
Mechanisms underlying navigational leadership hierarchies: studies with avian and fish models

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Abstract

For animals moving together in groups, navigating collectively requires group members to reach consensus decisions about, among other things, the direction in which to travel. This thesis focuses on how consensus collective decisions are made when certain individuals have a disproportionate influence on the group's movement decisions. The specific focus is on hierarchical decision-making during collective movement, whereby an individual's position in the hierarchy corresponds to its relative contribution to the directional decision-making process. I used two model species, homing pigeons (*Columba livia*) and the Characin fish (*Astyanax mexicanus*) to explore the mechanisms and consequences of leadership hierarchies, using a combination of GPS tracking and high-resolution video recording. Across several experiments, the following key results emerged:

Previous navigational experience contributes to structuring navigational leadership hierarchies in homing pigeons, but only at the most influential positions. Birds with local experience occupy the top hierarchical positions significantly more often than inexperienced birds. This suggests there is an advantage to individuals in having an experienced leader when homing as a group.

When leader birds hold highly inaccurate information, leadership hierarchies are spontaneously rearranged causing the original leaders to lose influence over flocks. This demonstrates the importance flexibility in decision-making structures, which may thus prevent the propagation of navigational errors – detrimental to all individuals within the flock – through the hierarchy.

Homing pigeon navigational leadership hierarchies can be stable over long periods of time, but only in flocks with high levels of inter-individual variation in age and experience. Flocks homogeneous in age and experience showed no hierarchy stability. This highlights the importance of flock composition in determining the stability of navigational leadership hierarchies, which potentially impacts on the advantages of these decision-making structures.

Three-dimensional data are not a necessary requirement for identifying leadership hierarchies in animals that move and interact in three dimensions. A two-dimensional directional correlation delay model was able to correctly identify leader-follower interactions in three-dimensional shoals of *Astyanax mexicanus*.

Overall, this thesis has shed light on the mechanisms of consensus decision-making, involving hierarchies of influence, during group movement. Through this knowledge we can further our understanding of the adaptive significance of collective behaviour.

Author Contributions

The work in this thesis is primarily my own.

This thesis is presented as a set of independent chapters laid out in scientific journal format, with a general introduction and discussion linking them together.

Chapter 2 is published and Chapter 3 is currently under review after being revised.

The following people contributed to one or more data chapters:

Dora Biro and Theresa Burt de Perera contributed their ideas and provided feedback for manuscript preparation for all chapters in this thesis.

Mate Nagy participated in data collection for Chapter 2, and contributed to the analysis and gave feedback during manuscript preparation for Chapters 2, 3 and 5.

Robert Holbrook offered ideas, participated with data collection and contributed feedback to Chapter 5.

Benjamin Petitt aided with the analysis in Chapter 2 by providing some of the initial code, although I altered and ran all the code, analysed the results and prepared the manuscript.

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Chapter 1

General introduction

This chapter outlines the background to the thesis.

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1.1 The importance of understanding leadership hierarchies in collective behavior

When moving together, animal groups must reach consensus decisions on the direction and length to travel if they are to maintain group cohesion and thus accrue the benefits of group living. For example, cohesive movement helps small fish (e.g. rudd, *Scardinius erythrophthalmus*) avoid being eaten by predators (Krause and Ruxton 2002), wild dogs (*Lycaon pictus*) to increase their food intake (Creel and Creel 1995) and pigeons (*Columba livia*) to increase navigational accuracy (Dell'Arciccia et al. 2008).

A consensus decision can be reached where all individuals equally contribute (i.e. fully shared) (Conradt and Roper 2005), where only one or a few individuals are responsible (i.e. despotic leadership) (Conradt and Roper 2003), or via a hierarchy of influences (i.e. hierarchical leadership) where an individual's position in the hierarchy reflects the weight of its contribution in the decision-making process (Nagy et al. 2010). Leadership hierarchies as a type of decision-making mechanism are particularly interesting as they lie between fully shared decisions and despotic leadership, and their discovery has widened our overall understanding of consensus decision-making. Leadership hierarchies are found in a range of species including homing pigeons (*Columba livia*)(Nagy et al. 2010), beef cows (*Bos taurus*)(Sarova et al. 2010) and medaka fish (*Oryzias latipes*)(Perez-Escudero et al. 2014).

This thesis is motivated by the desire to understand how decision-making operates within leadership hierarchies, what individual factors underpin them, their stability and their three-dimensional nature. Understanding the mechanisms and functional

consequences of group decision-making has important implications for broader questions in collective behaviour, such as in the design and control of self-organised systems. With these aims in mind, I have collected two-dimensional and three-dimensional data on group decision making during collective movement in bird flocks (homing pigeons *Columba livia*) and fish schools (the Characin fish *Astyanax mexicanus*). Birds and fish are two taxa where cohesive group formation is highly prevalent, with over half of all fish species forming schools (Shaw 1978) and roughly half of bird species forming feeding flocks (Lack 1968). I first present background information on each subject area, focusing on collective movement, collective-decision making, life in three-dimensions, and the two model species (*C. livia* and *A. mexicanus*) used in this thesis.

1.2 Collective motion

A necessary part of group living for many species is moving collectively. More specifically, collective motion refers to group movements where numerous conspecifics synchronously move together in the same direction whilst maintaining cohesion (Vicsek and Zafeiris 2012). Collective motion has been observed in a wide range of species including amoeba (*Dictyostelium discoideum*) (Kessler and Levine 1993), insects (e.g. desert locust, *Schistocera gregaria*) (Buhl et al. 2006), birds (e.g. starlings, *Sturnus vulgaris*) (Ballerini et al. 2008), fish (e.g. mosquitofish, *Gambusia holbrooki*) (Herbert-Read et al. 2011) and mammals (e.g. plains zebra, *Equus burchellii*) (Fischhoff et al. 2007). When travelling as a group, individuals must maintain group cohesion in order to sustain the benefits associated with collective movement. These include the dilution of predation risk, increased rate of food

discovery, enhanced navigation, cooperative hunting, cooperative defence, communal breeding and collective vigilance (Krause and Ruxton 2002). There are also costs associated with group formation, such as increased competition for resources, increased disease transfer and reduction of choice when making decisions (Krause and Ruxton 2002). However, for many animals the benefits vastly outweigh the costs. Homing pigeons and fish are thought to benefit primarily from reduced predation risk (Krause and Ruxton 2002, Rutz 2012). In homing pigeons, group formation has also been shown to enhance navigational efficiency (Dell'Arciccia et al. 2008), thought to be due to individuals being able to pool information and produce more accurate directional decisions by averaging out individual errors, or by following knowledgeable group members (Simons 2004).

1.3 Group decision-making mechanisms

Group composition is rarely homogeneous; instead individuals often possess conflicting information or interests. In the presence of such conflicts within the group a consensus decision must be reached. All members must agree to a decision otherwise the group will split, but not all members must contribute to the decision (Conradt and Roper 2005). There are two main features of collective decision-making that have allowed for cross-species and cross-context comparisons (for a review, see Conradt and Roper 2005): (1) whether it involves local or global communication and (2) the degree of information sharing.

1.3.1 Global versus local communication

The level (global or local) at which communication among group members occurs is important as it indicates whether the likely mechanisms involved in reaching

consensus are passive or active (Conradt and Roper 2005). In small groups, where individuals can communicate directly with all group members (i.e. on a global scale), there is room for active group negotiating behaviours or active leadership where individuals directly signal their intent to other group members who can choose to follow or not to follow (see King et al. 2009 or Petit and Bon 2010 for examples). This is enhanced by individual recognition and memory of previous interactions (Petit and Bon 2010).

However, groups can reach sizes of thousands of individuals, and it is in these cases where global communication becomes more difficult. In large groups, such as fish schools (Krause 2000), bird flocks (Conradt and Roper 2003) and ungulate herds (Prins 1996), individuals can only interact with a small subset of group members, principally their nearby neighbours (i.e. on a local scale). Mathematical modelling has shown how individuals following a set of simple local rules can cause cohesive groups to form passively, without the need for global organisation (Couzin et al. 2002). Taking the case of collective movement as an example, this concept of self-organising groups relies on three main principles: attraction, alignment and repulsion (Couzin et al. 2005). These principles are modelled as three interaction radii around a focal fish (Figure 1), where depending on a neighbours distance to a focal fish, the focal fish will follow one of the three interaction rules. The inner zone of repulsion (Z_r) prevents collision if individuals become too close. The middle zone of alignment (Z_{al}) facilitates collective directional motion by enabling individuals to match the orientation of others. Finally the outer zone of attraction (Z_{at}) enables groups to maintain cohesion, as individuals far away move towards the group to prevent isolation (Couzin and Krause 2003).

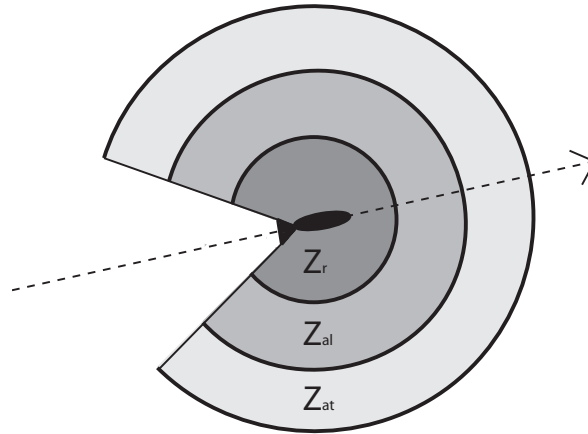


Figure 1: Representation of the interaction radii around a focal individual. Z_r is the zone of repulsion, Z_{al} the zone of alignment, and Z_{at} the zone of attraction. There is a blind angle behind the individual where no visual perception occurs. The figure is adapted from Couzin et al. 2002.

Empirical data collected in two dimensions (fish schools: Viscido et al. 2004 and Herbert-Read et al. 2011, pigeons: Pettit et al. 2013, and surf scoters, *Melanitta perspicillata*: Lukeman et al. 2010) and in three dimensions (starlings, *S. vulgaris*: Bellerini et al. 2008; Attanasi et al. 2014) have generally supported the model's three principles. However, the empirical data have highlighted important species-specific variations, potentially due to differences in the medium through which the animals move and the mechanics of their locomotion. For example, mosquito fish (*Gambusia holbrooki*) slow down to avoid collisions (Herbert-Read et al. 2011) whereas homing pigeons (*C. livia*) fly with a low variance of speeds and instead turn away from neighbours to avoid collisions (Pettit et al. 2013). In addition, empirical data have suggested that in some groups, such as starling flocks (*S. vulgaris*), individuals interact with a fixed number of neighbours (topological) (Ballerini et al.

2008) rather than with all neighbours within a certain distance (metric) as assumed by previous models (Couzin et al. 2002, Couzin et al. 2005). Therefore, recent attention has been targeted at designing species-specific models that expand the general principles of self-organisation with species-specific responses and behaviours. One such example is the starling model developed by Hildenbrandt and Hemelrijk (2010) that used avoidance, attraction, and alignment principles, with the addition of fixed wing aerodynamics and topological interactions to generate patterns remarkably similar to the empirical data.

This mechanism of self-organisation is thought to be able to lead to equally shared consensus decisions when group-living benefits are high relative to potential consensus costs (Conradt and Roper 2003) or when individuals differences in experience are low (Conradt and Roper 2003). However, through the principles of self-organisation some individuals can still have greater weight in decision-making, resulting in passive leadership (Couzin et al. 2005, Conradt et al. 2009, King et al. 2009). Without active communication (Conradt et al. 2009), or knowledge about who within the group is informed (Couzin et al. 2005), individuals can alter simple behavioural parameters, such as speed, assertiveness and social attraction range depending on their own internal states, which may in turn increase their likelihood of leading through local interaction rules. For example, the more beneficial it is for an individual group member to reach a target the higher degree of assertiveness they might adopt, even with an increased risk of group fragmentation (Conradt et al. 2009), and therefore they will likely lead group movements.

1.3.2 Degree of information sharing

The degree of information sharing within consensus decision-making has traditionally been classified into two extremes: either all group members contribute with equal weighting (fully shared) or one or a few individuals are responsible for the group's decisions (despotic leadership). Leading is thought to be advantageous to individuals (for a review, see Krause 2000), offering opportunities for increased food intake (Krause 1993, King et al. 2008), access to higher quality food (Krause 1993), enhanced learning speed (Pettit et al. 2015), and reduced probability of conflict between an individual's directional choice and that of the group (Krause 2000). There are also potential costs associated with leadership, including higher predation rates and increased energy expenditure (Krause 2000). For us to identify an individual as a leader requires other individuals to follow; thus in many cases even when a single individual initiates the activity, other group members will still be involved in the decision by either choosing to follow or to split (King et al. 2009, Petit and Bon 2010). Therefore, for leadership to occur the benefits to the rest of the group of maintaining cohesion and following must outweigh any potential costs of following (Conradt and Roper 2009).

Alternatively, a consensus decision can be made in which all individuals equally contribute to the decision, independent of their social status or individuals' identities (Conradt and Roper 2005). Generally, fully egalitarian decisions are thought to be more beneficial because they lead to less extreme decisions (Conradt and Roper 2003). Equally shared decisions can occur via quorum sensing. For example, in three-spine sticklebacks (*Gasterosteus aculeatus*) when deciding between two alternative routes, the probability of picking one route increased as a

function of the number of individuals having recently taken it (Ward et al. 2008). Alternatively an equally shared decision can occur via averaging out all the ‘votes’, as seen in African buffalo (*Syncerus caffer*) where the direction of group travel is decided by the mean gaze direction of adult females (Prins 1996) .

Although I have thus far discussed information sharing as being either egalitarian or despotic it is now generally agreed that in reality there are degrees of information sharing along a continuous spectrum between these two extremes (Nagy et al. 2010, Strandburg-Peshkin et al. 2015). Hierarchies of influence can be used to reach consensus decisions, where the weight an individual has in the decision depends on its position within the leadership hierarchy (Nagy et al. 2010). These decision-making structures are not solely despotic as all individuals can potentially contribute, nor are they fully egalitarian, as individuals contribute with different weights. Understanding such leadership hierarchies is the main focus of this thesis.

Currently, the most commonly used method to identify whether groups have a hierarchical decision-making structure is to use a directional correlation delay analysis (Nagy et al. 2010). If individuals fly in a flock then they will show high correlations in their directional movements (Cavagna et al. 2010). The direction correlation delay analysis takes a pair of individuals, A and B, and calculates the direction and magnitude of the temporal delay between A’s changes in direction and B’s matching of these directions. In these pair-wise comparisons, if, for example, individual B performs the same sequence of direction changes as A, but delayed in time, B is deemed the follower and A the leader. By analysing all pair-wise interactions within a group in this way, leadership networks can be constructed. These can be thought of as leadership hierarchies when the full set of pair-wise

leader-follower relationships condense into transitive (i.e. containing no loops), multilevel hierarchical networks.

1.3.3 Leadership stability and factors determining leadership

When individuals within groups are uniform the probability of leading may be random or may not occur at all. However, in many groups inter-individual differences occur in, for example, morphology, physiology, social status and experience (for review see Petit and Bon 2010 and King et al. 2009), which may bias an individual's propensity to lead. Whether individual positions within a leadership hierarchy are transient or consistent across time and/or context will depend on the factors that have resulted in certain individuals having greater influence over decisions than others. Below I will discuss some of the factors thought to be important in structuring leadership hierarchies, a topic I also examine further in Chapters 2, 3, and 4.

Leadership may operate differently depending on social context. First, in societies with strong social ties (e.g. baboons, *Papio ursinus* and rhesus macaques, *Macaca mulatta*), a dominant individual can dictate the decisions and fragmentation is reduced through strong social ties (King et al. 2008, Sueur and Petit 2008). This individual's leadership is maintained as long as it remains dominant. Secondly, in weakly bonded societies consistency will depend on the relevant factors involved. These factors include, but are not restricted to, the possession of superior knowledge (e.g. golden shiners, *Notemigonus crysoleucas*: Reeb's 2000, pigeons, *C. livia*: Flack et al. 2012, killer whales, *Orcinus orca*: Brent et al. 2015, Chapter 2), morphological factors such as size (Pettit et al. 2015) and intrinsic individual differences in temperament (three-spined sticklebacks, *Gasterosteus aculeatus*:

Harcourt et al. 2009). These factors have the potential to be stable across time. Alternatively, an individual's likelihood of leading can vary dynamically, depending on their physiological or energetic state, resulting in transient leadership. For example, individuals for whom reaching the goal is most crucial may initiate movement ("leading according to need") (Conradt et al. 2009). Examples of this can be seen in female lactating plains zebras (*Equus burchellii*) who initiate group movement because leading results in priority access to scarce water (Fischhoff et al. 2007). On the other hand, if for some individuals the benefits of remaining in a large group outweighs the benefits of reaching a particular destination, but this is not true for all individuals within the group, then the latter will have stronger influence on group movement ("leading according to social indifference") (Conradt et al. 2009). One possible example of this can be found in African buffalo (*Syncerus caffer*) where under some conditions females lead and males follow behind. This is thought to be because the males have a larger incentive in terms of mating advantages to avoid group fragmentation (Prins 1996).

Importantly, an individual's propensity to lead is often controlled by a combination of factors. For example, Nakayama et al. (2012) showed that when pairs of sticklebacks (*G. aculeatus*) had similar nutritional levels, bolder individuals initiated leaving cover to search for food. However, when nutritional levels varied, the individual in the lower nutritional state initiated leaving cover. In addition to this, recent social conditions have been shown to have a temporal effect on the boldness of the fish (Jolles et al. 2016), therefore potentially impacting on leadership. Understanding the factors influencing leadership and the stability of leader-follower interactions provides insights into the potential adaptive value of leadership

structures. However, few studies to date have taken consistency of leadership into account (Nagy et al. 2010, Burns et al. 2012, Santos et al. 2014, Chapters 3, 4 and 5).

1.4 Life in a three-dimensional world

Life exists in three dimensions and therefore there is an element of vertical travel in most animals' natural movement. However, while some taxa remain in contact with a surface (e.g. humans and rats) and move mainly in two dimensions (x and y), others (e.g. fish and birds) disengage from surfaces and move mainly in three dimensions (x, y and z). As such, we would expect models and analyses to reflect this extra degree of freedom of movement when modelling non-surfaced bound animals. Only recent interest in how groups interact in three dimensions has resulted in collective motion models being extended to include interactions in the vertical axis (Czirok et al. 1999, Couzin et al. 2002, Hildenbrandt et al. 2010, Camperi et al. 2012). However, models of leadership (e.g. Nagy et al. 2010; Katz et al. 2011) are still restricted to two dimensions, generating questions about their validity in explaining three-dimensional movement dynamics (Chapter 5).

1.4.1 Tracking animals in three dimensions

One key issue with the study of interactions in three dimensions is the difficulty of collecting high-resolution three-dimensional data (Viscido et al. 2004, Ballerini et al. 2008, Butail and Paley 2012, Attanasi et al. 2014). Until recently, the two main methods used to record three-dimensional movements of individuals within groups were the shadow technique and the stereo-technique (Cullen et al. 1965). The shadow technique, commonly employed in the case of fish kept in captive

conditions, involves shining light onto a tank and measuring the distance between a fish and its shadow, in order to calculate the individual's three-dimensional position. The stereo-technique involves two cameras positioned at different angles to a target, which are able to record photos simultaneously. Using photogrammetric techniques the two-dimensional coordinates from both views are matched to reconstruct the three-dimensional volume. I use this technique in Chapter 5. Over the last decade the stereo-technique has become the more popular method, due to increased camera resolution and the potential for automated recording, and although originally designed for fish schools (Cullen et al. 1965) it has been modified for and applied in bird flocks as well (Major and Dill 1978, Ballerini et al. 2008, Cavagna et al. 2008). For example, Ballerini and colleagues (2008) determined the three-dimensional positions of European starlings (*S. vulgaris*) in flocks of up to 2600 individuals, but not their individual tracks over time.

All optical techniques (including shadow and stereo-techniques) suffer from a significant drawback, that is, in order to reconstruct the three-dimensional positions of an object, images must be matched (Osborn 1997, Hartley and Zisserman 2003). For large compact groups with few distinguishing features, this is a very difficult task, because when individuals overlap it becomes hard to identify one from another. As such, ensuring the continuous tracking of an individual becomes highly problematic. This is especially hard for automatic tracking software (for examples see Viscido et al. 2004, Butail and Paly 2012, Cavagna et al. 2008). In addition, the cameras are fixed and can only record one area. Therefore, three-dimensional studies are often limited to small groups, where individual overlap is less frequently

compared to large dense groups, and to a fixed location (i.e. either a tank or a specific area in the sky).

Recent advances in technology have aimed to overcome some of the issues around the stereo-technique, namely the restriction to the laboratory or a small area, and the tracking of a large number of individuals simultaneously. Low-frequency band sonar has been used to track large fish schools in three-dimensions of Atlantic herring (*Clupea harengus*) in the wild (Makris et al. 2009). Although this technique can quantify the formation processes of ocean fish schools during spawning as school transition from disordered to highly synchronized, it is unable to track individual fish due to the technique's low resolution. A second technique applied to tracking fish is split-beam echo sounders that enable the determination of the precise location of single fish in the acoustic beam (Brede et al. 1990, Handegard et al. 2005). Therefore, at present in the wild we are unable to track multiple fish in three-dimensions at high resolution. In order to track birds over long distance, miniature Global Positioning System (GPS) devices have frequently been used to record the latitude and longitude of birds' positions (von Hunerbein et al. 2000, Bridge et al. 2011). However, the vertical measurement error for GPS altitude measurements can be an order of magnitude greater than the horizontal error (vertical uncertainty of ± 100 m) (Ladetto et al. 2000). GPS devices with ± 22 m vertical error have been used to measure the migration of bar-headed geese (*Anser indicus*) typically climbing to an altitude of 6000m (Hawkes 2011) but for measuring movements of individuals within a flock this error is still too high. Instead, a bird's altitude can be measured using a barometer that records atmospheric pressure and comparing this against the pressure at sea level (Cleasby et al. 2015). Recently

Cleasby et al. (2015) combined barometers and GPS devices in order to track in three-dimensions multiple individual northern gannets (*Morus bassanus*) over long distances with a vertical absolute error of 0.88 m (Cleasby et al. 2015).

1.4.2 What changes when we add the vertical dimension?

The addition of the vertical dimension expands the available space within which an individual can move and interact with other individuals, from a plane to a three-dimensional volume (Jeffery et al. 2013). Animals moving and interacting with neighbours in two dimensions are restricted to three degrees of freedom: two translational (forwards/backwards, and left/right) and one rotational (yaw). However, in three dimensions the degrees of freedom are increased to six: three translational (forwards/backwards, left/right, and up/down) and three rotational (yaw, pitch, roll) (Holbrook and Burt de Perera 2013) (Figure 2a).

In three dimensions, as neighbours can be located above or below an individual and assuming that vision is the main interaction sense for many groups, the vertical structure of the visual field of an animal will influence an individual's ability to interact with neighbours in the vertical. Many animals have a blind spot directly behind them resulting in no visual information being perceived from this direction (Figure 2b, c). This is thought to result in frontal bias leadership as described in Huth and Wissel (1992), that is, individuals pay more attention to those in front and are thus more likely to follow if they are behind others (pigeons, *C. livia*: Pettit et al. 2015, three-spined sticklebacks, *G. aculeatus*: Bumann and Krause 1993). There is no obvious vertical bias in the sensory system of *A. mexicanus* or *C. livia*, with animals likely to sense above and below them equally (Figure 2b) (Chapter 5). This will not be true for all species however. For example benthic fish (e.g. skate, *Raja*

eglanteria) have a reduced visual field directly below them due to the shape and position of the eyes (Figure 2c) (McComb and Kajiura 2008). This will result in individuals being unable to detect visual stimuli directly below them and therefore cannot respond to other individuals in this visual area.

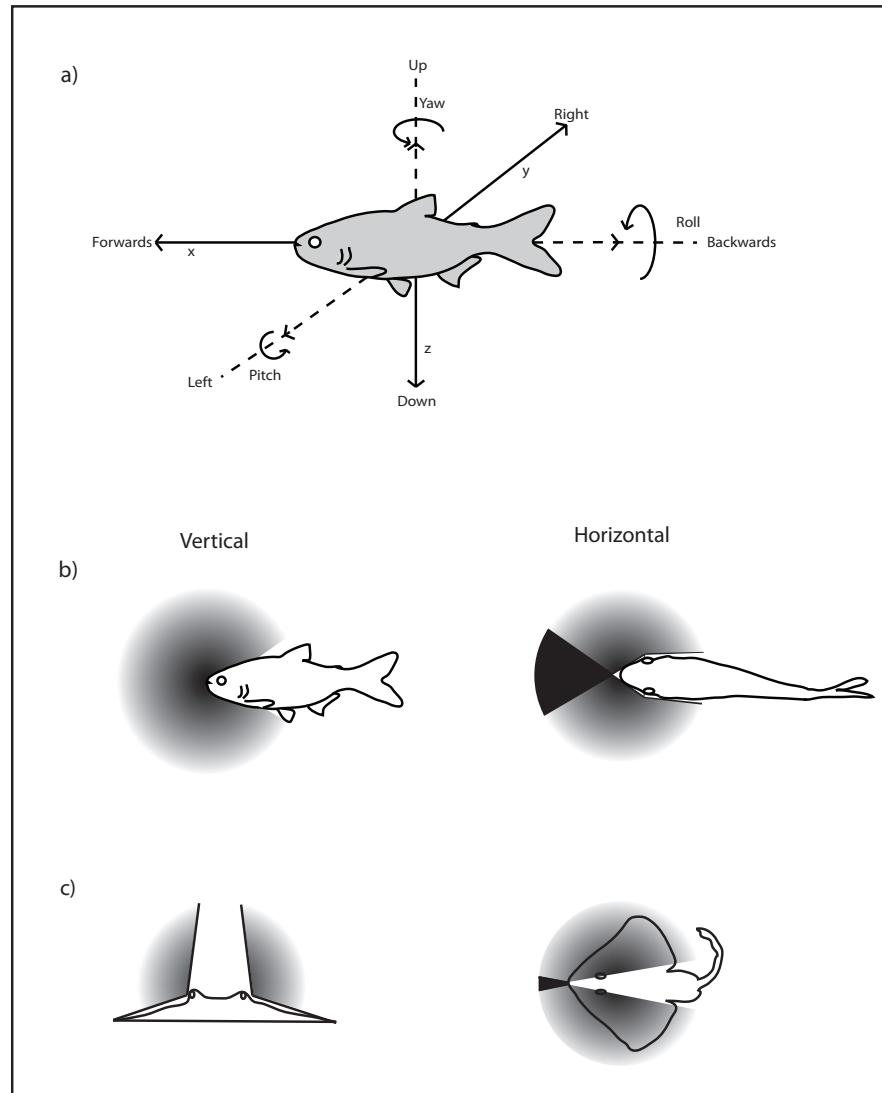


Figure 2: (a) Schematic diagram of the translational and rotational degrees of freedom and the three Cartesian axes in non-surface-bound animals. (b, c) Schematic diagram of the visual field in the vertical and the horizontal planes for (b) non-surface-bound animals *A. mexicanus* and (c) for the skate, *Raja eglanteria*. Grey shading represents where animals have monocular vision and black where binocular vision occurs. (c) Is adapted from (McComb and Kajiura 2008).

1.5 Homing pigeons (*Columba livia*) as a model species

Homing pigeons (*C. livia*) are derived from the domesticated rock pigeon, selected over numerous generations for their ability to return home after being displaced. They have been recorded returning home from novel sites over 1800km away (Walcott 1996). This ability to home from a distant unfamiliar location (true navigation)(Baker 1978) is not unique to homing pigeons. We can assume that such target-locating abilities are present in many species with a central “home” used for breeding or shelter. For example, displacement experiments have demonstrated this ability in a range of species including, Cory shearwaters (*Calonectris borealis*) (Gagliardo et al. 2013), northern elephant seals (*Mirounga angustirostris*) (Matsumura et al. 2011) and African elephants (*Loxodonta africana*) (Pinter-Wollman 2009).

The ease with which homing pigeons can be tracked during unconstrained homing flights makes them one of the most well studied species in the fields of both individual spatial cognition and collective behaviour. Early experiments investigating solo navigation involved estimated vanishing bearings of birds once released derived by using binoculars to follow the flight of pigeons to determine the direction in which they initially set off home (Keeton 1970). While this method has revealed many of the fundamental features of pigeons’ navigational strategies, it is limited, as it provides no detailed route information. In addition, identifying individual birds within a flock is difficult, limiting the studies to mainly solo or paired flights. With recent advances in on-board sensor technology, pigeons can now be tracked across their entire flight using lightweight GPS devices. These devices

provide a time-stamped series of high-resolution positional fixes (latitude/longitude) from which flight trajectories can be reconstructed in fine detail. Analysing fine-scale movements from release site to home loft using GPS devices has allowed investigation in to the navigational strategies individuals and groups employ throughout their journey For Chapters 2-4 using homing pigeons, I attach such GPS devices to all birds within experimental flocks, and set them joint navigational tasks by releasing them from specific sites 5.27-10.11km from their home loft. The devices used in this thesis (Qstarz BT-Q1300ST) weigh 13.5g, record positional fixes at 5 Hz and are affixed to birds using either a Velcro or a backpack attachment method (see methods in experimental Chapters for more detail). In the following overview, I will focus on how pigeons accomplish such navigational tasks, both individually and in groups.

1.5.1 Navigational mechanisms

A broad distinction commonly made in animal navigation research concerns whether individuals are navigating in areas familiar or unfamiliar to them. This divide is due to the difference in the cues being attended to and the difference in mechanisms by which individuals navigate in these areas.

Unfamiliar area navigation involves travelling through an area not previously visited by the individual. The theoretical basis for unfamiliar area navigation in homing pigeons is a two-step map-and-compass model (Kramer 1953). The “map” provides information on the birds’ location relative to home (Step 1) and the “compass” allows the birds to compute and assume the course towards home (Step 2) (Wiltschko and Wiltschko 2009).

