COLLECTIVE DECISION-MAKING IN HOMING PIGEON NAVIGATION

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Declaration

All work in this thesis is my own.

This thesis is structured as a set of independent chapters in the style of scientific journal articles with a general introduction and a final conclusion chapter linking them, as approved by the Director of Graduate Studies in the Department of Zoology, University of Oxford.

Chapters 2 and 3 are published, and Chapter 5 is currently under review.

The following people co-authored one or more of these articles and their contributions are as follows:

Dora Biro contributed her ideas and feedback for Chapters 2, 3 and 5 throughout planning phases and manuscript preparation.

Tim Guilford and Robin Freeman contributed their feedback during manuscript preparation of Chapters 2 and 3.

Benjamin Pettit participated in the data collection of Chapter 2

Zsuzsa Ákos participated in data collection, and data analyses of Chapter 5. Máté Nagy helped with the data analysis of Chapter 5. Tamás Viscek contributed his feedback during manuscript preparation of Chapter 5.

Collective decision-making in homing pigeon navigation

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Abstract

This thesis focuses on conflict resolution and collective decision-making in co-navigating pigeons, *Columba livia*. These birds have a remarkable homing ability and frequently fly in flocks. Group navigation demands that group members reach consensus on which path to follow, but the mechanisms by which they do so remain largely unexplored. Pigeons are particularly suitable for studying these mechanisms, due to their sociality and the fact that their possession of information can easily be altered and quantified. I present the results of a series of experiments that manipulated the experience of homing pigeons in various ways so as to observe the effect of information they had previously gathered on their group behaviour. Key findings were:

1. Previous navigational experience contributes to the establishment of leader-follower relationships. The larger the difference in experience between two co-navigating pigeons, the higher the likelihood the more experienced bird will emerge as leader.

2. Shared homing experience through repeated joint flights can allow two pigeons to develop into a "behavioural unit". They form spatial sub-groups when flying with less familiar birds, and perform a similar transition between compromise- and leadership-dominated flights as single birds, although they are more likely to accept compromise routes. Such previous association histories between birds can thus affect collective decision-making in larger flocks.

3. There is a trade-off between the amount of spatial information handled and the efficiency with which such information can be applied during homing. Leading/following behaviour is influenced by the recency of the route memories.

4. Leadership hierarchies in pigeon flocks appear resistant to changes in the navigational knowledge of a subset of their members, at least when these changes are relatively small in magnitude. The stability of the hierarchical structure might be beneficial during decision-making.

5. Mathematical modelling suggests that underlying hierarchical social structures can increase navigational accuracy. Hierarchically organised groups with the smallest number of strong connections achieve highest accuracy. Group leader-follower dynamics resemble the underlying social structure.

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To my family

"Everybody is interested in pigeons…"

An adviser to Darwin's publisher explaining why Darwin should
publish a book on pigeons instead of "The Origin of Species", 1857

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Chapter 1

General Introduction

1.1 Collective decision-making

1.1.1 Living in groups

Most organisms associate with one or more conspecifics during certain periods of their lifetime (Wilson 1980). Yet, we would not classify all those animals as social since even solitary species can live, temporarily, in small units while mating or rearing offspring. It is difficult to compile a broad definition of sociality that can be generalised across a wide range of species. Lee (1994) proposed seven levels of sociality characterised by the degree of interactions between individuals during different activities such as foraging, travelling or resting. One major factor that distinguishes between "social" and "gregarious" species is social attraction. Rather than aggregating temporarily due to external pressure ("gregariousness"), social animals actively seek out the proximity of conspecifics. Among bird species, for example, grouping is a widespread phenomenon; individuals maintain stable associations while breeding and, at the same time, form large aggregations while roosting or foraging (Lee 1994). Those aggregations may vary in size due to changing levels of competition among members of the group. In general, sociality involves a trade-off between the costs and benefits associated with coming together (Krause & Ruxton 2002).

Many of the benefits have associated costs that may become more harmful as group size increases. Advantages like an increased probability of detecting predators (Elgar 1989), or enhanced foraging efficiency (Brown 1986) might become disadvantageous as the group grows due to greater attack and capture probabilities (Lindström 1989). However, social tendencies during migratory journeys, for example, may allow birds to counteract some of the negative impacts of their costly trips (Beauchamp 2011) since flock migration can improve navigation by increasing the accuracy of orientation (Bergman & Donner 1964), or can result in energetic advantages during flight (Lissaman & Shollenberger 1970).

1.1.2 Types of group decisions

Animals that live in social groups have to reach consensus about the timing of daily activities such as foraging or resting. Furthermore, for species that travel collectively between different locations it is necessary to negotiate a joint route so as to maintain proximity. Each member of a collective has to weigh up the costs and benefits of several mutually exclusive actions. It is this weighing of alternative options in social animals that has been described as "group decision-making" (Conradt & Roper 2005).

Mathematical modelling has investigated how animal groups make decisions about activity synchronisation with a distinction between two possible mechanisms: "shared" and "unshared" decisions (Conradt & Roper 2003). In socially complex, heterogeneous groups with high levels of relatedness (e.g. primates, elephants, dolphins) unshared decisions are more likely to be observed. Here one particular group member, usually distinguished by higher levels of experience, age or dominance (Reebs 2000; McComb et al. 2011; King et al. 2008), initiates an activity change which the rest of the group follows. In contrast, shared decisions refer to behavioural changes of the group that are initiated by all or the majority of group members. This includes examples such as nest choice in eusocial insects (Seeley & Buhrman 1999; Franks et al. 2003) and the migration routes of ungulates (Prins 1995). Individuals can express their preferences using vocalisation (Harcourt & Stewart 1994) or ritualised motion patterns (Seeley & Buhrman 1999). Once a certain number of individuals reaches consensus, the whole group will undergo a change in activity. Such thresholds, or “quorums”, have been described in a variety of animal species (Prins 1995; Pratt et al. 2002; Ward et al. 2008; Sueur et al. 2010).

However, such distinction in shared and unshared decisions might be considered slightly arbitrary. Even in unshared decisions group members do not follow because of force. The group’s behaviour still originates from each individual’s decision to change its activity or not, which in turn arises from its motivational state and the strengths of its various behavioural tendencies (McFarland 1977). This means that even when a single animal initiates an activity change, other group members may still be involved in the collective decision (Petit & Bon 2010). A simple process by which this can be achieved is called mimetism. This means that the probability that a certain individual displays a particular behaviour depends on the number of others which are already engaged in this behaviour (King & Sueur 2011). Such process can be anonymous, hence it ignores the identity of the individual (Camazine et al. 2003; Couzin & Krause 2003), or it can also take the social relationships between group-mates into consideration (selective mimetism, Sueur et al. 2009; King & Sueur 2011).

1.1.3 Group movements

The size of animal groups can vary enormously. Fish shoals, starling flocks or locust swarms can consist of thousands of individuals. Especially in such large groups, decision-making must be highly synchronised and coordinated. Any group decision-making mechanism that relies on estimating the preference of the majority, like quorum responses, would exceed the sensory capabilities of individuals. Using mathematical modelling techniques, it has been shown that synchronised movement of large groups can arise from local interaction rules without centralised organisation (Vicsek et al. 1995; Couzin et al. 2002). For example, models posit that each individual avoids collisions by maintaining a minimum distance to its neighbours. At the same time, individuals tend to be attracted to others and align their travel direction with their closest neighbours. By using only those simple rules (avoid, attract, align), many collective behaviour movements can be explained. Furthermore, it has been shown that slight manipulation of the rules can explain many of the movement patterns and transitions exhibited by differently organised groups (Couzin et al. 2002).

How do such large groups reach consensus regarding their destinations and activities? Couzin et al. (2005) showed that information transfer within a group does not require signalling or individual recognition. Even with only a small proportion of informed individuals, the group can achieve high accuracy at reaching a given location. Furthermore, as group size increases, fewer informed individuals are necessary to guide the group to the goal accurately. Recently, due to advancement in digital image processing and high temporal resolution tracking, it has become possible to use data from freely interacting animals to infer interaction rules underlying collective motion. It has been identified that velocity changes in fish correlate with the position and velocity of neighbouring individuals (Herbert-Read et al. 2011; Katz et al. 2011). Moreover, Lukeman et al. (2010) showed that flocking surf scoters (*Melanitta perspicillata*) exhibit circular zones with specific, well-defined rules of interaction. Yet, more empirical data are needed to understand the principles of group decision-making fully and to benefit the most from a combination of theoretical and experimental work.

1.2 Pigeon navigation as a model system

The remarkable ability of pigeons to return home from distant locations has been known to humans for thousands of years. Descendants of wild rock doves have been used to carry messages in ancient civilizations such as Egypt and Rome, and during wartimes even as recently as the 20th century. However, scientific interest in pigeons' navigational skills intensified only during the last 60 years. Today, the "map and compass" model is the most accepted concept in explaining the mechanisms of avian navigation. According to this principle, avian navigation is "composed of two fundamentally different steps, one establishing the position of the release place, the other determining the direction of flight" (Kramer 1961). Those two steps are described as the "map" phase and the "compass" phase. Research since Kramer's time has focused on determining the sensory mechanisms underlying those two separate phases. In the case of homing pigeons, a variety of cues involved in orientation have been identified, including olfaction, magnetoreception, the position of the sun as well as visual perception of landmarks.

Despite extensive debate and controversial results, the most widely accepted model for determining the location relative to the goal is the olfactory map. According to this model, at the home loft, pigeons associate odour borne on the wind with the direction the wind is blowing from. This allows them to build a representation of odour distributions surrounding the loft. When displaced to a distant site, the composition of the local odours in comparison to that at home is used to determine the position of the site in relation to the loft (Papi 1991). There is overwhelming evidence supporting the olfactory hypothesis, including experiments that raised pigeons under deflected wind conditions (Ioalé et al. 1978) or exposed birds to odours of different locations while being released (Benvenuti & Wallraff 1985). However, olfactory navigation has been a matter of considerable controversy and counter-evidence continues to be reported (Jorge et al. 2009, 2010).

Once location is determined, pigeons preferentially use a sun-based compass mechanism to compute the direction of the loft (Kramer 1953). The sun compass was first experimentally shown by Schmidt-König (1958) using birds whose internal clock was shifted by an artificial light-dark cycle. Every shifted hour will cause predictable changes in the birds' orientation upon release, as they erroneously interpret the position of the sun in the sky with reference to an internal clock that is out of sync with the actual time of day. Although observed deflections usually fall below the predicted magnitude (Chappell 1997), clock-shift effects are a widespread, repeated and robust phenomenon. One feature that clearly influences the degree of clock-shift deflections is familiarity with the release site. The deflections of birds that have been released repeatedly from a given site are much lower than expected (Foà & Albonetti 1980; Füller et al. 1983), which suggests that the local features, most likely visual input from learned landmarks, conflict with the direction suggested by the position of the sun (Wallraff et al. 1999). This finding suggests that the cues pigeons use change after repeated experience with an area. Their usual orientation mechanisms, such as the olfactory map or the sun compass, might become less important; instead, birds pay more attention to memorised visual cues that guide them back to the loft. Those locations that an individual has visited before, including a certain radius around them, can be defined as the bird's "familiar area" (Wallraff 2001).

1.2.1 Familiar area navigation

Research interest in visually guided navigation has increased over the last two decades, after a period of almost complete neglect. This lack of interest originated from an experiment that fitted pigeons with frosted contact lenses in order to impair their vision (Schmidt-König & Schlichte 1972). According to the authors, vision does not play a major role in navigation, because most birds homed successfully despite their blurred sight. However, when closely examining their results, it is evident that of the 106 birds released, 70 individuals did not in fact return to the loft, or reached only the proximity of the loft and could not locate its final position. The authors' conclusion that vision is a dispensable sense for navigation might thus have been drawn too quickly.

Since the early 1990s, several studies have shown that providing pigeons with a five-minute preview of the landscape surrounding the release site prior to release improves the birds' homing times (Braithwaite & Guilford 1991; Burt de Perera et al. 1997; Gagliardo et al. 2001). Interestingly, such positive effect of the visual treatment is limited to the first kilometre around the release site (Biro et al. 2002) indicating that birds can process navigational cues before being released and benefit from a "head start" over birds not given a visual preview.

Due to past technological difficulties associated with tracking birds in flight, until recently much less was known about the pigeon's behaviour during its homeward flight and therefore about its use of visual and other cues for orientation once it left the release site. A few early studies observed birds from airplanes (Hitchcock 1952; Michener & Walcott 1967), but the on-board deployment of route recorders proved more cost-effective and allowed a far closer look at pigeons' individual trajectories. Early devices such as direction recorders revealed that in familiar areas underlying landscape features had an effect on orientation (Bonadonna et al. 1997, 2000; Holland et al. 2000).

Small, lightweight GPS loggers use global positioning system satellites to determine and record the precise location of animals at certain intervals. Their recent development has advanced our understanding of pigeon navigation within the familiar area dramatically. The first loggers small enough to be carried by a pigeon could record entire homing trajectories at a frequency of 1 s^{-1} (von Hünerbein et al. 2000). Early studies revealed that pigeons exhibit a roadfollowing orientation strategy, meaning they are attracted to roads and thus associate with underlying landscape features while returning to the loft (Biro 2002; Guilford et al. 2004; Lipp et al. 2004).

One of the most unexpected discoveries using GPS – and a key finding I extensively make use of in the present thesis – was that pigeons develop individually preferred paths that they remain faithful to when released repeatedly from the same release site (Biro et al. 2004; Meade et al. 2005). This phenomenon is also referred to as route recapitulation. Routes often differ largely between individuals, but each bird produces its own previous path, retracing bends and turns with a high level of accuracy. Rather than homing along a straight-line path, pigeon routes are tortuous and appear to correlate with salient features of the terrain. Also, when released laterally "off-route", birds are directly attracted back to their own preferred route, providing further strong support for a reliance on local landscape features (Biro et al. 2004). Using a number of analytic tools, it has been shown that linear topographical features are associated with orientation in that pigeons are attracted to edge-containing land features (Lau et al. 2006). Furthermore, analysing high fidelity areas of trajectories identified habitual route waypoints where multiple tracks converge over salient visual features (Mann et al. 2011). Overall, in recent years, compelling evidence supporting the role of visual landscape cues in pigeons' orientation has been accumulated.

Studies have also found that with an increasing number of releases from a given site, an increase in track efficiency and a decrease in variation between consecutive tracks is observed, suggesting that memorisation of landscape features plays a major role in the formation of habitual routes (Meade et al. 2005). Under natural conditions, foraging pigeons can visit up to ten locations per day (Rose et al. 2006). Thus, there is a natural demand for distinct spatial memories linked to various specific routes, but we might expect a trade-off between the amount of spatial information handled and the efficiency with which such information could be applied during homing.

1.3 Group navigation in pigeons

The majority of pigeon research focuses on navigational mechanisms employed by individual birds. However, pigeons are social birds in all their activities and actively seek out the proximity of conspecifics (Goodwin 1983). Especially when visiting feeding grounds far away from the loft, pigeons rely on flying in groups rather than alone (Goodwin 1983; Baldaccini et al. 2000). Such sociality gives rise to a number of questions concerning group navigation. For example, theory predicts that group travel should exhibit higher levels of navigational accuracy because overall error in estimating a target location decreases with the number of individuals present (Hamilton 1967; Wallraff 1978; Simons 2004). Previous experimental results on pigeons have been ambiguous. Some studies detect no difference in accuracy between single and group navigation (Keeton 1970; Benvenuti & Baldaccini 1985), whereas others show that vanishing bearings of flocks are less scattered around the mean than those of individually released birds (Tamm 1980). The latter finding is supported by more recent work using GPS recordings, which reveals that flocks home faster and along more direct routes than solo flying birds (Dell’Ariccia et al. 2008).

How are navigational decisions made when birds fly in groups? Wallraff (1978) was the first to propose two alternative mechanisms: the flock’s direction is determined by only one (or a few) individual(s) that act as leader, or by averaging the preferences of each flock member. Since then, both empirical and theoretical data have confirmed that both of these outcomes are observable in flocks (Conradt & Roper 2003; Couzin et al. 2005; Biro et al. 2006). Combining the birds' gregarious nature with their tendency to home along stereotypical routes provides a novel experimental technique for studying group decision-making in pigeons. Biro et al. (2006) released pairs of pigeons whose individually established homing routes differed to various degrees. They found that birds will take an intermediate route when the distance between the individual routes is low, but select one of the routes as the inter-route distance increases and exceeds a certain threshold. The outcome of this experiment is in agreement with predictions produced by decision-making models (Couzin et al. 2005; Biro et al. 2006). Interestingly, leadership does not correlate with homing efficiency, meaning the pair's joint path does not always lie closer to the shortest individual route. In fact, the identities of the leaders and followers condense into a fully transitive hierarchy (i.e. if A follows B and B follows C, then A would follow C), where the ranks of birds show no relationship to their individual route efficiencies (Biro et al. 2006).

Such leadership hierarchies can also be observed in large flocks, and in the absence of route recapitulation. A new generation of GPS-devices, which log an individual's position up to five times per second, has revealed an unexpected pattern in the ways in which individual members can influence the behaviour of a moving group (Nagy et al. 2010). The study analysed the directional choices of every pigeon while the flock was either performing spontaneous flights around the loft or homing flights from a distant release site. To measure the effect that a given bird's direction had on the other members of the flock, the authors looked at the temporal relationship between the directional choices of every possible pair of birds in the flock. Leading events, i.e. where one bird's direction was "copied" by another bird delayed in time, were determined using a measure referred to as the directional correlation delay time. In turn, they found that flocks are hierarchically organised, where individuals contribute with different weights to the movement decisions of the flock. Such hierarchical networks consist of transitive leader-follower relationships in which birds consistently copy the directional choices of individuals above them in the hierarchy, while being copied by those lower in rank. Additionally, there is a strong correlation between the average spatial position of a bird within the flock and its rank in the hierarchy, in that birds higher in the leadership hierarchy also tend to be nearer to the front of the flock (Nagy et al. 2010). However, it remains an open particularly interesting question whether individuals that contribute with more weight to the movement decision of the group are also more knowledgeable than others?

1.4 Individual features influencing group decision-making

As seen so far, leadership in pigeons has been defined according to two different criteria. On the one hand it can refer to route recapitulating birds which, when flying with other individuals, succeed in leading the group home along their own preferred route (Biro et al. 2006). The other case describes a leader as an individual whose movements are copied by another bird delayed in time (Nagy et al. 2010). It is still unknown how these two measures of leadership correlate with each other. If the two types of leadership coincide, we would observe a pigeon taking up a high rank in the leadership hierarchy during group flights while also influencing the group's route choice towards its own preferred route.

A more general definition by Krause et al. (2000) describes leadership "as the initiation of new directions of locomotion by one or more individuals which are then followed by other group members." This idea is in agreement with Nagy et al.'s (2010) treatment of leadership. Nonetheless, route recapitulation allows an interesting alternative way of examining an individual's social influence on others, and in a sense, it more directly reflects the functional outcome of conflict resolution. Yet, although we can determine which bird emerges as leader, the underlying mechanistic principles remain elusive. Leaders may be those individuals that are "reluctant" to deviate from their own route (Gautrais 2010), due to higher levels of navigational certainty (or indeed *un*certainty). Navigational certainty may arise from the ability to recapitulate routes most accurately with very little variation between consecutive tracks. However, high levels of route fidelity may also demonstrate a lack of flexibility, thus be a proof of navigational uncertainty. To elucidate the mechanisms of leadership and distinguish between these two cases successfully further studies are necessary.

1.4.1 What determines leadership?

Morphological, physiological or behavioural features may alter an individual's propensity to initiate a movement or activity change, and such features can be linked to dominance rank, sex, reproductive state, experience, temperament and other factors (Petit & Bon 2010). A frequently assessed variable in studies of leadership is dominance rank. In species with strong dominance hierarchies such as mountain gorillas (*Gorilla beringei beringei*) or wolves (*Canis lupus*), the alpha male consistently initiates the group's movements because of its social affiliations within the group (Schaller 1963; Peterson et al. 2002). Tendencies to initiate group movements successfully may vary throughout the day, or the season. For example, a state-dependent individual based model predicts that in pairs of foragers the individual with the lower energy reserve emerges as the leader of the pair (Rands et al. 2003). In line with this, a model by Conradt et al. (2009) suggests that group movements are directed by those specific individuals for whom reaching the goal is most crucial. Several empirical studies support the findings of these models. For example, fish that are deprived of food are more likely to take front positions in shoals than those that are satiated (Krause et al. 1992), and lactating zebra females (*Equus burchellii*) initiate movements more frequently than those without dependent calves (Fischhoff et al. 2007). Furthermore, consistent leadership in group movements might be influenced by the enhanced knowledge of certain individuals. In several species it has been shown that knowledgeable individuals can change the action of group-mates due to a greater knowledge about their environment: golden shiner (*Notemigonus crysoleucas,* Reebs 2000), bottlenose dolphin (*Tursiops* sp., Lusseau & Conradt 2009), and meerkats (*Suricata suricatta,* Bousquet & Manser 2011). Similarly, older elephant females (*Loxodonta africana*) who most likely have accumulated high levels of experience influence group behaviour when threatened by predators (McComb et al. 2011).

In pigeons, few experiments so far have tried to explore individual features that predict leadership. While, as described above, the efficiency of solo navigational routes is not a significant factor (Biro et al. 2006), it has been shown that the maximum fidelity with which highly experienced individuals recapitulate their routes can at least partly predict leadership. More specifically, birds that exhibit less variation between consecutive tracks when flying solo are more likely to emerge as leaders when released with other birds (Freeman et al. 2011).

From the perspective of the current thesis, one key question concerns how variation in navigational experience or knowledge influences the movement of the group. We would expect that experience plays a major role in group decisions, as inexperienced birds may benefit by following more experienced leaders. For example, juvenile migrants that travel long distances between breeding area and wintering ground can learn from knowledgeable adults during group migration about the route to be flown (Chernetsov et al. 2004). Two studies on pigeons reported that naïve birds home faster with an experienced partner, where the "experienced" bird's extra knowledge was based on a 5-minute preview of the surrounding landscape (Burt de Perera & Guilford 1999), or on previous homing flights (Banks & Guilford 2000). However, these studies recorded only vanishing bearings and arrival times – measures that provide no information concerning leadership. Pairs may, for example, have split up on their way home. In fact, Banks and Guilford (2000) found that many pairs returned separately, especially when one or both of them were unfamiliar with the release site. It has been described before that a pigeon's propensity to fly together with other birds is relatively low during its very first flight from an unknown site irrespective of its partner's knowledge (Heinroth & Heinroth 1941; Guilford & Chappell 1996). However, this behaviour may change as birds gain more experience. We still do not know what the relationship between the spatial knowledge held by a homing pigeon and the probability that it will follow the movements of a co-navigating partner is. We would expect that following the decisions of knowledgeable leaders may result in both fast and accurate collective decisions, and that social relationships may even reinforce such advantage.

1.4.2 The influence of social relationships on leadership

Until very recently, social relationships between individuals have not been taken into account when trying to understand the mechanisms of collective decision-making. Yet, social groups typically differ from random aggregations because of preferred and non-preferred connections between individuals (Whitehead 2008). Preferred connections might arise between, for example, familiar conspecifics, sexual partners or parents and offspring. Empirical studies have shown that dominance relationships can influence collective movements in rhesus macaques (*Macaca mulatta*) as seen from the fact that dominant males spend more time at the front of the movement

(Sueur & Petit 2008). Furthermore, stable relationships based on familiarity can modulate an individual's tendency to follow the movements of a preferred partner (Griffiths & Magurran 1999; Boissy & Dumont 2002; Ramseyer et al. 2009; Tóth et al. 2009). Recently such social preferences have been incorporated into individual-based models on collective motion (King et al. 2011). These models suggest that social relationships between certain members can influence the cohesion of the group, the spatial positions of specific individuals and the hierarchical organisation of the group (Bode et al. 2011). However, the impact of underlying social structures on group navigation is still unknown. For example, do shared experiences during past decision-making lead to familiarity between certain individuals and, if so, does that affect interactions with others?

1.5 Structure of this thesis

This thesis combines empirical and theoretical approaches in order to understand how group decisions emerge from individual interactions. I shall present four experimental chapters that explore both the relationship between individual and group performance during homing, and the influence of group members' past individual experience on group decision-making. Also, I present a theoretical chapter which uses a self-propelled particle model to examine the role of underlying social networks on the accuracy of group navigation.

Chapter 2 concerns the relationship between the spatial knowledge of a homing pigeon and the probability that it will follow the movements of a co-navigating partner during a joint trip back to the loft. It thus examines factors contributing to the establishment of leadership and followership, focusing on the role of previous navigational experience. On a homing task, I tested pairs of pigeons where the two partners had relatively greater and lesser prior experience generated through individual training. To quantify prior experience, I used homing efficiency and route fidelity measures. To examine the outcome of such paired releases, I measured the extent to which paths flown by the pair resembled the individually preferred routes of the more and less experienced partner.

Chapter 3 explores the influence of co-navigating conspecifics on route learning and group decision-making. By first training pigeons to home in pairs and then releasing them together with other pairs in quadruples, I examined two separate aspects of group navigation. First, I asked whether birds homing with conspecifics acquire navigational knowledge faster. To answer this question, I compared measures of homing efficiency and route fidelity from solo and pairwise trained pigeons. Second, I asked how conflicts arising from the different directional preferences of pigeon pairs are resolved during joint homing: I analysed the homing performance of the quadruples formed by the pairs that received separate training and measured their leading/following behaviour.

