Heppner 2009), 2) empiricists validate these claims by measuring behavioural responses of real animals to one another, and fitting "interaction rules" to the data. Starlings, for example are thought to change direction in relation to their seven nearest neighbours (Ballerini et al. 2008). Such a behavioural rule (simultaneously tracking and responding to only seven neighbours) is almost certainly a statistical property of the model fit to the data. Nevertheless, 3) the findings count as "evidence" for the hypothesis, and the cycle continues (Sumpter et al. 2012).

More recently, measurements of neighbour-to-neighbour responses within a local sensory environment (Strandburg-Peshkin et al. 2013) (e.g. a starling cannot respond to another starling that it cannot see), makes more intuitive sense than responding to zones of neighbours (Couzin et al. 2002) or fixed number of neighbours (Ballerini et al. 2008). Nevertheless, we still are not asking even basic

questions of an “interaction rules” hypothesis (Bajec and Heppner 2009). Once we think we know “how it works” we can simulate models and record the outcomes. This will provide the essential predictions by which scientific hypotheses are tested (Popper 1963), yet have been so surprisingly rare in our field (Bajec and Heppner 2009; but see a test of Couzin et al. 2005 in Biro et al. 2006; Fig. 7.1).

A defence of the philosophical approach

I have provided a broadly adaptationist approach to understanding how behavioural mechanism governs form and function in bird flocks (Tinbergen 1963; Davies et al. 2012). This behavioural ecological angle has its limitations which I have been careful to avoid. I have been careful to think within the realms of the physical limitations imposed by morphology and physiology (Feder et al. 2000): I have never suggested that geese would start swarming, or that starlings would fly in V-formations given an appropriate change in their ecological conditions, to illustrate with an over exaggerated, possibly humorous example. I may be guilty of dividing behaviours into unitary “traits” (e.g. attraction, alignment, leadership, speed and energetic costs), finding adaptive rationale for each, and asking questions within this framework (an approach criticised by Gould and Lewontin 1979, for not considering the organism as a whole agent). Nevertheless, I remained fully aware of the potential limitations of interpreting adaptive function in a domesticated flock of homing pigeons. As discussed in Chapter 5, captive animal systems are useful to

test functional hypotheses regarding *already well-established* evolutionary pressures via manipulations. Furthermore this criticism cannot be concluded of my approach to my study "animal personalities", which I have been careful to discuss as the emergent outcome of internal physiological or neurophysiological (i.e. risk-taking) mechanisms (Wolf et al. 2007; Biro and Stamps 2010).

Conclusions

Birds come together in flight for a multitude of reasons, and it is these same forces which govern the flock's startling structure and dynamics. We have discovered that the interactions which give rise to bird flocks are not immutable and fixed; changes in the internal or external conditions can modify individual responses, and thus group-level properties, such as the flock's speed, shape and stability. Adaptive and plastic responses to environmental and social stimuli may have been expected in bird flocks, however, supporting evidence and even conceptual accounts were surprisingly rare (but see Bode et al. 2011; Ling et al. 2019). This may be due to recent technological advancements (Berdahl et al. 2018). It could also be, in-part, due to theories of natural selection which place the ball firmly in the hands of the individual (Dawkins 1980), when we know behavioural responses are not independent of an individual's present and historical social interactions (Lehtonen 2016). This is still a complex question (Kramer and Meunier 2016), nevertheless I have not shied away from it. I trust that future work will further elucidate how the

striking visual phenomena of collective flight can evolve from their solitary precursors.

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