The sensory basis of the map component is still under debate with evidence for olfactory cues, magnetic intensity and magnetic inclination (Wiltschko and Wiltschko 2009). The olfactory map is presently thought to be most likely method to determine the location relative to home (Papi 1991, Wallraff 2014). According to the model, at the home loft, birds associate odour borne on the wind with the direction the wind is blowing from. This enables birds to build a representation of odour distribution around their home. When displaced to an unfamiliar site, birds compare the odours in the local environment to that at home which allows them to determine the position of the site relative to home (Papi 1991).

Once the birds' location is determined, homing pigeons navigate goalwards using two compass mechanisms to maintain heading: the sun and the magnetic compass (Wallraff 2005). The sun is thought to be the primary cue used by homing pigeons. In order to use the sun's change in azimuth across the day as a compass cue, birds must time compensate the azimuth using their endogenous body clock (Kramer 1953). Robust evidence for the use of a time compensated sun compass in pigeons, some other birds and reptiles has come from studies manipulating the animals' endogenous body clock via clock-shifting (Schmidt-Koenig 1958). For example, an individual aiming to fly south, but whose body clock has been shifted six hours forward and is released at noon, will mistakenly interpret the 'noon sun' as the 6:00 p.m. sun located in the west and thus rather than fly south will fly east instead. In addition to the sun compass, pigeons have access to a magnetic compass. Experiments manipulating the magnetic field in the lab, or attaching magnets to pigeons when homing, have demonstrated that magnetoreception can also provide

compass information, especially when the sun is not available (Wiltschko and Wiltschko 2009).

Once in a familiar area, the potential navigational mechanisms change. Familiar area navigation is thought to involve a familiar area map (Baker 1982). Recent work involving high-resolution GPS tracking has revealed that pigeons follow landmarks such as roads, rivers and hedgerows (Guilford et al. 2004, Lipp et al. 2004) and develop idiosyncratic routes over repeated releases (route recapitulation) (Biro et al. 2006, Meade et al. 2006). These routes were not disrupted by magnets or by changes in wind direction (Meade et al. 2005), suggesting that pigeons were able to learn series of landmarks rather than use alternative cues. In addition, when visual input was prevented first to one eye and then to the other by the application of temporary “eye patches”, pigeons formed new idiosyncratic routes after switching eyes (Martinho et al. 2015). These studies all lead to the suggestion that visual landmarks are important for the avian familiar-area map. The ability to follow a series of landmarks may either involve a compass component (mosaic map) or require no compass and just rely on the landmarks for guidance (pilotage) (Guilford and Biro 2014). The use of visual cues does not mean pigeons necessarily stop paying attention to other navigational cues in the familiar area. Experiments using clock-shifting from within the familiar area (and even in sight of the loft) place visual (and other local cues) and sun compass information into conflict, and have shown that birds fly a partially deflected route in the direction of the clock-shift (Biro et al. 2007, Armstrong et al. 2013). This suggests that time-compensated solar cues are accessed throughout the journey on a fine-grained scale, and may be combined with direct guidance from familiar landmarks.

1.5.2 Group decision-making during collective motion

Most relevant for this thesis is how pigeons make navigational decisions when flying as a group. Homing pigeons are a gregarious species that preferentially will fly in flocks making them ideal for studying collective movement. Pigeons' tendency to flock raises questions as to whether there are advantages associated with navigating as a group compared with travelling alone (Simons 2004). Despite early work using vanishing bearings having mixed results (Keeton 1970), more recent GPS work has shown that flocks had shorter homing times and took more direct routes home than solo birds (Dell'Arciccia et al. 2008). However, this increased navigational efficiency appears to come at a cost of increased metabolic energy expenditure due to flying in cluster formation when flying together, especially for followers (Usherwood et al. 2011).

More recently work has focused on how navigational group decisions are made in homing pigeon flocks. Biro and colleagues (2006) used pigeons' propensity to develop individually preferred routes to study how conflict over homing directions is resolved. They released pairs of experienced birds, each with its own idiosyncratically preferred homing route, and reported that when the degree of difference in routes was above a threshold, leadership emerged (or the birds split), but below the threshold pairs flew a "compromise" route. By looking at pairwise relationships a transitive leadership hierarchy was discovered among all birds tested, whereby if Bird A leads Bird B and Bird B leads Bird C, then Bird A will lead Birds B and C. Building upon this result, Nagy and colleagues (2010) analysed leader-follower relations in larger flocks up to (30 individuals) using the directional correlation delay method described above. They showed that such transitive

leadership hierarchies were evident in these larger flocks as well, where individuals in a hierarchy of influence made navigational decisions during both homing and flights around their home. Recent studies have highlighted that decision-making in homing pigeons also involves democratic decision-making. Xu et al. (2012) used the same data as Nagy et al. (2010) to show hierarchical decisions were a combination of both shared and unshared interactions. These navigational leadership hierarchies are stable over a small number of releases (4-8) (Flack et al. 2013, Santos et al. 2014, Pettit et al. 2015), but their long term stability and flexibility are unknown (Chapters 3 and 4).

These advances in identifying leader-follower interactions have led to increased interest in determining the factors structuring the leadership hierarchy. What makes certain birds leaders, and others followers? Although the exact factors involved are still unresolved, a number of candidate mechanisms have emerged. In pairs of pigeons, leader-follower interactions were shown to relate to experience (Flack et al. 2012), speed (Pettit et al. 2015), and partially to maximum fidelity with which experienced birds recapitulate their route (Freeman et al. 2011). When scaling up to larger flocks, solo ground speed has been shown to predict navigational leadership hierarchies (Pettit et al. 2015). Faster birds spontaneously assume positions at the front of the flock, and because birds respond more strongly to individuals in front than behind (Pettit et al. 2013), the birds at the front will have the greatest influence over the flock's directional decisions. This link to speed has led to the suggestion that leadership hierarchies develop due to passive mechanisms in self-organized flocks rather than active decisions made by certain birds to lead or others to follow (Pettit et al. 2015). However, as the authors point out, this result does not mean all

leadership is due to speed differences (Pettit et al. 2015). The flocks used in Pettit and colleagues study were of mixed-age and therefore age and or experience could also impact leadership. Experience has been shown to influence leadership in pairs of pigeons (Flack et al. 2012), but its role in flock hierarchies is ambiguous (Flack et al. 2013).

1.6 The Characin fish (*Astyanax mexicanus*) as a model species

We used the eyed morph of *Astyanax mexicanus* that inhabits small rivers and streams in North and South America. This fish species was an ideal model to use because they readily form schools (Parzefall 1983), the majority of the previous work on fish navigation in three dimensions has been carried out using this species (Holbrook and Burt de Perera 2009, Holbrook and Burt de Perera 2011b, Holbrook and Burt de Perera 2013), and they are a robust species that is easy to raise and maintain in captivity.

One of the main advantages of using fish to study leadership is the accuracy with which individuals' positions in groups can be tracked in three dimensions. As discussed previously GPS devices currently have too high an error in altitude (compared to accuracy in longitude and latitude) to accurately study birds' movements in the vertical axis in addition to the horizontal. On the other hand, the stereo-technique can only be used in a fixed location, ideal for a tank. Leadership in three dimensions is an understudied area, and it is unknown if leadership identified in data reduced to two dimensions matches that identified when three-dimensional data is used (Chapter 5). In this overview of *A. mexicanus*, I will focus on how informational cues are used by fish in schooling and on past studies on leadership in

fish schools.

1.6.1 Navigation in three-dimensional space

As non-surfaced bound animals, fish can move easily in the vertical and horizontal dimensions of space. When navigating in the horizontal dimension fish have access to a range of cues known to be important in navigation of some species including: olfaction (salmonid fish) (Hasler and Scholz 1983), visual landmarks (Amarillo fish *Girardinichthys multiradiatus*) (Burt de Perera and Garcia 2003), mechanosensory (*Astyanax fasciatus*) (Burt de Perera 2004, Windsor et al. 2008), electrolocation (Sloman et al. 2006) and magnetism (salmonid fish) (Wiltschko and Wiltschko 2005). Many of these cues are also available in the vertical dimension (e.g. landmarks) however, there are additional cues such as light intensity and hydrostatic pressure (Burt de Perera et al. 2005). The horizontal cues used by *A. mexicanus* to navigate have received little attention (but see Burt de Perera et al. 2004 for work on the blind morph), however much is known about their navigation in the vertical dimension (Holbrook and Burt de Perera 2009, Holbrook and Burt de Perera 2011b, Holbrook and Burt de Perera 2013). *A. mexicanus* learnt vertical and horizontal information at the same rate (Holbrook and Burt de Perera 2009) and used them with similar accuracy (Holbrook and Burt de Perera 2013). However, when the two information sources were placed in conflict, individuals had a preference for vertical information (Holbrook and Burt de Perera 2009) even in the presence of stable landmarks (Holbrook and Burt de Perera 2011b). This is thought to be because hydrostatic pressure is a stable global cue that varies linearly with vertical distance in the water column and therefore is very reliable (Taylor et al. 2010, Holbrook and Burt de Perera 2011a). It has been proposed that fish use their

swim-bladder to detect changes in hydrostatic pressure in order to navigate in the vertical. This works because the percentage change in pressure caused by a vertical movement decreases as depth increases; therefore the relative rate of change in volume of the swim-bladder also decreases with increased depth (Taylor et al. 2010, Holbrook and Burt de Perera 2011a).

1.6.2 The mechanisms behind schooling

Schooling is critical for fish, as by maintaining cohesion, schools can benefit from the advantages of group formation (Krause and Ruxton 2002). Specifically, by responding to the orientations of nearby neighbours (alignment), the location of predators or resources can be transmitted through a group much further than the direct interaction range of an individual (Couzin and Krause 2003, Ioannou et al. 2011). Throughout this thesis I define schooling as the tendency for fish to synchronise and align their behaviour. This behaviour is different from shoaling, which is just the tendency to aggregate (including schooling) with other fish of the same or different species (Pitcher 1983).

The sensory systems involved in schooling are believed to mainly involve a combination of sight and mechanosensory inputs (Partridge and Pitcher 1980). The mechanosensory lateral line is made up of populations of neuromasts, comprising directionally-sensitive sensory hair cells, and are located across the whole body but concentrated on the head and trunk (Coombs et al. 2014). These neuromasts allow fish to detect distortions in flow created by an object, such as a school member, in a process called hydrodynamic imaging (Hassan 1989).

There is a debate over the importance and exact functions of vision and the lateral

line in schooling. Experiments that involve placing fish (*A. mexicanus*) shoals in the dark (John 1964) and those temporarily blinding individuals (small rudd, *Scardinius erythrophthalmus* and club mackerel, *Scomber colias*)(Parr 1927, Keenleyside 1955) suggested that vision is fundamental for schooling as blind fish were unable to school. However, Pitcher et al. (1976) and more recently Faucher (2010) showed that temporarily blinded saithe (*Pollachius virens*) were able to school, but this ability was lost when their lateral line was cut. From these experiments a proposition has emerged that vision is primarily important for maintaining position and angle between fish and the lateral line for monitoring swimming speeds and direction of travel of neighbours (Partridge and Pitcher 1980), but the exact roles may be species specific.

1.6.3 Leadership in fish schools

Fish schools were once thought to be an example of a truly egalitarian state (Shaw 1978). Leadership was first shown experimentally in fish schools using cross correlation (Bumann and Krause 1993), where, for a given moment in time the average position of the front fish was compared with the average position of the rear fish up to 400ms earlier or later. It would be expected that if a fish at the back was following the movements of a fish at the front, it would be would have the same orientation as the front fish, but with a delay in time. Due to the increase in the resolution of data that can now be collected, much finer scale studies of leader-follower interactions can now be made. For example, recently the directional correlation delay method used by Nagy et al. (2010) has been applied to fish revealing that fish (golden shiners, *Notemigonus crysoleucas*) follow directional changes of the individuals in front of them (Katz et al. 2011) and certain species (e.g.

medaka fish, *O. latipes*) are able to form relatively stable hierarchies over nine days (Perez-Escudero et al. 2014).

1.7 Unifying questions

Interest in understanding how collectively moving groups make decisions has increased over the last decade. Recent work has identified the formation of navigational leadership hierarchies in a range of species, especially those moving in three-dimensional space (Sueur and Petit 2008, Nagy et al. 2010, Sarova et al. 2010, Nagy et al. 2013, Perez-Escudero et al. 2014). However, we have a poor understanding of the factors that influence these hierarchies' formation, stability, and flexibility. Importantly, how well two-dimensional hierarchy models fit three-dimensional data remains wholly unexplored. This thesis contains four empirical data chapters that aim to address these areas, using either homing pigeons *C. livia* or the Characin fish *A. mexicanus* as model species. The following chapters are presented as self-contained manuscripts that set out to answer the following questions:

- 1) What factors influence the structure of leadership hierarchies?

(Chapters 2, 3, 4)

In Chapter 2, I focus on the link between leadership and navigational experience in pigeons – a factor that has (1) been suggested previously to be important (Flack et al. 2012) and, (2) is particularly relevant in determining how group performance varies as a function of the identity of the leader(s). One way in which differences in knowledge can occur is through differences in navigational experience developed

through previous encounters with the landscape and other environmental cues. I construct two flocks of mixed navigational experience with greater experience differences among flock members than were used in Flack et al. (2013). Half of the birds are highly familiar with a specific release site and the other half are locally inexperienced (and vice versa at a second site). Using GPS loggers I obtain tracks for all birds within the flocks, and by using directional correlation delay analysis (Nagy et al. 2010) to identify the navigational leadership hierarchy, I investigate whether “stratification” occurs based on experience, predicting that experienced birds will be clustered at the top of the hierarchy and inexperienced birds at the bottom. Repeating the experiment at two sites, where the roles of the same birds are reversed, allows me to specifically pinpoint whether hierarchical ranks are indeed contingent on experience levels.

In Chapter 3 I further investigate the role of experience by testing how important inter-individual variation in experience is in structuring the leadership hierarchy in homing pigeons. Leadership is theorized to occur when individual differences in knowledge, experience, energetic states and/or temperament occur between individuals (Conradt et al. 2003). A recent paper by Santos et al. (2014) suggested that decreasing inter-individual differences in age/experience in homing pigeon flocks resulted in an increase in shared decision-making and a decrease in leadership stability. I compare navigational leadership hierarchy stability between three flocks with uniform ages (homogeneous) and three flocks with mixed-ages (heterogeneous).

In Chapter 4 I investigate what happens when previously established leaders in pigeon flocks are navigationally ‘misinformed’. I experimentally manipulate the

quality of the leaders' navigational information, with the expectation that if navigational information influences leadership, then "bad" information at the top of the hierarchy should cause reorganisation of the hierarchy. See question 3 for more details.

2a) How stable are leadership hierarchies?

Stable leadership hierarchies will probably depend on the factors that are involved in the structuring. Previous studies in homing pigeons have concluded that leadership hierarchies are, in general, highly stable, yet have looked only at stability over a small number of releases (4-8) and over a small time frame (5-19 days)(Nagy et al. 2010, Flack et al. 2013, Santos et al. 2014, Pettit et al. 2015). Thus, stability over extended periods is unknown. Interactions over extended periods are more likely to simulate daily foraging trips. In Chapter 3, I release six flocks of homing pigeons, three homogeneous and three heterogeneous in age, in a series of 25 releases conducted over approximately one month. I investigate the stability of navigational leadership hierarchies over this time frame, whether group composition impacts on stability, and test for consequences of stability in terms of route efficiency.

In Chapter 5, I look at leadership in schools of *A. mexicanus* to study whether as with medaka fish (*O. latipes*) (Perez-Escudero et al. 2014) stability leadership hierarchies occurred. I video and reconstruct the three-dimensional tracks of 10 fish in six schools. I then use a three-dimensional directional correlation model to identify leader-follower interactions throughout 30-second bursts of data, in order to identify and then investigate the stability of leadership hierarchies.

2b) Are there advantages associated with stable leadership hierarchies?

The benefit of hierarchical leadership has been proposed to come from the stability of the decision-making structure itself, in addition to the factors that place certain individuals into leading position (Flack et al. 2013). In Chapter 3, if I find variations in the long-term stability between homogeneous and heterogeneous flocks, as suggested by Santos et al. (2014), I will look at the potential advantages of stable leadership hierarchies. After the 25 flock releases, I release all birds as solos in order to investigate their route learning. I compare the efficiencies of routes during route formation over the 25 releases and birds' efficiencies when flown solo between stable and unstable leadership hierarchies.

3) What happens when leaders have “bad” information?

Previous studies have highlighted the stability of navigational leadership hierarchies in pigeon flocks (Flack et al. 2013, Nagy et al. 2013, Pettit et al. 2015). In Chapter 4, I set out to investigate the flexibility of these decision-making structures by testing a previous model by Flack et al. (2015). This model suggested that hierarchies would be unable to compensate when error occurred in the top hierarchical position, because leadership stability would result in the error being propagated down the hierarchy (Flack et al. 2015). If this were to occur in nature, then in these situations hierarchical decision-making could be detrimental to the flock. I identify leaders in eight flocks of homing pigeons, and manipulate the leaders' personal information using the clock-shift procedure. This procedure is known to systematically interfere with pigeons' use of the sun compass by altering the their perception of geographical direction (Schmidt-Koenig 1958). After clock-shifting I look at whether

inflexible leadership results in errors spreading through the hierarchy, causing the flock to be led astray or if some compensatory mechanism prevents this detrimental result from occurring.

4) What role does adding the third dimension of space play when identifying leader-follower interactions?

All previous leader-follower studies using directional correlation delay analyses have been used on two-dimensional data irrespective of the study species moving freely in three dimensions (Nagy et al. 2010, Katz et al. 2011, Pettit et al. 2015). Vertical information has been shown to be important in navigation in fish (Holbrook and Burt de Perera 2009) and combined with the presence of neighbours above and below an individual, suggests that information from the vertical dimension could be a potential source of information during shoaling. In Chapter 5, I use *A. mexicanus* to probe this question by testing whether leaders identified when tracking data are reduced to two dimensions match those identified when the analysis is run on the full three-dimensional dataset. I also examine whether there is a directional bias to information flow in the vertical.

Finally, in the general discussion (Chapter 6) I provide answers to the questions above by summarizing the key findings of the thesis, discussing the general implications of my findings and their relevance to the field of collective behaviour and suggesting some ideas for future directions of study. This thesis hopes to further our understanding of the mechanisms by which flocks and schools make consensus decisions but also to provide insights into the adaptive value of collective organisation and decision-making.

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Chapter 2

Lack of experience-based stratification in homing pigeon leadership hierarchies

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Abstract

In societies that make collective decisions through leadership, a fundamental question concerns the individual attributes that allow certain group members to assume leadership roles over others. Homing pigeons form transitive leadership hierarchies during flock flights, where flock members are ranked according to the average time differences with which they lead or follow others' movement. Here, we test systematically whether leadership ranks in navigational hierarchies are correlated with prior experience of a homing task. We constructed experimental flocks of pigeons with mixed navigational experience: half of the birds within each flock had been familiarised with a specific release site through multiple previous releases, while the other half had never been released from the same site. We measured the birds' hierarchical leadership ranks, then switched the same birds' roles at a second site to test whether the relative hierarchical positions of the birds in the two subsets would reverse in response to the reversal in levels of experience. We found that while across all releases the top hierarchical positions were occupied by experienced birds significantly more often than by inexperienced ones, the remaining experienced birds were not consistently clustered in the top half – in other words the network did not become stratified. We discuss our results in light of the adaptive value of structuring leadership hierarchies according to “merit” (here, navigational experience).

2.1 Introduction

During collective travel, individuals must maintain cohesion in order to sustain the benefits associated with group motion, including predator avoidance, increased foraging benefits and enhanced navigational efficiency (Krause and Ruxton 2002). Groups are rarely homogeneous; inter-individual differences in knowledge, motivation or social status may be present, resulting in potential conflicts of interest. When conflicts arise, leader/follower interactions can emerge from these inter-individual differences (Conradt and Roper 2003). A fundamental question of group living is how individual attributes allow certain group members to assume leadership roles over others. In systems where leadership is implicated, the benefits derived from, and ultimately the adaptive value of, collective decision-making will depend on the mechanism that places specific individuals into leadership positions.

Theoretical and empirical work suggests a variety of inter-individual differences can affect specific individuals' abilities to influence group movements (Reebs 2000, Conradt et al. 2009). For example, dominance has been shown to be associated with leadership in many mammalian species with strong social ties, including grey wolves (*Canis lupus*) chacma baboons (*Papio ursinus*), rhesus macaques (*Macaca mulatta*) and beef cows (*Bos taurus*) (Peterson et al. 2002, King et al. 2008, Sueur and Petit 2008, Sarova et al. 2010). Furthermore, observations suggest that leadership is assumed by knowledgeable individuals in golden shiners (*Notemigonus crysoleucas*) and pairs of homing pigeons (*Columba livia*) (Reebs 2000, Flack et al. 2012), or by the oldest individuals in elephants (*Loxodonta africana*) and dogs (*Canis canis*) (McComb et al. 2011, Akos et al. 2014) (with the caveat that age is

typically not independent of knowledge and experience). Empirical evidence also suggests a role for motivation, resulting in leadership “according to need” (Conradt et al. 2009). For example, frontal positions during group movements are taken up by hungrier individuals in several fish species (Krause 1993, Nakayama et al. 2012) and by lactating females in plains zebras (*Equus burchellii*) (Fischhoff et al. 2007). In groups where knowledge and motivation are similar across individuals, intrinsic factors such as temperament (boldness/shyness) have been shown to predict leadership in a range of species (Beauchamp 2000, Harcourt et al. 2009, Kurvers et al. 2009, Nakayama et al. 2012). Overall, however, it is important to note that these factors are not mutually exclusive, nor are they likely to operate independently. Instead, the mechanisms behind the emergence of leader/follower interactions are most likely to involve a combination of factors specific to each system. For example, when pairs of three-spined sticklebacks (*Gasterosteus aculeatus*) have similar nutritional levels, bolder individuals initiate leading events. However, when nutritional levels vary, the individual with the lower nutritional state initiates leaving cover (Nakayama et al. 2012).

Homing pigeons are an excellent model species for the study of collective decision-making due to their gregarious nature and the ease with which inter-individual differences within flocks can be manipulated. Early studies based on direct observation suggested that leadership, by one or a few birds, was operating in homing pigeon flocks ((Wagner 1982); see also (Jorge and Marques 2012)). With recent technological advances, birds’ movements within the flock can now be measured through on-board GPS loggers, yielding high-resolution data on collective movement dynamics and allowing more detailed insights into leadership in these

flocks. Such studies have revealed that pigeon flocks form transitive, multi-level navigational leadership hierarchies, with individuals contributing (on average) with different weights to the movement decisions of the flock (Nagy et al. 2010). The phenomenon itself appears robust, observable in flocks of different sizes (Nagy et al. 2013) and in different populations of pigeons (Nagy et al. 2010, Nagy et al. 2013, Santos et al. 2014). A recent study (Pettit et al. 2015) has confirmed individual flight speed as an important factor in structuring the leadership hierarchies, showing faster pigeons tend to lead flocks. Speed, in turn, has been shown to be influenced by morphological factors (Pettit et al. 2015) and motivation (Dell'Arciccia et al. 2009). However, the extent to which previous navigational experiences modulate these relationships remains unknown, since all birds in Pettit et al.'s study (Pettit et al. 2015) were equal in their lack of prior homing experience. Here we therefore focus on the link between leadership and navigational experience – an attribute that (i) is particularly relevant in determining how group performance varies as a function of the identity of the leader(s), and (ii) can be most easily manipulated experimentally.

Differences in knowledge can stem from differences not only in navigational experience through previous encounters with the landscape and other environmental cues, but also from individual differences in navigational skill or strategy. Although there is evidence that experienced birds are more likely to lead when flown in a pair (Flack et al. 2012), when scaled up to larger flocks of around ten birds, increases in experience do not improve a bird's chance of leading. In a study by Flack and colleagues (Flack et al. 2013), existing leadership hierarchies were resistant to change when specific individuals' navigational knowledge was selectively increased through additional solo flight training. One possible reason for

the differences in these findings was, as the authors suggested, that their latter experiment failed to generate large enough differences in knowledge to reorganise the hierarchies. Prior to the solo training, all birds had already participated in eight flock flights, and therefore most probably had already approached near-maximal levels of navigational efficiency (Guilford and Biro 2014), leading to a ceiling effect.

In the present study, we aim to resolve this problem, and to examine systematically how a specific individual attribute – navigational experience – contributes to structuring leader-follower relations in large-scale orientation tasks performed by homing pigeon flocks. We constructed two flocks of mixed navigational experience, in which half the birds were highly familiar with a specific release site while the other half were locally inexperienced (having never been released from the same site previously), and then repeated the design at a second site where the roles of the two halves in each group were reversed. We tracked flock flights from both sites using miniature GPS devices carried by all subjects, and then compared the hierarchical ranks obtained by the same individuals at the two sites. Our rationale was that if leadership was influenced by navigational experience, then the results should reveal clear differences in the ranks attained by birds at the two sites, depending on whether they belonged to the experienced or the inexperienced half of the flock. Essentially, at each site we predicted a form of “stratification” within the leadership network based on knowledge, with the more experienced birds consistently clustered together in the top half of the hierarchy, and less experienced birds clustered in the bottom half. Crucially, individual birds’ occupancy of the two clusters would be expected to reverse between sites, providing a clear diagnostic of experience-based structuring in the network.

2.2 Methods

2.2.1 Subjects

This study used 27 adult homing pigeons bred and housed in two lofts, of around 140 birds, at the University of Oxford Field Station at Wytham (51°6' 58.34" N, 1°19' 02.40" W). Throughout the experiment, birds had free access to food (standard homing pigeon grain mix), water, minerals and grit. All experimental birds were 2 years old and all had received basic training consisting of multiple flock and solo releases from sites 2-3 km from the loft. In addition, 23 of the 27 birds had experimental homing experience: the previous year they had flown both in solo and paired flights from a single release site (Kirtlington; distance to home: 10.45 km, direction to home: 196.4°), but none had ever visited the two release sites used in the current experiment.

Twenty of the Kirtlington-experienced birds were randomly selected and divided into four groups of five individuals (henceforth referred to as groups A, B, C and D). The remaining seven birds were assigned to a fifth flock ("reserves"), which also received training in parallel to flocks A-D, and from which we transferred birds to experimental flocks when any of the experimental birds were lost. This occurred in four cases: 1 bird in group A, 1 bird in group C and 2 birds in group D.

2.2.2 Experimental procedure

Two release sites were used: Site 1 near High Cogges (distance to home loft 9.36 km, direction to home loft 90.1°) and Site 2 near Beckley (10.11 km, 264.3°). Based on previous studies, these distances – approximately 10 km in each case – were

deemed far enough from the loft that we could assume that birds were initially navigationally inexperienced at our test sites. Several observations are relevant to this assumption. First, numerous past studies observed that birds that had not previously been released from sites as little as 5 km from their loft show initially steep learning curves in that they gradually improve their efficiency and route fidelity over a series of releases before these measures asymptote around the 8th-10th flight (an effect first reported in (Meade et al. 2005); see also review in (Guilford and Biro 2014)). Releasing birds a further 10-20 times causes either no or only limited increase in the efficiency of routes. Both of these are highly robust effects, reproduced reliably in every experiment so far conducted under comparable conditions to ours (Guilford and Biro 2014). Second, data from feral urban pigeons shows only 7.5% were documented to fly over 2 km during foraging trips (Rose and Nagel 2006), suggesting that even birds that do not have an *ad libitum* supply of food at their home loft or roost (as is the case with our subjects) do not typically undertake foraging or exploratory journeys long enough to bring them even halfway to our release sites. Third, while there is a possible alternative to a purely learning based account – i.e. that training causes a switch in navigational strategy rather than, or as well as, learning (see Discussion) – in either case considerable differences are evident in homing performance as a function of flight number. In sum, training birds from previously unvisited sites has clear, observable effects on birds' homing, and these effects can be ascribed to increases in experience.

At Site 1, groups B and C received the “Experienced” treatment (see below for details of experimental treatments), while groups A and D were the “Inexperienced” flocks.

The treatments were reversed at Site 2: groups A and D received the “Experienced” treatment and groups B and C the “Inexperienced” treatment.

For the training phase, the Experienced treatment involved the groups being released eight times (T1-T8) in succession at their respective sites, while the Inexperienced groups of the same site were never taken to that site. This ensured that between the two treatment groups the birds had very different levels of experience. The Site 1 releases and Site 2 releases were carried out in an alternating order, allowing all groups to experience similar weather conditions and time intervals between successive flights.

The testing phase followed completion of training. We combined a group of Site 1 Experienced and a group of Site 2 Experienced birds (groups B and A, respectively), and did the same for the remaining two flocks (groups C and D), thereby creating two mixed-experience flocks of 10 (groups AB and CD). The compositions of the two flocks are illustrated in Figure 1. Each flock of 10 had eight experimental test releases (E1-E8) from each site, alternating between sites. As one bird from flock A did not return from the first test release, for the remaining test releases group AB consisted of four A-birds and five B-birds.

	Composition of Flock AB	Composition of Flock CD
Experienced Site 1	Flock B 5 birds	Flock C 5 birds
Experienced Site 2	Flock A 4 birds	Flock D 5 birds
Total number of birds	9	10

Figure 1. Composition of test flocks (groups AB and CD) with respect to training experienced by their members.

During both the training and testing phases, releases were carried out on consecutive days when the sun was visible and wind speed was $<7\text{ms}^{-1}$. A maximum of two releases were performed each day and there was a minimum interval of one hour between releases.