Pigeons visit many distant places on a daily basis and **Chapter 4** explores whether and how learning multiple homing routes influences route development and leader-follower relationships. I performed an experiment using three release sites and three different experimental groups of pigeons. Each group had a distinct training protocol, defined by the sequence of releases from each of the three sites. The protocols consisted of either (i) “sequential-site” training (i.e. completing training at one site before commencing training at the next), (ii) “rotation” training (i.e. sequential single releases alternating in a consistent order across sites 1, 2 and 3), or (iii) “random-order” training (i.e. releases alternating across the three release sites in a semi-random order, that is, without repeating the most recent release site). I compared route development in the three different treatment groups. After training was completed, I performed triplet releases from all of the three release sites using one bird from each treatment group, and examined the influence of training protocol on leadership measures and group decision-making.

In **Chapter 5** I examine how the homing experience of individuals relates to the structure of a transitive leadership hierarchy arising in larger flocks. I conducted an experiment where I first trained three flocks of 10 birds to home eight times from a given release site. I calculated for each group the respective leadership hierarchy among flock members using the methods of Nagy et al. (2010). Then, I allowed three individuals from each flock to gain additional homing experience by training them individually from the release site 10 more times. Next, I released the entire flock again in order to evaluate any changes in the hierarchy's structure – in particular, whether the additional homing experience allowed the three individuals selected to assume higher ranks within the network. The study reveals whether and how the structure of hierarchical leadership networks during flock flights depends on individual properties such as navigational knowledge or homing efficiency.

In **Chapter 6** I use individual-based modelling in order to examine whether and how underlying social structures can influence the accuracy of group navigation by introducing different types of social networks into simulated navigating groups. I extended an existing model on collective movement (Couzin et al. 2005) by including both hierarchically and randomly organised group structures. I examined the effect of these types of structures on the navigational performance of the group. I also explored the group's leader-follower relationships using the method of Nagy et al. (2010) to compare the underlying social structure with the leadership dynamics arising from movement decisions.

Finally, **Chapter 7** provides a synthesis of the results obtained through my experimental and theoretical work. I summarise and link together my main findings, and propose potential future directions based on my work.

Chapter 2

What are leaders made of? - The role of individual experience in determining leader-follower relations in homing pigeons

N.B. Below I present this chapter in manuscript format. This manuscript has been published as:

Flack, A., Pettit, B., Freeman, R., Guilford, T., Biro, D., 2012. What are leaders made of? The role of individual experience in determining leader–follower relations in homing pigeons. Animal Behaviour 83, 703–709.

2.1 Summary

Negotiating joint routes during group travel is one of the challenges faced by collectively moving animals, on spatial scales ranging from daily foraging trips to long-distance migrations. Homing pigeons provide a useful model system for studying the mechanisms of group decision-making in the context of navigation due to the combination of their gregarious nature and the depth of our understanding of their individual orientational strategies. Previous work has shown that during paired flight, if two birds' individual "opinions" are sufficiently different, one will emerge as leader whom the other follows. What determines the identity of a leader has important implications for the efficiency of a moving collective, since leaders with better information can increase the navigational accuracy of the group. Here we examine factors contributing to the establishment of leader/followership, focusing on the role of previous navigational experience. We tested, on a homing task, pairs of pigeons in which the two partners had relatively higher and lower prior experience, generated through individual training. Analysis of the GPS-tracked routes taken by such pairs revealed a negative correlation between homing experience and the probability that a pigeon will follow a co-navigating partner. Thus, the larger the difference in experience between two partners, the higher the likelihood the more experienced bird will emerge as leader. Our results contribute to a better understanding of the mechanisms and potential payoffs of collective navigational decision-making in species that travel in mixed-experience groups.

2.2 Introduction

One of the most illustrative examples of group decision-making in collective animal behaviour concerns the coordinated movement of individuals. Many social animals travel together in groups, over a variety of different spatial scales, from daily foraging or ranging activities to large-scale migrations. Collective travel can yield a multitude of advantages to individual members (including predator avoidance, enhanced foraging efficiency, and increased navigational accuracy; Krause & Ruxton 2002). A central problem in the study of group movements concerns the question of how navigational information flows between group members, and of how such flow depends upon the navigational knowledge held by each member of the group (Couzin et al. 2005; Conradt et al. 2009). Differences in knowledge can stem from various sources, including inherent individual differences in navigational skill or strategy, as well as the amount of experience that group members have gathered through prior encounters with a landscape. Given such inter-individual variation in knowledge, how do groups reach consensus and solve the problem of maintaining a cohesively moving collective?

Over the past decade, collective motion and group decision-making have generated a great deal of theoretical interest (Couzin & Krause 2003; Conradt & Roper 2009; Sumpter 2010). Theoretical work focusing on individual movements and interactions has strengthened our understanding of how individual behaviours scale to coherent collective motion (Couzin & Krause 2003; Vabø & Skaret 2008; Hemelrijk & Hildenbrandt 2011). Additionally, theoretical approaches have generated predictions about the mechanisms through which such group decisions are made, with a broad distinction between processes where most or all group members contribute to a decision, and those where one or a small number of individuals make decisions for the rest of the group (Conradt & Roper 2009). Simulation models suggest the predictable occurrence of a transition from the latter to the former in groups containing members with divergent directional preferences. The transition is abrupt, and occurs at the point where conflict reaches a critical level (Couzin et al. 2005). Following the transition, leadership is typically assumed by the individual/subgroup with the highest certainty of information, or those that place the highest weight on their own information (Conradt et al. 2009). In line with such theoretical work, the role of individual knowledge in determining leadership in real animal groups is of fundamental interest – yet few experiments have attempted to provide the necessary empirical data (Guilford & Chappell 1996; Reebs 2000; Bousquet & Manser 2011).

Pigeons have long been a model species for the study of animal navigation, where emphasis has traditionally been on the mechanisms that individual birds use to navigate in the field (for a recent, comprehensive review, see Wallraff 2005). More recently, pigeons have emerged as a system suitable for the study of group decisions, mainly due to the ease with which coordinated movements of flock members can be studied (Biro et al. 2006; Dell'Ariccia et al. 2008; Nagy et al. 2010). Past studies have shown that following repeated releases from the same site, homing pigeons come to rely on stereotyped homing routes that show high levels of consistency *within* individuals but considerable divergence *between* individuals (Biro et al. 2004; Meade et al. 2005). When two such experienced, "route-recapitulating" pigeons are released together, they will either fly a compromise route intermediate between their individually preferred routes, or, if the distance between their routes rises above a critical threshold, one of the birds will follow the flight path of the other (Biro et al. 2006; Sumpter et al. 2008).

Interestingly, when experienced pigeons are tested repeatedly, in pairs with different partners, the identities of the leaders and followers condense into a fully transitive hierarchy (i.e. if A follows B and B follows C, then A will follow C; Biro et al. 2006). In fact, even in larger flocks, and in the absence of route recapitulation, a well-defined leadership hierarchy is evident in pairwise comparisons among group members in terms of the initiation and copying of small-scale directional changes (Nagy et al. 2010). These results suggests that in specific pairwise interactions there are one or more attributes of a flying bird that can reliably predict its propensity either to lead or to follow conspecifics. What such attributes are – in other words, what determines the probability that one bird will follow the movements of another – is still an open question.

Intriguingly, equally experienced pigeons show differences in route fidelity (i.e. the accuracy with which they follow their routes when flying solo), and route fidelity itself can, at least partially, predict the leading and following behaviour of two co-navigating pigeons. Birds with higher solo route fidelity tend to lead partners with lower solo route fidelity: a result suggesting that leadership may arise from the individual-specific emphasis that birds place on remaining close to their route versus remaining close to their partner (Freeman et al. 2011; Conradt et al. 2009 for a theoretical treatment of similar principles). Thus, route fidelity helps to predict leadership when pigeons have the *same* level of homing experience, but we have yet to explore the effect of *different* levels of homing experience on the establishment of leader-follower relations. If leading/following behaviour is a function of relative levels of homing experience, we should expect to observe more experienced birds emerge as leaders, supporting the predictions generated by models. Our question here therefore concerns the relationship between the spatial knowledge held by a homing pigeon and the probability that it will follow the movements of a co-navigating partner during a joint trip back to the loft.

To tackle this question, in the present study we used miniature GPS tracking during displacement experiments involving (i) the solo training of homing pigeons up to pre-defined levels of experience with a route, followed by (ii) releases of birds in pairs, constructed such that partners differed in their levels of homing experience. We then examined the outcome of such paired releases, focusing on the degree to which paths flown by the pair resembled the individually preferred routes of the more and less experienced partner.

2.3 Methods

2.3.1 Subjects and GPS tracking

We used 20 adult homing pigeons (*Columba livia*) bred at the Oxford University Field Station at Wytham (51^{0}46’58.34’’N, 1^{0}19’02.40’’W). They were kept in a social group of ca. 120 pigeons inside two lofts. Birds normally had free access to the outside, except on the days when the experiments were conducted. Food (a commercially available multigrain mixture), water, minerals and grit were provided *ad libitum* throughout the study. All experimental birds were between 3 and 7 years old, and had homing experience but had never visited the release sites used in the current study, nor had any experience with paired homing flights. They were trained to carry miniature GPS logging devices (~20 g; i-gotU GT-100 Phototrackers, Mobile Action Technology, Inc., Taiwan) attached to their back by a small Velcro strip glued to clipped feathers. The weight of the devices corresponded to approximately 4% of the average bird's weight (5% for the smallest bird). For every training and test flight, geographical longitude and latitude were logged by the devices at 1 Hz and a positional accuracy of approximately ± 2.5 m (i.e. when stationary, 50% of fixes remain within a radius of 2.5 m over 24 hours).

2.3.2 Experimental procedure

The experiment was performed at two release sites (Fig. 2.1): College Farm (henceforth: R1; distance and direction to home: 7 km, 74^0, respectively) and Forest Farm (henceforth: R2; distance and direction to home: 7 km, 260^0, respectively). Each of the 20 subjects was assigned randomly to one of two treatment groups, either a high-experience group (henceforth: E+ birds; 10 subjects) or a low-experience group (henceforth: E- birds; 10 subjects). Both groups had a distinct training and testing protocol (Table 2.1). Training and testing of all subjects was completed at the first site before training at the next site began. Training was conducted on consecutive days, interrupted only by days of unsuitable weather. This was consistent for both treatment groups and release sites.

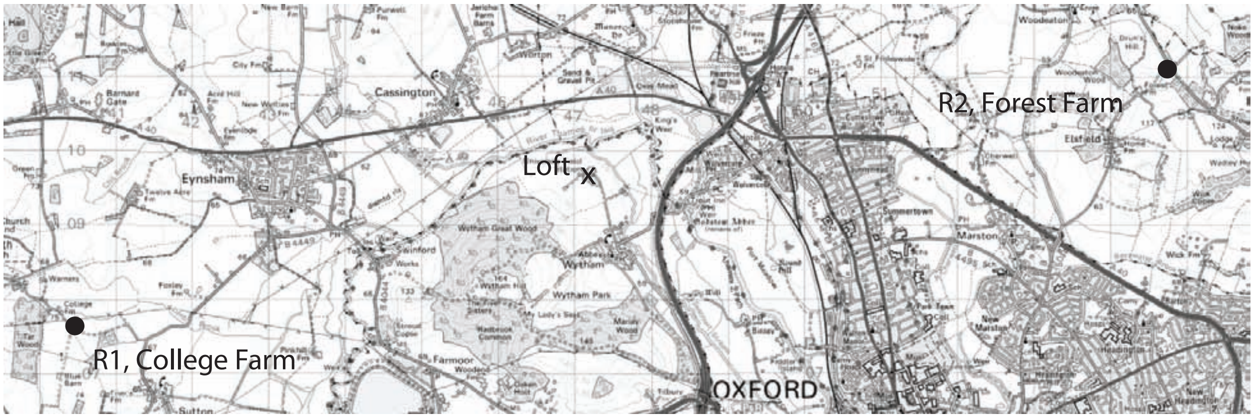

Figure 2.1 Ordnance survey map showing the locations of the release sites: College Farm (R1) and Forest Farm (R2). The release sites are indicated by black, filled circles, the home loft by an x.

Table 2.1 Training and testing protocol for the two treatment groups, E+ and E-. Training flights always involved solo releases; test flights were performed by releasing birds in pairs.

	No. of training flights	Test 1	No. of training flights	Test 2	No. of training flights	Test 3
E+ birds	15	E+/E-	1	E+/E-	1	E+/E-
E- birds	3	E+/E-	5	E+/E-	9	E+/E-

In the first stage of the experiment, birds from both groups were trained to fly individually from the release site, with the number of flights depending on the treatment group (15 and 3 flights; see Table 2.1). By choosing 3 and 15 flights, we ensured that the ensuing two groups of pigeons were at different stages of route development. Within the first three flights birds showed the highest level of improvement in homing efficiency, while by 15 flights increase in homing efficiency had reached a plateau (see Results). A maximum of three releases were conducted per day. To examine the influence of homing experience on leading/following behaviour, we then randomly assigned each bird a partner from the other group, and released those two birds simultaneously from the same release site as that used during training (E+/E- pairs; Test 1). Subsequently, we decreased the difference in homing experience in E+/E- pairs by giving birds additional solo training flights and repeated the paired test two more times using the same combination of pairs as in Test 1 (Tests 2 and 3; see Table 2.1). Test releases followed the completion of training with equal delay for both birds of a given pair (and were typically conducted the day after the final training flights of the two birds).

Finally, we repeated the entire protocol at a second release site, and switched the number of training flights assigned to each of the two groups. Thus, tests at the second site consisted of paired releases using same combinations of birds as at R1, but the E+ became the E- birds and vice versa. Thereby, we asked whether any possible relationship between homing experience and the probability to lead or follow was invariant to the release site or to some individual attribute other than experimenter-controlled homing experience. If experience was the key factor, we expected leader/follower roles to reverse within the same pairs in response to the reversal in levels of experience.

2.3.3 Data analysis and comparison methods

All analyses were conducted in Matlab (The Mathworks Inc.). Tracks were initially pre-processed by removing any point where the subject moved less than 1 m (which can be interpreted as a stationary bird), or any point after it reached within 100 m of the loft. To compare tracks, we analysed only those positional fixes that lay outside a radius of 1000 m from the release site. This enabled us to examine the similarities between the birds' routes and reduced potential noise created by the birds circling around the release site immediately after release, before assuming a homeward course.

We first examined the development of individuals' routes by focusing on homing efficiency on the one hand and route fidelity on the other. Homing efficiency is defined here as the ratio between the straight-line distance between the release site and the loft, divided by the sum of the direct distances between the neighbouring fixes. Route fidelity refers to the accuracy with which a bird reproduces the same route repeatedly. In order to estimate track similarity, we used two different methods to compare tracks. The first method, the nearest neighbour analysis, allowed us to estimate track similarity by computing the spatial proximity between tracks. For each point along the focal track, we determined the distance to the nearest neighbouring point along the comparison track, and used the average distance across all pairs of points as a measure of track similarity. While this analysis examines the absolute spatial proximity between tracks, homing pigeons may follow landmarks or the movements of co-navigating birds at a variety of distances, making it more difficult to determine leading/following behaviour on the basis of track proximity alone.

Hence, we developed a second method that compares the dynamics of tracks by using the birds' instantaneous flight direction, or heading. For bearing calculations, we determined for every two point along the track the birds' heading relative to the position of the loft. To estimate track similarity during training (within-individual comparisons) or to compare paired flights with previous individual training flights (between-condition comparisons), we defined different track segments according to the distance to the loft: We divided the straight-line distance between the release site and the loft into 18 equal parts (see below) and numbered them consecutively. We then calculated the mean bearings relative to the loft in each segment, and determined the degree of similarity between tracks. To do this, we computed the difference between the mean bearings of the single segments of any given track and the bearings from the corresponding segments of the paired flight. For all analyses involving bearings, we used circular statistical methods (Batschelet 1981). The number of segments (18) was determined using the relationship between efficiency and homing experience as a reference. We fitted nonlinear regression models to the data of homing efficiency as a function of the number of training flights. The equation that gave the best fit (r^2=0.96) was $Y=Y_0 + a * \exp(-b*X)$, where Y is a measure of the efficiency and X is the number of training flights (a and b are parameters that shape and scale the function). Next, we used this model to examine how variance of track similarity (Y) during training relates to both the number of training flights (X) and the number of segments. We found maximum r^2 values using 18 segments (r^2=0.97).

Next, in order to identify subjects as either leaders or followers, we used data from the highly efficient tracks of the single birds (i.e. tracks with an average efficiency larger than 0.75; for E+ birds flights 4-17 and 6-17 from release sites 1 and 2, respectively, see also Fig. 2.2) and calculated the expected range of individual track variation between those tracks. In order to do so, we determined the corresponding 99% confidence intervals arising from the two measures of track similarity. Using such intervals as a reference, we compared the paired flight of each bird with its own previous training flights and with the previous training flight of its partner. Leading/following behaviour was defined depending on whether or not both paired flights fell within the normal range of variation of the E+ birds. Our rationale for using this criterion was as follows. Since at the time of Test 1 and 2, E- birds had performed no or only few highly efficient tracks (see Fig. 2.2), the track variation between consecutive flights was relatively large. We calculated the ratios between the confidence intervals of both groups from the different tests (Table 2.2). At the time of Test 1, we found that the range of track variation of the E+ birds corresponded to 26% and 1% of the range of variation of the E- birds, according to the relative bearing and the nearest neighbour analysis, respectively. In Test 2, such range still corresponded to approximately 59% of the range of variation of the E- birds (see Table 2.2). Thus, paired flights were likely to fall within the range of the E- birds due simply to the large variation between these birds' tracks, while cases where pairs flew within the much smaller range of the E+ bird indicated more clearly that they followed the E+ bird's route. Hence, we tested whether or not the paired flights of both birds fell within the normal range of variation of the E+ birds.

Table 2.2 Ratio in percentage between the 99% confidence intervals of track variation in E+ and E- birds. Smaller percentage values indicate smaller confidence intervals for E+ than for E- birds.

Relative Bearing Analysis			Nearest Neighbour Analysis		
Test 1	Test 2	Test 3	Test 1	Test 2	Test 3
25.8	58.6	117	0.7	26.2	76

2.4 Results

We first examined the relationship among training regime, homing efficiency and the development of idiosyncratic routes. We found a positive correlation between path efficiency and the number of solo training flights completed (Fig. 2.2a, b). Pigeons needed only three flights to increase their homing efficiency drastically. At R1, the fourth flight of the E+ birds already had an average efficiency of 0.75, which then increased gradually until it became asymptotic after six flights (Fig. 2.2a). At R2, a similar level of efficiency was reached after only five flights (Fig. 2.2b). This increase in efficiency over consecutive releases did not differ between the two release sites ($F_{1,496}$=1.63, P=0.21, two-way repeated measures ANOVA). We also found that these experience-dependent changes in homing efficiency were invariant to the training protocol ($F_{1,496}$=0.10, P=0.75, two-way repeated measures ANOVA). While flying from the first release site, the E+ and E- birds had different efficiency levels only in Test 1, with the E+ birds significantly more efficient than the E- birds (P<0.001, t=5.5, df=18, two-sample t-test). Subsequently, in Tests 2 and 3, both groups were equally efficient during homing (Test 2: P=0.81, t=0.24, df=18; Test 3: P=0.81, t=0.24, df=18; two-sample t-tests). We obtained similar results for the second release site (Test 1: P<0.01, t=3.8, df=16; Test 2: P=0.48, t=0.73, df=16; Test 3: P=0.09, t=1.77, df=16; two-sample t-tests).

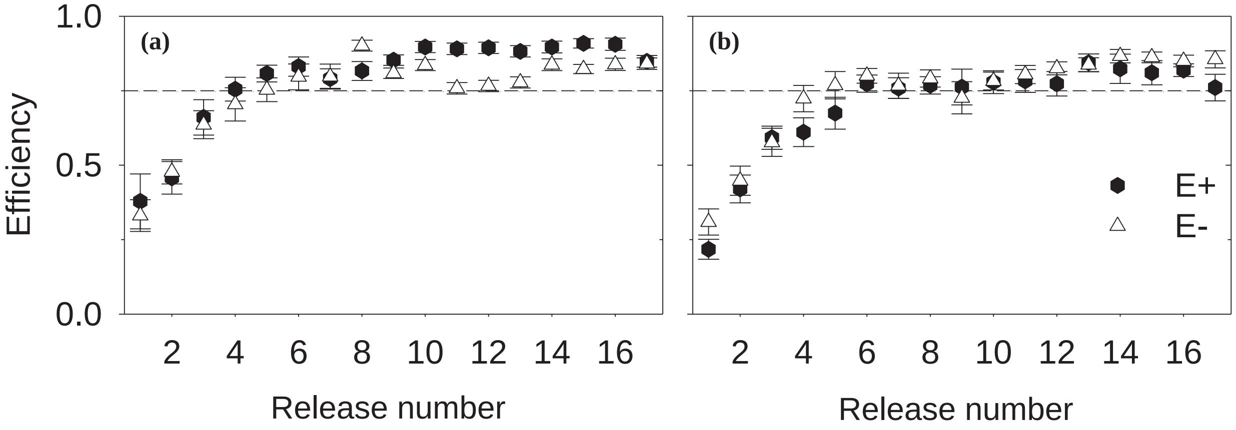

Figure 2.2 Homing efficiency (mean ± S.E.M.) as a function of training. Homing efficiency is the ratio between the straight-line distance between the release site and the loft, divided by the sum of the distances between all neighbouring position fixes along the length of the route flown. Data from different birds were averaged according to group identity and training release. **(a)** R1, College Farm, **(b)** R2, Forest Farm. Black circles and white triangles indicate high- and low-experienced birds, respectively. Dotted line indicates efficiency of 0.75.

Next, we examined the development of idiosyncratic routes. Fig. 2.3 illustrates route development of the E+ and E- birds at both R1 and R2 (Fig. 2.3a and 2.3d, respectively). Each column in Fig. 2.3a and d shows the mean difference in the bird's relative bearing as a function of both distance to home (top to bottom) and training (left to right). At the beginning of training (i.e. flights 1-5), individual homing routes were poorly developed and highly variable, but this variability decreased dramatically over the course of the birds' subsequent flights (Fig. 2.3). There is no evidence of any difference in route development with training protocol (Fig. 2.3b, e; R1: $F_{1,270}$=2.59, P=0.12; R2: $F_{1,240}$=2.98, P=0.054; two-way repeated measures ANOVA).

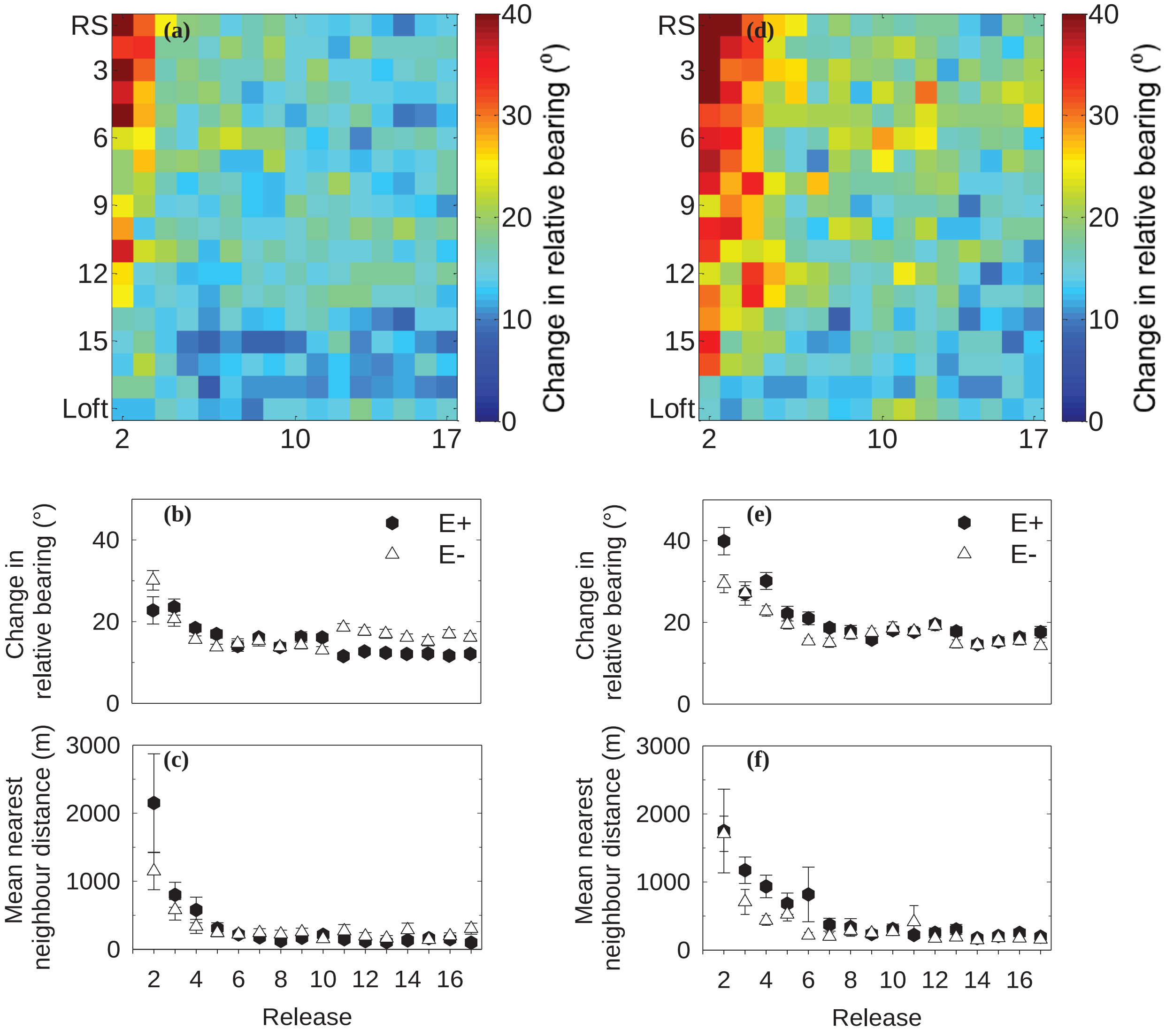

Figure 2.3 Development of the solo homing routes of birds released at R1 and R2. **(a, d)** We computed the difference between the mean relative bearing of given segments of any given track and the bearings from the corresponding segments of the preceding flight. Thus, each column depicts the mean difference in the instantaneous flight direction of the birds relative to the loft, or relative bearing, as a function of homing from the release site to the loft (top to bottom) and training flight number (left to right). Data are grouped according to release site: **(a)** E+ and E- birds at R1, **(d)** E+ and E- birds at R2. **(b, e)** Change in relative bearing (mean ± S.E.M.) and **(c, f)** mean nearest neighbour distance (mean ± S.E.M.) as a function of training. Data from different birds were averaged according to group identity.