2.2.3 Data logging

Subjects were tracked on all training and testing flights using commercially available GPS loggers (Qstarz BT-Q1300ST). These devices weighed 15.5g and logged time-stamped longitude and latitude coordinates at 5Hz (absolute spatial error: mean = 1.69m, 95th percentile = 4.33m, (Pettit et al. 2013)). They were attached using Velcro strips glued onto clipped feathers along the birds' back. Data was downloaded using QTravel (Qstarz V.3.2) software and all processing of data was carried out in Matlab (R_2012B) using custom-written code (Pettit 2014). The geodetic latitude and longitude coordinates provided by the GPS were first

converted to X and Y Universal Transverse Mercator (UTM) coordinates using UTM projection. Tracks were speed filtered using the same method as Pettit (Pettit 2014), to remove portions of the tracks when the pigeons had landed, by only keeping points where speed was continuously above 5ms^{-1} either for 10s before or 10s after the time point. Pigeons frequently circle near the start and at the end of a flight, so to focus on the homing portion of the tracks, only points 100m from the release point (start) and from the loft (end) were used.

2.2.4 Data analysis

Where possible we used Linear Mixed Models (LMMs) or Generalised Linear Mixed Models (GLMMs) to analyse the data, with the lme4 package in R (R Core Team 2014, Bates et al. 2015). For all LMMs and GLMMs in this study we checked the assumptions of linearity, normality and homoskedasticity by visual inspection of plotted residuals.

In order to evaluate the increase in birds' navigational experience through the training phase, we used two measures of homing performance: i) homing efficiency and ii) distance of route from the beeline. We defined efficiency as the straight-line distance between the release site and the loft divided by the actual distance travelled by the bird (Biro et al. 2006) and the distance from the beeline as the nearest-neighbour distance from each point on the track to a straight-line path composed of 100 points from start to finish (Pettit et al. 2013). These two measurements are often correlated (low efficiency with large distance from the beeline and high efficiency with small distance from the beeline), although not always (a bird may stay close to the beeline but fly a locally tortuous track, leading to low efficiency and small distance from beeline). In order to compare flock homing

performance across the training releases, we calculated the groups' mean efficiency and distance from the beeline (excluding birds that split). A bird was deemed to have split if it spent less than 75% of the flight within 100m of another bird. Using a LMM, with *release* and *site* as fixed factors and *group* as a random factor, we examined how efficiency and distance from the beeline changed as releases progressed from T1 to T8.

To measure leader-follower relationships in each experimental group during testing, we calculated the directional correlation delay for each possible pairing of birds using methods based on Nagy and colleagues (Nagy et al. 2010) and Pettit and colleagues (Pettit et al. 2015). This analysis measures the temporal relationship between a bird's flight direction and those of the other flock members, identifying birds as followers when they perform changes in direction that match those of others but are delayed in time. The directional correlation between pairs i and j is, $C_{ij}(\tau) = \langle v_i(t) \cdot v_j(t+\tau) \rangle$, where $v_i(t)$ is the normalized velocity of i at time t and $v_j(t+\tau)$ is the normalized velocity of bird j at time $t+\tau$. Normalized velocity is calculated by dividing the velocity vector by its magnitude (i.e. $v_i(t) = x_i(t)' / |x_i(t)'|$). The value of τ_{ij} (tau) that maximizes the $C_{ij}(\tau)$ correlation function across t , is the average time delay between a pair of birds (Supplementary Figure 1). The directional correlation time delay (τ_{ij}) for a pair of birds i and j , is the time taken for bird i to react to a change in direction of bird j . If $\tau_{ij} < 0$, then when bird i turns, j has already turned and therefore can be interpreted as j leading i . We resolved leader-follower relations between all pairs of birds that spent a minimum of 120s within 100m of each other during flight (Supplementary Figure 2).

To calculate unique hierarchical positions for each bird, we calculated the average directional correlation time delay of bird i with the rest of the flock (τ_i) weighted by duration (Pettit et al. 2015). The most positive value identifies the bird at the top of the hierarchy. To test individuals' positional consistency in the hierarchy across the testing phase releases (E1-E8), we calculated intra-class correlation coefficients using LMMs, with *individual* and *release* as random effects. This method is identical to that used in Pettit (Pettit et al. 2015). The formula $r = \sigma^2_{\text{individual}} / (\sigma^2_{\text{individual}} + \sigma^2_{\epsilon})$, where $\sigma^2_{\text{individual}}$ is the between-group variation and σ^2_{ϵ} is the residual variation, gives the repeatability measurement as the proportion of variance due to individual at a particular site (Nakagawa and Schielzeth 2010). To test for significance we used a randomization test, where we randomized the 10 (nine in case of group AB) τ_i values within each release and re-calculated r (r_{rand}) for each iteration. We calculated the p-value as the proportion of 10^4 randomizations with $r_{\text{rand}} \geq r$ (Nakagawa and Schielzeth 2010).

To test if experience affects hierarchical position in the flock, we calculated for each bird its average position within the hierarchy across the eight testing releases ($\tau_{i,\text{bar}}$) by averaging the τ_i values across the releases. Using a paired t-test we compared for each bird the mean difference in $\tau_{i,\text{bar}}$ values obtained when the bird flew from the site at which it was experienced and those obtained from the site at which it was inexperienced. As it was on the first release of testing from a given site that the inexperienced birds maximally naïve, we repeated this test for just the first release of testing. In addition, making use of the full data set of testing releases rather than just the per-bird averages as above, we examined whether experienced birds had

higher τ_i values in any given release, using a LMM. Finally, looking more specifically at only the birds at the very top and very bottom of the leadership hierarchy, we tested, using binomial tests, whether the highest- or lowest-ranked birds were more likely to belong to one treatment group (experienced or inexperienced, respectively) than from the other.

2.3 Results

2.3.1 Navigational performance

First, we evaluated the effect of training on homing performance. The number of birds used for each release during this analysis is reported in Supplementary Table 1. Across the eight releases of training (T1-T8), homing efficiency significantly increased by 0.529 ± 0.211 (mean $\pm$ s.d.), resulting in an average 71% reduction in path length compared to the first release (LMM with *release* as fixed factor and *group* as a random factor: Maximum Likelihood comparison to model without release $P < 0.001$). Distance from the beeline significantly decreased by an average of $62\% \pm 33\%$ from the first release (mean $\pm$ s.d.) (natural logarithm transformation on skewed response variable, LMM with *release* as a fixed factor and *group* as a random factor: Maximum Likelihood comparison to model without release $P = 0.034$). In both tests, including the fixed factor *site* did not significantly lower the AIC calculated by Maximum Likelihood and thus did not improve the models' fit so was removed (Supplementary Table 2). These results demonstrate that birds adopted increasingly direct routes home over the course of training, confirming that, while initially inexperienced, training resulted in an increase in their levels of navigational

experience.

2.3.2 Leadership

Transitive, multi-level leadership hierarchies were detected during our flocks' flights from both sites (see Figure 2 for an example). However, for two of the four groups, we found no significant individual repeatability in individuals' average directional correlation delay times across their eight testing releases (Table 1), indicating that the leadership hierarchy did not remain consistent across flights. Only at Site 2 was there low but significant repeatability for Groups AB and CD. We did not find evidence of significant repeatability between the two sites for any of the groups (Table 1), suggesting that individuals did not maintain consistent ranks when they were tested as experienced vs inexperienced flock members.

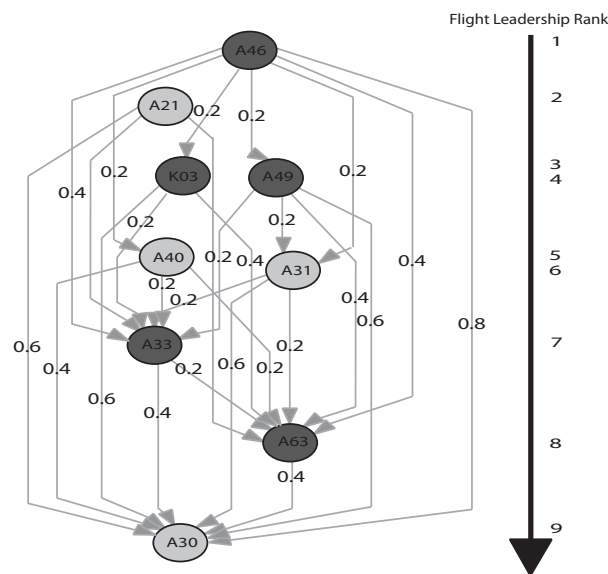


Figure 2. Example of leadership hierarchy. Network shown is for Flock AB Site 2, release 7. Nodes are individual birds, and for each pairwise comparison, edges point from leader to follower. The values represent the time delays (in seconds) between each pair. The lack of an edge means either the $C_{\max}$ value between the pair was below 0.99 or the delay was below 0.2, the lowest resolution of

the GPS device. Dark grey nodes show individuals experienced at the site shown, while light grey nodes are the inexperienced birds.

Table 1. Individual consistency in hierarchical position within leadership networks. r is the intra-class correlation coefficient from an LMM with the random effects shown. Six repeatability values were calculated across all eight testing phase releases (E1-E8); four are consistency of leadership among flock flights at a particular site (see top four rows of table) and two are consistency of leadership between sites for both flocks (bottom two rows). P-values were calculated using a randomization test as the proportion of 10^4 randomizations with $r_{\text{rand}} \geq r$. Rows in bold represent significant levels of consistency in leadership ranks.

Response	Random effects	r	p
Hierarchical position ($\tau_{i,\text{bar}}$) Group AB Site 1	individual, release	0.108	0.085
Hierarchical position ($\tau_{i,\text{bar}}$) Group AB Site 2	individual, release	0.244	0.004
Hierarchical position ($\tau_{i,\text{bar}}$) Group CD Site 1	individual, release	0.087	0.104
Hierarchical position ($\tau_{i,\text{bar}}$) Group CD Site 2	individual, release	0.234	0.013
Hierarchical position ($\tau_{i,\text{bar}}$) Group AB	Individual, site	0.000	1
Hierarchical position ($\tau_{i,\text{bar}}$) Group CD	Individual, site	0.420	0.137

Due to the low/non-significant repeatability of individuals' positions in the hierarchy across releases, comparing birds' average time delay values ($\tau_{i,\text{bar}}$) across testing (i.e. between sites where they were either experienced or inexperienced) should be evaluated with care. Birds did not have significantly higher mean time delay values at sites where they were experienced, compared with sites where they were inexperienced (Flock 1: Paired Two-Sample t-test $t_9 = 0.913$ $P = 0.372$, Flock 2: Paired Two-Sample t-test $t_{10} = -0.923$ $P = 0.367$). Although these results are based on average measurements across all eight releases, and may thus have been affected by the low repeatability scores across releases, the same results held true even when considering only the first release (Release E1) (Flock 1: Paired Two-Sample t-test $t_9 = 1.05$ $P = 0.305$, Flock 2: Paired Two-Sample t-test $t_{10} = -1.49$ $P = 0.159$). An additional analysis, which controlled for any potential bias due to low repeatability by the LMM taking into account the τ_i values calculated for each individual in every flight rather than averaging across them, further confirmed these results. Experience had no significant effect on the τ_i value of birds within a flock (LMM with *experience* as a fixed factor and *individual* nested in *group* as a random factor: Maximum Likelihood comparison to model without *experience* $P = 0.110$), showing that there was no stratification in the network based on birds' experience. Site and Release were non-significant factors and thus removed from the model.

The identity of the bird occupying the highest position in the hierarchy was significantly associated with experience (Binomial test, expected = 0.5, $P = 0.020$). In 23 out of 32 flights (72%) the highest ranked bird was experienced (Figure 3). Table 2 shows the number of different experienced birds that led across the 32 flights. In three of the four release series multiple different birds led, but this was not the case

for Group CD at Site 1 where leadership was dominated by just one bird. To examine the effect that this particular bird had on our results, we repeated our analysis after excluding the dataset from Group CD at Site 1. Our conclusions remain largely unchanged (leadership was still assumed by an experienced bird 71% of the time). This trend was strongest for the first two flights, where across all four flocks, the highest ranked bird was always an experienced individual. Furthermore, for three of the four flocks we did not observe an inexperienced bird occupying the top position before the 5th release. Birds at the bottom of the leadership hierarchy were more often inexperienced than experienced ones (21 inexperienced out of 32 releases; Fig. 3) but this difference was not significant (Binomial test, expected = 0.5, $P = 0.055$).

Table 2. Number of flights led by an experienced bird, and number of different birds that contributed to these counts, in each of the eight-release series performed by the two groups at the two sites. In three of the release series leadership is assumed by multiple different birds; only in one case (Group CD at Site 1) does one individual dominate all flights. Analyses (see main text) were repeated both with and without the inclusion of the latter dataset.

	Group AB Site 1	Group AB Site 2	Group CD Site 1	Group CD Site 2
Number of flights led by experienced bird	5	7	6	5
Number of different experienced birds who led	3	5	1	3

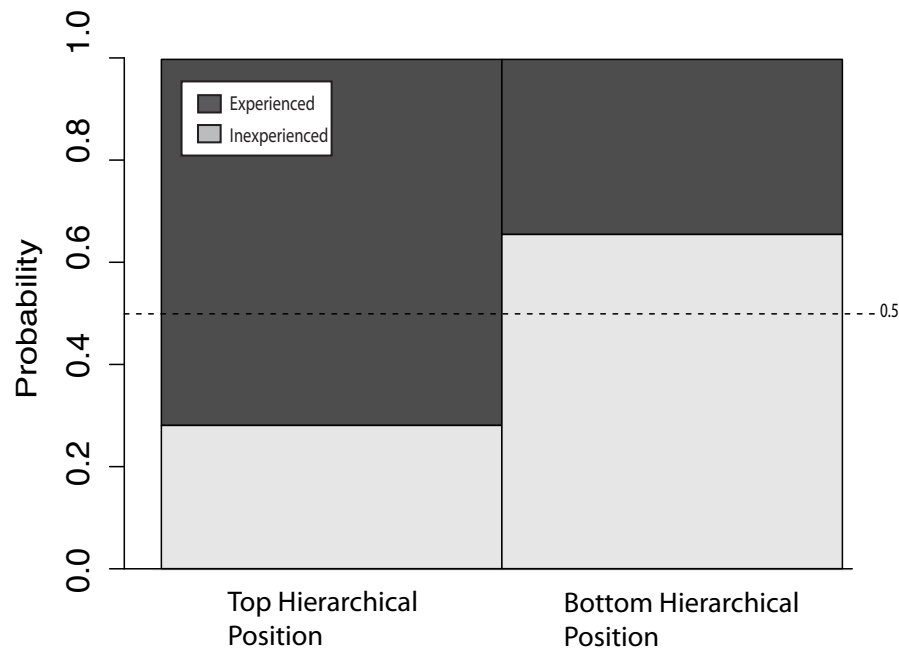


Figure 3 The probability that an individual occupies the top or the bottom leadership hierarchical position as a function of experience. Data are across all flights. Dark grey represents experienced birds and light grey inexperienced birds. The dashed line indicates chance level. Experienced birds occupied the top leadership hierarchical position more often than expected by chance (see main text for statistical detail).

2.4 Discussion

In animal groups in which at least some decisions are made by leaders rather than being fully “democratic” (i.e. rely on unequal rather than equal contributions from all group members), the accuracy of collective decisions will depend on the factors that place specific individuals into leadership positions. For flocks of birds navigating towards a target, for example, the flock can assume a more efficient route if the birds with greater navigational experience contribute with the greatest weight

to the flock's movement decisions. Previous research has suggested that experience may indeed be an important individual attribute that affects birds' propensity to lead during flock flights (Nagy et al. 2010), however, only in cases where inter-individual differences in experience are sufficiently large (Flack et al. 2012). Our present experiments were designed to examine whether the experience effect detected in pairs of birds by the latter study (Flack et al. 2012) would scale up to larger groups and to the context of leadership hierarchies. We identified an important subtlety: we found that while experience did not consistently affect the majority of positions in the hierarchy (in concordance with Flack et al. 2013), the top rank was predictably assumed by a relatively more experienced bird. This was especially prominent during early releases where the difference in experience between the two subsets was greatest. Overall, our results lend support to the suggestion that experience is an important factor in determining leadership during short-range homing flights, but also imply that additional individual attributes will influence the hierarchical structure of the flock as a whole, typically outweighing – or acting in combination with – experience as we move below the top ranks in the hierarchy.

It is worth noting that while our experimental design relied on large differences in experience between the two treatment groups, with the assumption that the Inexperienced group had never previously visited the release sites, we could not be fully certain that none of our birds had spontaneously ranged in the vicinity. As such, we could not guarantee that they were fully naïve. However, the steep increases we observed in route efficiency as a function of release number (consistent with numerous previous studies (Guilford and Biro 2014)) strongly suggest an increase

in birds' familiarity with the local landscape through learning, as a result of training. If we do hypothesise that birds were not fully naïve with the sites at the start of training, then it is possible that we were observing – rather than changes in familiarity – changes in navigational strategy (for example, a shift away from sun-compass-based towards more landmark-based navigation (Gagliardo et al. 2005)). Nonetheless, in either case, the increases we observed in route efficiencies and route recapitulation must be inferred to be the consequence of increases in experience, validating our experimental design.

That experience may be an important factor in structuring leadership hierarchies has a firm theoretical basis. When travelling in groups not all individuals will possess pertinent navigational information. Theoretical work by Couzin and colleagues (Couzin et al. 2005) has shown that a relatively small proportion of informed individuals are sufficient to guide a group, and that information can be transferred without knowledge of which individuals are informed. High navigational certainty may result in some individuals placing greater weight on their own decisions than on that of others or on maintaining group cohesion, resulting in them acting as leaders (whom others follow) and having the greatest input into the groups' movement decisions (see models in (Conradt et al. 2009)). Following an experienced member of the flock can benefit all members as it can increase the group's navigational accuracy, which in turn reduces, among other things, energy expenditure, time spent at risk of predation, and time spent away from the nest. We would argue that these benefits are maintained even if only the bird at the top of the leadership hierarchy is experienced, since by definition these birds' knowledge will have the greatest influence on the flock's overall movement.

Given that the effect of navigational experience does not seem to extend beyond the top rank, what other factors may be involved in structuring leadership hierarchies in pigeon flocks? Theoretical and empirical evidence suggests a number of potentially relevant individual attributes. Importantly, the model developed by Pettit and colleagues (Pettit et al. 2013) predicts that, with all else being equal, faster birds – i.e. those that attain higher speeds when flying solo – will fly at the front of flocks and therefore dominate the choice of route. This prediction has now been empirically confirmed in both paired (Pettit et al. 2013) and larger-flock flights (Pettit et al. 2015). However, it is important to note that speed may itself be a function of a variety of factors, including age, morphology, physiology and motivation. In addition, it is currently unknown whether temperament – a parameter that in many species has been shown to influence leadership (Beauchamp 2000, Harcourt et al. 2009, Kurvers et al. 2009, Nakayama et al. 2012) – has any impact the organisation of decision-making in pigeon flocks. These factors may act in combination to determine individuals' speed and positioning within the flock, and thus potentially their rank in the hierarchy.

An interesting, and unexpected, feature of our data was that the leadership hierarchy was not stable across releases for two of the four experimental flocks. This is in contrast to previous studies using both GPS-based quantitative analysis (Nagy et al. 2010, Flack et al. 2013, Pettit et al. 2015) and visual observations (Wagner 1982) which report repeatability in individual birds' relative ranks from flight to flight and even across contexts. Our observed lack of hierarchy stability also gives weight to the suggestion that while individual flight speed (or some correlate thereof) is an important factor in structuring leadership hierarchies (Pettit et al.

2015), it does not act as the sole or primary determinant of an individual's leadership rank, at least under some circumstances. One difference between this and previous studies was the relative homogeneity in the age of the subjects in our flocks: all of our subjects had hatched in the same year, whereas other studies have used mixed-age flocks. While experience naturally positively co-varies with age in most animal groups, the role of age in affecting speed in homing pigeons is unknown. Small differences in age have been shown to influence leadership in small flocks but only in very young pigeons (under one year) (Jorge and Marques 2012). Santos and colleagues (Santos et al. 2014) showed that same-aged flocks experienced a reduction in leadership stability (although they themselves did not test mixed-age flocks), which could explain the evident lack of stability across releases for two of the four flocks in our study. Another, potentially relevant, difference between our study and previous studies concerns the experimental procedure employed for releases. In previous studies that used multiple sites (Nagy et al. 2010, Flack et al. 2013, Pettit et al. 2015) all releases were carried out at one site before the experiment moved to another. In contrast, the releases in this study alternated between sites, in order to balance the experience level of the two groups between the two sites. Flack and colleagues (Flack et al. 2014) showed that gaining experience with multiple routes concurrently (i.e. being released in an alternating fashion from different sites) did not seem to hinder individuals' ability to learn routes. However, the effect of multiple-route learning on the formation and stability of navigational leadership hierarchies is unknown, and needs further investigation. The fact that significant stability was found at one of our sites may suggest that the effect is at least partially site-specific.

In conclusion, our results confirm an important effect of navigational experience on leadership in homing pigeons at the highest, most influential position of the leadership hierarchy. Intuitively, this would appear to make sense from an adaptive perspective: having an experienced bird as the one responsible for the greatest proportion of the flock's movement decisions is likely to be beneficial as it will increase the flock's navigational accuracy. However, why leadership ranks in the rest of the flock do not segregate between experienced and inexperienced birds presents an interesting puzzle. Does the fact that the remaining experienced birds were not clustered in the top half of the hierarchy suggest a sub-optimal arrangement? Empirically, we are unable to compare the navigational efficiencies of flocks with and without such segregation, since we cannot impose the segregated (or "stratified" (*sensu* (Henrich and Boyd 2008))) structure on the group ourselves. However, previous modelling work provides some important insights into the potential benefits of embedding naïve individuals among those better informed. First, agent-based simulations have suggested that merit-based stratification (which, in our case, we can interpret as sorting according to navigational experience) ultimately reduces the efficiency of information flow within networks of interacting individuals through the formation of "elites" who preferentially associate with each other rather than with those outside their subgroup (David-Barrett and Dunbar 2014). Second, adding uninformed individuals to groups can promote consensus decisions by "dampening" conflict among subsets of individuals (Couzin et al. 2011). While such conflict in our flocks is likely to have been low since all our experienced flock members had undergone training together, it is nonetheless possible that a form of buffering by naïve birds can enhance group performance within a hierarchical network. Future work into understanding not only the mechanisms

through which certain individuals are placed in leadership positions but also how uninformed individuals affect information flow through networks they share with knowledgeable group mates, will further inform us about the adaptive significance of hierarchical structures in decision-making by animal collectives.

2.5 Acknowledgments

We thank Julian Howe and Phil Smith for animal husbandry and technical support, and Ben Sheldon for the initial experimental idea from which this study was developed. We are also grateful to three anonymous reviewers for helpful comments on the manuscript.

2.6 Supplementary Information

2.6.1 Tables

Table S1: Table showing numbers of individuals in the flock that contributed to the efficiency and distance from beeline analyses across the training phase. Data from birds that did not remain within 100m of at least two other birds for 75% of their entire track were removed. In each case (x) identifies the number of birds who split and (x) identifies the number of birds for whom GPS data are missing.

Release	Number of birds in group			
	Group A Site2 5 birds	Group B Site1 5 birds	Group C Site 1 5 birds	Group D Site 2 5 birds
T1	2 ⁽¹⁾ (2)	2 ⁽²⁾ (1)	2 ⁽³⁾	3 ⁽²⁾
T2	4 ⁽¹⁾	5	5	4 ⁽¹⁾
T3	2 ⁽²⁾ (1)	3 ⁽²⁾	4 ⁽¹⁾	4 ⁽¹⁾
T4	3 ⁽¹⁾ (1)	5	5	2 ⁽²⁾ (1)
T5	5	3 ⁽¹⁾ (1)	5	3 ⁽¹⁾ (1)
T6	3 ⁽¹⁾ (1)	5	5	4 ⁽¹⁾
T7	4 ⁽¹⁾	5	4 ⁽¹⁾	5
T8	4 ⁽¹⁾	5	4 ⁽¹⁾	4 ⁽¹⁾

Table S2: Table showing the model deletion steps for the LMM testing if release significantly affects both efficiency and distance from the beeline. We calculated AIC using Maximum Likelihood and tested for significance using Chi-square. In both cases the Maximum Model (Model 1) contains *release* and *site* as fixed effects and *flock* as a random effect. In the simplified model (Model 2) we removed the non-significant fixed term of *site* and we then tested for significance of *release* (Model 3). Efficiency and distance from beeline are both significantly associated with release (Efficiency: ML comparison model with (Model 2) and without release (Model 3) $P < 0.001$, NND: ML comparison model with (Model 2) and without release (Model 3) $P = 0.034$).

Model	Response	Fixed effects	Random effects	AIC	Chisq	df	P
1	efficiency	release site	flock	-18.19			
2	efficiency	release	flock	-19.93	0.257	1	0.612
3	efficiency		flock	-8.01	25.9	7	<0.001
1	beeline	release site	flock	22.18			
2	beeline	release	flock	22.39	2.20	1	0.137
3	beeline		flock	23.54	15.2	7	0.034

2.6.2 Figures

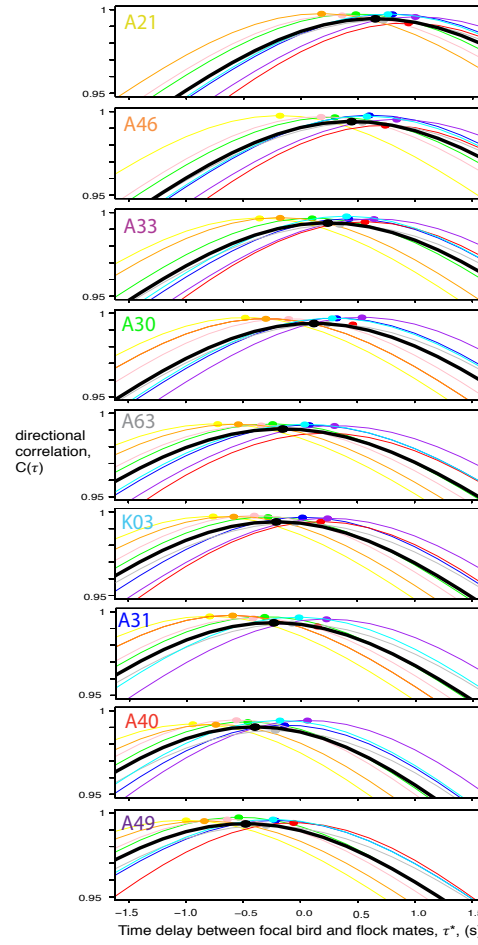


Figure S1: Example illustrating the calculation of leader-follower relations in homing pigeon flocks, as resolved by the directional correlation analysis. Each panel shows the focal bird's directional correlation function compared to every other bird in the flock for a single flight, against the time delay, τ . Group AB release 8 is shown here, with the birds ordered from leading to following (i.e. A21 is at the top of the leadership hierarchy). Each coloured line represents $C_{ij}(\tau)$, the correlation between bird the focal bird (i) and the non-focal bird (j). The black line shows $C_i(\tau)$, the duration weighted-average. The maximal correlation is associated with a time delay, τ_i . The coloured circles indicate the maximal correlation τ value for a pair, τ_{ij} . This quantifies the pairwise leader/follower relationship; $\tau_{ij} > 0$ indicates that bird i leads bird j . The black circle shows the overall leadership value for bird i , with respect to the rest of the flock.

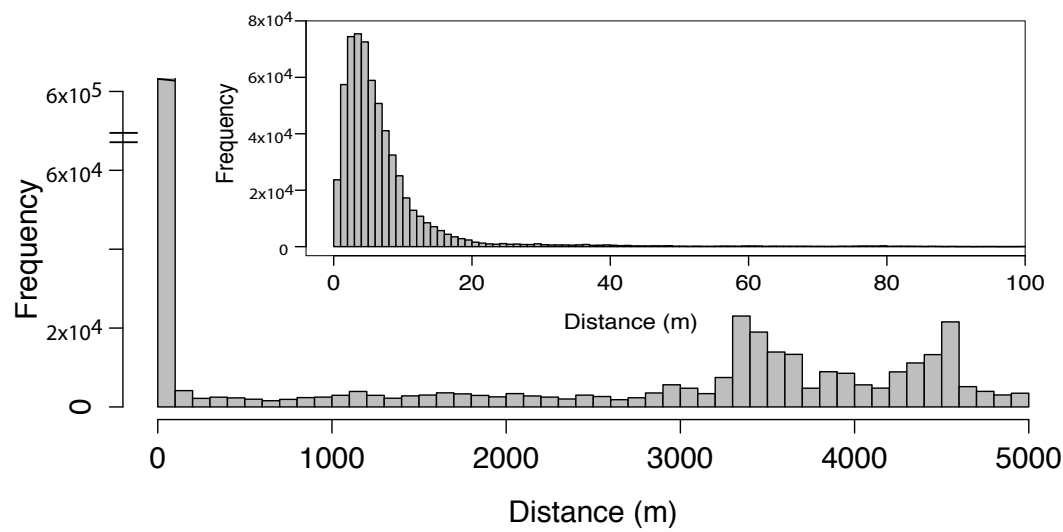


Figure S2: Histogram illustrating the frequency distribution of distances (bin=100m) between pairs of pigeons for all groups across all releases. Inset shows frequency distribution of distances (bin=1m) for birds up to 100m away. The shape of the distribution shows that the majority of birds are within 20m of each other during group flights, therefore using 100m as the cut-off for designating birds as having split is a conservative criterion.

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Chapter 3

Stability in homing pigeon leadership hierarchies: from inter-individual variation to functional consequences

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Abstract

Reaching a consensus decision in homing pigeons (*Columba livia*) has been shown to involve a hierarchy of influence. In this scenario all individuals contribute but their weight in the decisions-making process depends on their “rank” within the leadership hierarchy. It has been suggested that the advantage of decision-making structures could be derived not only from the benefit of putting certain leaders (such as those most experienced) in charge, but also from the stability of the structure itself. In homing pigeon flocks, little is known about the time-course over which stability manifests itself or the importance of inter-individual differences in enabling stability of leadership hierarchies. In this study we calculated leadership hierarchical stability over an extended series of releases and compared stability and navigational performance between flocks with a homogeneous-age structure and those with a heterogeneous-age structure. The results showed that stable leadership hierarchies were only displayed in heterogeneous-aged flocks. In addition, heterogeneous-age flocks reached saturation in route efficiency more quickly and were more likely to fly more similar routes in succession, perhaps due to the stability in the navigational leadership hierarchy. When released as solos, individuals were able to recapitulate their own flock’s route with higher accuracy compared to the homogeneous-age flocks. Our study shows that inter-individual differences in age are important for determining hierarchy stability and that there is potentially a spatial learning advantage to stable decision-making structures.

3.1 Introduction

The synchronised movement of groups creates eye-catching displays, but groups must reconcile navigational differences to prevent group fragmentation. Consensus decisions are required to maintain the benefits associated with group cohesion (Krause and Ruxton 2002). Although shared decisions are thought to be more prevalent in nature (Conradt and Roper 2005), leadership (Krause 2000, King et al. 2008) and hierarchical leadership (Nagy et al. 2010, Sarova et al. 2010, Perez-Escudero et al. 2014) also occur in many contexts. In leadership hierarchies all individuals contribute to the group decision, but the weight of their decisions will correspond to their 'rank' within the hierarchy. The study of collective motion has traditionally focused on the factors underlying the leadership hierarchy structure (e.g. Nagy et al. 2013; Pettit et al. 2015; Watts et al. 2016), in part because it has been thought that the adaptive value of collective decision-making might depend on the mechanism that places specific individuals into leadership positions. However, it has been recently suggested that the advantage of hierarchical decision-making structures might derive not only from the benefit to the group of putting certain leaders in charge (i.e., the most experienced), but also from the potential stability of the structure itself (Flack et al. 2013). Advantages could arise either due to enabling certain leaders to retain their influential positions or because the stability of the structure could enhance information flow and thus improve decision-making accuracy (Lusseau and Conradt 2009, McComb et al. 2011). Therefore, understanding the long-term stability of leadership hierarchies would be a necessary step in determining the functional consequences that these decision-making structures may have.

Leadership is theorized to spontaneously emerge when interacting individuals differ (Conradt and Roper 2003) in, for example, knowledge and experience (Reebs 2000, Couzin et al. 2005, Brent et al. 2015, Watts et al. 2016), energetic state (Rands et al. 2003, Fischhoff et al. 2007) and/or temperament (Nakayama et al. 2012). Depending on the factors involved in structuring leader-follower interactions, leadership may be stable or transient across time. A theoretical model by Conradt et al. (2009) suggests that leadership is assumed by those individuals for whom reaching the goal is most important. Such “leadership according to need” would be state-dependent, where the identity of the individual most in need will vary dynamically over time. For example, the hungriest fish will take up positions at the front of the shoal where it has the largest influence on the group’s movements and the largest food intake (Krause 1993). Alternatively, more stability in leaders during group movements might be expected if certain individuals consistently have greater knowledge relevant to the collective task at hand. Individuals with the greatest degrees of environmental knowledge lead group movements in a range of species including, golden shiners (*Notemigonus crysoleucas*), bottlenose dolphins (*Tursiops* sp.), African elephants (*Loxodonta africana*), killer whales (*Orcinus orca*), and homing pigeons (*C. livia*) (Reebs 2000, Lusseau and Conradt 2009, McComb et al. 2011, Brent et al. 2015, Watts et al. 2016). Agent-based simulations suggest that if there are multiple knowledgeable individuals within a group, repeated interactions among the same individuals would lead to stratification based on merit (i.e. informed individuals learning to “trust” other informed individuals and to ignore uninformed ones) (David-Barrett and Dunbar 2014). Over time this leadership hierarchy consistency would increase, which in turn, might cause a separation between the informed and uninformed subsets, though such an effect is yet to be

demonstrated empirically. Alternatively, it has been argued that the organisation of the decision-making structure could change based on an assessment of the group's previous performance (Biro et al. 2016). In this case we would expect hierarchy consistency to be a function of efficiency, rather than necessarily to increase with time.

Homing pigeon flocks have been shown to exhibit hierarchical decision-making structures (Nagy et al. 2010, Xu et al. 2012, Zhang et al. 2014). These navigational leadership hierarchies are robust to changes in, for example, individual experience levels (Flack et al. 2013), context (homing vs “free” flights, Nagy et al. 2010), changes in group size (Nagy et al. 2013), and when measured over a short number of successive flights (4-8) (Flack et al. 2013, Santos et al. 2014, Pettit et al. 2015). This has led to the overall impression that navigational leadership hierarchies are highly stable structures. Many of these studies, however, used flocks whose members were mixed in age and experience (e.g., Nagy et al. 2010, Nagy et al. 2013, Flack et al. 2013 and Pettit et al. 2015), both of which are factors that have been shown to influence leadership in homing pigeons (Flack et al. 2012, Jorge and Marques 2012, Watts et al. 2016). A recent study focusing specifically on hierarchical leadership stability as a function of inter-individual differences in pigeons reported that homogeneous-age flocks have reduced leadership stability compared to heterogeneous-age flocks, although both still showed significant stability over five releases (Santos et al. 2014). However, this study compared only a single flock in each condition (i.e. there were no independent replicates) and compared data sets collected in two different studies in two different locations. As such, the importance of age heterogeneity within groups in determining the stability of homing pigeon

navigational leadership hierarchies remains an open question, as does the stability of these decision-making structures over longer time-frames than previously tested.

To investigate the role of inter-individual variation in the long-term stability of navigational leadership hierarchies – as well as the potential benefits that such stability may confer on individuals – we compared leadership hierarchy stability between groups with a homogeneous age structure and those with a heterogeneous age structure. We used six flocks of seven birds each: three flocks of homogeneous-aged birds (i.e. birds all hatched in the same year) and three flocks of heterogeneous-aged birds. Flocks were repeatedly released from the same site 25 times, followed by a solo release, and all flights were tracked with miniature GPS devices. Our aims for this study were three-fold: (1) to test the stability of navigational leadership hierarchies over an extended series of releases, (2) to test the effect of inter-individual variation on leadership stability, and (3) to investigate whether hierarchy stability relates to (and thus potentially influences) route formation and individual spatial learning. We hypothesise that hierarchical stability should either increase with repeated releases with a process similar to merit-based stratification (David-Barrett and Dunbar 2014) or depend on previous efficiency if groups have a feedback mechanism (Biro et al. 2016). In addition, we predict that stability will be lower in homogeneous flocks due to smaller inter-individual differences resulting in an increase in shared-decisions (Couzin and Krause 2003, Santos et al. 2014). We expect to observe more consistency in the leadership of heterogeneous flocks and that, in turn, this might cause these flocks to take more stable routes and thus individuals to learn routes with better fidelity.

3.2 Methods

3.2.1 Subjects

We used 42 homing pigeons (age = 2-6 years), chosen from among the ca. 120 subjects housed at the University of Oxford Field Station at Wytham. We randomly selected seven birds hatched in 2012 and assigned them to Flock A, and 14 birds hatched in 2011 and assigned them to Flocks B and C. These were the homogeneous-aged flocks, where due to birds' uniform age, all subjects had similar levels of experience; Flock A had no prior releases and Flocks B and C had been released from three previous sites (47 times) up to 10.45 km from home. We then randomly selected three birds that hatched in each of 2012, 2011, 2008 and six birds that hatched in each of 2010 and 2009. These 21 birds were then randomly assigned to three flocks of seven (Flocks D, E and F), with the condition that each flock had the same age structure. These were the heterogeneous-aged flocks (aged 2-6 years), which due to their variation in age meant they varied widely in homing experience, having been on 0-70 homing releases, from a range of release sites (up to 10.6 km). For the remainder of the paper homogeneous-age flocks will be referred to as homogeneous flocks and heterogeneous-age flock as heterogeneous flocks. None of the birds had ever been released from the site used in this study. All birds received basic training prior to starting the experiment, consisting of five flock flights from sites 2-3km from the loft in the four cardinal directions while carrying plasticine dummy weights of a similar shape and weight as the GPS devices.

3.2.2 *Experimental procedure*

We released each flock as a group from the chosen release site (distance to home loft 7.34km, direction to home loft 135.9°) 25 times followed by a single solo flight. Owing to limitations on bird availability due to other on going experiments, the experiment was conducted using the homogeneous flocks first followed by the heterogeneous flocks. To minimise the differences between conditions experienced by each flock, releases were carried out on consecutive days when the sun was visible and wind speed was $<7\text{ms}^{-1}$. A maximum of three releases were performed each day and there was a minimum interval of one hour between releases. After the conclusion of the experiment all birds were weighed. Four birds went missing or sustained minor injuries and thus were removed partway through the experiment, one from homogeneous Flock C (B84 release 10), two from heterogeneous Flock D (B01 release 5 and A39 release 18) and one from heterogeneous Flock F (N36 release 18).

During all homing flights, positional data were logged using 5 Hz GPS loggers (Qstarz BT-Q1300ST; approx. 15.5g). Devices were either attached using Velcro strips glued onto clipped feathers (homogeneous groups) or, due to the age and thus feather quality of some of the birds, placed into elastic harnesses (heterogeneous groups). Several previous studies have used such harnesses (Nagy et al. 2010, Nagy et al. 2013, Pettit et al. 2015) and have reported no effect on hierarchy stability when compared with Velcro attached birds (Pettit et al. 2015). Upon the birds' return to the loft, data were downloaded using QTravel software (Qstarz V.3.2).

3.2.3 GPS data processing

We carried out data analysis in Matlab (Mathworks 2012b) and R (0.98.1014) (R Core Team 2014). The geodetic latitude and longitude coordinates provided by the GPS were first converted into Universal Transverse Mercator (UTM) coordinates. Tracks were processed by discarding all points other than those where speed was continuously above 5ms^{-1} for 10s before or after the given point (i.e. flight). In addition, tracks were trimmed 100m from the release site and loft to exclude circling behaviour.

3.2.4 Statistical analyses

3.2.4.1 Navigational leadership hierarchy stability

We determined leader-follower networks using the temporal relationships between a given bird's directional changes and those of all others in the flock: a directional correlation analysis (see Nagy et al. 2010 for a more detailed method). Taking a pair of birds i and j , the direction correlation is calculated as $C_{ij}(\tau) = \langle v_i(t) \cdot v_j(t+\tau) \rangle$, where $v_i(t)$ is the normalized velocity of i at time t and $v_j(t+\tau)$ is the normalized velocity of bird j at time $t+\tau$. The value of τ_{ij} (τ) that maximizes the $C_{ij}(\tau)$ correlation function across t is the average time delay between a pair of birds. If $\tau < 0$, then when bird i turns, j has already turned and therefore can be interpreted as j leading i . We resolved all pairwise interactions between birds that spent a minimum of 120s within 100m of at least two other birds. To summarise a bird's leadership position within each flock for every release, we then calculated the duration-weighted average directional correlation time delay of each bird with the rest of the flock ($\text{mean } \tau$). To investigate the consistency of an individual's position across releases

and between groups, we calculated the intra-class correlation coefficient (r) of individuals' *mean tau* values using Linear Mixed Models (LMM) with *bird* and *release* as random effects (`rpt.remlLMM` function in R, Schielzeth and Nakagawa 2010, R Core Team 2014). This function calculates r as $r = \sigma^2_{\text{individual}} / (\sigma^2_{\text{individual}} + \sigma^2_e)$, where $\sigma^2_{\text{individual}}$ is the between-group variation and σ^2_e is the residual variation. A randomization test with 10^4 iterations was then used to calculate p -values.

3.2.4.2 Inter-individual differences

To test if birds assigned to the two group compositions varied in inter-individual factors such as body mass or solo ground speed we calculated the variance of the two measures for every flock and compared the two group compositions variances using a Bartlett test. These two metrics are thought to be correlated with heavier birds flying faster (Pettit et al. 2015). Solo releases were conducted on different days for the homogeneous and heterogeneous flocks. Thus we could not compare the solo ground speeds directly due to potential differences in wind speed, and therefore we focused on the variance of solo ground speeds. Ground speeds were calculated using the distance between successive GPS fixes averaged over the track (Pettit et al. 2015).

Inter-individual variation is thought to be related to the type of decision-making mechanism groups use (Couzin and Krause 2003, Santos et al. 2014), and therefore we tested for differences in types of decision-making mechanism used by the two compositional groups, by calculating the proportion of mutual (shared) versus directed (leadership) interactions. Mutual interactions correspond to interactions between a pair of birds being correlated, but the interaction is not directionally

consistent (i.e. bird A leads bird B half the time, and follows bird B for the other half). This results in *tau* values between pairs across the whole flight of 0 seconds. In contrast directed interactions corresponded to interactions that occur in a consistent direction (i.e. bird A in the majority of case leads bird B) and therefore the *tau* values are > 0 seconds.

3.2.4.3 Route structure

To analyze flocks' and individuals' navigational performance in terms of route structure we used two measures. (1) We calculated route efficiency, which we quantified as the straight-line distance between the start and the finish divided by the actual distance flown. We calculated the efficiency of each bird in a flock and then averaged these values for a single flock measure to account for non-independence of birds flying together. (2) We determined nearest neighbour distances (NND) between routes, which we calculated as the distance from each GPS point on a focal route to the nearest neighbouring point on the other, applied reciprocally and averaged over the length of the route. To account for non-independence of individuals flying together, we calculated a flock route by calculating the mean latitude and longitude (flock centre) of the flock over each time point. We then used this flock route to calculate NND between successive releases. In both measures we removed birds that spent $<70\%$ their time within 100m of at least two other birds. In order to compare solo route structure measurements with flock routes, we constructed a mean final flock route over the last five releases (21-25), using the method of Freeman et al. (2011). Over 100 iterations, this method identifies a mean route of 1000 points which minimises the distance to nearest

neighbour points on the flock routes, whilst ensuring consecutive points on the mean route are more than five metres apart.

When using Linear Models (LM) and Linear Mixed Models (LMM) in the R (R Core Team 2014) package “lme4” (Bates et al. 2015), we used AIC to select the best models, and checked the assumptions of Gaussian error and homogeneous variance by visual inspection of the plotted residuals. We tested the significance of fixed factors using maximum likelihood, comparing the full model to a model without the relevant factor included. Throughout the models the binomial fixed factor *composition* was used to identify whether the flock is homogeneous or heterogeneous, i.e. of the same or mixed ages.

3.3 Results

3.3.1 Navigational leadership hierarchy stability

For the subsequent consistency analyses on leader/follower interactions, we removed the first two releases due to a high proportion of birds splitting during these early flights (Release 1: 26/36 and Release 2: 25/36 birds splitting). This is a common observation when flocks are released from novel sites (Guilford and Chappell 1996, Banks and Guilford 2000). Multi-level leadership hierarchies were detected during all flock flights. In heterogeneous groups individuals maintained consistent leader-follower interactions enabling leadership hierarchies to remain stable across the remaining 23 releases. This was not the case, however, for homogeneous groups where no consistent leader-follower interactions were found (Table 1, Figure 1). Lower consistency scores could be due to high within-individual variance and/or low between-individual variation. In the present study the

homogeneous flocks had high within-individual variation as birds often swapped ranks, resulting in low between-individual variation and thus the similarity in birds' mean ranks (Figure 1). Therefore, although hierarchies were formed in both heterogeneous and homogeneous flocks, in homogeneous flocks these were not stable between releases. In heterogeneous flocks, birds that most often assumed the highest rank (top leaders) were aged 5 (Flock D) and 4 (Flocks E and F), i.e., generally older but not necessarily the oldest from the full age range available (2-6 years).

Table 1: **Leadership consistency and percentage of mutual interactions in homogeneous and heterogeneous groups.** r is the intra-class correlation coefficient from an LMM with mean τ as the response variable and *bird* and *release* as random effects (Schielzeth and Nakagawa 2010). Mutual interactions correspond to pair-wise relationships with a time delay of 0 seconds.

	Releases	r	P-value	% Mutual interactions
Homogeneous (Flock A-C)	3-25	0.01	0.34	31.5
Heterogeneous (Flock D-F)	3-25	0.2	0.001	23.4

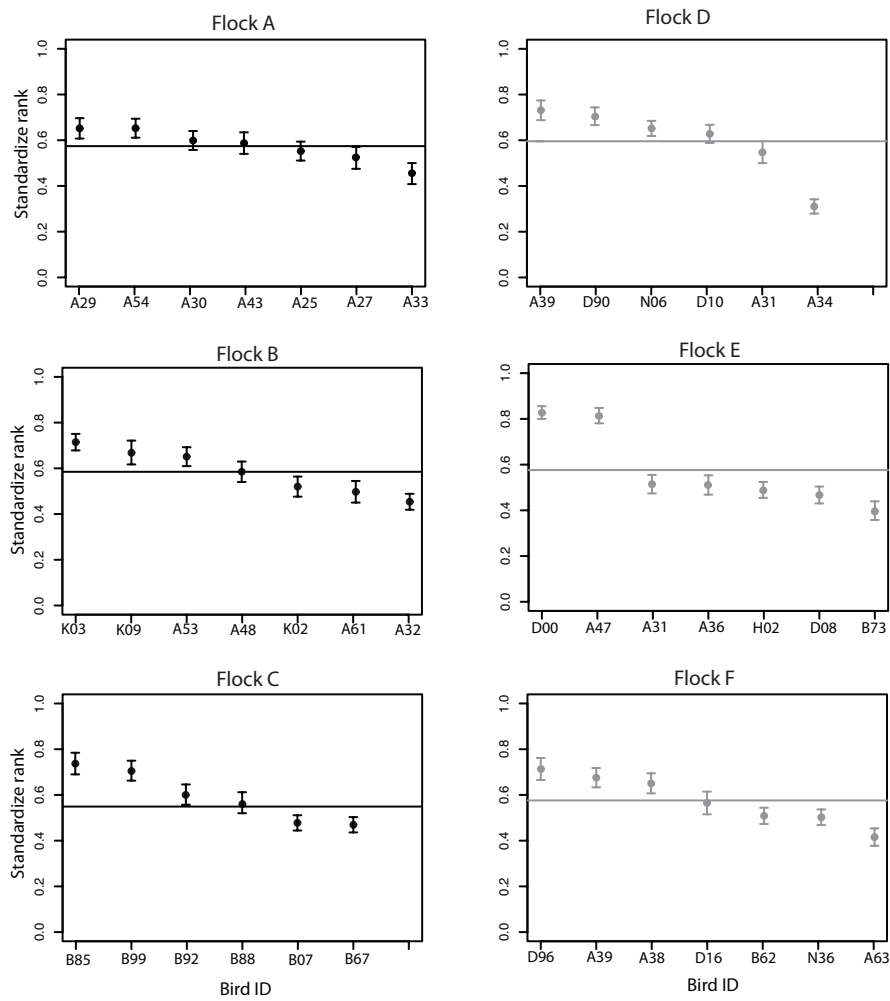


Figure 1: Mean standardized rank for each bird across the 23 releases. Standardized rank takes the number of birds in a flock into account. An mean score of 1 indicates that across the 23 releases the bird always assumed the top hierarchical rank, and 0 that the bird was always lowest ranked. The bars indicate the standard error of the mean (SEM), and the black line the mean standardized rank for the flock. Panels in the left column (black dots) correspond to the homogeneous flocks and those on the right (grey dots) to the heterogeneous flocks.

To understand the consistency of leader-follower interactions within the leadership hierarchy at a finer resolution we calculated the r for a moving window of eight releases (“release window”; Figure 2). There was a significant difference in the

leader-follower consistency scores across the moving release window between homogeneous and heterogeneous groups (LMM with *composition* and *release window* as fixed effects and *flock* as a random effect, tested against a model without *composition*: estimate: 0.163, $df = 1$, $\chi^2 = 8.33$, $P = 0.0039$), but not across release window (same model as above but tested against model without *release window*: estimate: -0.001, $df = 1$, $\chi^2 = 0.896$, $P = 0.344$). Therefore, both the lack of consistency in homogeneous groups and the consistency in heterogeneous groups were stable across the 23 releases. In line with this, we found no relationship between a flocks previous route efficiency and the consistency of individuals' ranks when comparing individuals' ranks between the current and previous release using a Pearson's product-moment correlation (LMM with *consistency* as the response, *previous efficiency* as the fixed effect and *release* crossed with *flock* as the random effects: estimate = -0.251, $df = 1$, $\chi^2 = 0.095$, $P = 0.757$). Therefore, a group's hierarchical structure was no more likely to change whether the flock flew a route with high or low efficiency on its previous release..

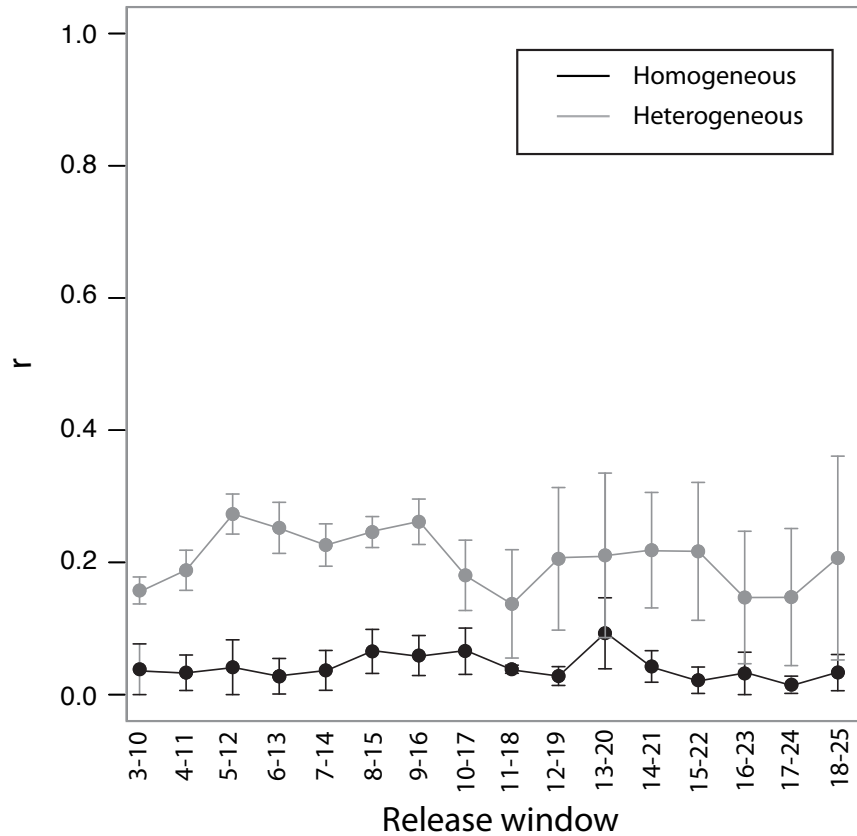


Figure 2: Hierarchical leader-follower consistency scores as moving averages. r was calculated across a moving window of eight releases. The error bars represent the SEM over the three flocks within each treatment. The SEM for heterogeneous flocks increased and the mean decreased from flight 11 onwards due to flock 6's rapid decrease in leader-follower hierarchical consistency after a bird was removed due to injury.

3.3.2 Inter-individual differences

We found no differences in the variance of solo ground speeds between heterogeneous and homogeneous flocks (Bartlett test: Bartlett's k -squared = 4.48, df = 5, P = 0.482) nor in body mass between flocks (Bartlett test: Bartlett's k -squared = 7.02, df = 5, P = 0.219). Therefore, flocks with greater hierarchical stability did not have a larger variance in solo speeds or body mass, suggesting these two measures were not related to stability.

Homogeneous flocks had a greater percentage of mutual interactions compared to heterogeneous flocks (Table 1). When between a given pair of birds $\tau = 0$, this could also indicate no interaction rather than a mutual interaction (Katz et al. 2011, Xu et al. 2012). We suggest that in the present experiment we observed mutual interactions rather than lack of interactions because the correlation ($C_{ij}(\tau)$) at $\tau = 0$ tended to be as high as values at larger time delays, as recorded in previous work on homing pigeons (Xu et al. 2012). This suggests that these interactions were still highly correlated, just not directionally consistent (see Figure 3) and that the strength of the mutual and directional links were equivalent.

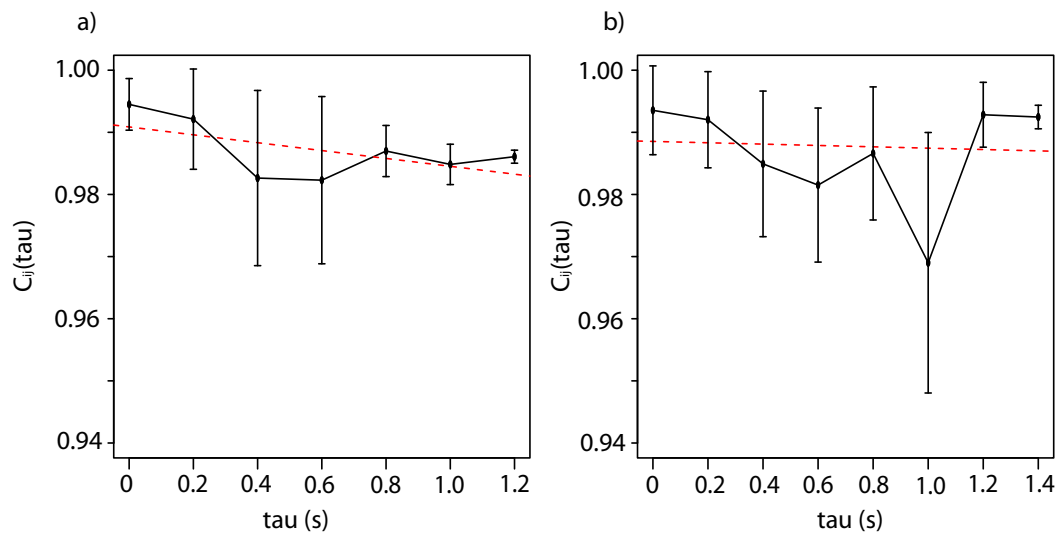


Figure 3: The change in maximum directional correlation with changes in τ for (a) homogeneous groups and (b) heterogeneous groups. The bars represent the standard deviation (sd) and the red dotted line indicates the correlation line plotted from a LM between the two variables.

3.3.3 Route structure

With repeated releases, flock routes became more efficient and their shape stabilised, becoming more consistent over time. This is shown by the increase in efficiency and decrease in NND over repeated releases (Table 2, Figure 4). Heterogeneous flocks had greater efficiencies overall across the 23 flights (Table 2), due to a faster increase to maximum efficiency compared to homogeneous flocks (Figure 4a). However, final efficiencies for heterogeneous and homogeneous flocks (releases 21-25) did not differ significantly (Figure 4a), reaching 0.81 ± 0.05 (mean $\pm$ sd) and 0.78 ± 0.08 , respectively. The difference in NND distance between homogeneous and heterogeneous flocks across the 23 flights was marginally significant (Table 2), due to the greater variance in NND distance in homogeneous flocks (f-test, $F_{59} = 3.67$, $P < 0.001$; Figure 4b). This suggests that heterogeneous flocks flew more consistent routes.

Table 2: Route structure results. Two LMM's testing for the effects of release and composition on either efficiency or NND as the response variable. The log of NND was taken to account for data skew.

Route structure measure	Model Fixed effects	Random effects	Significance tested factor	Effect size	χ^2	df	P-value
Efficiency	release * composition	flock	release	0.014	64.4	24	<0.001
			composition	0.139	6.7	1	0.009
NND	release + composition	flock	release	-0.026	26.3	22	<0.001
			composition	-0.339	3.96	1	0.046

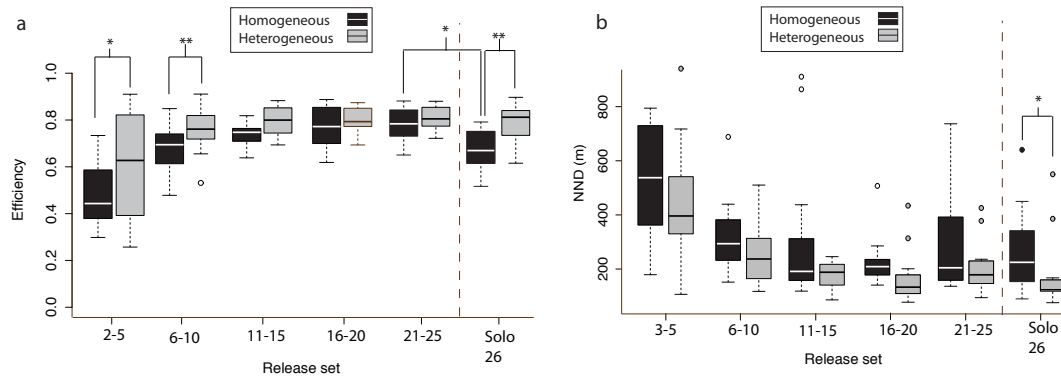


Figure 4: Changes in route structure as a function of release. (a) Mean flock efficiency and (b) Mean flock NND across successive blocks of five (“release sets”) in order to smooth the pattern for comparisons. For both efficiency and NND, statistical comparisons between homogeneous and heterogeneous flocks for each release set were performed using Tukey’s post hoc tests on an LMM (Lenth 2016) with *flock* and *release* as random factors and *release set* interacting with *composition* as categorical variables. Star indicates significance level (* <0.05 ; ** <0.001). The final bars (release 26) represent the solo releases conducted after the 25 flock flights. We removed one bird from Flock D during analysis, as this bird always split from the flock (as such, it did not have the opportunity to learn the flock route, making its solo performance irrelevant to our comparisons).

Birds from heterogeneous flocks demonstrated significantly more efficient routes when flown solo than birds from homogeneous flocks (Tukey post hoc test: estimate = -0.12, df = 11.79, $t = -3.08$, $P = 0.009$; Figure 4a). The homogeneous-flock birds flew solo routes with significantly lower efficiencies compared to the final mean flock route (averaged over releases 21-25) (Figure 4a). In concordance, NNDs between the solo and the final mean flock route (averaged over releases 21-25) were significantly larger for homogeneous- compared to heterogeneous-flock birds (Tukey post hoc test: estimate = 0.50, df = 10.81, $t = 2.35$, $P = 0.039$; Figure 4b). This implies that heterogeneous birds learnt and were able to recapitulate their flock’s route more faithfully when flying alone (Figure 5). For all flocks, birds’ solo routes

were more similar (i.e. had lower NNDs) to their own flocks' final mean route than to other flocks' final mean routes (Table 3; LM with log NND as response variable and *flock, own/different* interaction with *composition* as fixed effects: *same/different* estimate = -0.40, $t = -3.1$, $P = 0.002$), further confirming individual learning during flock flights.