Table 2.3 presents the results of the leadership analysis during Tests 1, 2, and 3 at both release sites. Here, we disregarded flights where partners split up during homing (pairs were considered to have split when the partners' instantaneous distance increased above 200 m and never fell below this threshold again). At the time of Test 1, the E- birds had less homing experience (3 flights) than the E+ birds (15 flights). While homing from R1, these less experienced pigeons followed the routes of their more experienced partners: the homing routes of all of the 6 pairs that did not split up during homing fell well within the 99% confidence intervals of the E+ birds ($P<0.01$, binomial test). This robust phenomenon was detected by both comparison methods. We obtained similar results for the second release site with the roles of individuals in a given pair reversed, further confirming experience as a key factor in determining leadership beyond other (un-manipulated) individual attributes. In Test 1, all 5 non-splitting pairs at R2 followed the routes of the E+ birds ($P=0.03$, binomial test) according to the relative bearing method (the nearest neighbour analysis indicated only 3 of the 5 pairs; $P=0.50$, binomial test). By pooling data from R1 and R2, we found that 11 and 9 ($P<0.001$ and $P=0.03$, binomial test) of the eleven pairs flew within the range of the E+ birds, according to the relative bearing and the nearest neighbour analysis, respectively.

At the time of Test 2, the E- and E+ birds had made 8 and 16 homing flights, respectively. Of the 9 non-splitting pairs released from R1 in Test 2, both methods identified that 7 pairs flew within the normal range of individual track variation of the E+ birds ($P=0.09$, binomial test). We obtained similar results for the second release site: of the 9 non-splitting pairs at R2 in Test 2, 7 pairs flew within the 99% confidence intervals of the E+ birds according to the relative bearing method ($P=0.09$, binomial test), although only 5 according to the nearest neighbour analysis ($P=0.50$, binomial test). By pooling data from R1 and R2, we found that 14 and 12 (P=0.02 and P=0.12, binomial test) of the 18 pairs flew within the normal range of the E+ birds, as determined by the relative bearing and the nearest neighbour analysis, respectively.

At the time of Test 3, both the E+ and the E- birds had performed 17 individual homing flights. Thus, by this stage both groups had gained the same amount of homing experience. By pooling data from R1 and R2, we found that 5 and 9 (P=0.20 and P=0.21, binomial test) of the 14 pairs flew within the normal range of the E+ birds, as determined by the relative bearing and the nearest neighbour analysis, respectively. The different results obtained through the relative bearing and the nearest neighbour methods demonstrate that the two measures work based on different assumptions, thereby capturing different aspects of track similarity. Nonetheless, they indicate similar general trends, strengthening the idea that our findings are robust.

Table 2.3 Leading/following behaviour of the E- birds in Tests 1-3. We compared the paired flight of each E- bird with the previous training flight of its partner (E+) and with its own previous training flights (E-). Y/N indicates whether the paired flight of the E-bird fell within (Y) or out of (N) the normal range of variation of either reference tracks (E+ or E-). The track comparisons were made using two methods: relative bearing (RB) and nearest neighbour analysis (NN). Each cell shows the number of cases found at R1 and R2. The columns SUM show the number of E- birds that flew within the range of the E+ birds' tracks and the total number of pairs observed at each release site. P-values show the results of binomial tests.

		R1					R2					Both Sites
		E+: Y E- : N	E+: Y E- : Y	E+: N E- : N	E+: N E- : Y	SUM	E+: Y E- : N	E+: Y E- : Y	E+: N E- : N	E+: N E- : Y	SUM	
Test 1	RB	**0**	**6**	0	0	**6**/6 $P<0.05$	**1**	**4**	0	0	**5**/5 $P=0.03$	**11**/11 $P<0.01$
	NN	**1**	**5**	0	0	**6**/6 $P<0.05$	**0**	**3**	0	2	**3**/5 $P=0.5$	**9**/11 $P<0.05$
Test 2	RB	**2**	**5**	1	1	**7**/9 $P=0.09$	**1**	**6**	0	2	**7**/9 $P=0.09$	**14**/18 $P<0.05$
	NN	**1**	**6**	0	2	**7**/9 $P=0.09$	**0**	**5**	1	3	**5**/9 $P=0.5$	**12**/18 $P=0.12$
Test 3	RB	**1**	**2**	2	3	**3**/8 $P=0.36$	**1**	**1**	1	3	**2**/6 $P=0.34$	**5**/14 $P=0.21$
	NN	**4**	**0**	0	4	**4**/8 $P=0.64$	**2**	**2**	1	1	**5**/6 $P=0.11$	**9**/14 $P=0.21$

Next, we examined how the probability of birds following the path of their co-navigating partner changed across the three tests. We measured (i) the extent to which the less experienced birds deviated from their solo routes while flying in pairs (calculated as the difference between the paired flight of each E- bird and its last solo training flight), and (ii) how closely the two birds flew together during the test. Figure 2.4 shows how these two measures related to each other in the three tests. In Test 1 (Fig. 2.4a), the cluster of data points shown in the upper-left area of the plot indicates that the E- birds deviated substantially from their own route while flying close to their partners. Pairs flying either within or outside of the 99% confidence interval of the E+ birds are depicted in black and white, respectively: the plot indicates that all pairs followed the routes of the E+ birds (see example in Fig. 2.4d). In Test 2, the majority of pairs followed the route of the E+ birds, but the E- birds deviated less from their original route in comparison to Test 1, as seen from the fact that the points in Fig. 2.4b lie closer to the reference diagonal. Moreover, in Test 2 we found pairs (those shown in blue) following the routes of the E- birds. In the final, third test, the E- birds again showed a smaller deviation with respect to their previous routes, as compared to Test 1. In contrast to the preceding tests, we found that more pairs flew outside the normal range of variation of the E+ birds than those that flew within (Fig. 2.4c). Fig. 2.4f illustrates an example in which we can no longer reliably evaluate leading/following behaviour due to the high similarity between the tracks of both – now similarly highly experienced – birds. Such cases became frequent at this stage of route development.

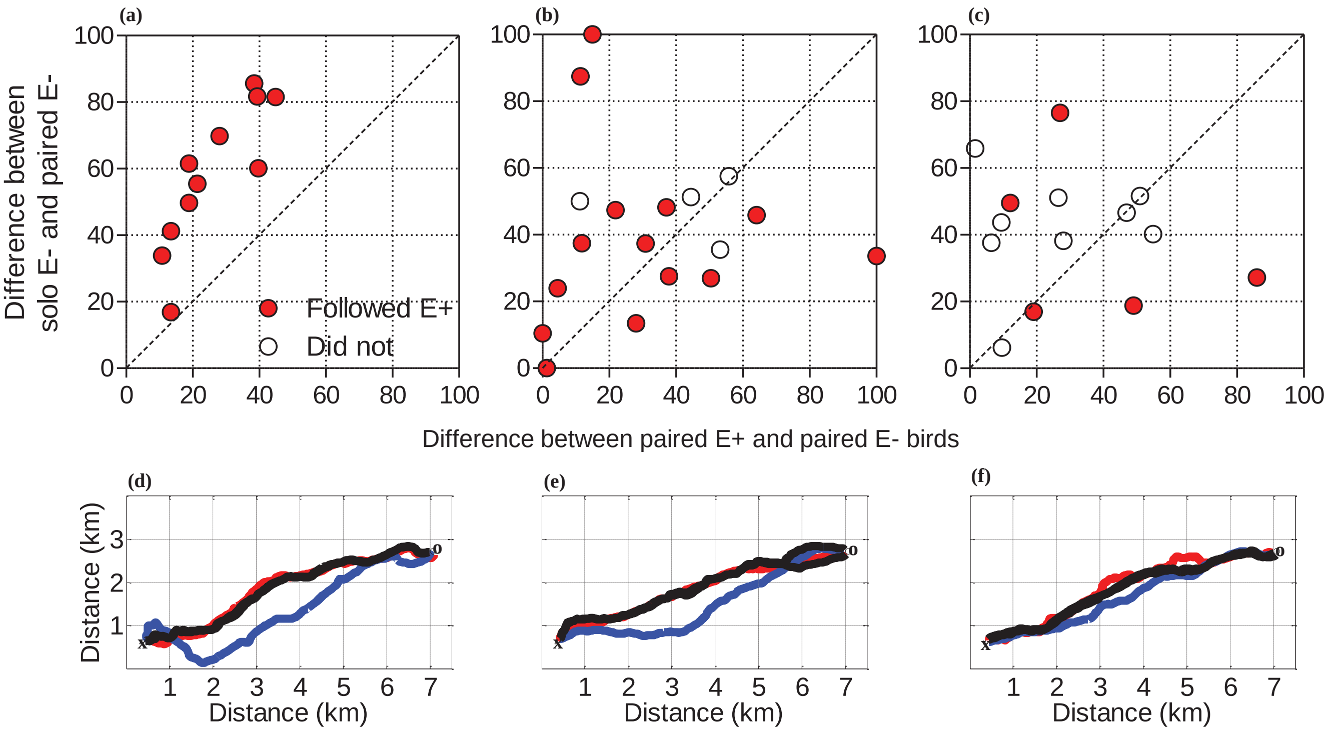

Figure 2.4 (a-c) The degree of similarity between the paired flight of each E- bird and its last solo training flight as a function of the degree of similarity between the flights of co-navigating pigeons for Test 1 **(a)**, Test 2 **(b)** and Test 3 **(c)**. Similarity was measured using the relative bearing method. Differences are expressed as percentages of the range between the minimum (0%) and maximum (100%) values recorded for each pair. Pairs that were identified to fly within or outside the 99% confidence interval of the E+ birds are depicted in red and white, respectively. **(d-f)** Examples of flights for Tests 1-3. In each panel, black lines show flights performed by E+ and E- birds of a pair when released together. Red and blue lines indicate tracks flown individually by E+ and E- birds, respectively, in releases immediately prior to the paired flight (**d** – Test 1; **e** – Test 2; **f** – Test 3). The release point is indicated by an x, the home loft by an o.

Finally, we explored whether birds were more likely to follow a partner with a more efficient route. We measured the difference in homing efficiency between the E+ and the E- birds' last training flight and the extent to which the E- birds deviated from their own route. We did not find a correlation between these two measures in any of the three tests we conducted (Pearson's correlation, Test 1: $r^2_9=0.04$, P=0.58; Test 2: $r^2_{16}=0.1$, P=0.19; Test 3: $r^2_{12}=0.1$, P=0.24). In other words, larger differences in route efficiency between the E+ and E- birds of a pair did not result in larger deviations by the E- birds from their own routes.

2.5 Discussion

Animal collectives travelling together must, if they are to maintain a cohesive group, be able to negotiate joint routes even in the presence of conflicting opinions over route choice. This can be achieved when certain individuals have a disproportionately large influence in making navigational decisions (which are then followed by others), or by averaging each group member's preferences for a more "democratic" decision. Previous work with homing pigeons has confirmed theoretical predictions that the two mechanisms (consensus and averaging) can indeed co-exist within the same decision-making scenario, as birds' propensity to rely on one or the other depends on the size of the conflict experienced. Furthermore, we also know that in specific pairwise interactions there are one or more attributes of a flying bird that can reliably predict its likelihood either to lead or to follow conspecifics (Biro et al. 2006; Nagy et al. 2010). Evidence indicates that leadership may derive from the shifting of the balance between the emphasis that birds place on remaining close to their individually preferred routes and the emphasis they place on remaining close to their partner (Freeman et al. 2011). What roles do individual knowledge and experience play in determining such leader-follower relations? Given that all previous studies have examined leadership phenomena in pigeons with equal levels of homing experience, in the present study we asked whether and to what extent the probability that a bird will follow the path of another depended upon its own level of homing experience relative to that of its partner.

Our results clearly demonstrated that less experienced pigeons are likely to follow more experienced conspecifics. The difference in homing experience between our two experimental groups of co-navigating pigeons was the largest in the first of our three tests. Under these conditions, all pairs flew within the range of the more experienced birds' preferred path. Similarly, we found that the majority of less experienced birds followed their more experienced partners in the second test, where differences in levels of experience were reduced but still existent. However, by the time the final test was conducted, and both groups had had the same number of training flights, we observed roughly equal probabilities to lead or follow in the same pairs of previously more or less experienced birds. This means that some of the birds that had previously followed a (more experienced) partner were able to become leaders once their experience rose to equal that of their partner. These results held at both release sites where we conducted replicates of the experiment, suggesting that the outcome is invariant to release site location. Further, interestingly, since the training regimes of the birds were reversed between the two sites (with more experienced birds at the first site becoming the less experienced ones at the second), the results also confirm the robustness of the effect over other individual differences that may determine the emergence of leaders. Taken together, the results clearly indicate that different levels of homing experience accounted for the observed group differences in leading/following behaviour.

In the present study we used homing efficiency and route fidelity as measures of a pigeon's level of experience and navigational knowledge, manipulated by controlled exposure to a specific navigational task during training. Our results document how, over the course of repeated releases from a given site, both homing efficiency and route fidelity increase first dramatically and later gradually until they become asymptotic. Such findings match previous results by Meade et al. (2005), who reported that as birds become more experienced, their routes become more efficient and increasingly stereotyped. Past experiments by Wallraff (1959) also suggested that homing success increases with experience, but that specific knowledge of a release point is of much less importance than general homing practice. If this were the case, the efficiency observed at our second site would have been higher than that observed at the first site, which would have prevented us from evaluating the behaviour at both release sites in a combined analysis. Interestingly, our results did not match these previous findings: the rate of increase in efficiency over consecutive releases did not differ between the two release sites.

Our results additionally suggest that there is a short sensitive period in the development of a route, during which pigeons are more likely to respond to conspecifics by following the latter's route. Past studies have described that a pigeon's propensity to fly together with other birds is relatively low during its very first flight from an unknown site irrespective of its partners' knowledge (Heinroth & Heinroth 1941; Guilford & Chappell 1996). This suggests that on encountering a new location, birds may prioritise the processing of available navigational information in order to compute their own directional decision, and that at this stage, stimuli arising from other birds (even those more experienced) may not be salient enough to initiate a following reaction. The present study shows that just a few additional flights are sufficient to induce different behaviour. After those initial flights, birds may have gained enough experience to allow them to attend to and to follow the movements of partners. Whether such following behaviour also represents a learning opportunity (i.e. whether birds following conspecifics during this potential sensitive period acquire navigational knowledge about routes) is an open – and highly interesting – question that will be the basis of future work.

Our findings are in line both with theoretical predictions and with empirical studies on different model systems suggesting that naïve or inexperienced individuals follow those more experienced. For example, several studies have reported, across a broad range of taxa, a relationship between information and leadership. Cliff swallows follow their colony neighbours (Brown 1986), while trained shoaling fish can manipulate the direction of the group (Reebs 2000). A recent study on meerkats has shown that trained individuals are more likely to initiate group departure than untrained individuals (Bousquet & Manser 2011). In agreement with these empirical reports, theoretical work by Couzin et al. (2005) and Conradt et al. (2009) has shown that individuals with the highest certainty of information or larger degree of assertiveness can spontaneously emerge as leaders during group movement.

Whilst our experiments necessarily involve a level of artificiality to provide experimental control, it seems likely that the same advantages found here in following more experienced birds when an individual is itself inexperienced should also exist in feral pigeon or ancestral rock dove populations. Group members are always likely to vary in local experience and age, providing information gathering advantages, and reducing navigational risks, to inexperienced individuals in following others. Indeed, we may expect these advantages to be quite general to socially foraging species that range widely.

In sum, our results have implications for a better understanding of how problems of collective decision-making are solved in species that travel in mixed-experience groups. We can assume that each member of a group possesses particular features (e.g. age, experience, social rank, or sex) that might modify its own behaviour towards others as well as the behaviour of its conspecifics towards it. Evidence indicates that numerous types of individual differences and state- or status-dependent characteristics, such as level of dominance (King et al. 2008), hunger (Krause et al. 2000), boldness (Harcourt et al. 2009) or lactation state (Fischhoff et al. 2007), can influence leadership and followership across a range of species (see also King et al. 2009 for review). Further studies on the role of individual variation among group members in determining the organisation of group decision-making are certain to prove fruitful for improving our understanding of both the mechanisms and the adaptive significance of information transfer, coordination, and learning in animal collectives.

Chapter 3

Pairs of pigeons act as behavioural units during route learning and co-navigational leadership conflicts

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3.1 Summary

In many species, group members obtain benefits from moving collectively, such as enhanced foraging efficiency or increased predator detection. In situations where the group's decision involves integrating individual preferences, group cohesion can lead to more accurate outcomes than solitary decisions. In homing pigeons, a classic model in avian orientation studies, individuals learn habitual routes home, but whether and how co-navigating birds acquire and share route-based information is unknown. Using miniature GPS loggers, we examined these questions by first training pairs (the smallest possible flocks) of pigeons together, and then releasing them with other pairs that had received separate pair-training. Our results show that, much like solitary individuals, pairs of birds are able to establish idiosyncratic routes that they recapitulate together faithfully. Also, when homing with other pairs they exhibit a transition from a compromise- to a leadership-like mechanism of conflict-resolution as a function of the degree of disagreement (distance separating the two preferred routes) between the two pairs, although pairs tolerate a greater range of disagreements prior to the transition than do single birds. We conclude that through shared experiences during past decision-making, pairs of individuals can become units so closely coordinated that their behaviour resembles that of single birds. This has implications for the behaviour of larger groups within which certain individuals have closer social affiliations or share a history of previous associations.

3.2 Introduction

Individuals in many bird species obtain a variety of benefits from moving collectively (Krause & Ruxton 2002). Although in pigeons *(Columba livia)* flying in a flock can be energetically more costly than flying alone (Usherwood et al. 2011), this is offset by a number of advantages. Besides the anti-predatory benefits of group travel, group cohesion can lead to more accurate navigation in situations where the overall orientation of the flock arises from averaging the directional preferences of the single members of the group (Hamilton 1967; Simons 2004; Dell'Ariccia et al. 2008). A combination of social habits and prodigious navigational skills (Wallraff 2005) makes homing pigeons a useful model system for the study of collective navigation (Biro et al. 2006; Flack et al. 2012). Pigeons benefit from route memories that develop over consecutive flights: once enough experience with a route is gathered, these memories will reliably guide birds back to the loft along a remarkably fixed flight path (Biro et al. 2004; Meade et al. 2005). Also, wild rock pigeons, the stock ancestral to homing pigeons, perform daily foraging trips from their colony to feeding grounds, and back, seemingly using stable routes (Baldaccini et al. 2000), a process that most likely involves visual memories and reduces the pigeons' level of navigational uncertainty across flights. Nonetheless, because under natural conditions pigeons often travel in small or large flocks rather than individually, one intuitive question that follows is how the presence of a co-navigating partner influences the development of stereotyped routes in homing pigeons. For example, do pairwise trained pigeons develop joint stereotyped homing routes? If so, do joint and individual routes develop in a similar fashion?

Importantly, when homing as a pair, pigeons that possess different preferred homing routes will fly along a path that lies between their two individual routes, provided that these individual routes are within a certain distance from each other (Biro et al. 2006). This suggests that these birds are compromising over their route choice, with the two birds' individual preferences being combined to give a shared route. However, if the distance between the two birds' routes rises above a threshold, one of the pigeons will emerge as the leader and the other as the follower, as seen from the fact that the pair will then follow the leader's path faithfully. In the present paper, we investigate whether and how such leader-follower relationships translate to quadruples composed of pairwise trained individuals. Although pair-routes may prevail during the homing flights of such quadruples, compromise routes may also be observed, depending on the spatial relationship between the previously established joint routes of the pairs. Furthermore, joint homing can improve navigational efficiency, particularly when decisions are shared (Simons 2004; Dell'Ariccia et al. 2008) - a phenomenon which could suggest an adaptive explanation for a pigeon's tendency to travel with a co-navigating partner in addition to the more commonly cited anti-predatory accounts. Social bonds and shared experiences developed through joint travel may in turn lead to inter-individual affiliations that enable close coordination of a pair's behaviour even when embedded within a larger flock, much like existing social relationships between familiar conspecifics, sexual partners or parents and offspring can modify the organisation of social groups in a variety of species (e.g. Griffiths & Magurran 1999; Sueur et al. 2010).

With these ideas in mind, we conducted a series of experiments in which we examined, first, whether and how pigeons establish homing routes when trained in pairs, and second, how such joint training influences the pairs' subsequent behaviour in larger flocks. Our work provides insights into both the impact of a partner on the speed and stability of route learning, and collective decision-making in large groups within which different dyads have different levels of prior association.

3.3 Methods

3.2.1 Subjects and experimental procedure

We used 16 adult homing pigeons (Columba livia Gmelin 1789) bred at the Oxford University Field Station at Wytham ($51^0$46’58.34’’N, $1^0$19’02.40’’W). All experimental birds were between 3 and 7 years old, and had homing experience but had never been released from the sites used in the present study. They were trained to carry miniature GPS logging devices (~15 g; i-gotU GT-120 Phototrackers, Mobile Action Technology, Inc., Taiwan) attached to their back by a small Velcro strip glued to clipped feathers. For every training and test flight, geographical longitude and latitude were logged by the devices at 1 Hz and with a positional accuracy of approximately ± 2.5 m (i.e. when stationary, 50% of fixes remained within a radius of 2.5 m over 24 hours). The experiment was performed at two release sites: Church Hanborough (henceforth, R1; distance and direction to home: 6.14 km, 129^0, respectively) and College Farm (henceforth, R2; distance and direction to home: 7.00 km, 74^0, respectively). Training at R1 consisted of paired homing flights: each subject was assigned a fixed partner (thus forming eight pairs in total), and the two birds were released 17 consecutive times as a pair, with a maximum of four releases per day. After completing training, we tested pairs in quadruples by releasing two pairs simultaneously from the same release site as that used during training. We repeated such quadruple releases until all possible combinations of our eight pairs had been tested; thus a total of 28 group releases were performed (i.e. seven quadruple releases for each pair).

In addition to these group releases, the same subjects also underwent individual training in order to provide reference data on homing efficiency and track variation changes in birds trained alone. Subjects were required to home singly from R2, 17 times in succession, with a maximum of three releases per bird per day (see Flack et al. 2012).

3.3.2 Data analysis

All analyses were conducted in Matlab (The Mathworks, Natick, MA, USA). Tracks were initially pre-processed by removing any point where the subject moved less than 1 m (which can be interpreted as a stationary bird), or any point after it came within 100 m of the loft. When comparing tracks, we analysed only those positional fixes that lay outside a radius of 200 m from the release site to reduce the effect of initial circling behaviour. We explored the acquisition of homing routes when birds were trained in pairs by analysing homing efficiency and route fidelity. Homing efficiency is defined here as the ratio between the straight-line distance between the release site and the loft, divided by the sum of the direct distances between the neighbouring fixes of the track. Route fidelity refers to the accuracy with which a bird (or a pair of birds) reproduces the same route repeatedly and is measured as the mean nearest neighbour distance between all constituent points of two tracks.

Additionally, we evaluated a subject's quadruple flight with reference to its immediately preceding paired training flight. To identify subjects as either leaders or followers, we first calculated the expected range of individual track variation between the final set of highly efficient training tracks (i.e. training flights 10 – 17). We measured the mean nearest neighbour distance between consecutive training tracks and determined their corresponding 99% confidence intervals. Second, we compared the path of each quadruple with the last training flight of both pairs. Leading/following behaviour was then assigned to each pair depending on whether or not quadruple flights fell within the confidence interval of one or the other pair (see also Flack et al. 2012 for further technical detail on these methods).

3.4 Results

We began by examining the development of homing routes in pigeons trained in experimenter-assigned pairs. During these paired flights, individual homing efficiency increased as training progressed (nonlinear regression, Paired flights: $r^2=0.47$, Fig. 3.1a). Furthermore, track variation (nearest neighbour distance to previous training track) decreased with training (Fig. 3.1b), eventually beginning to asymptote around the sixth to eighth flight and reaching an average inter-route distance of only 241 m by the end of training. Hence, homing pigeons trained exclusively in pairs were able to develop joint stereotyped homing routes, and their route development progressed with an accuracy and on a timescale comparable to those previously reported from individually trained birds (Meade et al. 2005). By also training our subjects in solo releases, we were able to provide a new set of reference tracks for individuals' ability to learn routes when flying alone (Fig. 3.1a, b). While no formal comparisons can be made because the birds were released from a different site during solo-training (by necessity, as they had already learnt about the first site during paired flights), this dataset nonetheless reinforces the similarities in route acquisition between the pair- and solo-training conditions. Note, for example, the similarities in the overall shapes of the two regression curves fitted to the increase in birds' homing efficiency under the two training conditions (Fig. 3.1a). The decrease in variation between consecutive tracks flown by pair-trained birds is also comparable to that of solo-trained birds (Fig. 3.1b), although it appears also to hint that at an early stage of route development birds may exhibit less inter-route variation when trained with a partner (this will, however, require further experiments for a formal comparison). Not all pairs stayed together throughout all of their joint training flights. Nonetheless, we found that the probability of pairs splitting decreased markedly as training advanced (Fig. 3.1c), a phenomenon also revealed by the reduction of the instantaneous distance between training partners during flight (Fig. 3.1c inset).