Table 3: NNDs between a bird's solo route and either the mean flock route from the bird's own flock or from a different flock.

Composition	Comparison to flock mean route	Mean (m)	sd (m)
Homogeneous	Own flock	256	147
	Different flock	374	191
Heterogeneous	Own flock	165	116
	Different flock	359	251

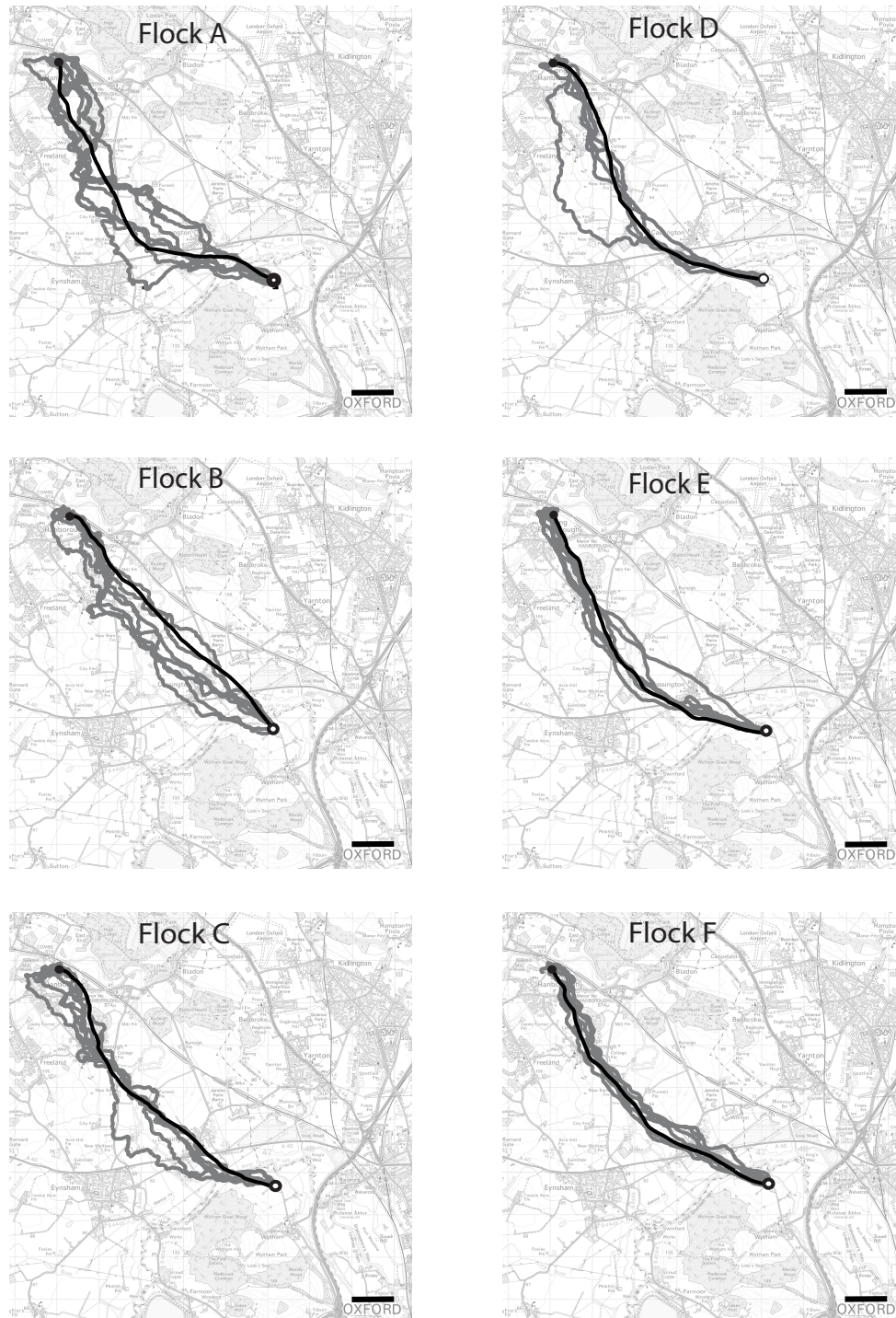


Figure 5: Birds' solo and mean flock routes. The black lines indicate for each flock the final mean flock route calculated from the mean flock routes for releases 21-25. The grey lines show the solo routes of birds belonging to each respective flock. Scale bar: 1 km. Ordnance Survey mapping © Corwn copyright 2012.

Heterogeneous leader birds did not have greater solo efficiencies compared to other flock mates (LMM with *mean tau* as a fixed effect and *flock* as a random factor, compared to model without *mean tau*: estimate = -0.015, $t = -0.065$, $\chi^2 = 0.001$, $df = 1$, $P = 0.99$). Therefore, leaders did not learn more efficient routes than followers.

3.4 Discussion

Our results demonstrated two advantages that may be associated with stable navigational leadership hierarchies: (1) groups with stable leadership hierarchies learnt consistent routes faster than those without, and (2) when flying singly, individuals from groups with stable leadership hierarchies were more likely to maintain the high efficiencies achieved by their flocks and recapitulated the flock's route more accurately. In addition, we also showed that groups heterogeneous in age had stable leadership hierarchical decision-making structures over a relatively long time period (25 flights on average over one month), while groups homogeneous in age did not. Taken together, these results suggest that flock composition could have important consequences for individual members in terms of spatial learning.

The long-term stability we identified in heterogeneous groups is in concordance with previous studies measuring stability over shorter time scales (< 8 releases) (Nagy et al. 2010, Flack et al. 2013, Santos et al. 2014, Pettit et al. 2015). The consistency scores of 0.2-0.3 we obtained on a fine scale using a moving time window of eight releases were similar to those of Pettit et al. (2015), who used the same method of repeatability calculation over four releases. This suggests that the

factors involved in structuring the leadership hierarchy are stable over a long time period, and thus there could be an adaptive value to certain individuals consistently leading. Importantly, the degrees of both the consistency (heterogeneous groups) and the lack of consistency (homogeneous groups) remained stable across our extended series of releases. We found no evidence that repeated interactions enabled individuals to settle into increasingly stable hierarchies, for example, by “learning” through experience whom to follow (David-Barrett and Dunbar 2014). This is in agreement with a previous study which showed that experience-based stratification of the leadership hierarchy did not occur in flocks composed of half experienced and half inexperienced birds (Watts et al. 2016), at least in the short term (eight releases). We also found no evidence for the consistency of the leadership hierarchy to depend on the performance (efficiency in this case) of the previous release (Biro et al. 2016). Flocks that previously flew low efficiency routes were not more likely to change their hierarchy structure and pay attention to different individuals than flocks that flew previously efficient routes.

There are two mechanisms by which leadership hierarchy stability could be established and maintained. The first requires recognition (enhanced by individual recognition and memory) of certain morphological, physiological or behavioural features in conspecifics. Leadership based on dominance (King et al. 2008) or familiarity (Flack et al. 2013) can, in this way, result in leader-follower interactions that are fixed over extended periods. Second, leadership hierarchies can emerge passively, involving interactions with individuals in consistent ways by following simple behavioural rules requiring no recognition of conspecifics status (Couzin et al. 2002). Individuals may interact consistently with others based inherent features

such as experience, preferred weighting between personal and social information, body size or characteristic flight speed. Speed, for example, has been shown to be important in determining individual pigeon's positions in the leadership hierarchy, with faster birds spontaneously flying at the front of flocks and assuming higher leadership ranks, irrespective of their navigational competence (Pettit et al. 2015). Therefore, hierarchical stability can be an inevitable consequence of inherent inter-individual differences, if these differences are large enough and stable enough to cause consistently directed leader-follower interactions. In our study we did not find that homogeneous and heterogeneous flocks differed in the extent of solo speed or body mass variance present within them, though they certainly did vary in terms of age and experience. How exactly the age/experience variation might have translated into hierarchy stability in the heterogeneous groups – whether through the first or the second of the mechanisms proposed above – remains unclear, but the strong casual link between inter-individual variation and hierarchy stability appears to be a robust finding.

The lack of hierarchical stability in homogeneous flocks could have been caused by the observed increase in the number of mutual (shared) interactions. This increase, in turn, is likely to have been due to the relatively small inter-individual variance in age/experience within such flocks (by definition). That a decrease in inter-individual variance should be accompanied by an increase in mutual interactions is in concordance with previous theoretical (Conradt and Roper 2003) and empirical studies (Santos et al. 2014). Nonetheless, hierarchies still formed in homogeneous groups, implying that another factor (or factors) is/are involved in enabling the emergence of a hierarchical decision-making network. Such a factor must be

dynamic, suggesting a role for factors shown to be important in other species such as motivation or nutritional levels (Krause 1993, Fischhoff et al. 2007, Nakayama et al. 2012) that can change day-to-day.

Consistent decision-making structures could be beneficial by enhancing information flow between group members, thereby increasing the accuracy of group-level decisions (Lusseau and Conradt 2009, McComb et al. 2011) or alternatively by enabling a ‘beneficial’ leader (e.g. experienced) leader to maintain its position where it has the greatest influence over group movements. Although our results do not necessarily distinguish between the two possible explanations, the results do support the notion of stability being beneficial, particularly in the early stages of the experiment when the navigational task was still unfamiliar to the flocks. Heterogeneous groups increased efficiency significantly faster than homogeneous groups, although both groups reached similar final efficiencies. In addition, homogeneous flocks flew less consistent routes over the last 15 releases. These results may suggest a benefit in terms of a more steady improvement in performance (through more effective spatial learning at the group level) for groups with stable decision-making structures. However, we are aware that due to the design of the experiment we can not rule out that the faster improvement in efficiency achieved by heterogeneous flocks was due to the flocks containing more experienced group members rather than the stability of the leadership hierarchy itself.

Consistent leadership has been shown, albeit over a smaller number of releases than those conducted here, to have an advantage at the individual level: leaders learn routes more effectively than followers, the explanation for which may lie in the

experience of having to make the majority of navigational decisions for their flock (Pettit et al. 2015). In the present study, we found that the birds which were the most consistent leaders over 25 flights did not necessarily have the highest route efficiencies when flying alone. The difference we observed was actually between the birds that had previously flown in heterogeneous flocks compared to homogeneous flocks. All birds demonstrated solo routes that were more similar to their own flock's mean than to other flocks' means, revealing individual learning during flock navigation. However, heterogeneous solo birds recapitulated their flocks' efficient routes with higher fidelity, resulting in them flying more efficient routes compared to homogeneous solo birds. We suggest that this difference between birds from the two flock compositions could be due to differences in leadership stability associated. Consistent hierarchical leadership in heterogeneous flocks could allow flocks to fly the same route repeatedly, exposing individuals to the same spatial cues each time, and thus enabling them to learn the route with higher accuracy. Therefore, consistent decision-making structures may endow group members with an additional benefit in the form of enhanced individual learning of a specific, successful navigational solution (route). This could be advantageous, as by flying the most efficient routes birds minimise energy expenditure and time spent at risk of predation or away from the loft.

Our results highlight the importance of inter-individual differences in age/experience in enabling multi-level navigational leadership hierarchies to form and remain stable over extended periods. The presence of a more stable leadership hierarchy in heterogeneous flocks compared to homogeneous flocks appeared to not only to enable faster emergence of a consistent flock route, but also allowed

individuals to better learn recapitulate efficient routes when flying singly. It is likely that flying a stable route, through having stable leadership, enables all members to learn the collective solution more accurately. This result is applicable to the wider context of collective decision-making, suggesting that groups with a wider range of age/experience may gain benefits in terms of making more accurate decisions faster and the individuals within the group may benefit from enhanced learning.

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Chapter 4

Misinformed leaders lose influence over pigeon flocks

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Abstract

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

4.1 Introduction

Animal groups faced with making joint decisions can exploit variation in the quality of members' personal information by sharing decision-making: when navigating, for example, they can pool their personal knowledge to reduce overall navigational error (e.g. (Simons 2004)). However, in some groups, decisions are not shared entirely "democratically", meaning that individuals do not contribute equally to decisions (King et al. 2008, Nagy et al. 2010). The group's performance then becomes disproportionately dependent on leaders' information quality. Because leadership does not necessarily correlate with competence (King et al. 2008, Pettit et al. 2015) the question arises whether (i) followers and/or leaders are sensitive to the quality of leaders' input, and, if so, (ii) whether groups have any scope for "overruling" inaccurate leadership.

Homing pigeon flocks form transitive leadership hierarchies where some individuals consistently contribute more to directional decisions than others (Nagy et al. 2010), although a degree of decision-sharing is also evident among members (Jorge and Marques 2012, Xu et al. 2012). These hierarchies are stable across time (Santos et al. 2014), and important factors structuring them include individual differences in, e.g., navigational experience (Flack et al. 2012, Watts et al. 2016) and speed (Pettit et al. 2015). Recent modelling work has shown that multi-level hierarchies can compensate for an increase in navigational error better than random networks (Flack et al. 2015), however, this advantage disappears when the most influential individuals have the highest error, as errors then propagate down the hierarchy. In such situations, hierarchical structuring could be detrimental.

Here, we examined whether this model prediction holds true in real homing pigeon flocks, by experimentally increasing the navigational error of an identified leader. We manipulated leaders' personal information through "clock-shifting": a procedure known to systematically interfere with pigeons' use of the sun-compass for directional guidance, where clock-shifted ("misinformed") birds fly a predictably deviated route home (Schmidt-Koenig 1958). We asked whether stable leadership results in such errors propagating down the hierarchy (i.e., the whole flock flies the incorrect, shifted route) or if some compensatory mechanism allows flocks to maintain a correct (non-shifted) route.

4.2 Methods

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

We trained flocks from our chosen site (Bladon, 51°49'23.48"N 1°21'26.29"W; distance and direction from home: 5.27km, 149.5°) through eight consecutive releases ("Stage 0"; figure 1a). We calculated leadership ranks for each member in each flock based on spatial positioning (with leaders nearer the front and followers nearer the back) and confirmed these through directional correlation delay analysis (figure S1; see (Nagy et al. 2010) for details of both methods). We designated as "Stage-0 leaders" birds with the highest average rank over the last four training releases.

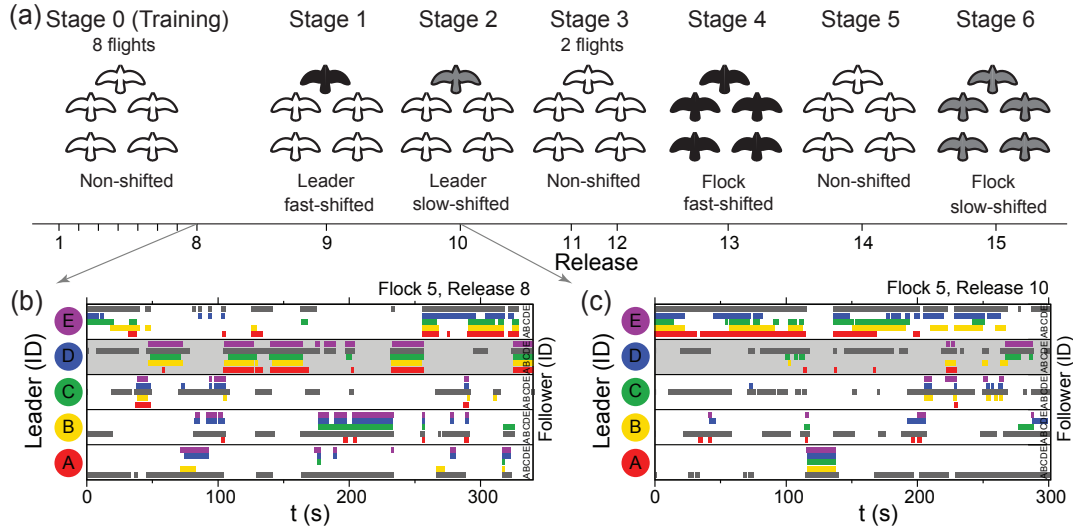


Figure 1. Experimental design and leadership analysis. (a) Release protocol for the eight experimental flocks. (b-c) Momentary leader-follower interactions over 10s time windows for an example flock in releases 8 and 10, respectively. Coloured bands indicate who is following a particular leader at each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

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

GPS tracks were analysed in Matlab (Mathworks 2012b) and R (0.98.1014). We explored the effect of misinformed (i.e. clock-shifted) leaders and flocks by

assessing, post-clock-shift (i) changes to the leadership hierarchy and (ii) deviations in the route flown. See electronic supplementary material for detailed Methods.

4.3 Results

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

flights in which the Stage-0 leader did not split and where at least three birds remained in the flock, on three occasions the Stage-0 leader assumed leadership.

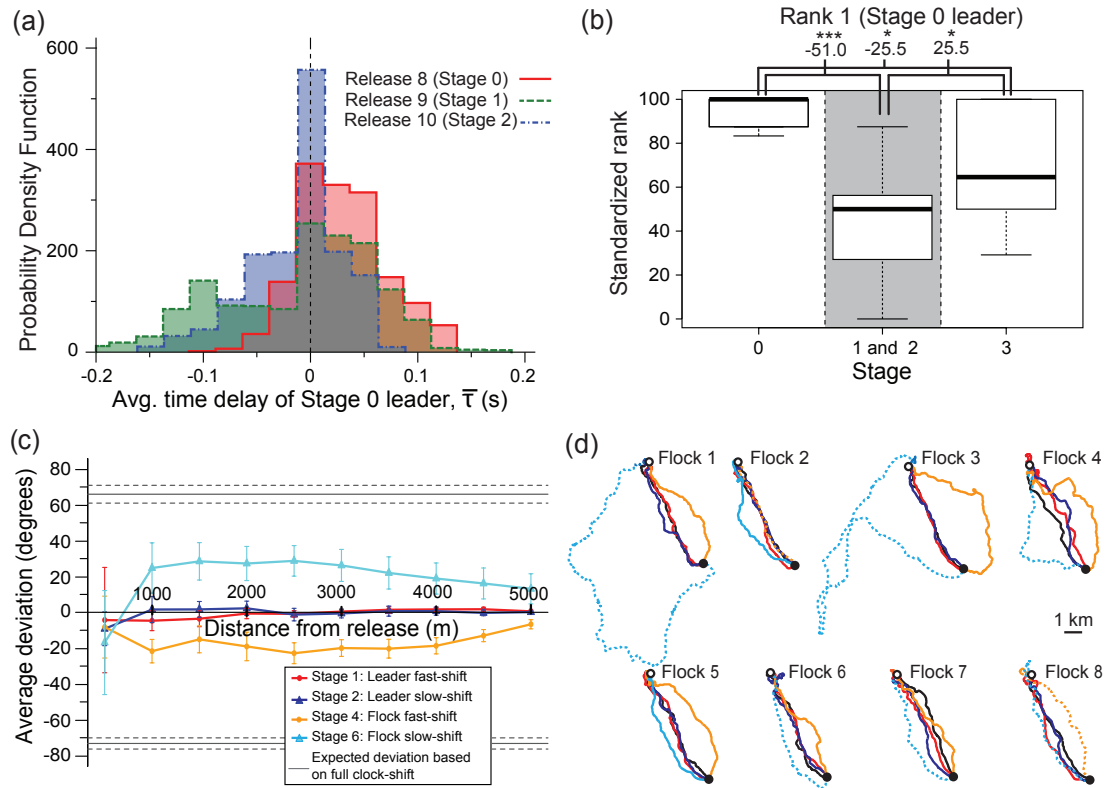


Figure 2. Effect of clock-shift on time delays, leadership ranks and routes. (a) Distribution of momentary time delay values (τ) for Stage-0 leaders for releases 8-10, averaged for each time step over the eight flocks. Positive values indicate being ahead of the mean of the flock. (b) Boxplots of median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

To detect clock-shift deviation in tracks, we used “virtual vanishing bearings”, calculated as the subjects’ heading at given points with respect to the release point (Biro et al. 2002). For each 500m concentric boundary centred around the release site, we calculated the flock medians of the difference in each individual’s heading between their last training release (non-shifted control) and test release for Stages 1, 2, 4 and 6 (figure 2c,d). A deviation of zero indicates that the track is, at the given distance from release, identical to the training track, i.e., displays no effect of clock-shift.

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

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

Table 1. Comparisons between the median flock virtual vanishing bearings for each Stage and their corresponding null expectation. Null expectation was calculated as a track with a mean deviation of 0, and a standard deviation exactly equal to that of each flock for the different Stages. We compared a Linear Mixed Model (LMM) with *stage*, and *distance* as fixed effects and *flock* as a random effect to a LMM without *stage* (Maximum Likelihood test: $\text{Chisq}=130.8$, $P<0.001$), then used post-hoc Tukey tests for pairwise comparisons between combinations of interest.

4.4 Discussion

Previous theoretical work predicted that in hierarchically structured decision-making errors by leaders propagate downwards, resulting in inaccurate collective decisions (Flack et al. 2015). By introducing incorrect navigational information of a specific magnitude at the top of the hierarchy, we found this potential disadvantage could be overcome in pigeon flocks: our results showed that when only leaders were misinformed flocks retained their existing routes, whereas when entire flocks were shifted they displayed deviated routes (albeit with a smaller-than-predicted deviation, as is common in birds familiar with the landscape, (Wallraff et al. 1999); although see (Wiltschko et al. 2005)). Thus we can infer that clock-shifting was

successful, but that leaders alone were not able to “mislead” their flocks on erroneous routes.

Importantly, we also documented a drop in many leaders’ hierarchical ranks (i.e. in the majority of flocks their input into the flock’s navigational decisions diminished) when they alone were clock-shifted. In considering this result, however, it is worth noting that Stage-0 leaders were not entirely stable in their leadership during training (figures S3, S4). Nonetheless, stability was greatest in releases 7-8, where all Stage-0 leaders ranked either in the top two (release 7) or the top (release 8) hierarchical positions. Thus the comparison with Stages 1&2 is clearest when considering the latter part of Stage 0. That leadership stability was gradually established is also supported by the observation that Stage 0 routes showed a clear learning curve, asymptoting also around releases 7-8 (figure S7). We therefore suggest that although there is noise in the system in the form of (i) flocks gradually settling on both leaders and routes and (ii) leaders varying in the extent to which they drop in rank, the combination of overall patterns within the leadership hierarchical data and analyses of route structures pre- and post-clock-shifting provide a sufficient (albeit noisy) signal for our conclusions.

We hypothesize that where a decrease was observed in leaders’ hierarchical rank, this could have been due to two non-mutually exclusive mechanisms. First, clock-shifting may have caused leaders to become uncertain in the quality of their own information. Clock-shifting places the sun-compass, an important navigational cue, in conflict with all other directional cues (e.g., visual, magnetic) in the bird’s environment. This conflict may have prompted leaders to place less weight on their personal information and more on social information (i.e. the copying of

flockmates). Uncertainty may also have reduced the flight speed of the clock-shifted leader, and since speed is associated with leadership in pigeons (Pettit et al. 2015), slower flight may result in birds dropping down the hierarchy (although see figure S6, showing that loss of leadership cannot be explained purely by changes in speed). This mechanism requires no recognition by followers that their leader has incorrect information. Alternatively, flock members may have actively ‘filtered out’ the low quality information, by reducing their reliance on social information received from leaders. This could have been due to recognising the increased conflict between their and the leader’s directional preference, or to detecting a cue (e.g. reduced speed) indicating uncertainty in the leader. Thus, the latter mechanism corresponds to followers ‘choosing’ not to follow, and the former to leaders ‘choosing’ not to lead. At present we cannot distinguish between these alternatives.

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

4.5 Acknowledgments

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4.6 Supplementary Information

4.6.1 Detailed methods

4.6.2 Subjects and materials

40 homing pigeons, aged 2 to 5 years and bred at the Oxford University Field Station in Wytham, Oxfordshire, UK, served as subjects. They were chosen from among the ca. 120 subjects living together at the facility, by randomly selecting eight birds that had hatched in each of 2009, 2011 and 2012, and 16 that had hatched in 2014. These 40 birds were then randomly assigned to eight flocks of five birds, with the condition that each flock had the same age structure: one bird hatched in 2009, one in 2011, one in 2012, and two in 2014. During all homing flights, positional data were logged using miniature GPS loggers (Qstarz BT-Q1300ST) attached to the birds' backs via Velcro strips glued to trimmed feathers. The devices weighed 15.5g and logged time-stamped longitude and latitude coordinates at 5Hz (absolute spatial error: mean = 1.69m, 95th percentile = 4.33m (Pettit et al. 2013)).

4.6.3 Training and testing procedures

Prior to starting the experiment, all birds received basic training, which consisted of multiple flock and solo flights from sites 2-3km from the loft in the four cardinal directions, while carrying plasticine dummy weights of the same shape and weight as the GPS devices. Subjects were transported to release sites by car and released at 10-minute intervals to prevent them merging en route.

We then trained flocks to home from our chosen site (Bladon, 51°49'23.48"N 1°21'26.29"W; distance and direction from home: 5.27km, 149.5°) through eight

consecutive releases, over a period of one week (“Stage 0”; see figure 1a of main manuscript for experimental design). We staggered the start of training, with four of the flocks only starting training once the other four had completed Stage 0 and had begun the clock-shifting procedure. This was due to space limitations in the clock-shift lofts.

We calculated leadership ranks for each member in each flock using two different methods. First, leadership ranks were assigned based on spatial positioning, using each bird’s average distance from the centre of the flock along the front-back axis projected onto the flock’s direction of motion. Birds nearer the front of the flock were given higher ranks, while those nearer the back were given lower ranks. Second, we calculated ranks through directional correlation delay analysis, which evaluates the temporal relationship between directional changes that each possible pairing of birds within the flock performs. In these pairwise comparisons, the bird that performs the same sequence of movement changes as another bird, but, on average, delayed in time, is designated the follower, and the other the leader. We resolved leader-follower relations between all pairs of birds, giving each pair a tau value (the average time delay between the two given birds). These pairwise leader-follower relations were then used to construct leadership hierarchies for each flock. A given bird’s leadership score was calculated as the average of its tau values, with the most positive value identifying the bird at the top of the hierarchy. Ref. (Nagy et al. 2010) provides further detail on both methods.

We found a significant correlation between the leadership values obtained through the two methods (Linear Mixed Model (LMM) with *flock* as a random factor: comparison to model without time delay using Maximum Likelihood, $\text{Chisq} = 9.90$, P

= 0.002; figure S1). In other words, birds at the front of the flock were also those whose directional changes were consistently copied by birds further behind. In our subsequent analyses we used the leadership ranks obtained through analysis of spatial positioning, and identified as “Stage-0 leaders” the birds with the highest average rank over the last four training releases. The Stage-0 leader was positioned at the top of the hierarchy in 21 of the total of 32 (8 flocks x 4 flights) Stage 0 flights, and positioned in the top two in 29 of the 32 flights. Therefore, in 91% of Stage 0 flights the bird we identified as the Stage-0 leader was positioned in one of the two positions with the greatest influence on the flocks’ directional decisions. Figure S2a shows the standardized ranks of the Stage-0 leaders over Stage 0.

After training we conducted six experimental stages. We performed four clock-shifts (Stages 1, 2, 4, and 6; see figure 1a), during which selected birds were placed in light-tight chambers until their internal clocks had readjusted to an artificially shifted day-night cycle. All shifts corresponded to either an anticlockwise (fast) or clockwise (slow) 70° shift in the sun’s azimuth on the dates of release. The experiment was run over a three-month period, with a six-week break before Stage 3 for half the flocks and before Stage 5 for the other half, due to the staggered starts. Therefore, birds were clock-shifted either two or three hours depending on the time of the year, in order to maintain a roughly 70° shift.

When only Stage-0 leaders (n=8) were being clock-shifted (Stages 1 and 2), we also placed the remaining members of the flocks (n=32) in a light-tight chamber, but their experimental sunrise and sunset times coincided with true sunrise and sunset. Birds remained in the clock-shifting chambers between four and seven days (depending on weather conditions) before being transported in light-tight

containers to the release site and released in their original flocks. Light-tight containers were used to ensure clock-shifted birds were unable to begin re-adjusting their internal body clocks already prior to being tested, i.e., while being transported to the release sites.

4.6.4 GPS data processing

Upon birds' return to the loft, we downloaded their data using QTravel software (Qstarz V.3.2). GPS tracks were analysed in Matlab (Mathworks 2012b) and R (0.98.1014). The geodetic latitude and longitude coordinates provided by the GPS were first converted to X and Y Universal Transverse Mercator (UTM) coordinates using UTM projection. We then processed tracks by discarding all points other than those where speed was continuously above 5ms^{-1} for 10s before or after the given point (i.e. flight) and trimmed tracks to end once birds had reached to within 100m of the loft.

4.6.5 Figures

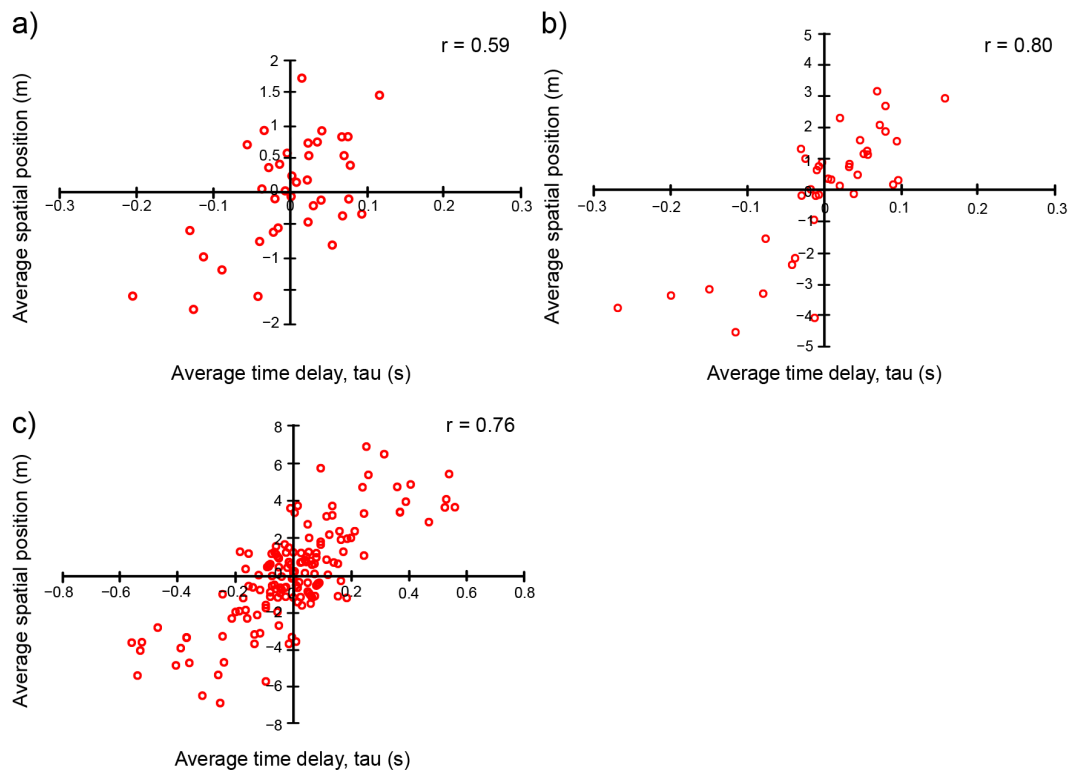


Figure S1: Correlation between time delay (τ) values and those based on birds' spatial positioning within the flock. Correlations between τ and spatial positioning were calculated for each bird as an average over each pair in releases 5-8 with **a)** a distance filter of 10m, and **b)** a distance filter of 30m. Distance filters refer to a threshold value: for data fixes where the distance between two birds is greater than this threshold, those fixes are not used in the calculation of τ or spatial positioning. **c)** Shows the pair-wise average τ for each release, plotted against a pair's spatial positioning. Correlations were calculated using Pearson correlation tests between the two variables in question.

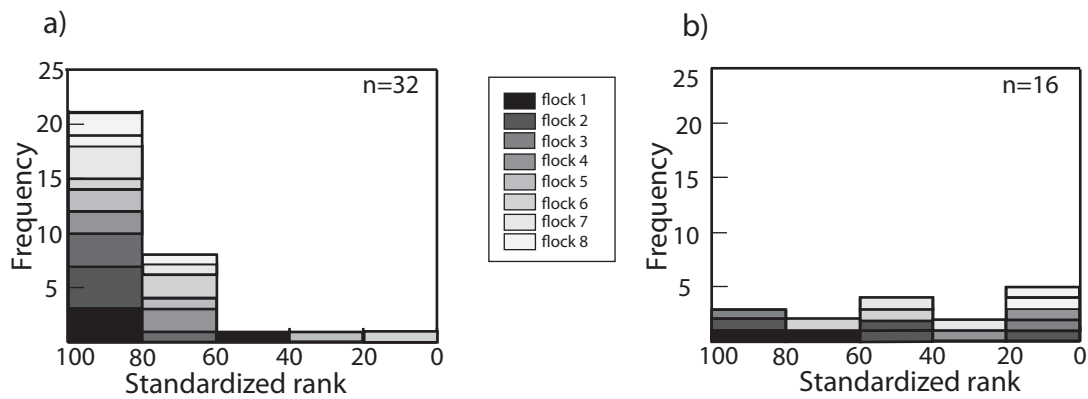


Figure S2: Histograms of the standardized rank positions of the Stage 0-leaders during a) Stage 0 and b) Stages 1&2 (clock-shift). During stage 0, leaders were posited at rank 1 in 21 of the 32 flights and positioned rank 1 or 2 in 29 of the 32 flights. Rank standardization accounts for the varying size of flocks in some releases due to birds splitting. Standardized rank 100 is equivalent to rank 1 (top of the hierarchy) and standardized rank 0 is equivalent to the bottom of the hierarchy. These two distributions are significantly different (Kolmogorov-Smirnov test, p-value calculated using bootstrapping $n=1000$, $D = 0.62$, $P < 0.001$).

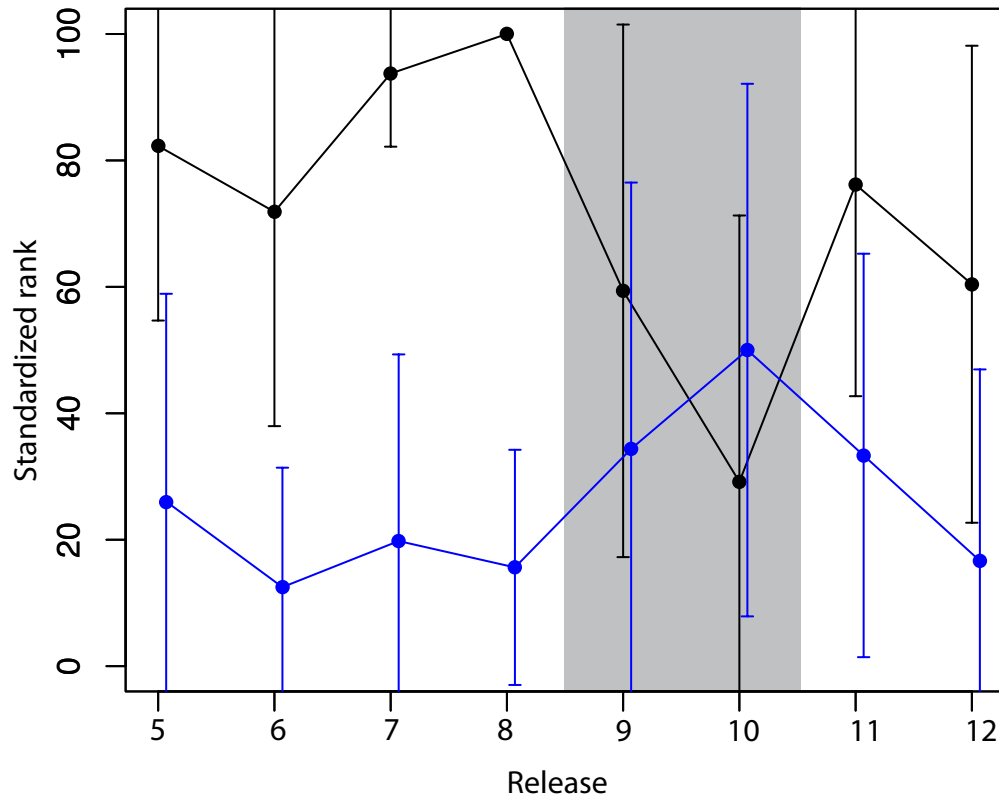


Figure S3: Mean standardized ranks of birds identified as the highest and the lowest ranked after Stage 0 (i.e. in releases 5-8), across Stages 0, 1, 2 and 3. The black line indicates the bird with the highest average rank during Stage 0 (i.e. the Stage-0 leader), and the blue line the bird with the lowest average rank (i.e. 5). Error bars indicate the standard deviation around the mean. Rank standardization accounts for the varying size of flocks in some releases due to birds splitting. Standardized rank 100 is equivalent to rank 1 (top of the hierarchy) and standardized rank 0 is equivalent to the bottom of the hierarchy.

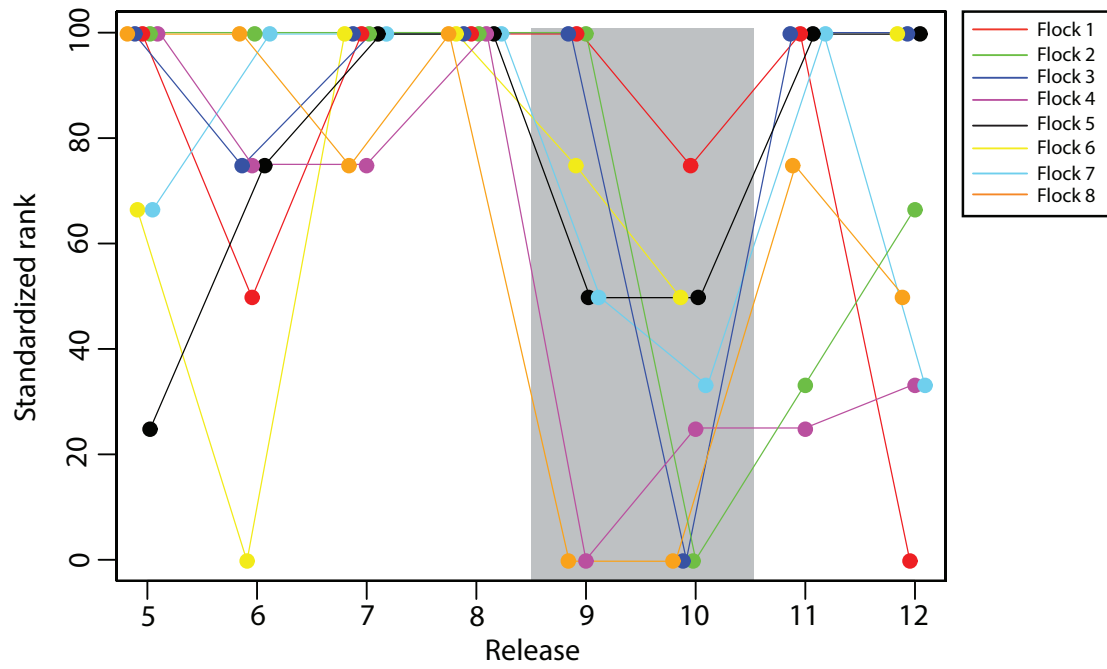


Figure S4: Standardized ranks of birds identified as Stage-0 leaders (i.e. those with the highest rank in releases 5-8), across Stages 0, 1, 2 and 3. Points are spread on the x-axis to enable identification of different flocks. Rank standardization accounts for the varying size of flocks in some releases due to birds splitting. Standardized rank 100 is equivalent to rank 1 (top of the hierarchy) and standardized rank 0 is equivalent to the bottom of the hierarchy.

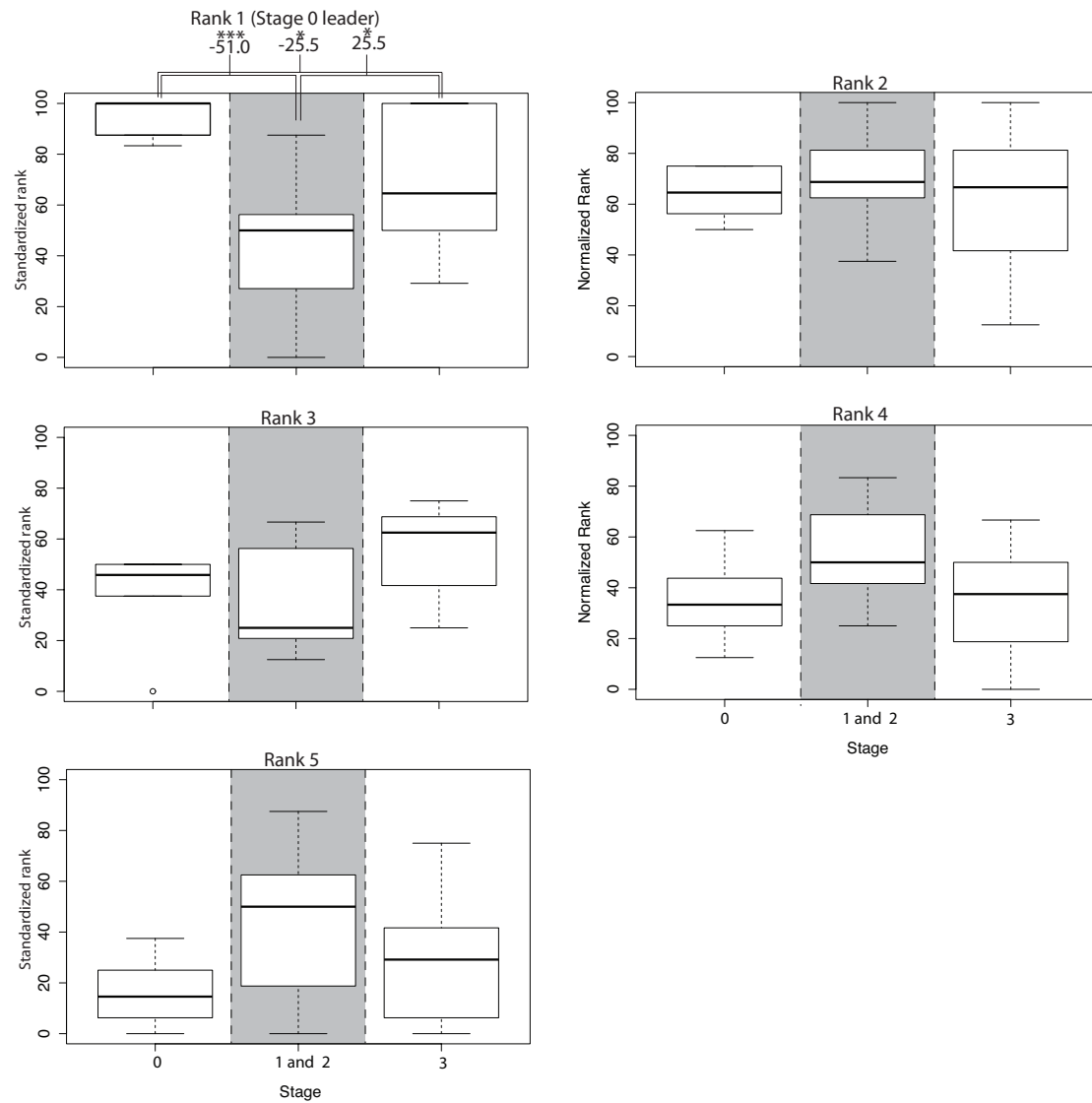


Figure S5: Standardized ranks of each bird ranked after Stage 0, in Stages 0, 1&2 and 3. Box plots show the change in standardized rank for all flocks over each stage. Grey shading represents the clock-shift stages. We tested for significant differences in the mean ranks between the three stages by comparing a LMM for each plot with *standardized rank* as the response variable, *stage* as a fixed variable and *flock* as a random factor, to a model without *stage* using a maximum likelihood ratio test. Significance was only found for Rank 1 ($P < 0.001$), thus for all other birds the standardized ranks did not significantly change between stages. The lowest-ranked birds' position is useful for comparison, since they, like leaders, are subject to a ceiling/floor effect. We then used a post hoc Tukey test to compare the means of the three stages within Rank 1: Stage 1-2, $P < 0.001$, effect size = -51.0; Stage 1-3, $P = 0.02$, effect size = -25.5; and Stage 2-3, $P = 0.02$, effect size = 25.5).

These levels of significance are shown as asterisks and the effect sizes as numerals below them (in the top left panel).

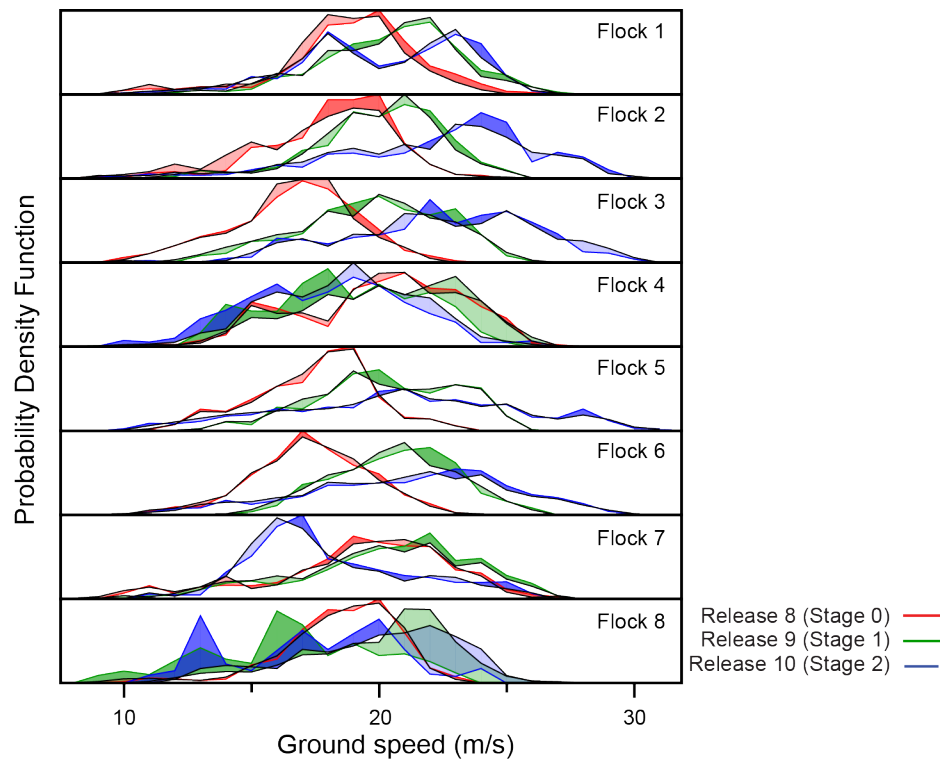


Figure S6: Ground speed distribution for the Stage-0 leaders compared to the rest of the birds for all 8 flocks. Ground speed was calculated for each bird from the GPS trajectories. Ground velocities are the vectorial sums of two vectors: the flight velocity compared to the air and velocity of the air due to wind. Only those data points were used where a bird had at least two neighbours within a radius of 30m. Assuming that all birds of a flock were flying under similar conditions, the Stage-0 leader's Probability Density distribution (coloured line) was compared to that of the rest of the flock (shown in black). Dark shaded areas indicate where the distribution for the Stage-0 leaders is above the rest of the flock, and light shaded areas indicate where the distribution for the Stage-0 leaders is below the rest of the flock. In Flocks 1, 2, and 3 the Stage-0 leaders flew faster compared to the flock in all non-shifted and the two clock-shifted releases. In Flocks 4 and 8 the Stage-0 leaders flew with similar speeds as the rest of the flock in the non-shifted release, but flew

slower in the two clock-shifted releases. In flocks 5, 6 and 7 the Stage-0 leaders flew with similar speeds as the rest of the flock in all non-shifted and the two clock-shifted releases.

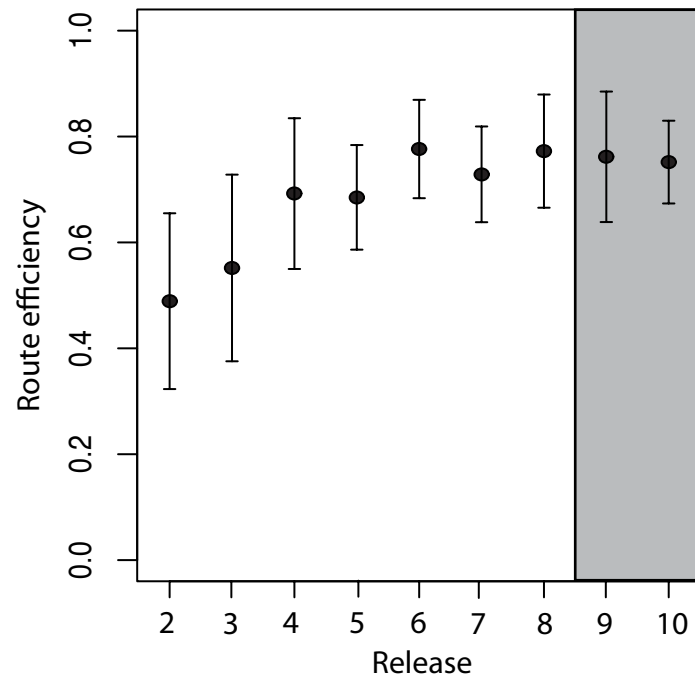


Figure S7: Mean route efficiency of the eight flocks across Stages 0-2. Route efficiency was calculated as the straight-line distance between the release site and the home loft, divided by the actual distance travelled by the bird. Individual birds' efficiencies were then averaged to obtain a single value for each flock (note that this was done since within the same flock birds' efficiencies were not independent). The grey shading around releases 9 and 10 represents the clock-shift Stages 1-2. Error bars indicate the standard deviation around the mean of the eight flocks.

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Chapter 5

A validation of the use of two-dimensional collective behaviour leadership models on three-dimensionally structured fish schools.

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This manuscript is prepared for publication.

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Abstract

Identifying leader-follower interactions is crucial for understanding how a group decides where or when to move, and how this information is then transferred throughout the group. Although many animal groups have a three-dimensional structure, previous studies investigating leader-follower interactions have often ignored the transfer of vertical information. This raises the question as to whether the commonly used two-dimensional hierarchical leadership models can be used justifiably on groups that interact in three dimensions. To address this we quantified the individual movements of banded tetra fish (*Astyanax mexicanus*) within shoals by computing the three-dimensional trajectories of all individuals using a stereo-camera technique. We used these data firstly to identify and compare leader-follower interactions in two and three dimensions, and secondly to analyse leadership with respect to an individual's spatial position in three dimensions. We showed that previous two-dimensional hierarchical leadership models correctly identified the leader-follower interactions 95% of the time when compared to three-dimensional models, and we revealed that fish attend to vertical information received from the same fish from which they gained horizontal information. Our results show that three-dimensional models are not a necessary requirement for identifying leader-follower hierarchies in animals that move freely in three-dimensions.

5.1 Introduction

Important information about the environment (e.g. location of predators or resources) can be acquired and transmitted throughout a group through individuals responding to the position, orientation and speed of nearby neighbours (Ioannou et al. 2011). By identifying who leads whom in these interactions, the direction of information transfer can be determined. Many animal collectives, such as fish schools or bird flocks, often have a three-dimensional group structure where individuals interact in the vertical and horizontal dimensions. Understanding how directional information is transmitted effectively in three-dimensional space within a group is important, as any directional biases in information flow could impact the chance of individuals surviving within the group (Krause and Ruxton 2002, Sumpter et al. 2008).

Individuals that align with nearby neighbours (i.e. change their direction in response to the direction change of a nearby neighbour) can quickly transfer information through the group beyond the direct interaction range of an individual (Radakov 1973, Couzin and Krause 2003, Cavagna et al. 2010). By observing how the direction of a focal individual is correlated with the direction of a non-focal individual after a time delay (directional correlation delay), leader-follower interactions can be determined within groups (i.e. who follows whom) (Nagy et al. 2010). Previous studies have used leader-follower interactions in order to detect leadership hierarchies in homing pigeon (*Columba livia*) flocks (Nagy et al. 2010, Nagy et al. 2013, Pettit et al. 2015, Watts et al. 2016) and medaka fish (*Oryzias latipes*) schools (Perez-Escudero et al. 2014), as well as the direction of information transfer within

golden shiner (*Notemigonus crysoleucas*) schools (Katz et al. 2011). These studies are based on animals that move freely in three dimensions, yet the models used are restricted to two dimensions – the horizontal plane. It is unknown whether vertical and horizontal information is transferred in a similar way and consequently, whether leaders that emerge when only considering horizontal information remain leaders when information from all three dimensions is considered.

Vertical information is known to be an important component of three-dimensional navigation for a range of species, for example honey bees (Dacke and Srinivasan 2007), hummingbirds (Flores-Abreu et al. 2013), and fish (Holbrook and Burt de Perera 2009). During navigation tasks, individual *Astyanax mexicanus* (the fish species used in this present study) were able to learn vertical information at the same rate (Holbrook et al. 2009) and used it with a similar accuracy (Holbrook and Burt de Perera 2013) as horizontal information. When cues from the two spatial axes were positioned in conflict, there was a preference for vertical information (Holbrook and Burt de Perera 2009, Holbrook and Burt de Perera 2011b). The importance of vertical information in navigation suggests that it might also be a useful source of information in other three-dimensional behaviours, such as schooling. During vertical navigation, it is thought that one of the most important cues is hydrostatic pressure, an allocentric global cue (Burt de Perera et al. 2005, Taylor et al. 2010, Holbrook and de Perera 2011a, Davis 2016), and this cue might also inform the dynamics within a fish collective. Currently, it is unknown what the role of either information gained from the allocentric pressure cue or from an alternative social vertical cue informed by body orientation (responding to changes in pitch of neighbours) plays during schooling behaviour.

Many animal collectives move in three dimensions. We used schools of fish (*A. mexicanus*) to investigate the validity of two-dimensional hierarchical leadership models on three-dimensional data and whether there was a vertical directional bias of information flow. We reconstructed high-resolution three-dimensional movement data, for six schools of ten fish over a 30 second period, using a standard photogrammetry technique. We then identified leader-follower interactions using two- (x-y plane) or three- (x-y-z volume) dimensional directional correlation delay models after which we analysed the three-dimensional spatial position of leaders relative to followers, using two vertical frames of reference - gravity and body orientation. We examined first whether fish attend to vertical information from the same fish from which they gain horizontal information, and therefore whether two-dimensional models could predict the same three-dimensional leaders. If this were the case we would expect the leaders that emerged when only horizontal information was considered would remain leaders when information from all three-dimensions was included in the model. Secondly, we examined whether the flow of information in the horizontal and vertical space had a directional bias. We predicted that information would flow front to back, as seen in previous studies (Katz et al. 2011), but in the vertical there would be no bias, and thus individuals would interact with those above and below them equally.

5.2. Methods

5.2.1 Subjects

We used 60 captive-bred Mexican banded tetras, *A. mexicanus* (eyed morph). The fish were approximately 24 months old and raised in the lab from fry in 54-litre

aquaria (60 × 30 × 30 cm) with biologically filtered water enriched with Java moss (*Taxiphyllum barbieri*). The laboratory and aquaria were illuminated with overhead fluorescent lighting on a 12h:12h light:dark cycle and were maintained at 24°C. After completing the experiment, we transferred the fish into a separate set of aquaria to ensure that new fish were used each time.

5.2.2 Experimental set up

We lined three walls and the floor of a cubic glass tank with white sheets of PVC and filled it with water to provide a swimming area of 76 × 76 × 76 cm. Two video cameras (AVT Prosilica GX2300) were placed perpendicular to each other: one pointing perpendicular to the centre of the surface water (to record x-y movements), and one pointing perpendicular to the centre of one of the sides (to record x-z movements) (Figure 1). The cameras recorded at a frame rate of 32 Hz and at a pixel resolution of 2336 × 1752. Frames were synchronised using a master/slave trigger configuration driven by one camera, providing synchronisation to within 8 ms. Monitors were housed behind a screen allowing the observer to operate the cameras without disturbing the animals. We used StreamPix 5 (NorPix, Inc.) to video the fish and used a combination of Matlab (The MathWorks, Inc.2013b), R (RStudio 3.2.1) (R Core Team 2014), Perl (5.18), and CUDA (7.5) for analysis.

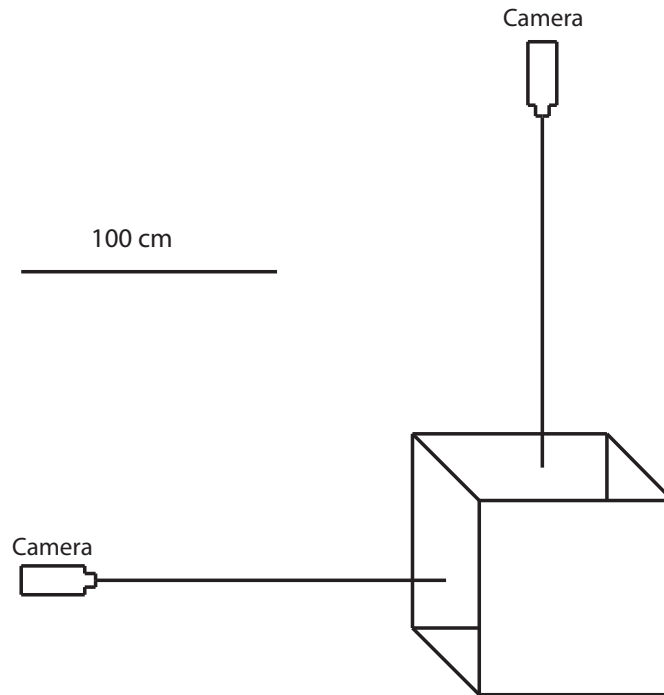


Figure 1: A schematic of the experimental tank set up and the positions of the two cameras relative to the swimming area.

5.2.3 Experimental procedure

Each fish was carefully removed from its holding tank and placed in the experimental tank. We used six shoals of 10 fish. Prior to experiments each shoal was left in the experimental tank for 10 hours to allow fish to acclimatize. Once this time had elapsed, we initiated video recording for 65 seconds. We elicited a predator response in order to record polarized schools, where leader-follower interactions would indicate the direction of information transmission through the group (Wilson 1975, Partridge 1982). After 20 seconds a researcher walked past the tank in order to elicit the anti-predator response. The same researcher walked past the tank on all occasions. Following fishes' anti-predator response we continued to record their

behaviour for the next 45 seconds. Once the trial was completed, all fish were individually photographed (Canon 30D) on 1 mm squared graph paper in order to record the length of each fish.

5.2.4 Three-dimensional trajectory calculation

In order to reconstruct the three-dimensional trajectories of the fish shoals we first calibrated the volume they were moving through by solving the camera geometry. To do this we recorded images of a flat two-dimensional rectangular calibration grid (9 by 12 dots, spaces at 30 mm intervals) visible by both cameras and located the points on each of these grids automatically using computer vision. We then used photogrammetry to solve for camera geometry. This allowed us to reconstruct new points from both cameras (i.e. the individual fish and the corners of the tank) in the three-dimensional volume. This procedure was performed using custom-written software as detailed in Walker and colleagues (2009) and applied by Holbrook and colleagues (2013). We manually located all fish in the shoal for each camera for frames 600-1600 (18.75-50 seconds) to ensure our analysis encompassed the anti-predator response.