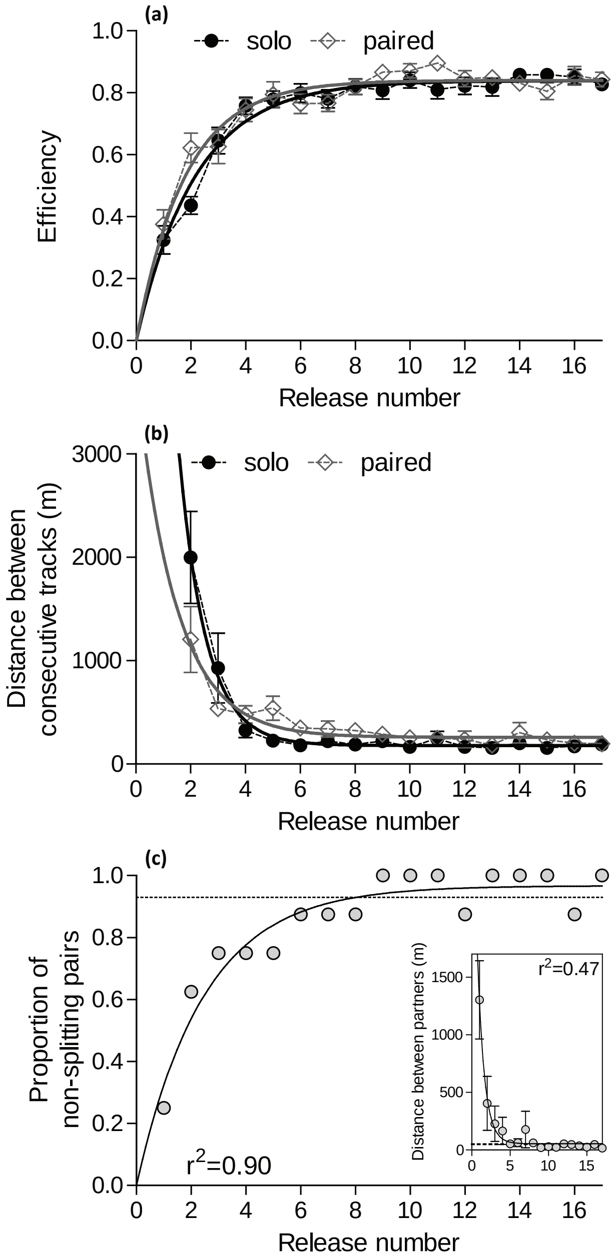


Figure 3.1 (a-c) Training data from homing pigeons released 17 times consecutively from a release site, either singly or in pairs. **(a)** Homing efficiency (mean ± S.E.M.) and **(b)** nearest neighbour distance (mean ± S.E.M.) between consecutive training tracks as a function of training. Data from different birds were averaged according to training protocol. Black circles indicate solo training, white diamonds paired training. Solid lines correspond to fitting of nonlinear regression curves. **(c)** Proportion of non-splitting pairs as a function of training. Inset is mean (± S.E.M.) instantaneous distance between training partners as a function of training. R^2 shows goodness of fit for nonlinear regression.

We next examined the homing flights of quadruples composed of pairwise trained individuals. First, we determined the instantaneous distance among the four pigeons involved in every quadruple release at all points (i.e. every second) during homing. For each of the four pigeons, we calculated the distance to its known training partner as well as the distance to the remaining two birds. Next, for each of these two sets of data we determined the proportion of the homing flight during which such distance remained below 50 m, a distance that corresponds to the plateau reached during training (see Fig. 3.1c inset). We found that individuals spent more time flying closer to their training partners than to the unfamiliar pigeons of the quadruple (Related Samples Friedman ANOVA, N=28, Q=4.48, P=0.034, Fig. 3.2a).

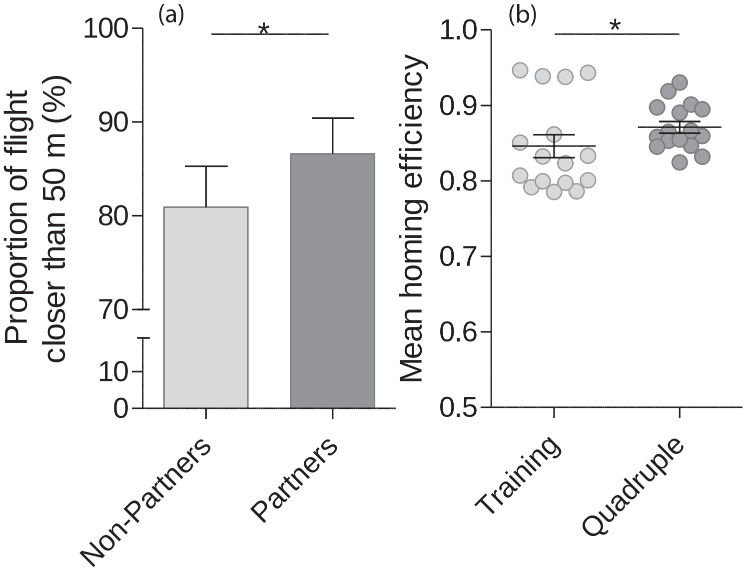


Figure 3.2 (a, b) Distance between birds and homing efficiency during quadruple flights. **(a)** Mean ± S.E.M. of the proportion of each group flight (N=28) during which distance between partners and non-partners is less than 50 m. **(b)** Scatter plots of mean homing efficiency during training (averaged across flights 10-17) and quadruple flights (N=16). Asterisks represent significant differences ($P<0.05$).

In these quadruple flights, we also observed that the birds increased their homing efficiency, as compared with the average of the final seven paired training flights (paired t-test, t_{15}=2.57, P=0.022, Fig. 3.2b). We therefore determined the extent to which each of the pairs deviated from their pair-routes during quadruple flights. One quadruple split before arrival at the loft (one bird homed individually), and in three cases the inter-route distances were too small to clearly assign leader-follower behaviour. Among the remaining 24 quadruples, in 9 cases the birds flew along a compromise route, defined as an intermediate path that deviated from both pair-routes (Fig. 3.3a; see also example tracks in Fig. 3.3e). In 15 cases, the group followed one of the previously established pair-routes (Fig. 3.3a; see also example tracks in Fig. 3.3c, d). Based on these observations, we composed a network of leadership during the quadruple flights. The nodes of this network represent individual pairs, and the edges point from the pair that remained on its own route (i.e. led) to the pair that left its route (i.e. followed the leading pair). The network showed a hierarchical structure with transitive properties (no loops). There was no correlation between a pair's rank in the hierarchy and its route efficiency during previous paired flights (Pearson's r=-0.44, n=8, P=0.272, Fig. 3.3b). This finding closely mirrors what has been found in individually trained birds (Biro et al. 2006), indicating that the behaviour and interactions of pairs resembled those of individuals.

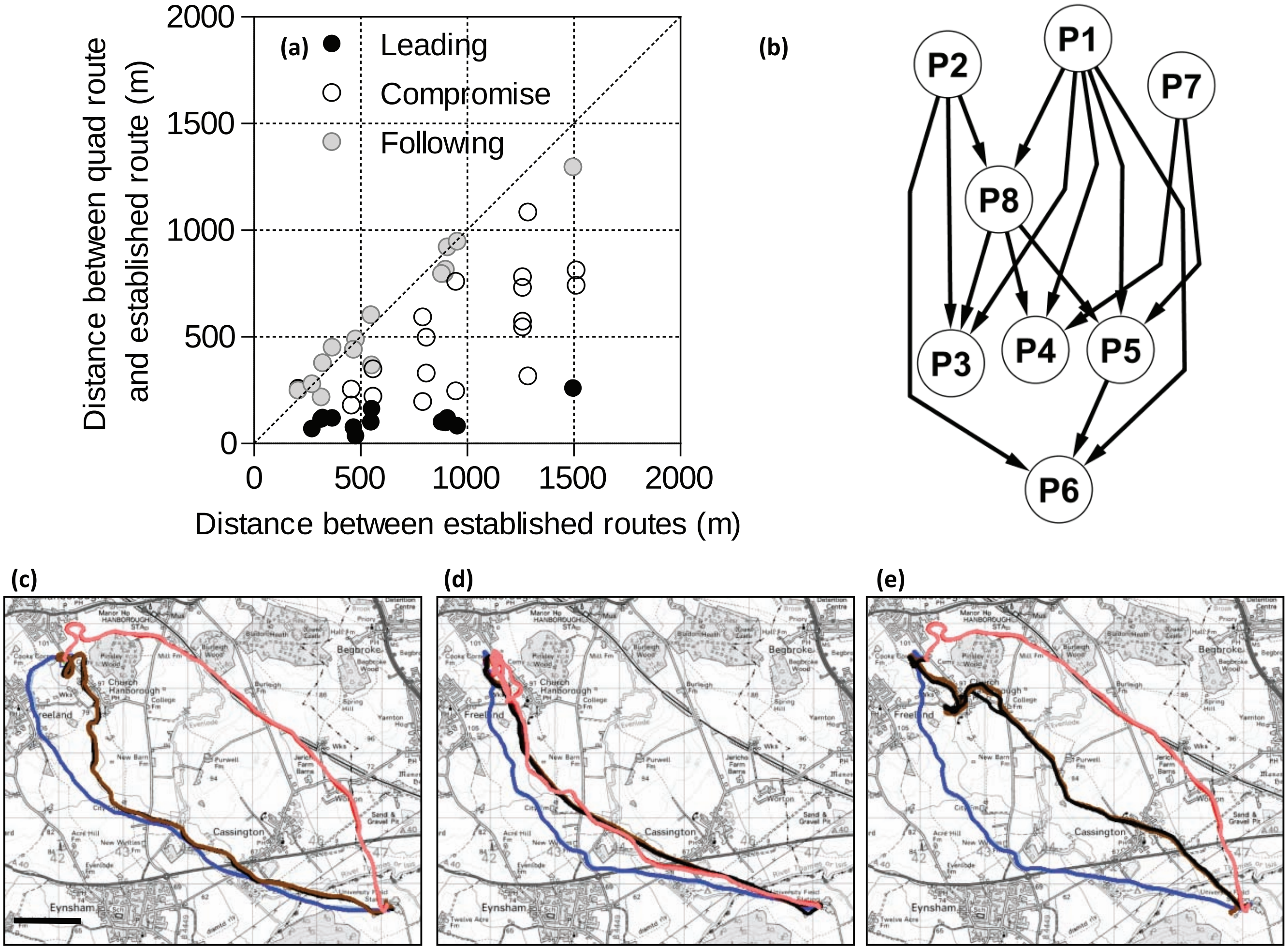


Figure 3.3 (a-e) Leadership and compromise during quadruple flights. **(a)** Mean distance of birds from their own established routes during quadruple flights as a function of the distance between their own and the other pair's established routes. Birds that followed their own route or the routes of their partners are depicted in black and grey, respectively. Birds that flew along a compromise route are depicted in white. **(b)** Outcome of specific pairings of pairs. Circles indicate pairs, numbers correspond to the relative rank attained by each pair in terms of homing efficiency during the last training flight (1=most efficient). Solid arrows point from the leading pair of a quadruple to the follower pair. **(c-e)** Examples of flights performed by training pairs released in quadruples. In each panel, blue and red lines indicate tracks flown during training by pair 1 and pair 2, respectively, and black and brown lines show the flight paths of pair 1 and pair 2 when released together as a group of four. Scale bar, 1 km.

3.5 Discussion

We examined how pigeons learn homing routes when trained in pairs, and how such training influences their subsequent leader-follower relationships when flying in larger flocks. We found that, much like solo-trained birds in our previous experiments (Biro et al. 2004; Meade et al. 2005; Flack et al. 2012), pairs of pigeons trained together also developed idiosyncratic routes over the course of consecutive homing flights. Crucially, the timescale over which the routes developed and the accuracy with which stable routes were recapitulated towards the end of training were clearly comparable between solo- and pair-trained birds, suggesting fundamental similarities in the mechanisms of acquisition and in the navigational processes underlying the recapitulation behaviour. While pair-trained birds tended to split up at some point during the journey in their first few flights, the probability of splitting decreased as training progressed, and birds began reliably to fly close to each other. After this initial phase, pigeons exhibited close coordination of movement with their partners, with potentially both birds' individual navigational experiences contributing to the development of the joint route. This finding is in agreement with previous results showing that there is a short sensitive period in the development of a route, during which pigeons are more likely to respond to conspecifics by following another's route (Flack et al. 2012).

Furthermore, we found that the link between partners established during training continued to be maintained during quadruple flights, as pair members spent more time flying closer to each other than to the two other unfamiliar birds. This link between pair members may have emerged spontaneously, from the pigeons' individual attraction to a common route. While passing over specific features of the landscape, pairwise-trained pigeons might have been attracted towards common familiar homing paths, thereby deviating from other co-navigating birds. Alternatively, repeated interactions during training may have promoted the formation of affiliative bonds based on individual recognition or increased social tolerance between partners, which were then maintained in the form of spatially defined sub-groups during quadruple flights. We argue that pigeons may identify familiar partners among flock members and exhibit a propensity to follow their path, which, as confirmed by joint experience, would lead to a common goal. Past work on different species demonstrated how the establishment of stable relationships based on familiarity can modulate an individual’s tendency to follow the movements of a preferred partner (Boissy & Dumont 2002; Ramseyer et al. 2009). This is in agreement with recent theoretical work on the impact of social networks on collective motion in animals, which suggests that social relationships can affect leader-follower dynamics, the positioning of individuals within the group and the cohesion of the group (Bode et al. 2011).

Next, we explored how the different directional preferences of sub-groups of pigeons in a small flock are resolved during homing, by releasing quadruples composed of sub-groups (pairs) of pairwise trained pigeons. Among quadruples in which the two pairs possessed sufficiently dissimilar routes to lead to conflict, we observed two main outcomes, broadly defined as leadership (groups following one of the two pair-routes) and compromise (groups homing along a route intermediate to their established pair-routes). Our results provide empirical evidence to support previously developed theoretical work that investigated the mechanisms by which such group decisions can emerge, with a distinction between processes where a small number decides for the rest of the group and those where the decision is equally shared among members (Conradt & Roper 2009). Biro et al. (2006) had previously found that pairs of individually trained pigeons will fly along a compromise route if the distance between the birds’ previously established routes lies below a certain threshold (approximately 575m). By contrast, if this distance exceeds the critical threshold, one bird will follow the path of the other. These findings are in line with theoretical predictions (Biro et al. 2006; Couzin 2009) indicating that attraction to a route and to a partner will lead to intermediate routes only when the familiar landmarks of each individual are within a critical distance of each other, presumably corresponding to a sensory range. Interestingly, compared with past results describing following behaviour in pairs of individually trained birds, in quadruples we not only observed a greater proportion of intermediate routes overall, but also that these intermediate routes continued to occur at high inter-route distances. Even at average inter-route distances as high as 1500 m we detected quadruples flying along compromise routes (Fig. 3.3e), indicating that pairwise-trained individuals tolerate a greater range of disagreements between routes than solo-trained birds. Pigeons appear to be less attracted to their routes when flying in quadruples, a behaviour that seemingly increases their probability of flying along compromise routes. This might be due to birds in larger flocks maximising flock cohesion by reacting more readily to signals from conspecifics, thereby reducing responses to landmarks. Also, pigeons flying in quadruples increased their efficiency relative to paired flight. This result is in agreement with previous data showing that the homing performance of pigeons flying as a flock can be higher than that of birds released individually (Biro et al. 2006; Flack et al. 2012) and supports the predictions of group navigation models (Hamilton 1967; Simons 2004; Codling et al. 2007).

The perhaps most surprising aspect of the quadruple tests was the emergence of a fully transitive leadership hierarchy among our pairs. This matched exactly results obtained previously from solo-trained birds tested in pairs, in a design otherwise identical to ours (Biro et al. 2006), and closely resembled the behaviour of single birds in larger flocks, where hierarchies based on initiation and copying of small-scale directional changes (rather than on overall route choice) also showed very high levels of transitivity (Nagy et al. 2010). This suggests that pairs, much like single individuals, may possess stable attributes that they carry over into interactions with new partners, and which thus predict the outcome of any specific pair vs. pair contest. The lack of a correlation between pair-route efficiency and pair leadership rank suggests that such attributes are independent of the pair's navigational capability in a broad sense (again agreeing with results from solo-trained birds released in pairs; Biro et al. 2006). Instead, leadership may emerge out of the relative levels of motivation that different pairs of birds place on following conspecifics vs. following landmarks along their learnt route, with the pair that attaches more weight to landmarks being the one that emerges as leader. In addition, whatever the attributes that correlate with leadership, whether they arise from some combination of the two birds' individual preferences, or whether they are simply equivalent to the more "extreme" of the two individuals, are fascinating questions for future experiments.

In summary, we conclude that social bonds and a tendency to travel in groups can influence pigeons' behaviour during route learning and collective decision-making. Pairs develop into a unit through their shared experience of repeated joint flights. Furthermore, such relationships also affect collective decision-making in larger flocks, in that pairs are able to exert their influence as a unit (much like individual birds), form spatial sub-groups when flying with less familiar birds, and are more likely to accept compromise routes than birds in smaller flocks. Therefore, our results not only confirm theoretical predictions that the movement of a flock will depend strongly on its specific composition and on the nature of social relationships within it, but also imply, more broadly, the importance of past histories of joint decision-making among constituent members in shaping the behaviour of groups.

Chapter 4

Multiple-route learning and its influence on leader-follower relationships in homing pigeons

4.1 Summary

The following chapter explores whether and how learning multiple homing routes influences route development and leader-follower relationships. I performed an experiment using three release sites and three different experimental groups of pigeons. Each group had a distinct training protocol, defined by the sequence of releases from each of the three sites. I found that pigeons are able to establish and apply route memories successfully for more than one release site concurrently. They can effectively develop routes, even if they had recently homed from either one or two different release sites. Furthermore, I demonstrated that recency of route memories can predict leading/following behaviour meaning that birds were more likely to follow their conspecifics when homing from routes that they had learned last. This is most likely because more recently established routes are recalled better than those learned earlier. The results of my study broaden our understanding of route learning and open new possibilities for using manipulations of memory to study collective decision-making.

4.2 Introduction

The life of many social bird species centres at a focal point in the environment, the colony or roosting site. This is where group members rest during the night, interact frequently with conspecifics, and raise their offspring. The ability to return reliably to this home location from different places in the environment is of highest importance. Such homing abilities are present widely across different species, but have been most extensively studied in the pigeon, *Columba livia*. It is well known that pigeons are highly accomplished navigators, and can find their way back to their colony from sites hundreds of kilometres away and over unfamiliar terrain (for a comprehensive review, see Wallraff 2005). In recent years, through the use of miniature GPS devices, we have also greatly advanced our understanding of the navigational strategies that pigeons use in areas close to their breeding site. It has been shown that pigeons gradually come to rely on fixed routes when repeatedly homing from the same release site. Rather than approximating a straight line, these routes are often surprisingly tortuous and show a high level of inter-individual variation (Biro et al. 2004; Meade et al. 2005).

Such idiosyncratic homing routes develop in a distinctive manner. Pigeons show high levels of track variability and, therefore, also low levels of homing efficiency during the first few releases from a given site. Throughout the next flights homing efficiency increases while track variability decreases rapidly as pigeons begin to recapitulate routes within the same narrow flight corridor (Meade et al. 2005). These changes in track variability and homing efficiency as a function of time are thought to depend on increasing knowledge of the terrain, a view that is in line with the pigeons' capacity to store and subsequently recall and use spatial memories (Biro et al. 2003, 2004). Indeed, the existence of idiosyncratic routes in pigeons exposes the importance of spatial memory for successful homing. Under natural conditions, pigeons, alone or in small flocks, carry out daily foraging flights to locations distant from the colony, always returning to their central resting and breeding location (Rose et al. 2006). Thus, there is a demand for distinct allocentric spatial memories linked to the various routes: landmarks provide information about current position and are potentially stored together with information on directions and distances to travel before the next memorised cue (Biro et al. 2004). One intuitive question that follows is how efficiently pigeons can cope with the task of learning multiple homing routes. While simultaneous storage of multiple targets (such as feeding sites) and associated routes is likely to be the norm for pigeons – for example, foraging individuals can visit up to ten different locations per day (Rose et al. 2006) – we do not yet know how higher numbers of routes are handled within the scope of birds' learning and memory capacities.

Under laboratory conditions it has been shown that pigeons have a remarkable capacity to store and recall visual memories (Vaughan & Greene 1984; Cook et al. 2005). How does this ability relate to their visually mediated navigation skills? How does learning multiple homing routes influence the development of idiosyncratic routes and homing efficiency? It is reasonable to assume that relating a sequence of allocentric cues to a specific homing path will reduce the level of navigational uncertainty over consecutive post-displacement flights from the same site. Learning multiple routes simultaneously, however, may lead to a trade-off between the amount of spatial information that has to be handled and the efficiency with which such information can be gathered and subsequently applied during homing. Accordingly, the simultaneous development of multiple routes might slow down improvements in homing efficiency, and increase across-track variability.

In addition to their well-developed individual navigational skills, pigeons flying in a flock have the ability to reduce their uncertainty by relying on cues from co-navigating partners. Indeed, pigeons' social nature may allow them to profit from the movements of conspecifics. In the wild, pigeons often forage in flocks and they follow conspecifics on their way home or while flying to new foraging grounds (Goodwin 1983). In Chapter 2 I showed that less experienced homing pigeons tend to follow more experienced individuals. While the exact mechanisms underlying this effect remain to be elucidated, one consequence of following others is that it allows less informed pigeons to compensate for their relative deficiency in navigational information. Combining this finding with the hypothesis that learning multiple routes concurrently can lead to less efficient homing (effectively producing the equivalent of a less experienced bird), one could predict that a bird that has been challenged by having to remember more routes is likely to become a follower when flying with a bird that has had less demanding learning experiences.

With these ideas in mind, I examined the effect of concurrently learning to home from multiple sites on the development of idiosyncratic routes in pigeons. I constructed three different experimental groups of pigeons that were sequentially released from three different sites (Fig. 4.1). In the first group, pigeons were consecutively released several times from the same release site, R1. Once this training protocol was complete, they were released from a different site, R2, and exposed to the same training protocol there. Next, I repeated the entire procedure from a third, unfamiliar site, R3. The first group of pigeons was thus trained to fly home from three different sites experienced one at a time. By contrast, pigeons from the remaining two groups were trained from the three different sites in parallel, with releases alternating across the sites in either a consistent or semi-random order. I first asked whether and how these different training protocols influenced the speed and accuracy of individual route learning. Next, to examine the effect of the different training protocols on the pigeons’ probability to follow conspecifics, I released triplets of pigeons (composed of individuals from the above three groups) from each site, and quantified how far they deviated from their own, previously established route when flying with others.

4.3 Methods

4.3.1 Subjects and GPS device

I used 30 adult homing pigeons (*Columba livia*) bred at the Oxford University Field Station at Wytham (51^{0}46’58.34’’N, 1^{0}19’02.40’’W). All experimental birds were between 1 and 2 years old and had not participated in any previous experiment. However, birds normally had free access to the outside, which enabled them to perform spontaneous exploratory flights at any time. All subjects carried miniature GPS logging devices attached to their back by a small Velcro strip glued to clipped feathers. For every solo training flight, geographical longitude and latitude were logged by the devices at 1 Hz (i-gotU GT-120 Phototrackers, Mobile Action Technology, Inc., Taiwan; ~15 g). For every flock test flight, I recorded positional data at a frequency of 5 Hz (Qstarz BT-Q1300S, Qstarz International Co., Ltd., Taiwan; ~15 g).

4.3.2 Experimental protocol

The experiment was performed at three different release sites (see Fig. 4.1): Stonesfield (henceforth: R1; distance and direction to home: 10.4 km, 144°, respectively), Weston-on-the-Green (henceforth: R2; distance and direction to home: 10.2 km, 212°, respectively) and Beckley (henceforth: R3; distance and direction to home: 10.2 km, 264°, respectively). I used three different experimental groups of pigeons (henceforth: A-, B- and C-pigeons). Each group (N=10) had a distinct training protocol, as defined by the sequence of releases from each of the three sites. Training consisted of either (A) "sequential-site" training (i.e. completing training at one site before commencing training at the next), (B) "rotation" training (i.e. single releases cycling in a consistent order through R1, R2 and R3), or (C) "random-order" training (i.e. releases alternating across the three release sites in a semi-random order, Fig. 4.2a). By the end of training, each bird had performed 18 homing flights (6 from each site). A maximum of two releases were conducted per day. After completing training, I assigned birds to triplets, where triplets consisted of one bird from each treatment group (ABC), and released them together in the same composition from all three release sites in a randomised order (i.e. each triplet experienced a different release sequence). Due to the challenging training protocols, one bird of the A-pigeons (N=9) and three birds of the B-pigeons (N=7) did not return to the loft and therefore did not participate in the triplet releases. In order to reach a triplet sample size of 9, two birds from group B were assigned to two different triplets.

Figure 4.1 Satellite photograph of the topography around and the locations of the release sites: Stonesfield (R1), Weston-on-the-Green (R2) and Beckley (R3). The release sites are indicated by red dots, the home loft by a red x. Red bar indicates 1 km.

4.3.3 Data analysis

All analyses were conducted in Matlab (The Mathworks Inc.). Tracks were initially pre-processed by removing any point where the subject moved less than 0.5 m per second (which can be interpreted as a stationary bird), or any point after it reached within 250 m of the loft (to remove any circling around the loft, which birds often perform for extended periods prior to landing).

I explored how homing routes developed in the three treatment groups by focusing on homing efficiency and track variation. Homing efficiency is defined as the ratio between the straight-line distance between the release site and the loft, divided by the sum of the direct distances between the neighbouring positional fixes (i.e. total distance travelled). Also, when measuring the variation between tracks, I analysed only those positional fixes that lay outside a radius of 150 m from the release site, to remove initial circling behaviour (which was analysed separately, see below). Track variation refers to the accuracy with which a bird reproduces the same route repeatedly and is measured as the mean nearest neighbour distance between all constituent points of two tracks (Biro et al. 2007).

I separately analysed and compared orientation behaviour around the release site in the three treatment groups. To assess birds' accuracy in orientation during this early part of their journey, past studies have relied on "vanishing bearings" (the direction in which pigeons disappeared from visual contact at approximately 1.6-2.2 km from the release site; Wallraff 2005). Here I used GPS tracks to calculate for every consecutive pair of points along the track the birds' heading relative to the position of the loft. To estimate the directional accuracy of the orientation phase for each bird, I then calculated the mean of these bearings relative to the loft between the moment of release and when a bird's distance to the release point exceeded (and never again fell below) 2000 m using circular statistics (Batschelet 1981). Pigeons that took a straight course to the loft had a small mean angle, but birds that circled around and set off on a course not well directed towards the loft had a mean angle that deviated substantially from zero.

Pigeons received only six training flights from each release site meaning that variation between consecutive tracks remained relatively large (habitual routes are usually formed within six to ten flights, Meade et al. 2005; see also Fig. 2.3c, f and Fig. 3.1b). In order to assign leading/following behaviour reliably, I first calculated for each pigeon its mean routes from all three sites using the last four training tracks, applying the method developed by Freeman et al. (2011). Over 100 iterations, this method finds a mean path of 500 points that minimises the distance to nearest neighbouring points on the four original tracks, while ensuring that the distance between consecutive points on the mean path is more than 5 m. Next, I measured for each bird the deviation from its mean route while flying with its two partners by calculating the nearest neighbour distance between its triplet flight and its mean solo path. In order to compare the three different sites and groups, I expressed deviations as percentages of the range between the minimum (0%) and maximum (100%) nearest neighbour distance values recorded.

4.4 Results

4.4.1 Comparison of route learning as a function of training protocol

I first examined how the different training protocols and release sites (Fig. 4.2a) influenced homing efficiency. I used a linear mixed-effects model to test the effect of release number, training group and release site and their interaction on homing efficiency (binomial distribution). All data were analysed using R (R Development Core Team 2009) and the R packages lme4 (Bates & Maechler 2009) and languageR (Baayen 2008, 2009). Subject identity was included as a random factor (GLM: Akaike's information criterion, AIC=92.14). When examining homing efficiency as a function of training, I did not find site- or group-specific differences (see Table 4.1).

Table 4.1 GLMM analysis of the relationship between homing efficiency within each group, release site, and the respective interaction; showing estimates, standard error, z-values and probability (P).

	Estimate	**S.E.**	**z-value**	**P**
(Intercept)	-0.91	0.65	-1.41	0.16
Release	0.29	0.17	1.72	0.09
GroupB	0.26	0.90	0.29	0.77
GroupC	0.38	0.88	0.46	0.65
SiteR2	-0.02	1.71	-0.01	0.99
SiteR3	-2.41	2.66	-0.91	0.36
Release:GroupB	-0.16	0.18	-0.88	0.38
Release:GroupC	-0.20	0.18	-1.1	0.26
Release:SiteR2	-0.14	0.24	-0.60	0.55
Release:SiteR3	-0.05	0.24	-0.23	0.82
GroupB:SiteR2	0.36	1.94	0.19	0.85
GroupC:SiteR2	0.48	1.88	0.25	0.80
GroupB:SiteR3	3.05	2.83	1.08	0.28
GroupC:SiteR3	2.13	2.78	0.77	0.44
Release:GroupB:SiteR2	0.09	0.25	0.35	0.72
Release:GroupC:SiteR2	0.11	0.25	0.46	0.65
Release:GroupB:SiteR3	-0.03	0.25	-0.10	0.92
Release:GroupC:SiteR3	0.07	0.25	0.29	0.77

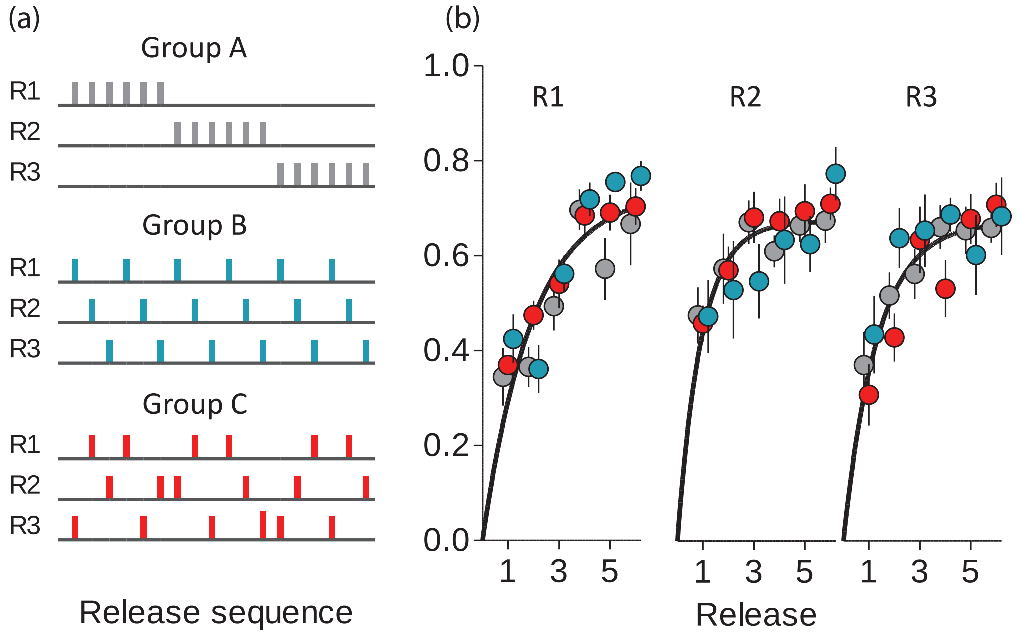


Figure 4.2 (a) Training protocol for the three experimental groups A, B and C. **(b)** Homing efficiency (treatment group mean ± S.E.M.) as a function of training at R1, R2 and R3 with the corresponding regression lines. Grey, blue and red circles/lines correspond to A-, B- and C-pigeons, respectively.

4.4.2 Effect of site change on homing performance

To investigate the impact of encountering a different release site compared to the previous release, I examined the link between release site change and the resultant changes in homing efficiency. Calculating how this measure changes as a bird experiences a change in release site will inform me about the level of navigational uncertainty faced upon release (averaged across site changes i.e. one value per bird). I examined the effect of release site change only for highly efficient tracks (i.e. using data from flights that led to efficiency values larger than 0.64, the average maximum from the different regression curves). This way I made sure that B- (N=7) and C-pigeons (N=10) had reached a comparable level of efficiency as the A-pigeons (N=9) at the time of release site change. By comparing the three different groups, I found that changing release site caused a larger efficiency decrease in the A-pigeons, as compared to the B- and C-pigeons (one-way ANOVA, $F_{(2,25)}=17.14$, $P<0.001$, Bonferroni post hoc, $P<0.05$; Fig. 4.3a).

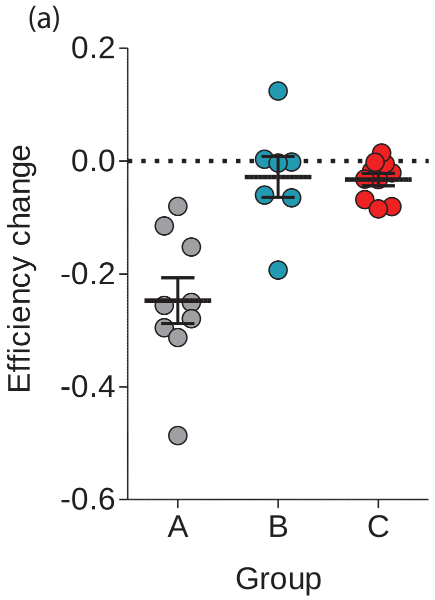


Figure 4.3 Scatter plot of the change in homing efficiency after change of release site for the three experimental groups. Grey, blue and red circles correspond to A-, B- and C-pigeons, respectively. Black bar with error bars indicate mean ± S.E.M.

In order to observe differences in the orientation phase, I measured a bird's directional accuracy within a radius of 2000 m around the release site. To compare the directedness of the orientation phase during the entire training (without being able to use repeated measures ANOVA on circular data), I first plotted for each individual the directional accuracy as a function of training (Fig. 4.4a-c), and then determined the total sum of these values (Fig. 4.4d). I found that C-pigeons exhibited the highest degree of orientation upon release, as the sum of directional accuracy is significantly larger than that of group B (unpaired t-test with Welch's correction, t_{12}=2.20, P=0.048). I found no differences between groups A and B (unpaired t-test with Welch's correction, t_{10}=0.54, P=0.60), and a borderline non-significant difference between groups A and C (unpaired t-test, t_{17}=2.10, P=0.051; Fig. 4.4d).

4.4.3 Route development

Next, I explored whether the three groups differed in their ability to develop idiosyncratic routes. I measured the nearest neighbour distance between consecutive training tracks from the same site in order to estimate the birds' ability to recapitulate their previous flights. I did not find differences between the three groups at any of the three release sites (Two-way repeated measures ANOVAs: R1: $F_{(2,92)}$=0.85, P=0.44; R2: $F_{(2,92)}$=1.31, P=0.29; R3: $F_{(2,92)}$=1.16, P=0.33). In order to compare the level of route fidelity throughout the training between the three groups, I determined the total sum of all values (Fig. 4.4e-g). I did not find any differences between the three different groups (Kruskal-Wallis test, K=2.48, P=0.29; Fig 4.4h).

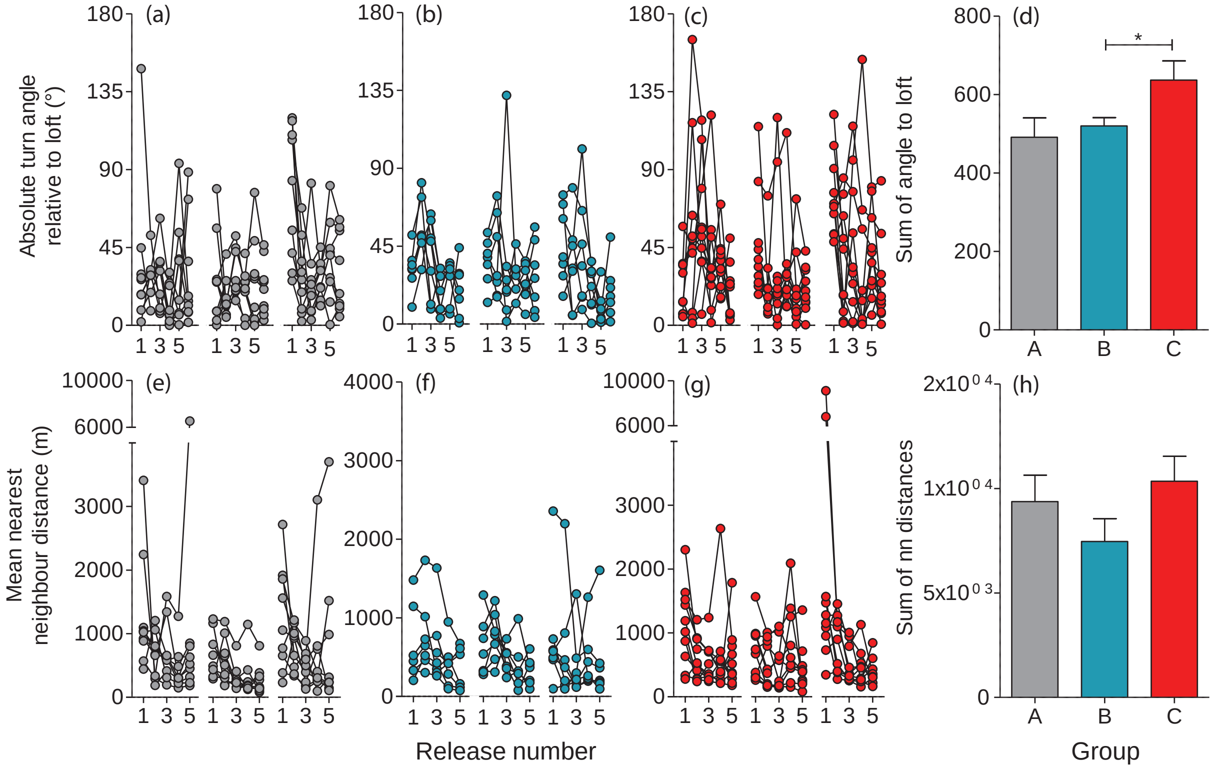


Figure 4.4 (a-d) Orientation behaviour upon release and **(e-h)** track variation for A-, B- and C-pigeons. Orientation behaviour is measured as a bird's directional accuracy within a radius of 2000 m around the release site. Track variation is measured as the nearest neighbour distance between consecutive training tracks. The three release sites are shown separately. **(d, h)** Mean ± S.E.M. of total sum of values of a-c and e-g. Grey circles/bars correspond to A-pigeons; blue and red circles/bars correspond to B- and C-pigeons, respectively. Asterisk shows $P<0.05$.

4.4.4 Leading/following behaviour

Finally, I examined how past experiences with multiple release sites influenced a pigeon's leading/following behaviour during flock flights. I measured the similarity between the flock (triplet) flight of each bird and the mean path of its last four solo training flights at all three release sites (see Methods). I found that release site had a significant effect on leading/following behaviour (Two-way repeated measures ANOVA, $F_{(2,46)}=4.79$, $P=0.018$, Fig. 4.5). Specifically, the three groups differed in their propensity to home along their partners' routes only at R1 (Friedman test, Q=7, P=0.030), with A-pigeons deviating significantly more from their own route than C-pigeons (Dunn's Multiple Comparison Test, P<0.05, see also Table 4.2).

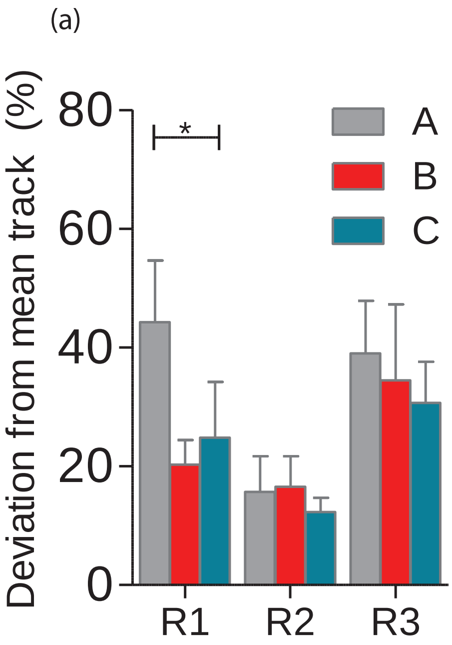


Figure 4.5 (a) Mean deviation (± S.E.M.) from mean track measured as average nearest neighbour distance between mean path and triplet flight for A-, B- and C-pigeons at three release sites. Measures are expressed as percentages of the range between the minimum (0%) and maximum (100%) values recorded. Asterisk shows P<0.05

Table 4.2 presents the results of the leadership analysis (identifying the bird that flew closest to its mean path during triplet releases; see Methods) for A-, B- and C-pigeons at the three release sites. Here, I disregarded flights where triplets split up during homing (triplets were considered to have split when the instantaneous distance between at least two birds increased above 200 m and never fell below this threshold again). While homing from R1, A-pigeons followed the routes of their partners: none of the homing routes of the 8 triplets analysed lay closest to the routes of the A-pigeons (P=0.03, two-tailed G-test, Table 4.2). However, at R2 and R3 I did not find any differences between the three different training groups (see Table 4.2).

Table 4.2 Leading/following behaviour at R1, R2 and R3. I identified and counted the bird of the triplet that flew closest to its mean path at the three release sites. Bottom column shows results of two-tailed G test.

	R1	R2	R3	TOTAL
A	0 (0)	55.6 (5)	22.2 (1)	26.9 (6)
B	37.5 (3)	33.3 (3)	55.6 (5)	42.3 (11)
C	62.5 (5)	11.1 (1)	22.2 (3)	30.8 (9)
Two-tailed G-test	G=6.93; P=0.03	G=2.91; P=0.23	G=2.91; P=0.23	G=1.51; P=0.47

4.5 Discussion

I examined how pigeons learn to home from multiple release sites simultaneously, and how such training influences their probability of leading or following conspecifics with different learning histories. I found that despite the different training protocols, all three experimental groups successfully established and applied route memories. Overall homing efficiency increased throughout training regardless of the release site location. Past studies found that although a pigeon's homing performance improves slightly when released repeatedly from the same site, the effect of general homing experience is stronger than site-specific experience. The more flights they perform, irrespective of the familiarity of the release site, the more efficient (higher speed, shorter flight durations) their homing flights become (Hoffmann 1959; Wallraff 1959). Interestingly, my results did not match these previous findings: the rate of increase in efficiency of the groups did not differ between the three release sites. Interestingly, the site-specific developments also indicate that the B- and C-pigeons effectively applied route memories from past flights, even if they had recently homed from either one or two different release sites.

The most widely accepted concept characterising the mechanism of homing is the "map and compass" model, which depicts homing as consisting of two sequential and independent steps (Kramer 1961). The first step (the "map" component) establishes the geographic position of the release site relative to home, whereas the second step (the "compass" component) consists of identifying the deduced homing direction. While being exposed to changing release sites, pigeons might experience added difficulties in determining their location in the field. It has been shown that previous homing flights can affect pigeons' vanishing bearings, in the sense that they may induce birds to fly in the same compass direction that allowed them to home from the previous release point (Michener & Walcott 1967; Wallraff 1974). In the present study, I clearly demonstrated that B- and C-pigeons became less susceptible to the influence of a release site change compared to the A-pigeons. One possible explanation is that these two groups learned to anticipate the altered sets of cues and landmarks upon release thereby coping with the changing sites more efficiently. Alternatively, B- and C-pigeons may be able to recognise the new release sites faster as they had more opportunities to memorise them compared to A-pigeons, which encounter the new site for the first time.

C-pigeons that experienced the most unpredictable training protocol showed the highest level of orientation upon release. Several studies showed that providing pigeons with a five-minute preview of the landscape surrounding the release site prior to release improves the birds' homing times (Braithwaite & Guilford 1991; Burt de Perera et al. 1997; Gagliardo et al. 2001). Interestingly, such positive effect of the visual treatment is limited to the first kilometre around the release site (Biro et al. 2002), indicating that birds can process navigational cues before being released and benefit from those through being able to more quickly assume a homeward route than birds not given preview. This is further evidenced by the finding that denying pigeons such visual preview leads to more circling behaviour (Biro et al. 2002). Due to the training protocol, C-pigeons have no possibility to predict the new release site. This irregularity can be compared to not having advance visual information. In comparison to the two groups that experienced more predictable training protocols and potentially benefit from prior information about the next release site, C-pigeons spent more time exploring the release sites to gather information about their position.

All three groups exhibited a similar increase in route fidelity indicating that pigeons are able to store several sequences of allocentric cues concurrently, which reliably guide them back to the loft. However, since I released pigeons only six times from each of the release sites, I cannot make clear statements concerning the comparability of the final level of accuracy with which the routes of the three groups are recapitulated. After only six releases from a single site, the variation between tracks is still relatively high (Meade et al. 2005). This means that if there are limitations on pigeons' spatial memory in terms of accurately storing and recalling a large number of landmarks, these might become evident only after further releases. Past studies on route recapitulation released birds up to 24 times from a single release site and observed their highly stereotypical homing paths (Meade et al. 2005). It might be more demanding to recreate accurately the bends and turns of several of such routes, rather than only of one route at a time. By analysing high fidelity areas of trajectories, Mann et al. (2011) identified habitual route waypoints where multiple tracks converge over salient visual features. They revealed that a bird requires only a small number of such waypoints (median value of seven) to memorise its route. Considering that under laboratory conditions pigeons can memorise more than a thousand pictorial stimuli (Vaughan & Greene 1984; Cook et al. 2005), I can assume that the limit of a pigeon's spatial memory lies beyond three homing routes. It remains for future studies to reveal the limits of pigeons' spatial memory capacities, and whether the order of learning multiple release sites (like the different training protocols of A-, B- and C-pigeons) influences track variability.

Next, I explored how the different training protocols influenced a bird's probability of leading or following its conspecifics. I found that leading/following behaviour was influenced by the recency of the route memories, as A-pigeons were more likely to follow others at the site they encountered first (and therefore the site they had least recently visited). Few experiments have tried to explore individual features that predict leadership in pigeons. It has been shown that the fidelity with which highly experienced individuals recapitulate their routes can partly predict leadership. More specifically, birds that exhibit higher peak route fidelity when flying solo are more likely to emerge as leaders when released with other birds (Freeman et al. 2011). Furthermore, in Chapter 2 I showed that less experienced homing pigeons tend to follow more experienced individuals, suggesting that following behaviour may be caused by an imbalance between pigeons in terms of the amount of navigational information they possess. In the present study, I detected that A-pigeons were more likely to follow the homing path of their conspecifics, but only at the site that was learned earliest. The training protocol of A-pigeons was such that they completed learning R1 before commencing training at R2, then completed at R2 before commencing at R3. A-pigeons' propensity to follow others at R1, but not at R2 and R3, may suggest that a deterioration in memory associated with less recent visits to a site may effectively turn birds into "less experienced" flock members. This finding can be compared to the enhanced recollection of the last objects in a list of items, known as the recency effect, documented in many species including pigeons (Wright et al. 1985). Such effect, together with the primacy effect (superior memory for the first items of a list), has been studied extensively in the laboratory using serial-probe-recognition tasks in human and non-human primates, rodents and pigeons. Wright et al. (1985) found primacy and recency effect in pigeons depending on the length of the retention interval. Short and long intervals produced recency and primacy effects, respectively (Wright 1994). A-pigeons followed the routes of their partners more frequently at R1 indicating better route recapitulation of those routes that were learned last (recency effect). B- and C-pigeons did not show such an effect, because they received training from all three sites at the same time. This means that their route memories had the same recency from all three sites. Taken together, the results indicate that the recency of a pigeon's route memories can be added to the list of individual features that influence leading/following behaviour in these birds.

Considering that primacy effects are usually indexed as long-term memory, it would be interesting to observe the leading/following behaviour of the A-pigeons at R1 after a longer retention interval to test for any potential changes.

In summary, my study exposed a pigeon's capacity to store, recall and eventually apply spatial memories from multiple sites in parallel. Furthermore, I demonstrated that recency of route memories can predict leading/following behaviour, likely due to the fact that lastly established routes are recalled better than those learned earlier. Using comparatively natural conditions and free-flying animals, I was able to demonstrate the recency effect, a phenomenon which so far has mainly been observed in the laboratory. The results of my study broaden our understanding of route learning and open new possibilities for studying other well-known learning and memory phenomena like the primacy and interference effects on navigating pigeons.

Chapter 5

Robustness of flight leadership relations in pigeons

N.B. Below I present this chapter in manuscript format. This manuscript has been published as:

Flack, A., Ákos, Z. Nagy, M., Vicsek, T. & Biro, D., 2013. Robustness of flight leadership relations in pigeons. Animal Behaviour

5.1 Summary

Collective animal movements produce spectacular natural phenomena that arise from simple local interactions among group members. Flocks of homing pigeons provide a useful model for the study of collective motion and decision-making. During homing flights, flock members are forced to resolve potentially divergent navigational preferences in order to stay together and benefit from flying in a group. Recent work has demonstrated that some individuals consistently contribute more to the movement decisions of the flock than others do, thereby generating stable hierarchical leader-follower networks. Yet, what attributes of a flying pigeon reliably predict leadership remains an open question. Here we examine the flexibility of an individual's hierarchical leadership rank (i.e. its ordinal position when flock members are ranked according to the average time differences with which they lead or follow others) as a function of changes in its navigational knowledge. We manipulate already established hierarchical networks in three different flocks, by providing certain individuals with additional homing experience. We find that such training does not consistently lead to an increase in birds' leadership ranks, and that, in general, the nature of leader-follower interactions between trained and untrained birds remains unaffected. Thus, leadership hierarchies in pigeon flocks appear resistant to changes in the navigational knowledge of a subset of their members, at least when these changes are relatively small in magnitude. We discuss the implications of our results in light of the potential benefits of structural stability in decision-making networks.

5.2 Introduction

A flock of birds circling over its roosting site is a magnificent aerial display. Theoretical work suggests that these highly synchronised and coordinated movements arise from simple interaction rules, without the need for centralised organisation (Vicsek et al. 1995; Couzin et al. 2002; Vicsek & Zafeiris 2012). Nonetheless, we are only just beginning to understand how rules implemented in models relate to those applied by animals. Progress in digital image processing and high temporal resolution tracking has allowed the inference of interaction rules in bird and fish species (e.g. Ballerini et al. 2008; Lukeman et al. 2010; Herbert-Read et al. 2011; Katz et al. 2011). Furthermore, in line with researchers' increasing interest in the role of inter-individual differences in shaping interactions (Conradt et al. 2009; Nakayama et al. 2012a), it has been found that homing pigeon flocks are hierarchically organised, where individuals contribute with different weights to the movement decisions of the flock (Nagy et al. 2010). Such hierarchical networks consist of transitive leader-follower relationships in which birds consistently copy the directional choices of individuals above them in the hierarchy, while being copied by those lower in rank. Little is known about what attributes of a flying pigeon can reliably predict leadership in flocks, although it has been suggested that leadership may be related to individual navigational efficiency (Nagy et al. 2010).