5.2.5 Statistical analysis

To investigate how fish respond to individuals in vertical and horizontal space, for each pair of fish we looked at how the direction of the focal fish was correlated with the direction of the non-focal fish in time (directional correlation delay analysis (Nagy et al. 2010), across two- and three- dimensional space. In these pairwise comparisons, the fish that performed the same sequence of direction changes as another fish after a time delay, was designated the follower, and the other the

leader. To identify leader-follower interactions in two (x-y plane) and three (x-y-z volume) dimensions, we used an extended version of the directional correlation delay method as used in Nagy et al 2010. The correlation was calculated by taking the dot product of the velocity vectors of the two fish at successive time intervals (for more information and equations see Supplementary Information). We calculated the dot product using the three-dimensional data and the horizontal components of the data independently. The time delay value (τ) was calculated by taking the time delay that maximises the correlation between a pair of fish. τ values were calculated for the two- (τ_{2d}) and three- (τ_{3d}) dimensional data. We calculated the directional time delay values over short trajectory segments within a 50-frame time window (as in (Nagy et al. 2013, Akos et al. 2014)), enabling us to identify short-term interactions. We removed interactions where the maximum correlation was below 0.7 (where 1 is perfect correlation in directional movements between two individuals, 0 is the expected value for uncorrelated random tracks, and -1 is perfect anti-correlation where two individuals move in opposite directions) or the distance between pairs was over 200 mm (75% interactions occurred within this distance). This enabled us to identify and compare leader-follower interactions in the three dimensions.

To investigate the structure of information flow within the school, for each pair we measured the three-dimensional angular orientation of the leader fish in relation to the direction of motion of the follower fish. For each pair we calculated the horizontal angle, azimuth (ϕ), from the direction of movement of the follower fish and the vertical elevations informed by either gravity (θ_g) or body orientation (θ_b) (Figure 2). We did not directly measure the body orientation of the fish; instead, to

determine body orientation we used the angle perpendicular to the direction of motion. These angles allowed us to determine whether a leader was positioned behind/in front, to the left/right and above/below the follower. We repeated this for all combinations of pairs within the shoal and for all time frame segments.

We split each shoal trajectory into 50 frame segments, and used Linear Mixed Models (LMM) and Generalised Linear Mixed Models (GLMM) from the lme4 package in R (Bates et al. 2015). Due to non-independence of individuals within pairs if we took all pairwise combinations, for all LMM and GLMM models we randomly selected five pairs containing no duplicated individuals for each shoal (all analysis were checked using other random sets of pairs – see supplementary information). We then accounted for pseudo-replication caused by segmenting the data by crossing the random factor *pair* with *section* and nesting *pair* within *shoal*. The presence of auto-correlation in models was checked for by testing for a significant slope between the residuals of a model at time t against the residuals at $t-1$.

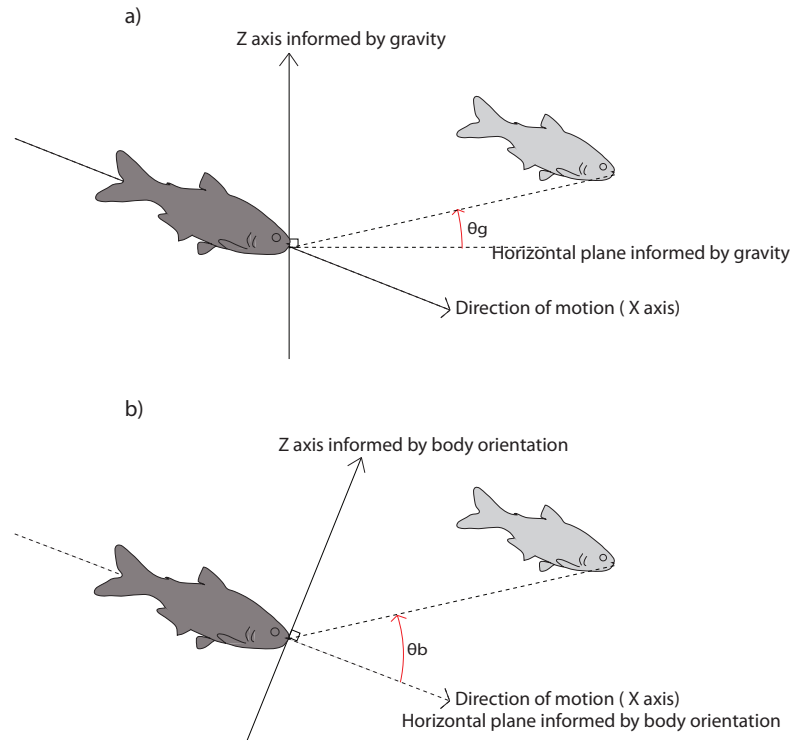


Figure 2: Schematic detailing the two elevation angles (θ) calculated. Two vertical reference frames were used for the spatial positioning calculations based on either (a) gravity (θ_g) or (b) body orientation (θ_b). We placed the follower (dark grey) at the centre of the coordinate system and calculated the relative position of the leader (light grey) with respect to the follower fish's heading. θ indicates the angle from the respective horizontal (x-y plane) and a straight line between the two fish.

5.3 Results

The fish schools moved in three-dimensional space (Figure 3 and SI figure 1) with a mean distance from the bottom of the tank of 232 mm (± 87 mm SD) and had a three-dimensional structure with a mean school height of 144 mm (± 43 mm SD). Schools moved equally up and down throughout the time frame (47% of movements were down and 53% up; figure S1).

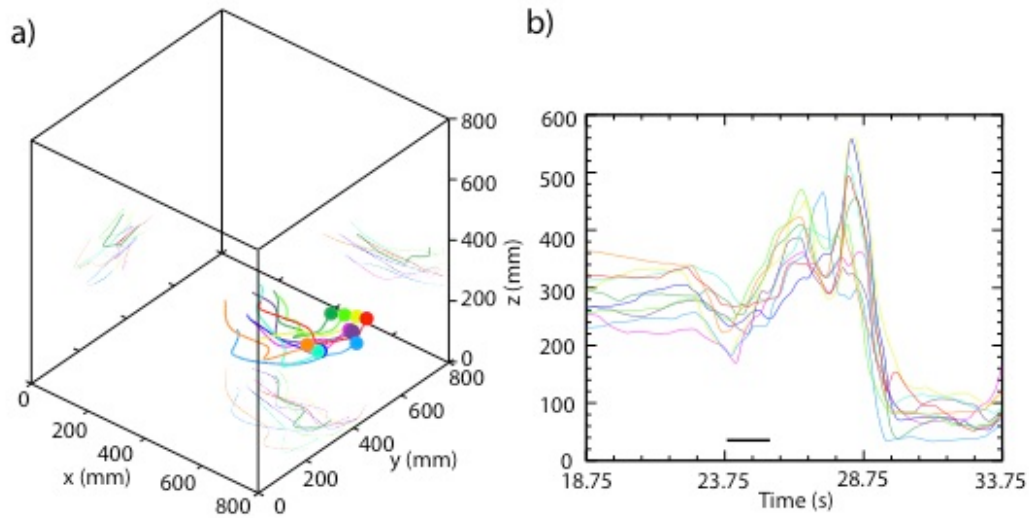


Figure 3: Illustration of the three-dimensional shape of a school. (a) A 50-frame (1.56 seconds) segment of shoal 4 in three-dimensions. Colours indicate each fish and are maintained in b and Figure 4. (b) The elevation profile for shoal 4 over the first 15 seconds of reconstructed data (480 frames). The black bar indicates the 50-frame segment plotted in A.

5.3.1 Leader-follower interactions

We resolved all pairwise leader-follower interactions for each fixed 50-frame segment, using the two different dimensional models with gravity as the vertical reference, revealing a series of hierarchies with transient leadership (Figure 4).

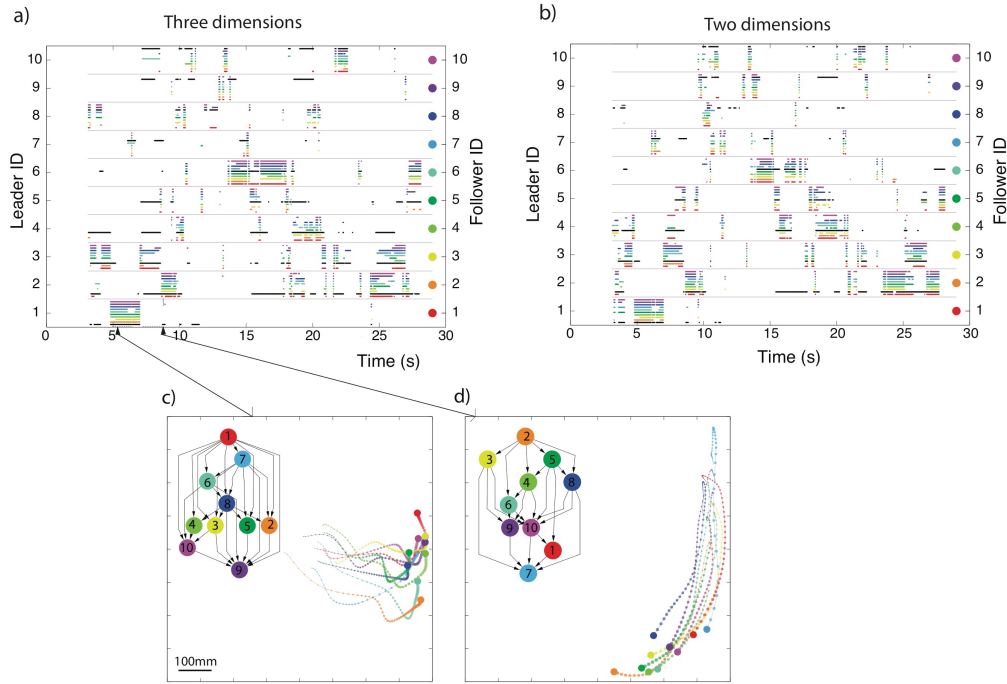


Figure 4: Hierarchical leadership in two and three dimensions. (a) Momentary leader-follower interactions over 50 frame time windows for an example shoal 4 using data in (a) three dimensions and (b) two dimensions. The coloured bars indicate the identities of the fish following the leader fish denoted on the left y-axis. Solid black bars indicate that the leader fish on the left y-axis was not following anyone, either because it was leading the hierarchy, or because it was not interacting with anyone else at that time point. The triangles on the x-axis indicate the exact frame used to plot the hierarchies in (c) and (d).

The mean three-dimensional correlation of pairs was $0.82 (\pm 0.15 \text{ SD})$ very similar to the mean in two dimensions of $0.86 (\pm 0.14 \text{ SD})$, suggesting fish responded to changes in direction made in the horizontal and vertical planes by other fish. Adding vertical information into the directional correlation model did not significantly alter the size or direction of time delay values (τ_{2d} vs τ_{3d}) calculated between pairs. There was a high significant correlation between τ_{2d} and τ_{3d} (Figure 5a; Table

S1; LMM linear regression: correlation estimate = 0.80, chisq = 530.7, df = 1, $P < 0.001$ from comparison to model without the continuous fixed variable *two-dimensional tau*) and 90% of the differences between the two tau values were less than 0.2 seconds (Figure 5b; Figure S2).

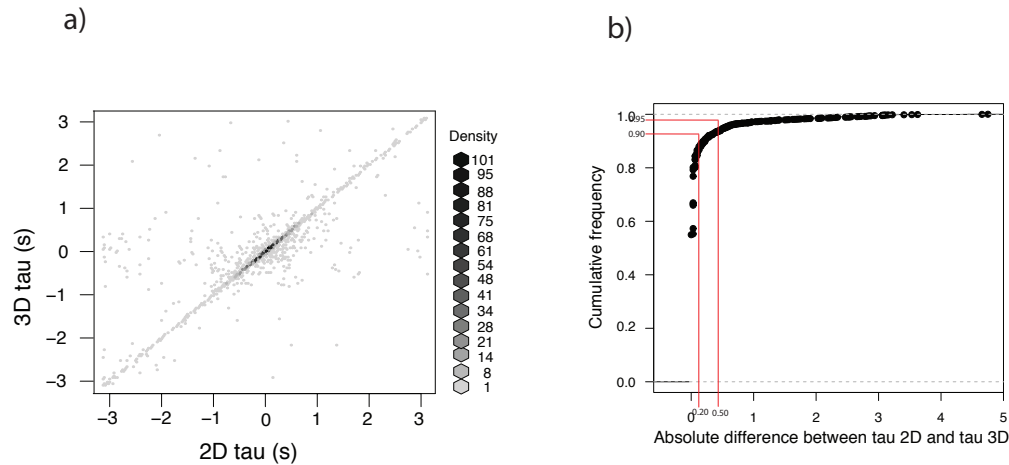


Figure 5: Comparison of two-dimensional and three-dimensional tau values. (a) A density correlation plot of two-dimensional and three-dimensional tau values. (b) Cumulative frequency plot of the absolute differences between two-dimensional and three-dimensional tau values. The red lines indicate where 90% and 95% of the values lie.

For identifying leader-follower interactions we removed points where $\tau < 0.1$ seconds, to ensure mutual interactions were excluded. In pairs of fish, by using the sign of the tau value to indicate who was leading, the two-dimensional model predicted 95% of the time the same leader as the three-dimensional models. Therefore leaders identified with the two-dimensional model were very similar to those identified using three dimensions (Binomial GLMM: $Z = 10.8$, $P < 0.001$, $R^2 = 74\%$; Figure 4a, b and Table S2). There was no significant auto-correlation in the model (Maximum likelihood test: estimate = -0.09, $t_1 = 1.64$, $P = 0.103$). Thus, in our schools, follower fish attended to horizontal and vertical information from the same

leader fish.

5.3.2 Three-dimensional spatial structure

Leader individuals had distinct spatial positions in the horizontal plane (x-y) and in the vertical (z) axis (Figure 6). Independent of the vertical reference frame used, the heat maps revealed a striking pattern of leaders being significantly spatially distributed in front of the followers (Figure 6, Table 1). Independent of the combination of the five random pairs chosen, leader fish were located in front of followers around 70% of the time (Table 1 and SI Table 1). Thus, fish respond more strongly to individuals turning in front of them compared to those positioned behind them. In the vertical axis informed by body orientation, leaders were located 74% of the time between -45° and $+45^\circ$. The significance of proportion of leaders located below the follower for both reference frames depended on the random five pairs in each shoal used for the analysis with proportions varying from 0.52 to 0.60 (Table 1 and Table S3). Even when significance was present the effect size was very low. Together, this suggests that fish respond similarly to fish positioned above or below them.

Table 1: Spatial position of the leaders relative to followers. Table of results for the four binomial GLMM's with random factors of *pair* nested in *shoal* and crossed with *section*, run using averages from 50 frame fixed sections of the track. The response variables were binomial, indicating whether a leader fish occurred in front/behind (model 1 and 2), above/below (model 3) or left/right (model 4) of the follower fish. All model significances (shown with grey shading) were tested against the Holm-Bonferroni step-wise correction for multiple tests and remained significant.

Model Number	Binary response variable	Proportion of points	Estimate	SE	Z	P
1	Elevation Body Orientation	0.52 below	-0.085	0.16	-0.52	0.60
2	Elevation Gravity	0.53 below	-0.13	0.18	-0.74	0.46
3	Font/Back	0.70 front	-0.90	0.17	-5.33	<0.0001
4	Left/Right	0.52 left	-0.11	0.13	-0.87	0.39

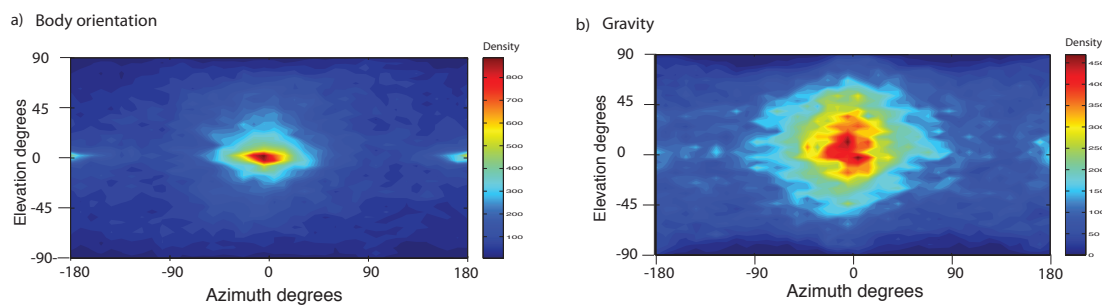


Figure 6: The density of the angular orientation of the leader fish in relation to the follower. Calculations used two vertical reference frames, (a) body orientation and (b) gravity. Elevation has the range -90° : 90° and azimuth -180° : 180° . The centre of the map ($\theta = 0^\circ$, $\phi = 0^\circ$) corresponds to directly in front of the follower fish and the same elevation as the follower fish, the points ($\theta = 0^\circ$, $\phi = 180^\circ$ and $\theta = 0^\circ$, $\phi = -180^\circ$) correspond to directly behind the follower fish and $\theta = 90^\circ$, $\phi = 0^\circ$ corresponding to directly above the follower fish.

To ascertain if the positions of the leaders relative to the followers using body orientation were non-random, we identified the proportion of points within a leading area (LA) of the mean azimuth and elevation $\pm$ one standard deviation. We then calculated the proportion of points within the defined LA for a random (null) model where individuals were randomly assigned into a shoal and the leader was randomly assigned to one member of each pair for every time window. Significance was calculated as the proportion of 10^3 randomizations where $LA_{\text{random}} \geq LA$. The position of the leaders was non-random ($P < 0.001$). Leaders had a mean distance of 70 ± 65 mm (mean $\pm$ SD) in front of followers or 8 ± 85 mm (mean $\pm$ SD) behind followers in the x-axis and were either 56 ± 48 (mean $\pm$ SD) mm below or 62 ± 56 (mean $\pm$ SD) mm above followers in the vertical axis.

Follower fish used the egocentric cue of body orientation as their vertical frame of reference, by matching their body orientation to that of the leaders. The distribution of the elevation angles using the two vertical reference frames were significantly different (Figure 6 and Figure S3; two-sample Kolmogorov-Smirnov test: $H = 1$ at 1% significance level), with a large proportion of points clustering around zero for body orientation.

5.4 Discussion

By resolving pair-wise interactions for high-resolution three-dimensional movement data in fish schools, we have demonstrated that two-dimensional leadership models can correctly identify leader-follower interactions in three dimensions. This result is important in validating previous two-dimensional directional correlation delay models used on three-dimensionally structured groups.

In addition to this we suggest that leaders were equally likely to be positioned above as below followers, and thus that information transmission was likely to flow equally in both vertical directions (up and down).

Information flowed through the three-dimensional structure of the school as fish responded to the changes in the vertical and horizontal directional movements of leaders. Importantly, our results showed that three-dimensional time delay values, the identification of who was leading whom, and the structure of the hierarchy were very similar when using either the two-dimensional or three-dimensional models. The two-dimensional model correctly identified the pairwise leader in three dimensions 95% of the time. These results indicate fish attended to the same leader for vertical and horizontal information. Therefore, in this species at least, the current two-dimensional models are able to identify the majority of the leaders in three-dimensional groups.

Leadership in this study was shown to be transient through time, with individuals swapping position within the school, although this is not necessarily the case for all fish species (Perez-Escudero et al. 2014). Independent of who was leading whom within a pair, followers seemed to adjust their direction to correlate with changes in the direction of neighbours directly in front of them, resulting in front-biased leadership as described in Huth and Wissel (1994). This is found in a range of species including fish and birds (Bumann and Krause 1993, Katz et al. 2011, Pettit et al. 2013). The bias towards paying attention to individuals in front causes information to be transferred front to back through a school. Interestingly, we found no major vertical directional bias to information transfer, with leaders positioned equally above and below the followers. This result did vary depending on the

random pairs chosen, although when significance occurred it was accompanied by a very low effect size. Therefore we suggest that generally leaders were positioned equally above or below followers but there is some bias in certain pairs. Schools did not swim more in one vertical direction, eliminating this as a possible source of bias.

We hypothesise that the difference in strength of bias between information transfer in the vertical and horizontal space could be due to spatial biases in the sensory systems used to mediate local interactions. Schooling is thought to involve a combination of the mechanosensory (lateral line) and visual systems, although their exact roles and importance is an area of controversy (Keenleyside 1955, Partridge and Pitcher 1980, Faucher et al. 2010). Vision is thought to maintain an individual's relative position and orientation with respect to a neighbour (Partridge and Pitcher 1980). The structure of the visual system means there is a blind spot directly behind the fish, where individuals receive no visual feedback. Through human visual inspection the vertical axis of visual field of *A. mexicanus* is thought to be uniform, unlike the visual field of certain benthic-dwelling fish (e.g. clearnose skate, *Raja eglanteria*) probably due to the differing shape and position of the eyes (McComb and Kajiura 2008). However, further studies into the visual systems of *A. mexicanus* are required to ensure this is the case. Our results are restricted to one fish species over a short time frame, and species-specific differences may occur in the potential biases in the transmission. Therefore, our study leads the way for further experiments looking at leadership in three dimensions.

Fish moved vertically towards their leaders, and as forward thrust in *A. mexicanus* is mostly provided by their tail rather than their median and paired fins (Webb 1994), the likely explanation is that fish altered their pitch to align themselves with their

neighbours' body orientations in vertical as well as the horizontal. The increased clustering around zero of elevation angles in body orientation suggests that fish used the social cue from leaders to inform their vertical position rather than using their own personal vertical cue informed by pressure. This does not mean that fish do not pay attention to pressure while schooling, as this global cue is likely to be important in whole school movements in response to vertical locations of interest, especially in the natural environment. Followers kept leaders within a range of -45° to 45° in elevation (using body orientation), similar range of angles to those observed in saithe (*Pollachius virens*), cod (*Gadus morhua*) and herring (*Clupea harengus*) (Partridge et al. 1980). One explanation for this is that followers are maintaining leaders in their binocular field of view. As the eyes are positioned on the side of the head, most fish only have a small field of binocular vision directly in front (Gerking 1994) and therefore it may be advantageous to a fish to keep a leader within this area.

Our results validate the use of previous two-dimensional directional correlation delay models used on three-dimensional groups. The identity of leaders and the structure of the leadership hierarchy were very similar when using either the two-dimensional or three-dimensional models on schools of ten fish. We show that collective three-dimensional data were not a necessary requirement for identifying leader-follower interactions in animals that freely move in three dimensions. The results from this study raise the question as to whether other models of collective behaviour (e.g. attraction and repulsion models) that currently are predominately performed on two-dimensional data sets would hold up when applied to high resolution three-dimensional movement data.

5.5 Supplementary Information

5.5.1 Directional correlation delay analysis

We used an extended version of the directional correlation delay method as used in Nagy et al 2010, which used gravity as the vertical frame of reference (z) for the relative coordinate system of an individual, in order to identify leader-follower interactions in two (x-y plane) and three (x-y-z volume) dimensions. For a pair of fish i and j , the directional correlation is, $C_{ij}(\tau) = \langle v_i(t) \cdot v_j(t+\tau) \rangle$, where $v_i(t)$ is the normalised velocity of i at time t and $v_j(t+\tau)$ is the normalised velocity of fish j at time $t+\tau$. The normalised velocity is calculated by dividing the velocity vector by its magnitude (i.e $v_i(t) = x_i(t)' / |x_i(t)'|$). The number of dimensions used for the velocity vector depended on whether we ran the analysis in two dimensions (v_x, v_y) or three dimensions (v_x, v_{yi}, v_{zi}). The value of τ_{ij} (τ) that maximizes the $C_{ij}(\tau)$ correlation function across t , is the average time delay between a pair of fish. The correlation coefficient will be 1 if the fish are perfectly aligned and 0 if their directions are uncorrelated. When $\tau_{ij} > 0$, this is interpreted as fish j is following fish i , as when fish j turns, fish i has already turned. We identified the average τ_{ij} for each 50-frame segment using a moving time window, used in Figure 4 a and b. To calculate unique hierarchical positions for each fish, we calculated the average directional correlation time delay of fish i with the rest of the school (*mean tau*). We filtered out points where the fish were more than 200mm apart (roughly 4 body lengths) or when the correlation was less than 0.7. 75% of the interactions occurred within this distance.

5.5.2 Supplementary results

All shoals had an equal range of individual sizes (Brown-Forsythe Levene-type test: $P = 0.4845$), which was potentially important, as fish size has been shown to correlate with leadership (Reebs 2001). The mean fish length was $50 \pm 0.4\text{mm}$ (mean $\pm$ SD, $N = 60$ fish measured from the mouth to the end of the tail).

5.5.3 Supplementary tables

Table S1: Correlation between tau values calculated on three-dimensional and two-dimensional data. The table indicates the result for six iterations on a different set of five random pairs chosen from each shoal to remove the issues of pseudo replication on individuals in multiple pairs. The results are from a LMM between the two variables. Note that the correlation estimates are all significant and highly correlated.

Iteration	Estimate	Chisq	df	P
1	0.80	530.7	1	< 0.0001
2	0.77	421.8	1	< 0.0001
3	0.89	567.9	1	< 0.0001
4	0.88	673.4	1	< 0.0001
5	0.75	273.9	1	< 0.0001
6	0.72	357.7	1	< 0.0001

Table S2: The identification of leaders using three-dimensional and two-dimensional data. The table shows the significant similarity between the identification of leaders within a pair between the two models for the six iterations of different sets of five random pairs chosen from each shoal. The results are from a binomial GLMM. Note that the results are very similar for all pairs.

Iteration	Z	P	R ² (%)	Proportion
1	10.8	< 0.0001	74	95
2	7.25	< 0.0001	70	94
3	6.96	< 0.0001	72	95
4	6.08	< 0.0001	70	94
5	6.25	< 0.0001	76	96
6	7.27	< 0.0001	70	94

Table S3: The spatial position of leaders relative to followers. Results are shown from four binomial GLMMs identifying if leaders are located in a certain position more often than by chance. The table shows the results for the six iterations of different sets of five random pairs chosen from each shoal. Note that for front/back and left/right the results are consistent across interactions but not for up/down.

Response variable	Iteration	Estimate	Z	P	Proportion
Up/down Body orientation	1	-0.085	-0.524	0.60	0.52
	2	-0.238	-1.69	0.09	0.56
	3	-0.379	-3.01	0.003	0.60
	4	-0.204	-1.30	0.19	0.55
	5	-0.459	-3.04	0.002	0.61
	6	-0.563	-3.39	<0.001	0.63
Up/down Gravity	1	-0.131	-0.736	0.46	0.53
	2	-0.27	-2.18	0.02	0.57
	3	-0.34	-2.40	0.02	0.59
	4	-0.25	-1.93	0.05	0.56
	5	-0.46	-2.80	0.005	0.60
	6	-0.45	-2.18	0.03	0.61
Front/back	1	-0.90	-5.33	< 0.001	0.70
	2	-1.11	-5.63	< 0.001	0.75
	3	-0.78	-5.57	< 0.001	0.69
	4	-0.87	-5.13	< 0.001	0.70
	5	-1.10	-5.12	< 0.001	0.73
	6	-0.82	-5.90	< 0.001	0.70
Left/right	1	-0.109	-0.86	0.39	0.52
	2	-0.17	-1.24	0.22	0.53
	3	-0.17	-0.67	0.57	0.52
	4	-0.03	-0.22	0.83	0.51
	5	-0.22	-0.084	0.08	0.55
	6	0.10	-0.79	0.43	0.47

5.5.4 Supplementary figures

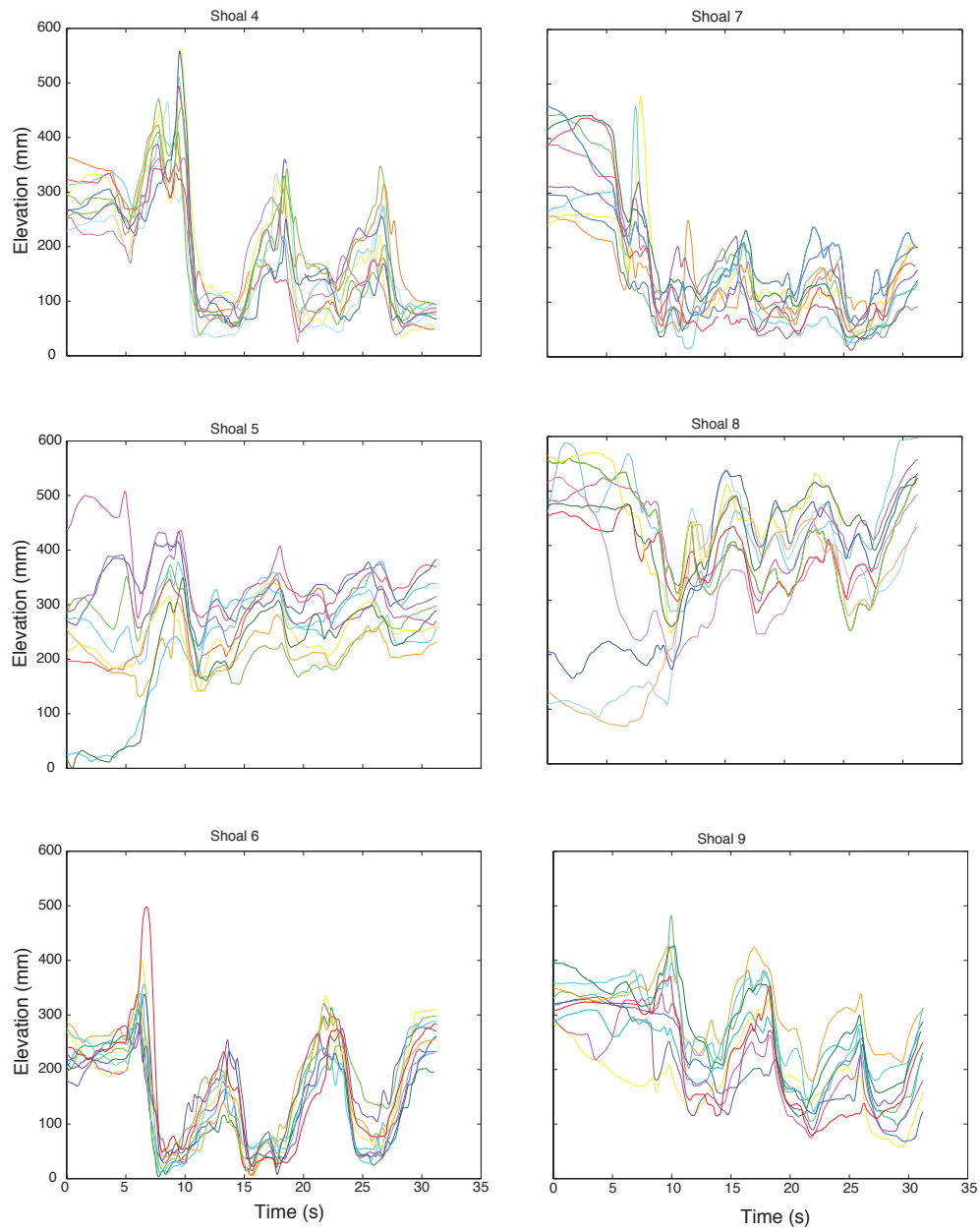


Figure S1: Elevation profiles for the six shoals over the 31.25 seconds. Coloured lines indicate the different fish within the shoal.