Empirical studies have identified a variety of traits (e.g. age, experience, social rank, and motivation; (McComb et al. 2011; Reebs 2000; King et al. 2008; Nakayama et al. 2012b) that can modify an individual's propensity to initiate a movement or activity change. Along similar lines, a model by Conradt et al. (2009) suggests that group movements are directed by those specific individuals for whom reaching the goal is most crucial. Several empirical studies support the findings of these models. For example, fish that are deprived of food are more likely to take front positions in shoals than those that are satiated (Krause et al. 1992), and lactating zebra females (*Equus burchellii*) initiate movements more frequently than those without dependent calves (Fischhoff et al. 2007). Furthermore, consistent leadership in group movements might be supported by the enhanced knowledge of certain individuals. In several species, including golden shiners, bottlenose dolphins and meerkats, it has been shown that better informed individuals can change the action of group-mates, using their greater knowledge about their environment (Reebs 2000; Lusseau & Conradt 2009; Bousquet & Manser 2011).

With respect to the context of collective motion, recent work has demonstrated that navigationally less experienced birds are likely to follow more experienced conspecifics (Flack et al. 2012). More specifically, the larger the difference in homing experience between two partners, the higher the likelihood that the more experienced bird will emerge as the leader. Additionally, in highly experienced birds the accuracy with which individuals recapitulate previously established idiosyncratic routes when flying solo has been suggested to predict relative influence when flying in pairs (Freeman et al. 2011), suggesting that some aspect of navigational certainty (or perhaps inflexibility) may promote leadership. These findings raise new questions about how variations in navigational knowledge possessed by individual members influence group dynamics in pigeon flocks. If a bird's position in the hierarchy correlates positively with its own navigational experience, we should be able to manipulate the network by providing selected individuals with the opportunity to acquire additional spatial knowledge. Here we evaluate whether it is indeed possible to alter individuals' ranks attained during flock homing flights by providing them with additional homing experience before re-testing them with their group mates.

5.3 Methods

5.3.1 Subjects and experimental procedure

We used 30 adult homing pigeons (*Columba livia*) bred at the Oxford University Field Station at Wytham (51°46’58.34’’N, 1°19’02.40’’W). They were kept in a social group of ca. 120 pigeons inside two lofts. Birds normally had free access to the outside, except on the days when the experiments were conducted. Food (a commercially available multigrain mixture), water, minerals and grit were provided ad libitum throughout the study. All experimental birds were between 4 and 8 years old, and had homing experience but had never visited the release site used in the current study. They carried miniature GPS logging devices (see below) attached to their back by a small Velcro strip glued to clipped feathers. All releases were performed from Radford (distance and direction to home: 15.7 km, 151°, respectively). The experiment had three phases. First, we trained three flocks of 10 birds (designated groups A, B and C), by releasing all 10 birds of a flock simultaneously at the release site (Phase I: group training). Each flock performed eight group training flights, with a maximum of two releases per day. We then calculated for each group a leadership hierarchy among flock members using the methods described in (Nagy et al. 2010). In Phase II (solo training), we allowed three randomly chosen individuals from each flock to gain additional homing experience by performing 10 individual flights from the same site (one of these nine birds was lost during its 8th individual training flight, and therefore did not participate in the third phase for group C). Finally, in Phase III (group tests), we released each original flock six more times in order to evaluate any changes in the hierarchy’s structure – in particular, whether the additional homing experience resulted in any changes in the ranks attained by the three individuals that had received additional solo training. Phase I was completed in 10 days, Phase II in 6 days, and Phase III in 3 days, with releases conducted on all consecutive days when weather conditions were favourable (dry and with winds<7 m/s).

5.3.2 GPS device and data handling

The GPS device was based on a commercially available product (Gmsu1LP, from Global Top), weighed 13 g, and was capable of logging time-stamped longitude, latitude and altitude data at 10 Hz. The geodetic coordinates provided by the GPS were converted into x, y and z coordinates using the Flat Earth model. These coordinates were smoothed by a Gaussian filter (σ=0.2 s), and we used a cubic B-spline method to fit curves onto the points obtained with the 0.1 s sampling rate. Only the x and y coordinates were used for analysis (average number of data points recorded per bird was 176107 (S.D.=15423)). In independent tests, using the devices in fixed relative positions to each other, the deviation between real and measured distance was 0.00 ± 0.34 m (mean ± .S.D.). This degree of accuracy is sufficient for calculating directional correlation delay functions that characterise relations among the birds' motion (see Figure 5.A1 and Appendix for further details).

5.3.3 Data analysis

To evaluate the effect of training on homing performance, we calculated homing efficiency and homing time for each flight. Efficiency was measured by dividing the straight-line distance between the release site and the loft with the actual distance travelled by the bird to reach home. Homing time was the length of time that elapsed between release and the bird reaching a radius of 250 m from the loft. It should of course be noted that the two measures are not independent of each other, although the relationship between them can vary to some extent as a function of the bird's speed. In addition, to measure the trained birds' change in homing performance, we calculated the difference in efficiency and homing time between the average of the first two and the average of the last two solo training flights in Phase II.

To determine leader-follower relations inside the flock, we calculated the directional correlation delay for each pair of birds i and j ($i \neq j$). The directional correlation delay of a pair is $C_{ij}(\tau) = \langle \vec{v}_i(t) \cdot \vec{v}_j(t+\tau) \rangle_t$, where $\vec{v}_i(t)$ is the normalised velocity of bird i at time t and $\vec{v}_j(t+\tau)$ is the normalised velocity of bird j at time $t + \tau$. That means we calculated the cross-correlation $C_{ij}(\tau)$ between the time series of movement directions for pairs of individuals (i, j) after shifting the time series of individual j by τ seconds (therefore $C_{ij}(\tau) = C_{ji}(-\tau)$: the cross-correlation for pair (j, i) after shifting the time series of individual i by $-\tau$ seconds). We then determined the maximum value of the $C_{ij}(\tau)$ correlation function at τ_{ij}^*, $C_{ij}(\tau_{ij}^*)$. We identified the corresponding τ_{ij}^* as the directional correlation delay time. τ_{ij}^* values focus on the relationship between specific pairings of individuals while ignoring hierarchy changes caused by other flock members. Negative τ_{ij}^* values mean that the flight directional changes of bird i fall behind that of bird j, and can thus be interpreted as a case of j leading (or i following given that $\tau_{ij}^* = -\tau_{ji}^*$). In order to compare relationships among flock members before and after the solo training we focused on pairwise τ_{ij}^* values, averaged across pre- and post-training separately. For every specific pair ij, we averaged those τ_{ij}^* values that exhibited a $C_{ij}(\tau_{ij}^*)$ larger than 0.95. Because the relationships between specific pairings are non-independent data points, we used the number of individuals as our sample size for correlations between pre- and post- training τ_{ij}^* values. Only edges with values higher than 0.02 were retained. We chose this conservative value as our threshold to reduce the amount of erroneously introduced edges while ensuring that there is no loss of information.

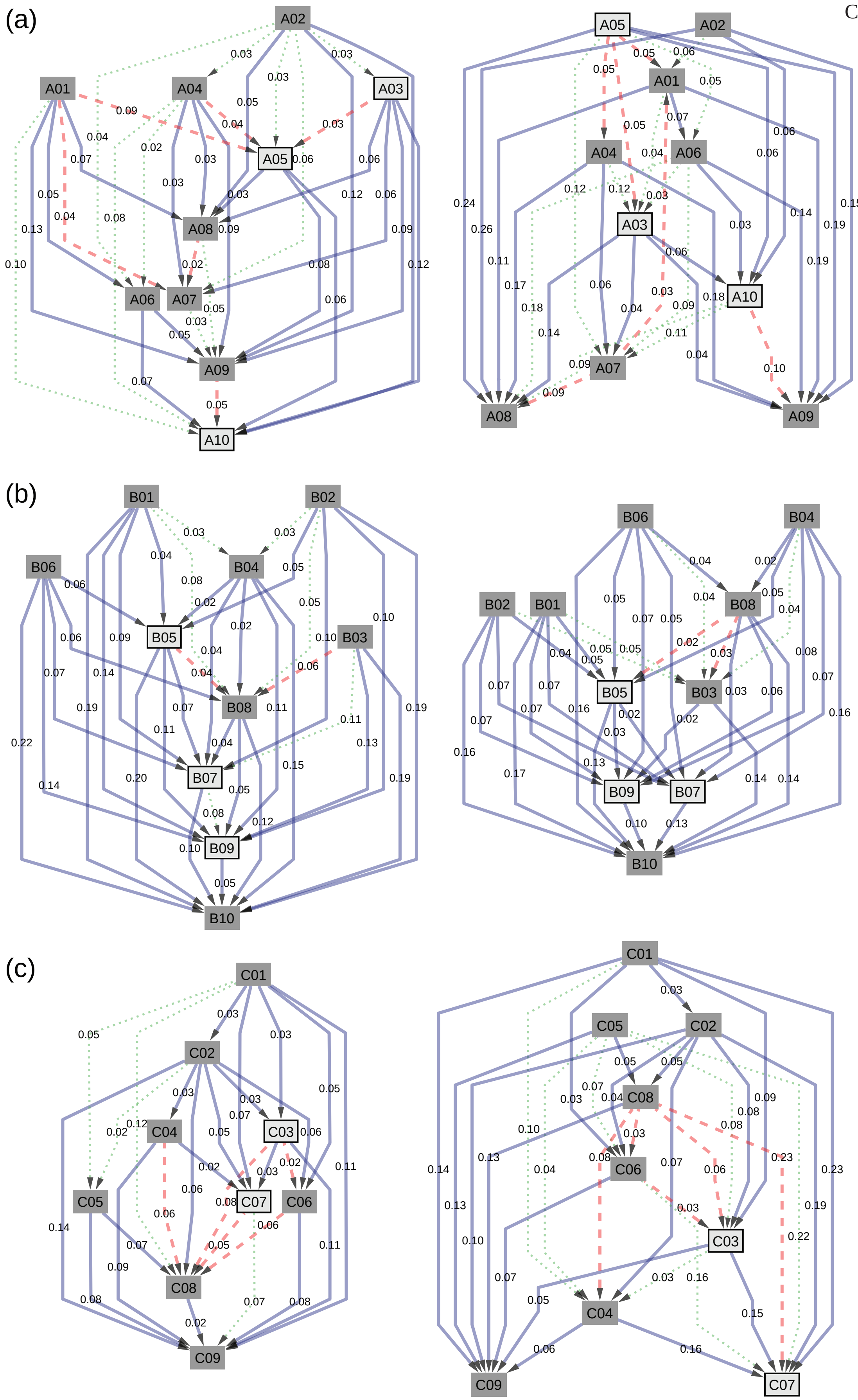
For the calculation of the $C_{ij}(\tau)$ correlation function, we included only those pairs of data points from birds i and j where the two birds were a maximum of 100 m apart (i.e. $d_{ij}<100$ m). We chose this threshold based on the distributions of inter-individual distances (see Fig. 5.A2). A bird's closest neighbour was less than 10 m away in 71% of all recorded data points (see inset of Fig. 5.A2). However, to be able to detect potential interactions between more distant flock members we used a threshold of 100 m, although only few data points fall into this bin category.

By averaging the τ_{ij}^{*} values of bird i and the rest of the flock, we obtained a second measure, denoted τ_i. Because of full transitivity of each hierarchy, this measure allowed us to resolve fully the hierarchical order among all group members (defined as hierarchical rank). On two occasions, the τ_i-value was 3.4 times higher than the standard deviation of all values (see Fig. 5.A3); in these cases we removed the two birds from these particular flock flights and re-ran the analyses without them (see Table 5.A1 for the results including the outliers). We calculated for each bird the average of the τ_i values for the flights before (Phase I, 8 flights; $\bar{\tau}_i^{pre}$) and after (Phase III, 6 flights; $\bar{\tau}_i^{post}$) the individual training period. $\bar{\tau}_i$ values have similar properties to linear ranks (positive and negative values correspond to leading and following behaviour, respectively). We tested our data for normality using Kolmagorov-Smirnov test ($P<0.05$). We used Pearson's correlations for samples with equal variances (F test for equal variance), and Spearman's correlations for those with unequal variances.

5.4 Results

Following the group releases of Phase I, we identified fully transitive hierarchies in each of our three flocks (Fig 5.1, top row). Besides confirming the findings of (Nagy et al. 2010), this initial result also provided the necessary premise for Phases II and III.

Figure 5.1 Pre- and post-training hierarchical networks of three flocks, generated using τ_{ij}^{*} values. Rectangles correspond to individual birds; trained birds are shown with black borders. The three-digit alphanumeric codes indicate in which group the subject was tested (A, B or C) and its rank during the pre-training flights. Edges indicate leader-follower relations pointing from the leader to the follower (only edges where $\tau_{ij}^{*} \geq 0.02$ are shown). Edges that have the same directionality in pre- and post-training networks are indicated as thick blue lines; those that undergo a change in direction between pre- and post-training are shown as red lines; those that appear in only one of the networks are shown as dotted green lines. Numbers on edges correspond to τ_{ij}^{*}. (a), (b) and (c) Pre-training (left column) and post-training (right column) hierarchies of groups A, B and C, respectively.


(a)
A01
A02
A03
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(b)
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B05
B06
B07
B08
B09
B10
(c)
C01
C02
C03
C04
C05
C06
C07
C08
C09

First, we evaluated the effect of the training (flock and solo flights) on homing performance, by examining homing efficiency and homing time over the course of Phases I, II and III (Fig. 5.2a, b). Birds improved in both measures of homing performance during the flock releases of Phase I. Furthermore, during Phase II the solo trained birds increased their efficiency by an average of 0.13 (S.D.=0.06, difference between the average of the first two and the average of the last two solo training flights in Phase II, Fig. 5.2c) and decreased their homing time by -343.4 s (S.D.=209.0 s, Fig. 5.2d). Both these changes differed significantly from zero (one-sample t-tests, efficiency: t_7=5.77, P<0.001; time: t_7=4.65, P=0.002).

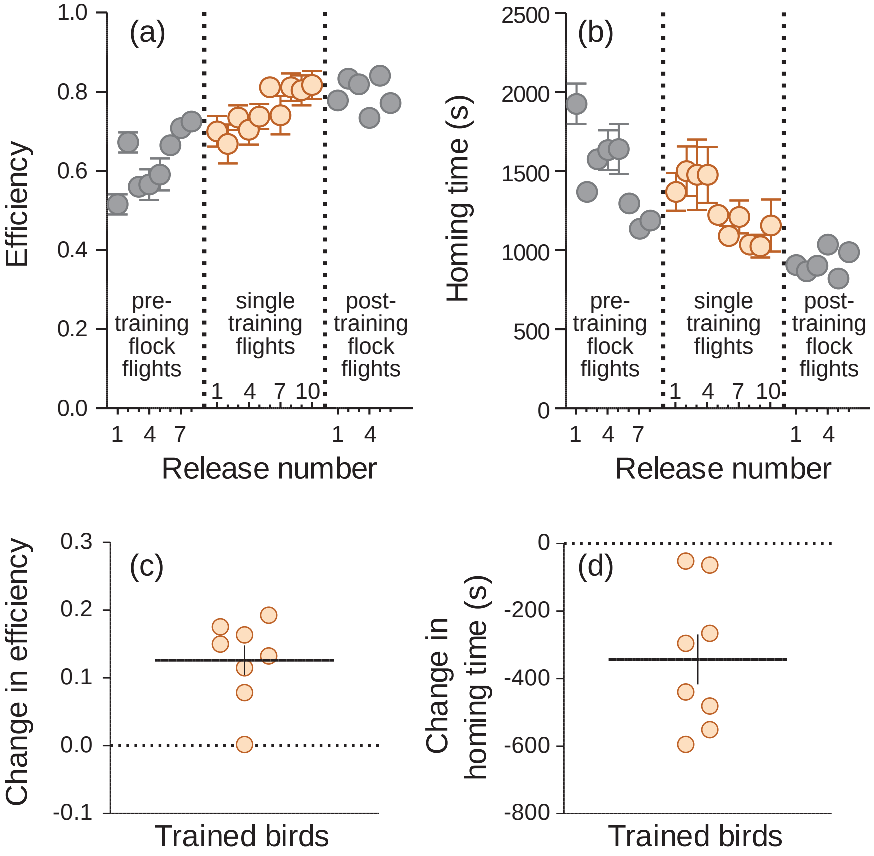


Figure 5.2 (a, b) Homing efficiency (mean ± S.E.M., **a**) and homing time (mean ± S.E.M., **b**) as a function of release number. Data from all groups were averaged according to release number. Grey circles indicate Phases I (N=30) and III (N=29). Inset shows trained individuals in Phase II (N=8). **(c, d)** Changes in homing efficiency **(c)** and homing time **(d)** during solo flights by trained individuals. Black line corresponds to mean (± S.E.M.).

We next used data from Phase III to measure the stability of the hierarchies by comparing the relative ranks of the untrained birds before and after solo training ($\bar{\tau}_i^{post}$ vs. $\bar{\tau}_i^{pre}$). We found a positive correlation between $\bar{\tau}_i^{pre}$ and $\bar{\tau}_i^{post}$ (Pearson's correlation, group ABC together: r_{20}=0.72, P<0.001, Fig. 5.3a, group A: r_6=0.80, P=0.030, group B: r_6=0.87, P=0.011, group C: r_6=0.69, P=0.090), which indicates the persistence of a robust hierarchical order among untrained flock members. However, the ranks of the trained birds exhibited variability: we found no correlation between $\bar{\tau}_i^{pre}$ and $\bar{\tau}_i^{post}$ (Pearson's correlation, r_7=-0.08, P=0.846, Fig. 5.3a), with some birds experiencing a rise and others a drop in $\bar{\tau}_i$. Also, the change in the birds' relative rank did not correlate with their changes in homing performance (Pearson's correlation, efficiency: r_7=0.247, P=0.556; time: r_7=0.072, P=0.866).

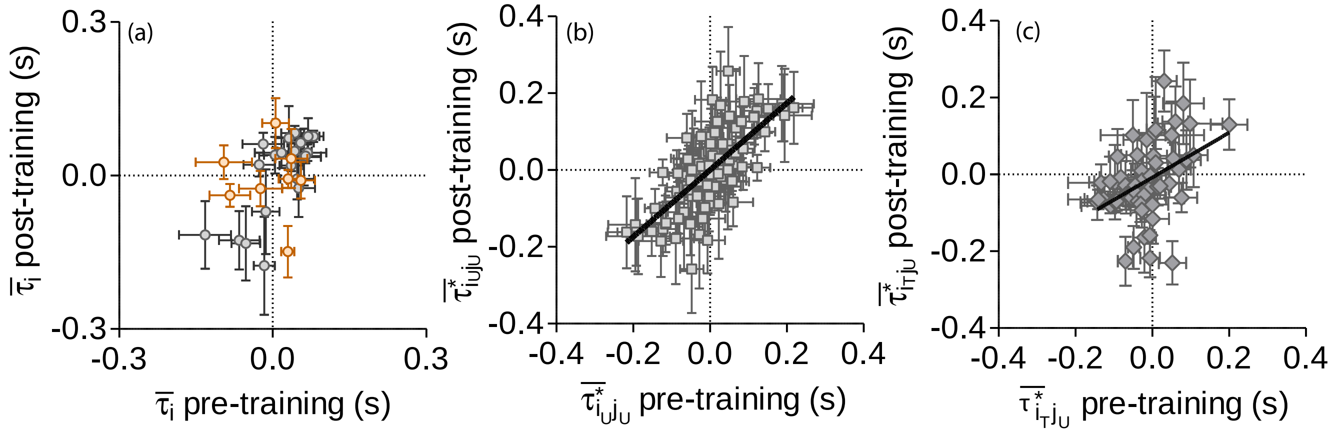


Figure 5.3 Relationship between τ before and after individual training flights (mean ± S.E.M.) (a) $\bar{\tau}_i^{post}$ as a function of $\bar{\tau}_i^{pre}$ for solo-trained (orange circles) and untrained individuals (light grey circles). (b-c) averaged τ_{ij}^* after individual training as a function of averaged τ_{ij}^* before individual training for untrained-untrained pairings (b) and trained-untrained pairings (c).

We further investigated the changes the hierarchies underwent using pairwise directional correlation time (τ^{*}_{ij}). We observed a positive correlation between pre- and post-training for the untrained birds when pooling the data from the three flocks (Spearman's correlation, group ABC together: r_{20}=0.66, P=0.001, Fig. 5.3b), further confirming the stability of their relationships over time and over repeated interactions. However, when examining the three flocks separately, we do not find a positive correlation in two cases which might be due to the small sample size of each flock (Spearman's correlation, group A: r_{6}=0.67, P=0.098, Pearson's correlation, group B: r_{6}=0.92, P=0.004, group C: r_{6}=0.62, P=0.138). Moreover, pairwise $\tau^{*}_{i_T j_U}$ values enable us to compare the changes in pairs consisting of a trained (i_T) and an untrained (j_U) individual. The relationship between trained and untrained pigeons also remained stable, as evidenced by the positive correlation between their pre- and post-training $\tau^{*}_{i_T j_U}$ (Spearman's correlation, r_{28}=0.44, P=0.018, Fig. 5.3c). Despite the extra experience gathered by certain flock members, their positions in the hierarchy relative to untrained birds showed, on average, no improvement: the difference in directional correlation delay times in trained-untrained pairs before and after the individual training was on average 0.00 s (S.E.M.=0.01 s) and did not differ significantly from zero (one-sample t-test, t_{55}=0.005, P=0.996). Thus, although the overall hierarchical rank of the trained individuals changed slightly, the direction of these changes was not consistent. In addition, the changes were small enough that across the flock as a whole the position of the untrained birds in relation to trained flock members remained mostly unchanged. The extra training had an even smaller effect on the positions of the untrained birds relative to each other (Fig. 5.1). Separate examination of the three flocks showed that in group A two of the trained birds improved their relative ranks and one maintained its position (the average change in τ^{*}_{ij} before and after training, A: $\Delta\tau^{*}_{ij}$=0.06s (S.E.M.=0.02s), one-sample t-test, t_{20}=3.34, P=0.003,

Fig. 5.1a). In group B, no clear change was found (B: $\Delta\tau_{ij}^{*}$=0.02 s (S.E.M.=0.01 s), one-sample t-test, t_{20}=1.77, *P*=0.09, Fig. 5.1b), whereas in group C the trained birds decreased their relative ranks C: ($\Delta\tau_{ij}^{*}$=-0.11 s (S.E.M.=0.02 s), one-sample t-test, t_{13}=5.30, *P*<0.001, see Fig. 5.1c). An additional statistical analysis, making use of the full dataset rather than per-bird averages as above, further confirmed the robustness of the measured hierarchies (see Appendix).

5.5 Discussion

Previous research has shown that group decision-making in pigeon flocks is hierarchically organised, with certain individuals consistently contributing with relatively more weight to movement decisions than others (Nagy et al. 2010). Here, we re-confirmed the existence of such hierarchical flight dynamics, demonstrating distinct leadership hierarchies in three separate flocks during repeated homing flights. Moreover, we showed that additional solo training given to specific group members did not affect the overall hierarchy of the flock: although trained birds increased their navigational efficiency during these solo flights (thus suggesting that they had gained additional navigational knowledge), this increase in efficiency was not accompanied reliably by improvement in their hierarchical position. Overall, pairwise leader-follower relations between flock members remained stable, and thus the hierarchies themselves remained robust. We use the term “robustness” to mean that the inter-individual relationships – and hence the whole systems of hierarchical leadership networks we observed – were resistant to perturbations (introduced here in the form of experimentally changing the knowledge of certain flock members). Our results imply that leadership ranks within flocks do not directly relate to individual navigational experience, but that some other intrinsic property, or a combination of several properties, defines the organisation of the hierarchy.

Two possible mechanisms might allow the establishment and maintenance of robust flight hierarchies. The first requires recognition of conspecifics' morphological, physiological or behavioural features that determine leadership ranks, and may be complemented by individual recognition and memory of previous interactions. Flock members may have fixed leader-follower relationships that are based on dominance (King et al. 2008), familiarity (Flack et al. 2013) or individual affiliations (Jacobs et al. 2011b) and are consequently maintained across multiple flights. Alternatively, hierarchies might derive from individuals reacting in consistent ways to other group members' movements, without necessarily identifying them or their status. Each individual may respond to flockmates in a way that is defined by its own specific features, such as experience or motivation. This would allow leadership to emerge passively as a consequence of simple interaction rules (Vicsek et al. 1995; Couzin et al. 2002). In other species these responses have been described to vary in line with multiple factors. For example, fish might emerge as leaders depending on their level of satiation (Nakayama et al. 2012b), or experience with a foraging task (Reebs 2000). We know that in pigeons individual morphological differences like body mass do not act to structure networks (Nagy et al. 2013). Yet, on which set of individual traits flight hierarchies are based remains open.

The fact that we found no consistent effect of the extra training on birds' leadership ranks is a somewhat surprising result, given previous suggestions of the effect of navigational experience and skill on leadership (Nagy et al. 2010; Freeman et al. 2011). One possible explanation is that solo and group homing flights affect birds differently meaning that flying in a flock might overshadow individually gained navigational advantages. In order to explore the effect of experience on leadership hierarchies further, one would need to test whether giving certain flock members additional group training flights will cause changes in an already established leadership hierarchy. Also, the trained birds' increase in experience might not have been large enough to induce changes in the organisation of the flock. Prior to the solo training, each subject had already performed eight flock homing flights and reached high, asymptotic levels of homing efficiency (Meade et al. 2005). Even though solo training did improve birds' solo homing efficiency, their advantage over the rest of the flock remained small or was only temporal. This interpretation is in agreement with past results showing that birds with more experience will more clearly emerge as leaders when the difference in experience between them and their flight partners is large (Flack et al. 2012). Future research should focus on the effect of experience while birds are still far from asymptotic levels of efficiency (e.g. with tests run after fewer homing flights for the most inexperienced birds). Furthermore, a control group in which every flock member receives extra solo training flights in Phase II would be useful as a baseline measure of how flock homing efficiency changes in response to training given equally to all group members.

Flack et al. (2012) tested mixed-experience pairs of pigeons and found that navigational experience had an effect on leadership, with birds that had performed more training flights more likely to emerge as leaders. In the present study, using groups of ten birds, no such effect was detected, which may indicate that influencing flockmates' movements is easier in smaller groups. Recent work by Herbert-Read et al. (2013) showed that individual movement characteristics become increasingly homogenised in larger groups supporting the idea that the potential for an individual to exert an effect on collective movements diminishes with increasing group size. Investigating the potential link between group size and group dynamics – both empirically and theoretically – is a promising avenue for future research.

Although flock dynamics can be observed without hierarchical organisation (Xu et al. 2012), such structure might be beneficial for establishing a “flight routine” that demands less attention from group members. The fact that hierarchies seem resistant to small changes once they are established indicates that rather than benefitting from particular features of the leader (such as navigational experience) their advantage might lie in the stability of the structure itself. Robust social structures may enhance information transfer among group members, thereby increasing the accuracy of group-level decisions (Lusseau & Conradt 2009; McComb et al. 2011). Recent theoretical work has found that underlying social structures can improve the navigational accuracy of large, leaderless groups (Bode et al. 2012a). Furthermore, it is suggested that hierarchical group dynamics could be based purely on social preferences (Bode et al. 2011). This is in agreement with what has been described for different species of group-living primates: King & Sueur (2011) suggest that leader-follower dynamics are embedded in inter-individual relationships, which may result in more efficient decision-making and coordination among group members. Social relationships can be found between relatives, familiar conspecifics or individuals of similar attributes such as size, personality or sex. Hence, the stability in our hierarchical networks may arise from preferential attachments that may have developed during early training and that may not be susceptible to changes in individuals’ navigational experience.

5.6 Appendix

5.6.1 Spatial and temporal error of the GPS devices

To test the spatial and temporal error originating from the GPS devices, we performed a variety of tests. 10 GPS devices (labelled 0 to 9) were attached to a rigid, 3 m long pole with an inter-device distance of 33 cm. We moved the pole along a free path in an open field using 3 different orientations: (1) with the pole's orientation parallel to the direction of motion (GPS 0 at the front and 9 at the back, Fig. 5.A1a); (2) with the pole in a fixed orientation relative to the field (Fig. 5.A1b); and (3) with the pole's orientation perpendicular to the direction of motion (Fig. 5.A1c) Each test lasted 10 minutes, and the pole moved between 1 and 3 m/s (typical flight speed of a pigeons is 18-22 m/s).

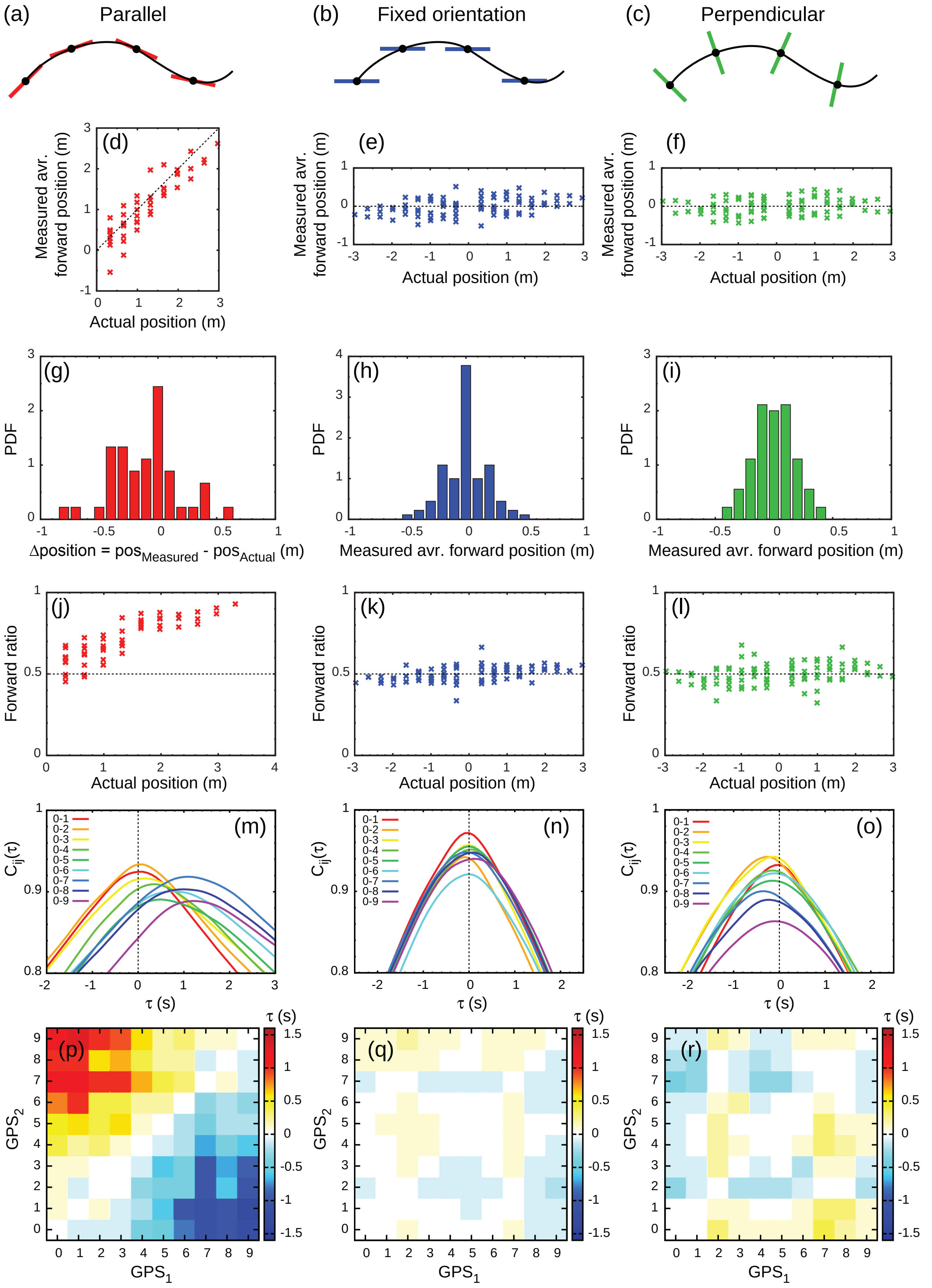
An important aspect of analysing flock flights is the relative position of each device within a pair in relation to the movement direction of the whole flock. This is why we measured the average forward position of each device (Fig. 5.A1d-f). In both the perpendicular and the globally-fixed orientation cases, we expect an average forward position of zero. In the parallel case we would expect a forward ratio of 1 for (i<j). Any deviation from such value is due to noise which is lower at small inter-device distances. We show the probability density function of this measure in Figure 5.A1g-i. We also measured the time a device was detected to be in front relative to the direction of motion, and calculated the time ratio for the 10-min test (Fig. 5.A1j-l). We also performed directional correlation delay analyses for all devices (Fig. 5.A1m-o). The absolute error of the GPS device arises from the relative error of the velocity which decreases as speed increases. Hence, our tests give an upper approximation of the noise due to the fact that each test lasted only 10 minutes and the pole was moved at low speeds.

5.6.2 Additional test of hierarchy robustness

We used a linear mixed-effects model to test the robustness of the hierarchies, using as our dataset the τ values calculated for each individual in every flight of phases I and III. All data were analysed using R (R Development Core Team 2009) and the R packages lme4 (Bates & Maechler 2009) and languageR (Baayen 2008, 2009). We included Subject as a random effect. As fixed effects, we added Training Phase (Phase I, pre-training or Phase III, post-training) and Treatment Group (trained or untrained individuals) to the model, as well as the interaction term between them.

We verified that the normality of error and homogeneity of variance assumptions of parametric analysis were statisfied by visual inspection of plots of residuals against fitted values. To assess the validity of the mixed effects analysis, we performed likelihood ratio tests comparing the model with fixed effects to the null model with only the random effect. The model that included fixed effects did not differ significantly from the null model (P=0.222), hence fulfilled the validation test. The following P-values were based on Markov-chain Monte Carlo sampling. We found no significant differences between pre- and post-training τ values (P_{MCMC}=0.656), or trained and untrained individuals (P_{MCMC}=0.203). The interaction between Training Phase and Treatment Group was not significant (P_{MCMC}=0.321). Together, these results further confirm that the solo training had no effect on the groups' hierarchies.

Figure 5.A1 Spatial and temporal error of the GPS trajectories and the directional correlation delay method for parallel (first column), globally fixed (second column) and perpendicular (third column) orientation tests. The pole (illustrated as coloured lines) was moved along a path (black line) in parallel **(a)**, globally fixed **(b)** and perpendicular **(c)** orientation relative to the movement direction. (d-f) Relative position of each device in a pair relative to the direction of motion as a function of its actual position. (**d)** shows only one value of each pair ($i<j$). **(e)** and **(f)** show both values. **(g-i)** Probability density function (PDF) of the measured forward position of panel **(d-f)**. **(g)** shows the deviation between measured and actual position for each pair. **(j-l)** Forward ratio defined as the time ratio a device was detected to be at front relative to the motion direction. **(j)** shows only one value of each pair ($i<j$). **(k)** and **(l)** show both values. **(m-o)** Directional correlation function ($C_{ij}(\tau)$) between GPS 0 and all other devices. **(p-r)** The directional correlation delay time (τ_{ij}) of each pair.


(a)
Parallel
(b)
Fixed orientation
(c)
Perpendicular
(d)
(e)
(f)
Measured avr. forward position (m)
Actual position (m)
(g)
(h)
(i)
PDF
Δposition = pos$_{Measured}$ - pos$_{Actual}$ (m)
Measured avr. forward position (m)
(j)
(k)
(l)
Forward ratio
Actual position (m)
(m)
(n)
(o)
$C_{ij}(\tau)$
τ (s)
0-1
0-2
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0-4
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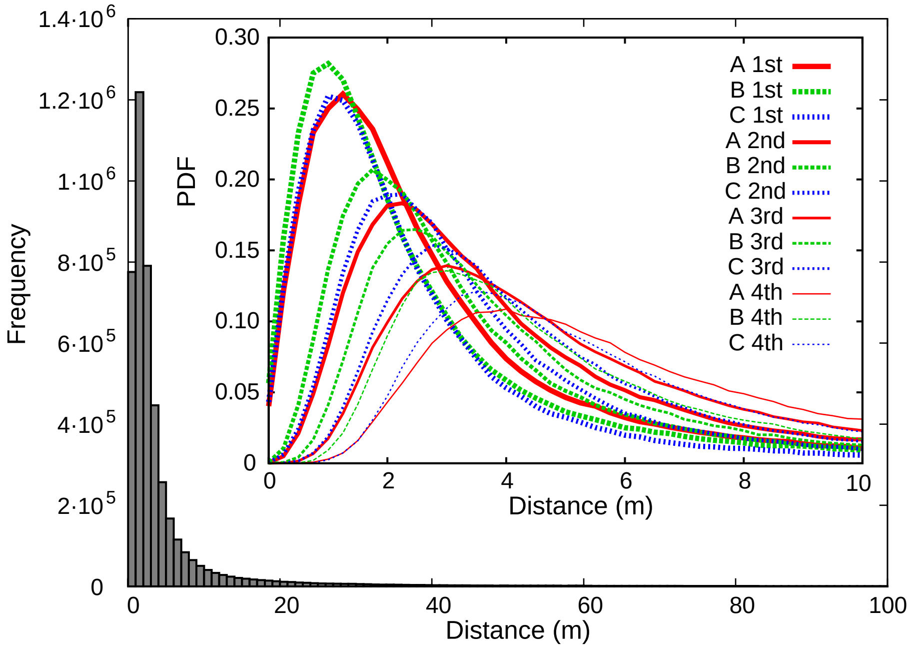

Figure 5.A2 Histogram illustrating the frequency distribution of distances (bin=1 m) to the first nearest neighbour of all three groups and flock flights (before and after solo training) pooled. Inset shows probability density functions of distances (bin=0.25 m) to the first, second, third and fourth nearest neighbours in groups A, B and C in red solid, green dashed and blue dotted lines, respectively (data shown only up to the fourth nearest neighbours for better visibility).

Table 5.A1 Results of the $\bar{\tau}_i^{pre}$ vs $\bar{\tau}_i^{post}$ correlation analysis with and without two outliers

Correlation between $\bar{\tau}_i^{pre}$ and $\bar{\tau}_i^{post}$	**Without outliers**	**With outliers**
untrained ABC	**r_{20}=0.72, P<0.001**	**r_{20}=0.62, P=0.003**
untrained group A	**r_6=0.80,P=0.031**	**r_6=0.80, P=0.031**
untrained group B	**r_6=0.87, P=0.011**	r_6=0.61, P=0.149
untrained group C	r_6=0.69, P=0.090	r_6=0.69, P=0.090
trained ABC	r_7=-0.08, P=0.846	r_7=-0.176, P=0.677

Values in bold indicate significant correlations.

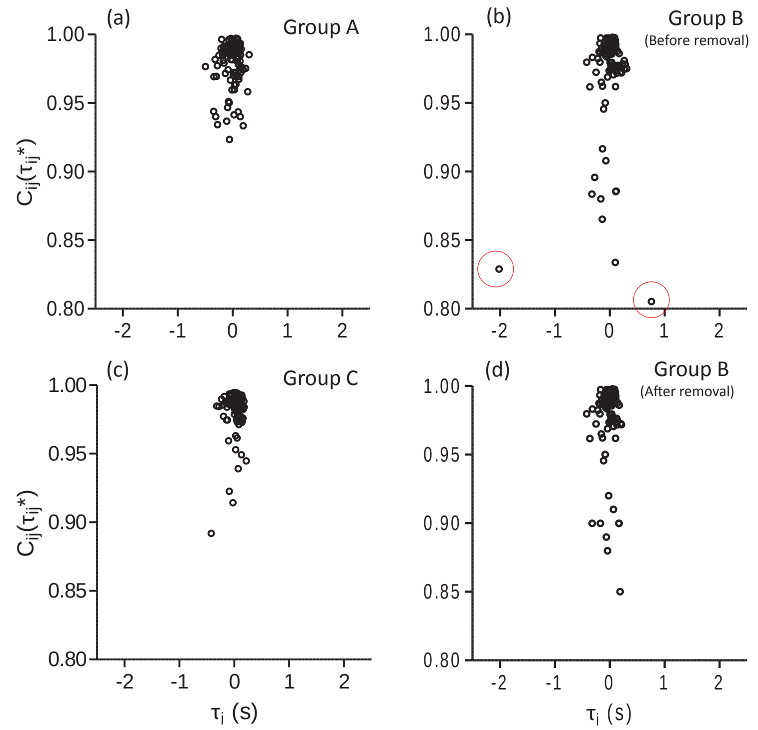

Figure 5.A3 Scatter plot of the relationship between an individual's $C_{ij}(\tau^*_{ij})$ value and τ_i for groups A, B and C (panels **(a)**, **(b)**, and **(c)**, respectively) for each flight. Red circles in **(b)** indicate τ_i-outliers with low correlation values. Panel **(d)** shows the re-calculated $C_{ij}(\tau^*_{ij})$, τ_i value pairs for group B after excluding those two outliers.

Chapter 6

Modelling group navigation: Transitive social structures improve navigational performance

6.1 Summary

Collective movements of large groups have been studied successfully in the past using individual-based modelling. However, so far most of these models have neglected the role of social connections between their interacting members. In Chapter 3, I found that familiarity between two pigeons arising from frequent navigational interactions can influence their positioning within a larger flock. In the present chapter, I investigate the impact of social preferences on group navigation by introducing social network structures into a model of collective motion. My results show that groups achieved the highest level of accuracy when they were hierarchically organised with the minimum number of connections per individual. I also observed that the social structure of the groups is mirrored in the group's leader-follower dynamics. These findings contribute to a better understanding of the potential payoffs of collective migration in species that possess social affiliations.

6.2 Introduction

Travelling collectively can be beneficial for a variety of reasons. Flocking may enhance navigational accuracy due to the fact that collating estimates from multiple individuals can reduce the navigational error of the group, as long as these estimates are distributed around a mean with no consistent directional bias (Hamilton 1967; Simons 2004). This has been supported by several empirical studies on birds (Bergman & Donner 1964; Dell'Ariccia et al. 2008) and humans (Faria et al. 2009). Theoretical work focusing on individual movements and interactions has strengthened our understanding of how individual behaviours scale to coherent collective motion (Couzin & Krause 2003; Vabø & Skaret 2008; Hemelrijk & Hildenbrandt 2011). These studies have demonstrated that synchronised movements of large groups can arise from three basic rules determining local inter-individual interactions (Vicsek et al. 1995; Couzin et al. 2002). First, each individual avoids collisions with others by maintaining a minimum distance to its neighbours. Second, individuals are attracted to their closest neighbours, and, third, align their direction of movement with those of their closest neighbours. These simple rules (avoid – attract – align) can produce group movements that closely resemble those of real animal collectives. Furthermore, such models have been used to examine the effect of moving as a group on navigational accuracy, showing that group membership can be beneficial under certain conditions (Grünbaum 1998; Codling et al. 2007).

However, until very recently, models examining collective motion and decision-making have neglected the role of underlying social relationships between group members. Many social groups differ from random aggregations due to the presence of preferred associations and interactions between certain individuals (Whitehead 2008). Such social relationships can be based on sexual partnerships, parent-offspring relations or a previous history of associations between certain group members. Empirical studies have observed that familiarity between individuals can modulate an individual's tendency to follow the movements of a preferred partner (Griffiths & Magurran 1999; Boissy & Dumont 2002; Ramseyer et al. 2009; Tóth et al. 2009; see also Chapter 3 of the present thesis). Similarly, the organisation of human groups is influenced by social interactions among members (Moussaïd et al. 2010). Incorporating such social preferences into a model of collective motion recently showed that social structure can influence group cohesion, the positioning of specific individuals and the movement dynamics within the group (Bode et al. 2011).

In this chapter, I aim to investigate further the role of social connections on group navigation. More specifically, what is the effect of preferred attachments between certain individuals on the accuracy of group navigation, and which form of group organisation endows the collective with the greatest advantages? Bode et al. (2012a) investigated the impact of social networks on the navigation of large, leaderless groups and found that underlying social networks can improve navigational accuracy of such groups and reduce group fragmentation. Here, I further explore the impact of social networks by simulating groups that specifically resemble flocks of pigeons in their organisation, and thereby draw on the findings of this thesis (e.g. Chapters 3 & 5). All generated networks in Bode et al. (2012a) were undirected – in other words they assumed that preferences between individuals were reciprocal. When examining large schools of fish or swarms of insects this assumption is reasonable because of the assumed lack of individual recognition. However, considering social relationships in smaller groups of animals which potentially distinguish between group members, such a premise seems less realistic. For example, using high-resolution GPS tracking, it has been shown that decision-making in flocks of homing pigeons is hierarchically organised, where given pairs of individuals within the group exhibit relatively stable, directed leader-follower relationships (Nagy et al. 2010). This in turn means that some individuals are able to contribute consistently with greater weight to the movement decisions of the flock. Drawing on this interesting empirical finding (the robustness of which was further confirmed by experiments reported in this thesis; see Chapter 5), here I use individual-based modelling to simulate flocks with different underlying social structures and examine their impact on navigational performance and their group dynamics.

6.3 Methods

6.3.1 Group motion model

In order to examine the effect of group organisation on navigational accuracy, I extended an existing collective motion model (Couzin et al. 2005) by incorporating internal group structures. I simulated a group of N individuals, represented by position vector $c_i(t)$ and direction vector $v_i(t)$, moving through a two-dimensional environment towards a fixed target location. Individuals interact with other group members within their "sensory range". This sensory range is divided into three interaction zones: avoidance zone (radius r_R), alignment zone (r_O) and attraction zone (r_A, Fig. 6.1). At all times, each individual tries to maintain a minimum distance between itself, i, and others, j, by turning away from individuals within the avoidance zone:

$$d_i(t + \Delta t) = - \sum_{j \neq i} \frac{c_j(t) - c_i(t)}{\left|c_j(t) - c_i(t)\right|} \tag{1}$$

d_i represents the individual's preferred direction to travel. This step has the highest priority. If there are no individuals within the avoidance zone, individuals will be attracted to, and align with their neighbours within the attraction zone and the alignment zone. The preferred direction is calculated as:

$$d_i(t + \Delta t) = \sum_{j \neq i} \frac{c_j(t) - c_i(t)}{\left|c_j(t) - c_i(t)\right|} + \sum_{j=1} \frac{v_j(t)}{\left|v_j(t)\right|} \tag{2}$$

Each individual has information about a target g. While navigating towards this target, individuals must balance their preference to maintain group cohesion with their preferred direction resulting in their new preferred direction d_i':

$$d_i'(t + \Delta t) = \frac{\tilde{d}_i(t + \Delta t) + w g_i}{\left|\tilde{d}_i(t + \Delta t) + w g_i\right|} \tag{3}$$

where w is a weighting factor between the individual's social interaction and their preferred directions, with higher levels of w giving greater weight to the preferred direction.

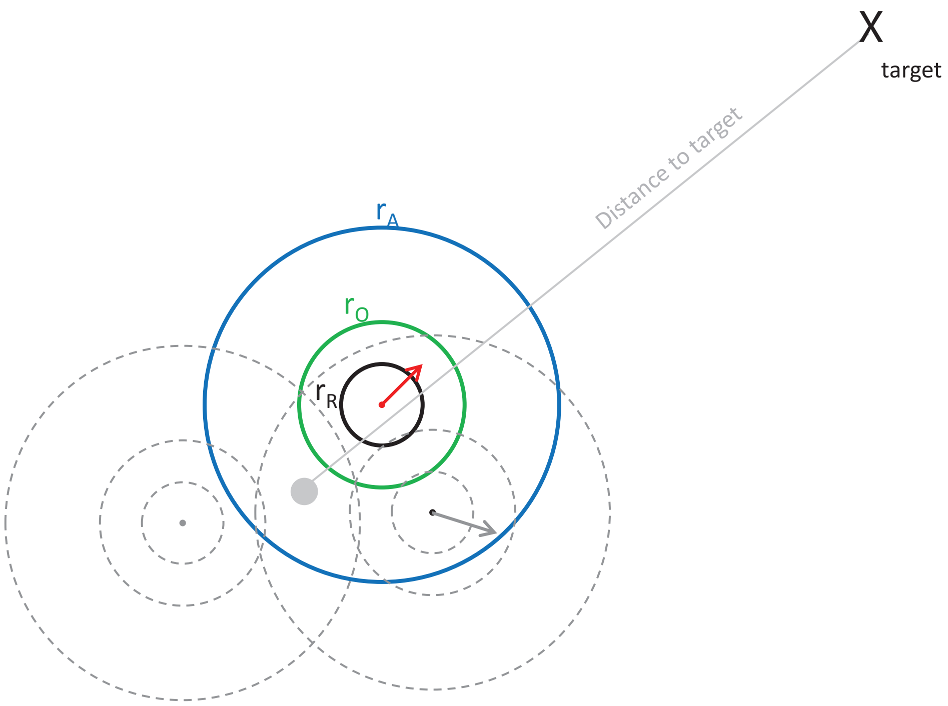

Figure 6.1 Schematic of an individual's three interaction zones which influence its behaviour within a group (here, two other group members with their respective interaction zones are depicted in grey). Blue, green and black circles indicate the repulsion zone (r_R), alignment zone (r_O) and attraction zone (r_A), respectively. Arrows show an individual's direction of motion. x indicates the target location. The grey dot represents the group's centre of mass.

In order to examine the effect of social relationships within the group on navigational performance, I extended the above model by including a "social preference" factor *h*. This affects the social relationships between the individuals by weighting their interactions:

$$d_i(t + \Delta t) = \sum_{j \neq i} \mathrm{h}_j \frac{c_j(t) - c_i(t)}{|c_j(t) - c_i(t)|} + \sum_{j=1} \mathrm{h}_j \frac{v_j(t)}{|v_j(t)|} \qquad (4)$$

where *h* varies with each individual. Higher values of *h* will cause interactions with the given individual to have greater influence on the group (i.e. leadership).

As in Couzin et al. (2005), I simulated random influences on an individual's movement. In order to do so, I modified its desired direction d_i', by rotating it by a random angle taken from a circular wrapped gaussian distribution, centred on 0, with standard deviation σ=0.01 radians. Furthermore, the maximum turning angle of an individual at each time step was θ=0.2 radians. The new position vector of individual i is given by $c_i(t+\Delta t) = c_i(t) + v_i(t+\Delta t)\Delta t s_i$, where s_i (s=3) is the speed of individual i and Δt is the time step (Δt=0.1). Based on data from real pigeon flocks I collected and reported in the previous chapters (especially Chapter 5), I confined the parameters to the following: N=10, r_A=50, r_O=6, r_R=1. I used 1000 replicates for each simulation, each run for 250 iterations (T=250).