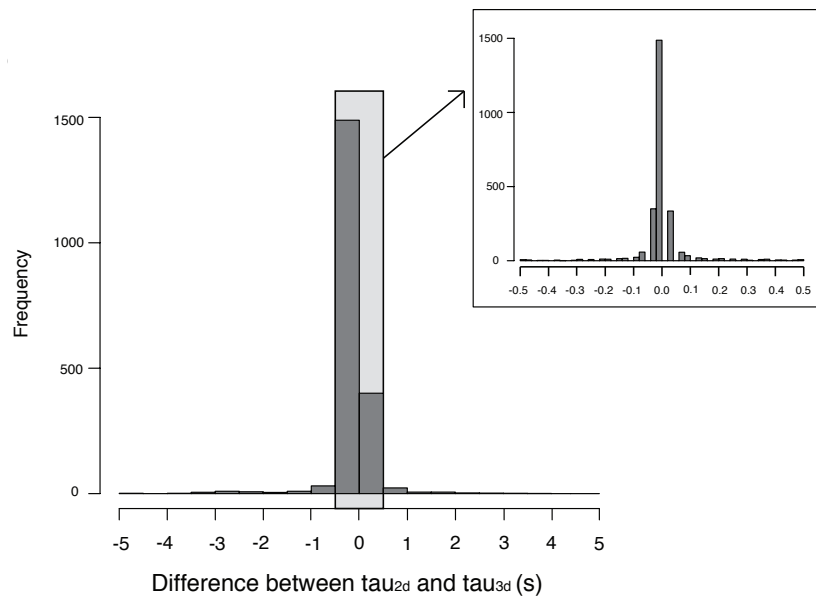


Figure S2: Frequency of the difference between the two-dimensional and three-dimensional tau values.

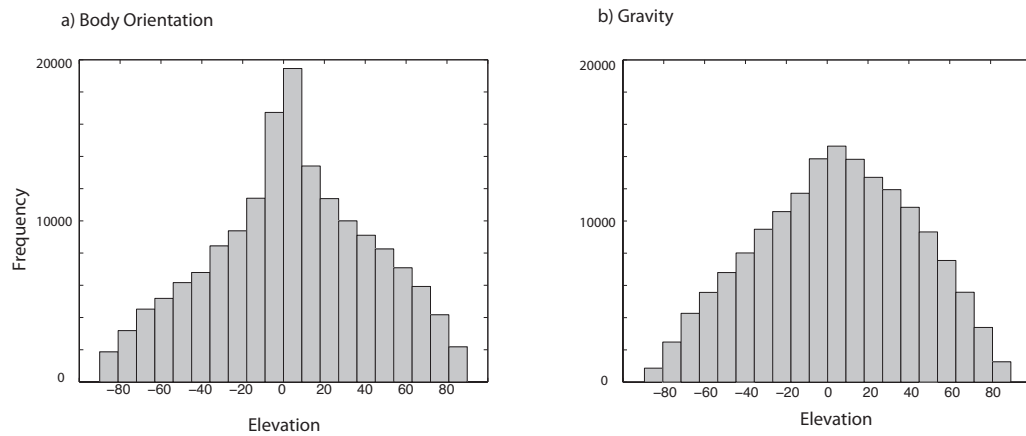


Figure S3: Frequency distribution of elevation angles. (a) Body orientation or (b) gravity was used as the vertical frame of reference when calculating elevation angles.

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Chapter 6

General discussion and conclusions

This chapter contains a general discussion of the findings from previous chapters.

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6.1 Summary of thesis aims

In some animal groups, while travelling together directional decisions can be reached via a hierarchy of influence. This involves all group members contributing to decision-making processes, but with individuals having different weights of influence depending on their “rank” in the hierarchy. This decision-making mechanism lies on a spectrum between the two extremes of group decision-making i.e. fully egalitarian and despotic leadership. Previous research into group navigational leadership hierarchies has primarily concentrated on using homing pigeons (*Columba livia*) as a model species (Nagy et al. 2010, Xu et al. 2012, Flack et al. 2013, Nagy et al. 2013, Santos et al. 2014, Pettit et al. 2015). Investigating hierarchical decision-making in one species in detail is helpful when trying to elucidate precisely how and why hierarchies form in that species. This can be useful in trying to understand principles that might be applied to other species, which are harder to study. However, due to constraints in present technology not all questions can be explored using homing pigeons. The tightly-schooling Characin fish *Astyanax mexicanus* is an excellent alternative model to use as they also move and interact in three dimensions, and much is known about their spatial cognition (Davis 2016).

My aim in this thesis was to investigate the nature of hierarchical consensus decision-making. Using data from birds (*C. livia*) and fish (*A. mexicanus*), I examined how individuals’ prior experience influences the hierarchical leadership structure and its long-term stability and flexibility. In addition, I also validated the use of two-dimensional leadership models in describing leadership behaviour in three-dimensionally moving groups. For each question posed in Chapter 1, I shall

demonstrate how this thesis advances our current understanding of leadership hierarchies and establish directions for future work.

6.2 Unifying questions revisited

6.2.1 What factors influence the structure of leadership hierarchies?

A major theme of this thesis is how differences between individuals create decision-making structures. Leadership hierarchies involve all members of a group, but allow some to have a disproportionally greater weight in the decision-making process (Nagy et al. 2010). It is thought that the benefits derived from and ultimately the adaptive value of leadership hierarchies will depend on the factors that place specific individuals into leadership positions. However, little is known about what determines where individuals are positioned in such hierarchies and therefore the weight of their input. My experiments have supported the idea, previously proposed, that a combination of factors are responsible for structuring leadership hierarchies. In particular this thesis focused on the role of navigational experience and information quality.

Navigational experience has previously been proposed as a key factor in determining the structure of hierarchies in homing pigeons (Flack et al. 2012). Experience arises from previous encounters with the environment. In Chapter 2, I demonstrated how large differences between individuals' navigational experience resulted in top leadership roles being filled by experienced birds more often than inexperienced birds, although throughout the rest of the hierarchy clustering by level of experience was not evident. In several other species, more knowledgeable individuals have greater influence over group movements (Reebs 2000, Maransky

and Bildstein 2001, Brent et al. 2015). For example, older female killer whales (*Orcinus orca*) with greater ecological knowledge lead their pods when salmon are in low supply and therefore the pressure to locate food is highest (Brent et al. 2015). As finding salmon is crucial to an individual's fitness during low salmon abundance years, there seems to be an advantage to the individuals of a group to having an experienced leader. For homing pigeons, as discussed in Chapter 2, having an experienced leader might increase the navigational efficiency of individuals within groups, enabling flocks to fly shorter routes and therefore individuals spend less time at high risk of predation and away from the loft.

Homing pigeon flocks, much like other animal collectives, are thought to consist of individuals with varied levels of navigational experience. Inter-individual differences in experience are theorized to be important in enabling leadership to emerge in the absence of explicit signals, allowing experience to have a role even in large groups such as fish schools (Conradt and Roper 2003, Couzin et al. 2005). In Chapter 3, homing pigeon flocks that were homogeneous both in age and by proxy experience had unstable leadership hierarchies, with an increase in the number and strength of mutual interactions (shared decision-making) compared to more heterogeneous flocks. The latter exhibited stable leadership hierarchies. In this chapter age and experience were correlated with older birds also having the most navigation experience. As suggested by a previous study (Santos et al. 2014), the increase in mutual interactions between pairs can lower the stability of the hierarchies. Therefore, the level of variation in age within a group can influence the structure of the navigational leadership hierarchy; it affects how individuals interact, which impacts the stability of the decision-making structure as a whole.

Other studies have shown in both homing pigeons (Biro et al. 2006, Xu et al. 2012, Santos et al. 2014) and baboons (*Papio anubis*) (Strandburg-Peshkin et al. 2015) that decision-making can involve a combination of shared decisions and leadership, depending on circumstance. When conflict arises over the direction of movement, baboon groups and pairs of homing pigeons have been shown to choose one direction over the other (unshared) when the angle between them is large, but otherwise compromise (shared) (Biro et al. 2006, Strandburg-Peshkin et al. 2015). The results from Chapter 3 agree with these findings, and highlighted further that the relative strengths of shared and unshared decisions are dependent on group composition.

Taken together the results from Chapters 2 and 3 highlight the importance of a variation in age and experience in the formation, structuring and stability of multi-level leadership hierarchies. The exact mechanisms enabling leadership by experienced birds and those behind inter-individual differences in age affecting stability are currently unknown. One potential explanation could be linked to speed. Speed has been shown to be particularly important in structuring leadership hierarchies, with faster pigeons shown to be positioned at the front of the flock where they have the highest input in the decision-making process (Pettit et al. 2015). However, at present it is unknown whether speed correlates with other factors and as such could underlie various factors that have previously been revealed to be important in leadership. Navigational experience could impact a bird's speed, for example, by altering its "confidence" in a route. Therefore, one explanation could be that experienced birds fly faster, resulting in experienced birds leading and inexperienced, slower birds trailing behind (following). This would

require no active recognition of who was experienced and instead rely on a self-organised mechanism related to individual differences in flight speed (Pettit et al. 2015) due to variances in experience. As such, variation in birds' experience levels may, via variation in their speeds, result in a stable hierarchy. In Chapter 3, I showed that the difference in stability between homogeneous and heterogeneous flocks was not due to differences in speed variances, which might have been expected if speed was correlated with experience. Nonetheless, this study was not designed to directly test this hypothesis and therefore this inference is not conclusive. A better test would have been to compare speeds of birds with different levels of experience of a route, not just the variances within the homogeneous and heterogeneous flocks. Future work will need to investigate whether birds with more local experience of the landscape fly faster, irrespective of other determinants of speed (such as body size). One way would be to experimentally manipulate birds' speeds, for example by adding small extra or attachments that cause aerodynamic interference to selected birds. This would reveal if increasing followers' speeds is sufficient to turn them into leaders, or, conversely, if decreasing leaders' speeds is sufficient to turn them into followers. Alternatively, if experience itself were more important than speed we would expect the leaders to continue to lead. This could be either because other flock members recognise the experienced bird alter their speeds to allow the experienced but slower bird to remain in front or because leader-follower relationships are established primarily through differential attendance to social versus personal information rather than speed.

Previous studies have suggested that a combination of factors may be involved in structuring navigational leadership hierarchies in homing pigeons (Pettit et al.

2015). The lack of large-scale stratification based on experience in Chapter 2 and the presence of unstable hierarchies in homogeneous compared to heterogeneous flocks in Chapter 3 supports this idea. Social dominance during feeding has been shown to be unrelated to navigational leadership (Nagy et al. 2013). In Chapter 4, I investigated another potential factor: quality of navigational information. Clock-shifting the highest-ranked leader in flocks introduced incorrect directional information at the top of the leadership hierarchy, I revealed that when hierarchy leaders possessed inaccurate “bad” information they lost their top positions. This resulted in flocks effectively “correcting” leaders’ errors, and flying non-deviated routes home. As I discussed in Chapter 3, clock-shifting comes with potential uncertainty for an individual in terms of their direction home, as navigational cues are placed into conflict. Uncertainty may have caused a reduction in speed of the leader resulting in its subsequent displacement further down the hierarchy or by acting as a cue to other flock mates, causing them to reduce their reliance on social information from the ‘misinformed’ leader. In both cases there is no active transmission on the part of the leader: it does not choose whether or not to pass on its information. In six of the eight flocks I tested, the speed of the leader was not affected by being misinformed, strongly suggesting that changes in speed were not responsible for the observed change in the structure of the hierarchy in this experiment. Considering this, I suggest it is more likely that flock members were able to pick up on other cues, such as recognising the increased conflict between their personal and the leader’s directional preferences. This does not have to involve active recognition but could result from individuals interacting consistently based on relatively simple rules; for example if a leader turns more than a certain bearing from what a follower judges to be the correct direction, the follower will not copy

the turn (i.e. will not follow). To test the operational presence of such simple rules, one could vary the conflict between leaders and followers by changing the duration of the clock-shift and examining whether leaders only lose their leadership when the level of conflict is above a certain threshold.

Taken together, the results from Chapters 2-4 highlight the idea that leadership hierarchies are structured by a combination of factors that may override each other depending upon the circumstances (i.e. composition of flock, motivation and information quality). The notion that leadership is determined by a combination of factors, some relatively stable (e.g. age, experience, temperament) and other factors that change depending on context (e.g. nutritional levels and information quality) has support from other species. In pairs of sticklebacks (Nakayama et al. 2012), bold fish, in general, emerged as leaders, but this was not the case when shyer fish had low nutritional levels. In this context the shy fish initiated leading, suggesting that transient factors can, under some circumstances, override more stable ones. Further research is necessary in order to establish whether there are other individual features of homing pigeons, for example temperament or motivation related to breeding state or hunger, that can work in combination with experience, speed and information quality to influence leadership in collective decision-making.

6.2.2 How stable are leadership hierarchies?

Although leadership is generally a widespread phenomenon throughout the animal kingdom (Conradt and Roper 2003), relatively few studies have looked at stability, especially over many repeated interactions and extended periods (Dumont et al. 2005, Burns et al. 2012, Flack et al. 2013, Nagy et al. 2013, Perez-Escudero et al. 2014, Santos et al. 2014, Pettit et al. 2015). Recently it has been proposed that the

potential advantages of hierarchical structures in decision-making may come not only from the benefit of certain individuals leading (i.e. those most experienced) but also from the stability of the structure itself (Flack et al. 2013). In homing pigeons, previous work has suggested that navigational leadership hierarchies are very stable structures, which are stable during a small number of flights (4-8), both round-the-loft “free-” (Nagy et al. 2010) and homing-flights (Nagy et al. 2010, Santos et al. 2014) and are robust to small changes in individual experience (Flack et al. 2013) and to the merging of small groups together (Nagy et al. 2013). However, little is known about whether hierarchies are stable over longer time frames or whether consistency depends on the context, such as flock composition or turning verse straight flight. Consistent leadership could arise through active recognition of certain morphological, physiological or behavioural features in conspecifics, such as seen in dominance hierarchies in chacma baboons (*Papio urinus*) (King et al. 2008) or passively via simple behavioural rules (Couzin et al. 2002).

In Chapter 3, using heterogeneous flocks comprising individuals varied in age experience, I showed that navigational leadership hierarchies could be stable over a much longer time period than previously evidenced (25 flights, conducted over a period of one month). The consistency scores I obtained were comparable to previous studies using heterogeneous pigeon flocks over a smaller number of releases (4) (Pettit et al. 2015). As I discussed above, the precise reasons for stability in heterogeneous flocks, but not in homogeneous flocks, is presently unknown, but highlights the importance of flock composition when studying leadership in homing pigeons.

Interestingly, in Chapter 5, I did not find stable leadership hierarchies in schools of *A. mexicanus* during anti-predator response behaviour over a 30 second period using a fine-scale analysis (32Hz compared to 5Hz in pigeons). One difference when comparing the results from fish in Chapter 5 with previous studies on leadership hierarchy stability in homing pigeons is that, I studied leadership during an anti-predator response, something not previously examined in pigeons. Homing pigeons are commonly tested in one of two scenarios: “free-” or “homing” flights. An interesting extension would therefore be to examine the leadership hierarchies in *A. mexicanus* during behavioural manoeuvres similar to those exhibited in homing pigeons to see if leadership stability in this species is dependent on behavioural context. In an experiment where schools of mosquitofish (*Gambusia holbrooki*) were released into a Y-maze, some individuals were found to consistently occupy frontal positions. This was found to be independent of dominance, size or sex suggesting that certain individuals were predisposed to leadership roles (Burns et al. 2012). Similarly, a stable leadership-hierarchy was found to occur in freely swimming medaka fish (*Oryzias latipes*) over three days, although this fish species is known to have a consistent group structure (Perez-Escudero et al. 2014). As discussed above, other studies involving the observation of feeding rates of roach (*Rutilus rutilus*) in the field show that leadership was only transient as it depended upon the nutrition levels of fish (Krause 1993). These results suggest that leadership stability in fish varies across species and also, as with homing pigeons, varies according to the context.

6.2.3 *Are there advantages associated with stable leadership hierarchies?*

The variation I found in hierarchy stability between homogeneous and heterogeneous pigeon flocks, raises the question arises of whether there are advantages associated with stability as Flack et al. (2013) proposed. Potential benefits to stability could help explain the adaptive value of these structures. My results from Chapter 3 are not conclusive, but indicate two potential benefits of stable leadership hierarchies during homing.

The first is suggested by the finding that heterogeneous groups with stable leadership hierarchies learnt routes faster, as shown by the rapid increase in route efficiency compared to homogeneous groups that had unstable hierarchical decision-making structures (although both groups reached similar final efficiencies). Faster learning enabled by hierarchy stability could be caused by enhanced information flow enabling improved mixing of the groups' information (Lusseau and Conradt 2009, McComb et al. 2011) or by the presence of a stable experienced leader (Chapter 2). As discussed above and shown in Chapter 2, experience is important in structuring the leadership hierarchy, and in particular key in determining the identify of the highest-ranked bird. This suggests stable experienced leaders could be beneficial to the flock. However, my results cannot distinguish between the two mechanisms. An alternative explanation is that the presence of more experienced birds within the flock might have resulted in enhanced learning independent of stability. For example, a study in whooping cranes (*Grus americana*) showed that flocks took straighter migratory routes if they contained older, more experienced birds (Mueller et al. 2013). In Chapter 3, I cannot rule out the possibility that the presence of older birds in the heterogeneous flocks

was responsible for their enhanced navigational abilities initially, rather than the presence of a stable leadership hierarchy per se. In my design, homogeneous and heterogeneous flocks did not span exactly the same age ranges; homogeneous flocks consisted of relatively young birds (one flock of naïve 2-year-old birds, and two flocks of more experienced 3-year-olds), with none of them composed of birds as old as the oldest subjects used in the heterogeneous flocks (4-6 years old). An interesting extension would thus be to examine homogeneous flocks comprised only of older birds – this would help disentangle whether hierarchical stability itself was the cause of the improved early efficiency or, rather, whether it was due simply to the presence of older, more experienced birds within the flock. Independent of the mechanism behind the increased learning rate in heterogeneous aged flocks, this advantage could be particularly crucial in migrating species where flock composition can range from all naïve juveniles to fully mixed-age flocks. The information transfer from more experienced older individuals, who often have greater navigational capabilities and knowledge than juveniles (Mettke-Hofmann and Gwinner 2003), to inexperienced individuals is important for navigational success (Chernetsov et al. 2004).

The second possible advantage of leadership hierarchical stability was suggested by data from solo releases conducted after the flock flights. Birds that had flown in a stable hierarchy were more likely to maintain the high-efficiency routes achieved by their flocks. I discussed that this could be due to the presence of stable leaders, which enables flocks to consistently fly similar (efficient) routes on each successive release, and thus to aid individual learning by exposing birds to the same route repeatedly and consistently.

However, previous work has suggested that not every flock member is expected to benefit equally from flock flights in terms of learning. Pettit et al. (2015) showed that leaders learnt routes more efficiently than followers, probably through the experience of having to make the majority of the navigational decisions. In Chapter 3, I looked at whether birds that were the most consistent leaders during flock flights also had higher solo efficiencies. I did not find this to be the case; the most efficient birds did not end up leading as observed Pettit et al. (2015). One reason for this difference could be the difference in the number of releases between the two studies (4 in Pettit et al. 2015 versus 25 in Chapter 3). Therefore, it may be that the advantage to leaders in terms of improved spatial learning is limited to the first few flock flights, but the additional experience of flying the same route many more times gives followers ample chance to learn it just as well. In other words, the results from Chapter 3 suggest that there is a spatial learning benefit to the individuals within the group after 25 flights but that the benefit is equal among them irrespective of their leadership status. Elucidating the relationship between spatial learning and leadership is important to understanding how individuals learning in a social context (“collective learning”; Flack et al. 2013) plays out over repeated journeys.

It is important to note that the advantages of stability on which I have focused are linked to the accuracy of orientation while retuning home. Belonging to a group is also beneficial for flock members, especially in terms of predator avoidance (Krause and Ruxton 2002). Certain landscape types may increase the chance of predation and therefore, we would not expect routes to be optimized only for accurate navigation. Even after repeated solo releases, birds do not necessarily take the straightest path. For solo birds, efficiency values reach around 0.8 (Meade et al.

2005) and this is similar to the values I found with the flocks in Chapters 2, 3 and 4. Therefore, although taking a shorter route would be beneficial for a flock, there are other considerations to take into account. If minimising risk was the main priority, staying as a flock might be more important than maximising individual efficiency.

6.2.3 What happens when leaders have “bad” information?

The description of leadership hierarchies as ‘stable’ (e.g. Nagy et al. 2013, Santos et al. 2014, Pettit et al. 2015, Chapter 3) or ‘robust’ (e.g. Flack et al. 2013) may give an impression of them as inflexible structures. A recent model by Flack et al. (2015) predicted that if the most influential individual in the group was also the one with the highest error, then this error would propagate down the hierarchy causing a decrease in the accuracy of the groups’ decision-making. If this indeed occurred in nature then stable, inflexible hierarchical structures would be detrimental in some situations. In Chapter 4, I found this potential disadvantage could be overcome in pigeon flocks. I clock-shifted leaders to introduce an error of a specific magnitude at the top of leadership hierarchy, and showed that this error did not cause entire flocks to fly ‘bad’ routes: instead, hierarchies appeared to reorganise, with the misinformed leaders dropping in rank and losing their previous level of influence. This highlights that rather than being inflexible, hierarchical decision-making can be flexible under certain circumstances, with incorrect information being ignored.

The fact that flocks flew ‘good’ (i.e. non-shifted) routes when their leader was clock-shifted could also be explained if groups decision-making was fully shared rather than hierarchical. Previous studies have suggested that shared decisions are important in homing pigeons (Jorge and Marques 2012, Xu et al. 2012), although their ratio to unshared decisions may vary according to context (such as level of

individual variation within the group; see Chapter 3). However, the presence of consistent time delay values between pairs of birds in Chapter 4 indicated that some birds influenced the flock's directional decisions more than others, i.e. the flocks were not fully democratic. Those designated as leaders prior to clock-shifting had (by definition) the highest positive time delay values, indicating that they were likely to have the greatest influence over the flock's movements. After the leaders had been clock-shifted their time delay values decreased, revealing that they no longer influenced flock decisions to the same extent. In Chapter 4, I discussed in detail the possible mechanisms behind this result, which range from a drop in rank by leaders due to increased uncertainty in their own information, to active recognition by followers that their leader is 'misleading' them. In either case, however, the results suggest that hierarchies have the capacity for flexibility in circumstances where leaders are 'bad' (although whether they have to be worse than some specific threshold remains to be explored).

Chapter 4 represents the first time clock-shifting has been utilised in studies of collective movements to introduce incorrect information into a system. This incorrect information is accompanied by potential uncertainty as birds' navigational cues are placed in conflict, and I have argued that this uncertainty could have been key to leaders losing their leadership positions. A future study could disentangle the effects of incorrect information and uncertainty on hierarchical reorganisation. This could be achieved by releasing flocks with clock-shifted leaders from a novel site – in such cases birds would be less likely to experience a conflict (i.e. 'realise' that their compass is faulty) or at least experience it to a lesser degree in the absence of guidance by familiar visual landmarks. Overall, I propose that introducing

misinformation into flocks through clock-shifting is an exciting new technique that will enable us to address many open questions, such as the role majority rules play in homing pigeon flocks.

6.2.4 What role does adding the third dimension of space play when identifying leader-follower interactions?

In recent years, there has been increasing interest in how individuals within groups interact in three dimensions (e.g. The STARFLAG project: Cavagna et al. 2008). However, when looking specifically at leadership in groups using the directional correlation delay method, the vertical axis has been ignored (Nagy et al. 2010, Katz et al. 2011, Nagy et al. 2013). This raises the question as to whether the commonly used two-dimensional hierarchical leadership analysis can be used justifiably on groups that interact in three dimensions. Chapters 2-4 suffer from this potential issue due to the lack of accurate altitude measurements from GPS devices. Therefore, in Chapter 5 I set out to explore the extent to which two- and three-dimensional analyses of group movements exhibit differences, using the fish species *A. mexicanus*. I found that the two-dimensional direction correlation delay model was able to correctly describe leader-follower interactions in three dimensions. This result is important as it validates previous two-dimensional leadership models (Nagy et al. 2010) and suggests that in terms of leadership, two-dimensional analyses are able to accurately evaluate three-dimensional data. Since, as previously discussed in more depth in Chapter 1, high resolution three-dimensional data is presently difficult to collect on a large scale, particularly for some wide-ranging animals, this validation is an encouraging finding for the field of collective behaviour as a whole.

In the horizontal plane fish respond preferentially to the movements of neighbours positioned in front (Katz et al. 2011). Results from Chapter 5 confirmed this interaction rule, as I found that leaders were positioned in front of followers. However, whether fish preferentially interacted with neighbours positioned below or above them was less clear. Generally it seemed that there was no significant preference for fish to interact with others located above or below them, although, as discussed in Chapter 5, between some pairs such significant sorting did occur although the effect sizes were small. Therefore, this is an area that requires further investigation. Specifically, with the anticipated development of automated tracking in three dimensions for large groups, the analysis of longer time series will be valuable.

A. mexicanus was chosen as the study species due to it previously being used in three-dimensional navigation studies, hence much was known about individuals' spatial cognition (Holbrook and Burt de Perera 2009, Holbrook and Burt de Perera 2011, Holbrook and Burt de Perera 2013). Holbrook and Burt de Perera (2009) found that *A. mexicanus* preferentially used vertical information during navigation when it conflicted with previously learnt horizontal information. They later proposed that using hydrostatic pressure was a likely mechanism to allow this separation of horizontal and vertical information (Taylor et al. 2010, Holbrook and Burt de Perera 2011). In Chapter 5, I found that individuals pay attention to vertical information during schooling, but that vertical information is more likely to come from social cues from the body orientations of other individuals, shown by the high correlation between pairs' directional movements in three dimensions. This means that individuals pay attention to the same fish for vertical and horizontal

information, and thus adding the third dimension does not significantly affect the results of leadership models.

In Chapter 5 I only used one fish species, *A. mexicanus*, leaving open the possibility for further exploration of the role of the vertical axis in leadership in other fish species and in birds. Different fish species may vary in their ability to respond to movements of neighbours in the vertical due to variations in the shape and position of their eyes altering the angles of vision. For example, benthic fish such as skate (*Raja eglanteria*), have their eyes positioned on the top of their head and therefore have no visual access to what is below them (McComb and Kajiura 2008). This would be predicted to create a vertical bias in whom individuals pay attention. Therefore, further studies could investigate the role of vertical information in leadership in other species to examine (i) which factors are species-specific and which are general, and (ii) what drivers in the species' ecology, morphology or lifestyle are responsible for any species-specific effects.

A three-dimensional study in European starlings (*Sturnus vulgaris*) revealed that individual birds had no vertical bias in where they were located with respect to their nearest neighbours. Neighbours were positioned between -45° and $+45^{\circ}$ elevation angles (Ballerini et al. 2008), the same as I found in *A. mexicanus*. To what extent they hold true in my other study species, homing pigeons, will only be formally testable once altitude measurements by GPS devices (or attached altimeters) reach comparable levels of accuracy to measurements of longitude and latitude. Once this is achieved, existing studies of homing pigeon leadership in two dimensions will receive additional validation.

6.3 Concluding remarks

When I began this thesis, hierarchical decision-making in collective animal behaviour was a relatively new concept, with many open questions regarding mechanism and function. Work from this thesis has helped shed light on both of these angles, through elucidating in more detail how hierarchical decision-making operates in groups, and what benefits such decision-making structures can have for individuals in those groups. My thesis has revealed that in homing pigeons a diverse array of individual features work in combination to determine the structure of leadership hierarchies, and thus how information flows through the group. From this work we can infer not only that there is an advantage to individuals within flock in having an experienced leader, but potentially also an advantage to heterogeneity in terms of experience and/or age in enabling stable leadership hierarchies to form. This stability may come with two advantages for individuals within the flock: firstly in terms of enhanced group navigation in the early stages of familiarisation with the landscape, and secondly, the ability to learn the (more efficient) homing routes taken by the flock and recapitulate them even when flying alone. Leadership hierarchies can be stable over many repeated releases but this stability does not necessarily equate with inflexibility. When low-quality information is present at the top (i.e. the leader is misinformed), hierarchies spontaneously reorganise; the leader drops in rank, which in turn prevents errors propagating downwards and affecting the whole flock. This also shows a benefit to these hierarchical structures. Therefore, the potential benefit and thus ultimately perhaps the adaptive value of these structures may come from a combination of different aspects of the decision-making structure. Crucially, as all of this work is on a species that moves in three-

dimensions, I validated the use of two-dimensional leadership analyses on three-dimensionally interacting schools of fish and explore how individuals interact in the vertical dimension. As the field grows and technology advances, we will be able to further our understanding of hierarchical decision-making in a greater variety of species, explore underlying mechanisms, use comparative analyses to generate universal principles as well as species- or context-specific effects, and elaborate on the evolution and adaptive value of the phenomenon.

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