6.3.2 Social structures of the group

Following Bode et al. (2012a), I restricted the weightings in underlying social preference networks to "strong" and "weak" connections. Individuals react to every conspecific due to the presence of weak connections throughout the group, however strong connections will have a greater impact on the group. Values of h are generated to mimic preferred and non-preferred connections between individuals. I set weak connections to h=1 and strong connections to h=100. I developed two types of group structures, based on (a) asymmetrical Erdös-Rényi random, directed models in which strong connections are added randomly (Erdös & Rényi 1960, henceforth: random network, Fig. 6.2A, B), and (b) asymmetrical directed Barabasi-Albert models, which start with a small number of nodes and expand by the addition of new nodes until the final group number is reached. New nodes attach preferentially to already well connected nodes (Barabási and Albert, 1999, henceforth: hierarchical network, Fig. 6.2C, D). These two network types cover many of the possible group structures. Each network is described by its average out-degree, i.e. the average number of strong connections per individual. An average out-degree of 0.9 (in a group of ten individuals) corresponds to one strong, directed connection per individual in the case of hierarchical networks (Fig. 6.2C), whereas a group with an average out-degree of 1.7 has two strong, directed connections per individual (Fig. 6.2D). Within the social structure, highly influential individuals are referred to as “social-leaders” which affect the movements of “social-followers” more strongly (Fig. 6.2). In groups without network structure all individuals are connected through weak connections meaning every member is influenced equally by every other member (Fig. 6.2E).

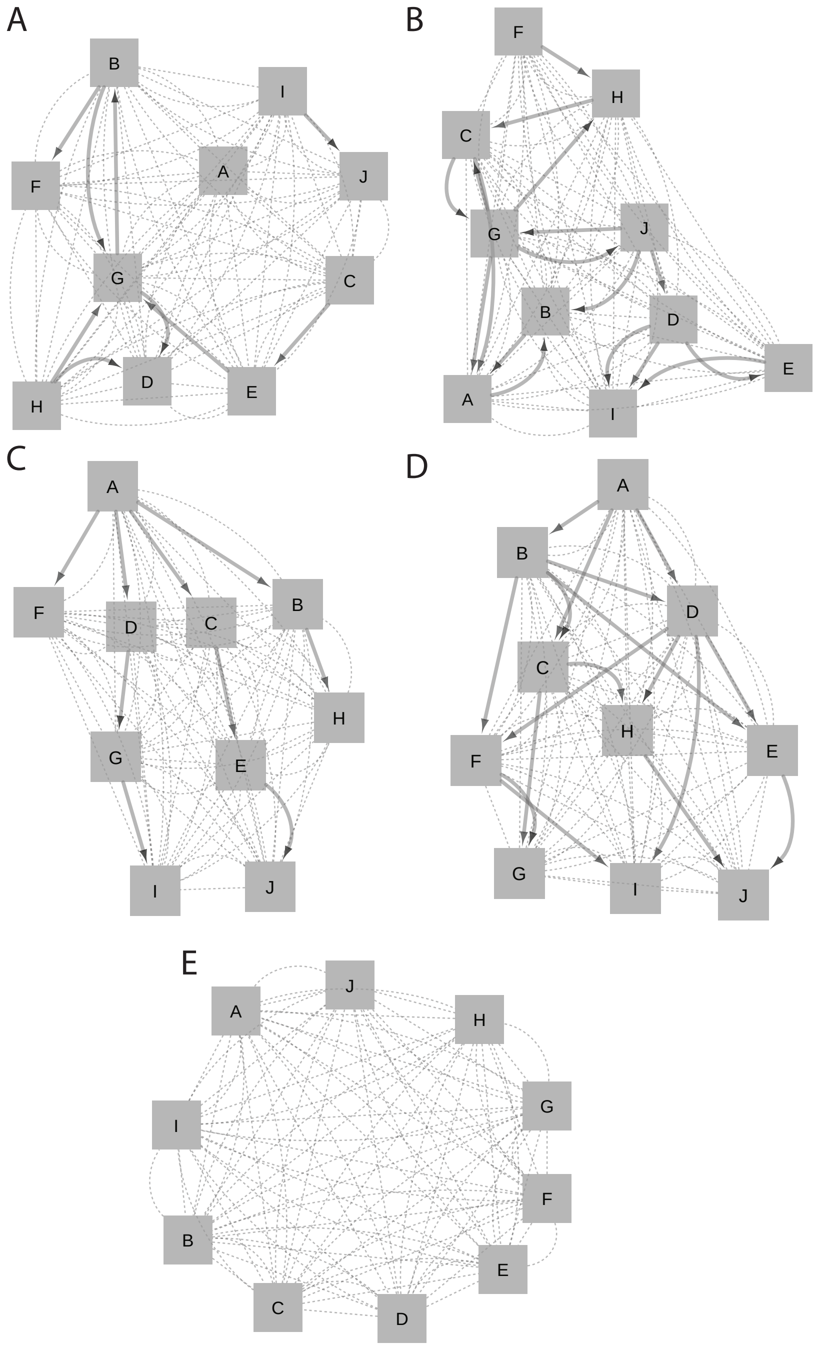

Figure 6.2 Examples of generated networks used to represent underlying social group structure. The top row shows Erdös-Rényi random, directed models with an average out-degree of **(A)** 0.9 and **(B)** 1.7; the middle rows show directed Barabasi-Albert models with an average out-degree of **(C)** 0.9 and **(D)** 1.7; the bottom row shows a group with no network **(E)**. Nodes represent individuals. Strong connections are shown as solid edges pointing from the social-leader to the social-follower; weak connections are shown as dotted edges.

6.3.3 Data analyses

In order to explore the impact of a group's underlying social structure on navigational performance, I measured navigational error defined as the group's distance to the target location at the end of the simulation (i.e. the further the group from the target after T time steps, the higher the navigational error). As in Bode et al. (2012a), I measured for each simulation the probability of fragmentation defined as the proportion of simulations that resulted in more than one group. A cohesive group is defined as groups in which all individuals are connected (within a distance of r_A).

To determine movement leader-follower relationships inside the group, I calculated the directional correlation delay for each pair of individuals i and j ($i \neq j$; see Nagy et al. 2010, and Chapter 5 of the present thesis for the full rationale behind this method) which looks at the temporal relationship between the directional choices of pairs of group members. Leading events, i.e. where one individual's direction was "copied" by another one delayed in time, were determined using the directional correlation delay time. The directional correlation delay of a pair is $C_{ij}(\tau) = \langle \vec{v}_i(t) \cdot \vec{v}_j(t+\tau) \rangle$, where $\vec{v}_i(t)$ is the normalised velocity of i. I then determined the maximum value of the $C_{ij}(\tau_{ij})$ correlation function, τ^*_{ij} which I identified as the directional correlation delay time. Negative τ^*_{ij} values mean that the movement direction of the i^{th} individual falls behind that of the j^{th} individual, and can thus be interpreted as a case of j leading. For every pair, I extracted from $\tau^*_{ij} = -\tau^*_{ji}$ the positive value as the directed edge pointing from the leader to the follower. By averaging the τ^*_{ij} values of individual i and the rest of the group, I obtained $\bar{\tau}_i$, which allowed me to fully resolve the organisation of the group. For every specific pair ij, I averaged those τ^*_{ij} values that exhibited a $C_{ij}(\tau^*_{ij})$ larger than 0.97. $\bar{\tau}_i$

values have similar properties to linear ranks (positive and negative values correspond to leading and following behaviour, respectively).

6.4 Results

6.4.1 Influence of out-degree

First, I explored a group's navigational error as a function of its underlying social structure and the degree of connectedness within the group. With a weighting factor w=0.3, groups with hierarchical networks increased their navigational error as a function of the mean out-degree of the group. The slope of the changes in navigational accuracy relative to the mean out-degree was significantly different from zero (linear regression, $P<0.001$, $F_{1.8998}=59.74$). As the number of strong connections distributed across group members increased, the navigational error of the group increased. However, I did not observe this relationship for random networks (linear regression, $P=0.820$, $F_{1.8715}=0.05$, Fig. 6.3A). Furthermore, the difference in navigational error between groups with random and hierarchical networks was significant when the average out-degree was 0.9 (Mann Whitney test, $P<0.001$, $U=452523$, Fig, 6.3A). Such an out-degree provides a fully connected hierarchical group with only one strong connection between pairs in the case of the preferential attachment networks (Fig. 6.2C). With an average out-degree of 1.7 (two strong connections per individual, see Fig. 6.2B, D), I no longer found any differences in the navigational error between random and hierarchical networks (Mann Whitney test, $P=0.488$, $U=488574$). Therefore, to explore the largest possible difference in the navigational error between groups with random and directed networks, I focus in all remaining simulations on the first case (out-degree=0.9) in which such difference is significant.

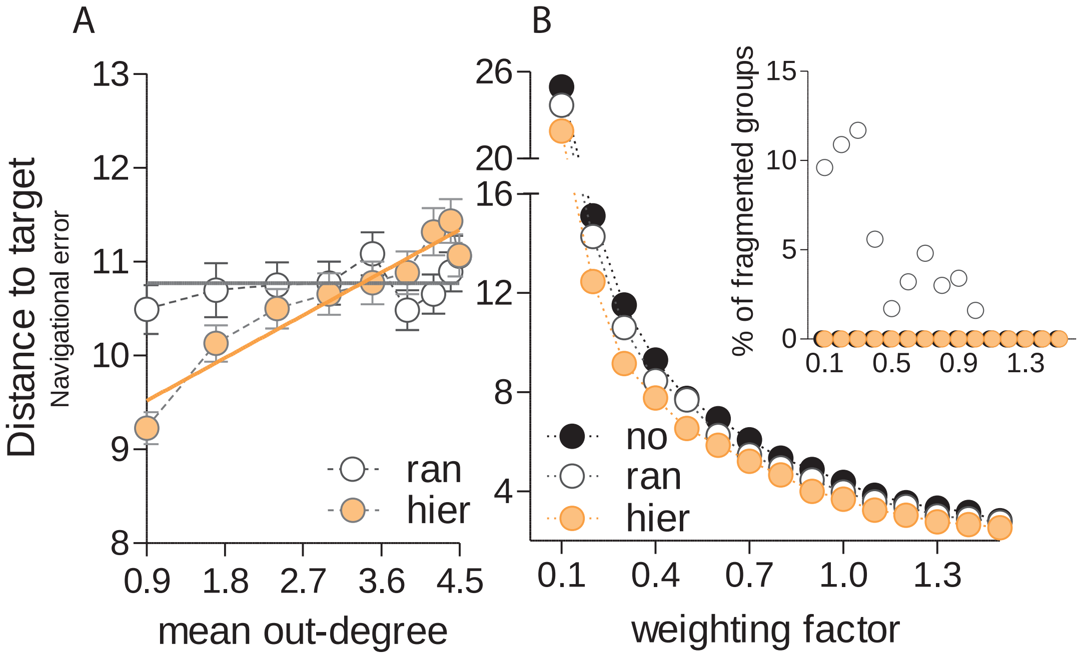

Figure 6.3 Navigational error (i.e. distance to target; mean ± S.E.M.) as a function of **(A)** average out-degree (w=0.3) and **(B)** weighting factor for different underlying network structures (out-degree=0.9). Navigational error is calculated as the distance of the group's centre of mass to the target at the end of the simulation. Groups with no, random or hierarchical networks are shown as black, white and orange circles, respectively. Inset shows the percentage of fragmented groups (i.e. those in which not all individuals remained within a distance of r_A from their nearest neighbour) as a function of the weighting factor.

6.4.1 Influence of the weighting factor

I examined the effect of different types of internal group structure for different weighting factors, w. When w=0 the preferred direction g has no influence, and the individuals have no preference for any particular direction. As w exceeds 1, the individual's preferred direction has more influence than the information arising from social interactions. First, each member of the group had the same weighting factor irrespective of its position in the network. When examining a range of different weighting factors between 0.1 and 1.5, I observed that both the weighting factor and the type of network structure influenced the navigational error of the group with a significant interaction (see Table 6.1 for results of the two-way ANOVA). The navigational error decreased significantly as the weighting factor increased, and groups with hierarchical networks navigated more accurately than those without or with random networks (Fig. 6.3B). The overall effect of *w* on groups with different network structures is relatively small because in my simulations all individuals are informed about the target location, as opposed to the model by Couzin et al. (2005), in which only a small number of individuals are informed. In the present chapter, groups without networks are still highly efficient, because all individuals are aware of the target location. For future simulations, it would be interesting to see how uninformed individuals would change the navigational error of groups with different underlying social structures.

Table 6.1 Results of two-way ANOVA

Source	*Df*	SS	MS	F
network type	2.0	10040	5020	146.8 (P<0.001)
weighting factor	14.0	1.284e+006	91749	2683(P<0.001)
Interaction	28.0	5554	198.3	5.80 (P<0.001)
Residual (error)	44400.0	1.518e+006	34.19	
Total	444444.0			

Because I was only interested in the navigational performance by cohesive groups, I excluded those groups that fragmented (i.e. those in which not all individuals remained within a distance of r_A from their nearest neighbour). I observed a difference in the proportion of fragmented groups between the three different network structures (Two-way ANOVA, $P<0.001$, $F_{2,28}=12.33$) with groups with random networks fragmenting significantly more than those groups with no or hierarchical networks (Fig. 6.3B inset). This is most likely because random social structures allow the formation of several unconnected subgroups, which then navigate independently of each other, whereas in hierarchically organised groups every member is connected to every other member.

6.4.2 Relationship between weighting factor and number of social-followers

I next explored the effect of changing an individual's weighting factor depending on its number of social-followers. I distributed weighting factors in the range of 0.05 to 0.5 among group members (see Fig. 6.4A-C for distribution of weighting factors in groups with hierarchical networks; groups with no or random networks not shown). I assigned each individual with a weighting factor, either (a) randomly, irrespective of its network position, (b) positively correlated with the number of the individual's followers (out-degree), or (c) negatively correlated with the out-degree.

When the weighting factor was randomly distributed among all group members irrespective of the number of followers (example for hierarchically organised groups Fig. 6.4A), I found that groups with a hierarchical network exhibited a smaller error than those with no (Mann Whitney test, $P<0.001$, $U=368579$) or randomly generated networks (Mann Whitney test, $P<0.001$, $U=430856$, Fig. 6.4D). Next, I looked at groups in which the weighting factor correlated positively with the number of followers (i.e. the more followers an individual had the higher its weighting for its own preferred direction was, Fig. 6.5B). That means if an individual followed many others (but was not itself followed) its own weighting was low, and therefore its own preferred direction had lower impact on the group. I found that under such conditions groups with hierarchical networks navigated more accurately than groups with no network (Mann Whitney test, $P<0.001$, $U=360660$), or those with random networks (Mann Whitney test, $P<0.001$, $U=426064$, Fig. 6.4E). Groups with random networks in turn navigated more accurately than those with no network (Mann Whitney test, $P<0.001$, $U=430553$). When I reversed the relationship between out-degree and weighting factor, so that they were negatively correlated (Fig. 6.5C), I observed the same navigational error for all three group types (Fig. 6.4F).

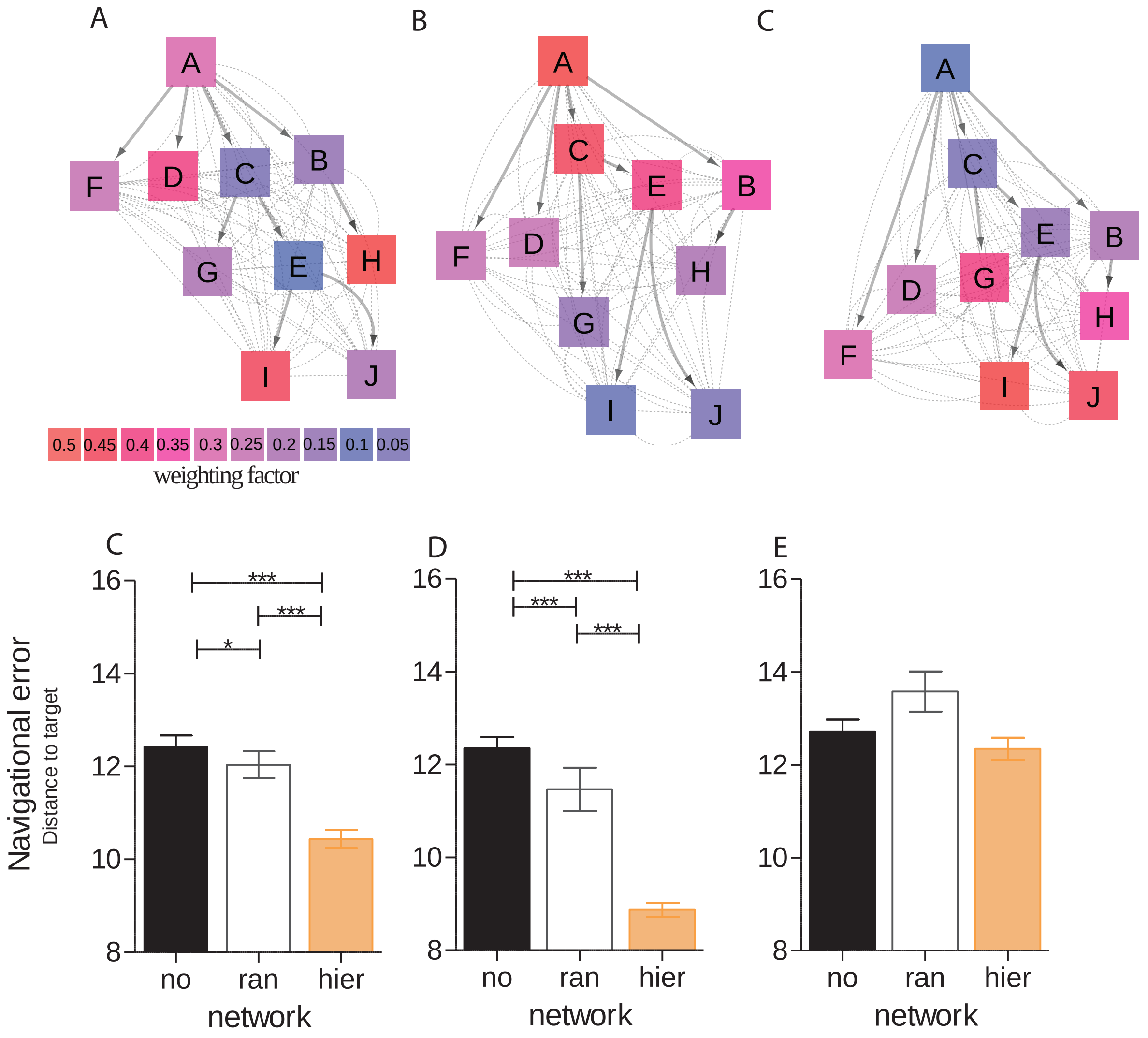

Figure 6.4 (A-C) Example of hierarchically organised groups with different relationships between weighting factors and number of followers: **(A)** randomly, irrespective of an individual's network position, **(B)** positively correlated with individuals' respective number of followers (out-degree), or **(C)** negatively correlated with the out-degree. Nodes represent individuals. Colour corresponds to weighting factor (between 0.05 and 0.5). Strong connections are shown as solid edges pointing from the social-leader to the social-follower; weak connections are shown as dotted edges. **(D-F)** Navigational errors (mean ± S.E.M.) as a function of relationship between weighting factor and number of followers for different networks. Groups with no, random and hierarchical networks are shown as black, white and orange bars, respectively. Asterisks represent significant differences (* – P<0.05; *** – P<0.001)

6.4.3 Group dynamics

Finally, I tested how the underlying network structure related to the group dynamics arising from the delay times between individuals' directional choices. I examined an individual's effect on the movement of the whole group, by calculating for each individual the average directional correlation delay time between it and every other member of the group. As in Section 6.4.2, I varied the relationship between an individual's weighting factor and its number of social-followers (range of 0.05 to 0.5). Again, the relationship was either positively or negatively correlated (see inset of Fig. 6.5 B, D). I found that the correlation between weighting factor and $\bar{\tau}_i$ coincided with the originally assigned relation between weighting factor and out-degree. For both random and hierarchical networks, weighting factor and $\bar{\tau}_i$ were positively (random: r=0.98, N=10, P<0.001; hierarchical: r=0.92, N=10, P<0.001, Pearson, Fig. 6.5A) or negatively (random: r=-0.92, N=10, P<0.001; hierarchical: r=-0.65, N=10, P=0.04, Pearson, Fig. 6.5C) correlated in agreement with their initial relation to out-degree. Hence, when examining the relationship between out-degree and $\bar{\tau}_i$, I found a positive correlation in both assignment groups for random and hierarchical networks (positive: random: r=0.98, N=10, P<0.001; hierarchical: r=0.93, N=10, P<0.001 Fig. 6.5B; negative: random: r=0.97, N=10, P<0.001; hierarchical: r=0.97, N=10, P<0.001, Fig. 6.5D) indicating that group dynamics are mirrored by social structures.

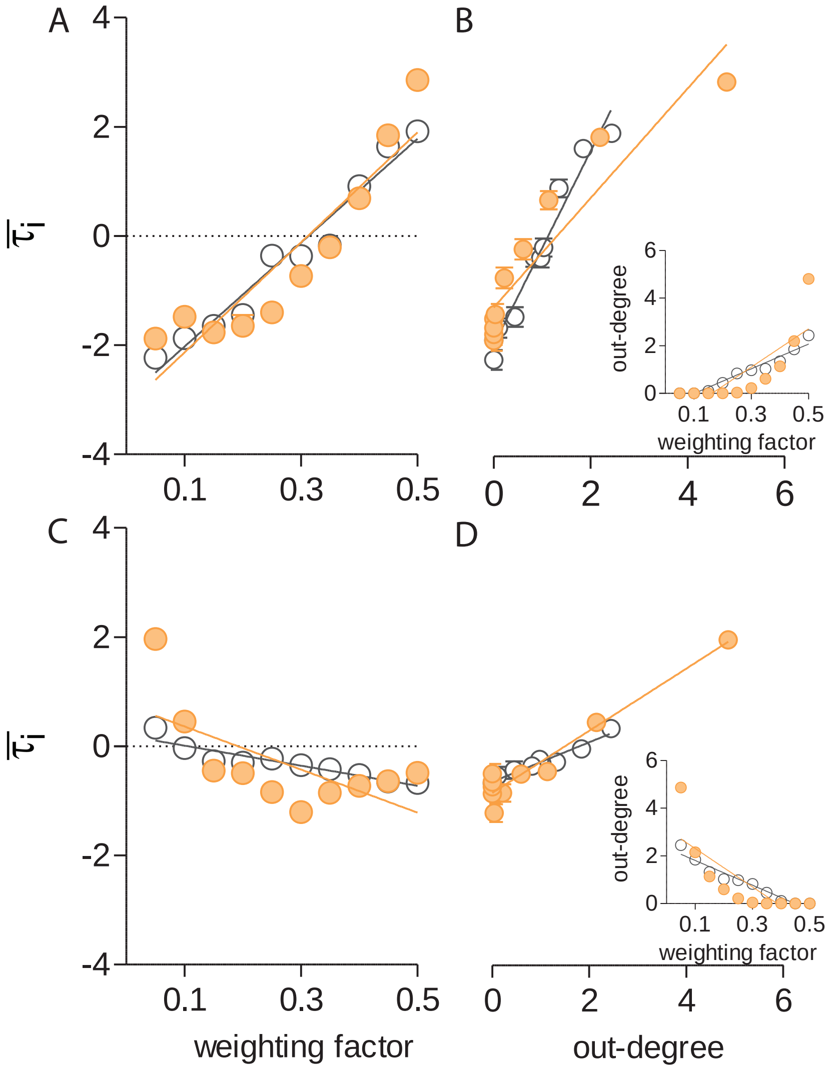

Figure 6.5 (A, C) Relationship between weighting factor (mean ± S.E.M.) and average directional correlation delay time $\bar{\tau}_i$(mean ± S.E.M.). **(B, D)** Relationship between out-degree and average directional delay time $\bar{\tau}_i$(mean ± S.E.M.). Groups in which weighting factors (between 0.05 and 0.5) were assigned as positively correlated **(A, B)**, or negatively correlated **(C, D)** with out-degree (see insets). Groups with random and hierarchical networks are shown as white and orange circles, respectively.

6.5 Discussion

The aim of the present chapter was to employ a mathematical modelling approach to study how various forms of underlying social organisation may affect navigational performance during collective movement. I simulated small groups of navigating individuals with varying social network structures and measured both navigational error and group dynamics within the resultant “flocks”. Previously, also using mathematical modelling, Bode et al. (2012b) found that underlying social networks can reduce navigational error in leaderless groups. However, this work focused mainly on the effect of undirected networks on large groups, which is why here I further explored such effect on small groups that better resemble the pigeon flocks that I studied in my previous chapters. I firstly confirmed the finding by Bode et al. (2012b) that the introduction of an underlying social structure decreases navigational error. Furthermore, I found that in groups with hierarchical social structures, navigational performance decreases with the average out-degree value. Groups achieved lowest error when each individual had only one strong connection. Interestingly, groups with randomly distributed social preferences exhibited a stable level of error irrespective of the number of strong connections among members. Although individuals still react to conspecifics to which they had only weak connections, the group exhibits a predetermined “chain” along which movement decisions cascade. By paying attention to more than one member of the group, information about how to reach the target accurately might be weakened by predominantly distracting interactions with conspecifics. Many animal species exhibit hierarchical group organisation based on, for example, dominance (King et al. 2009). My findings suggest that such groups move most accurately when each member’s movement decision are mainly influenced by one other focal individual (e.g. the dominant male). However, under natural conditions, animal groups often consist of individuals with differing levels of experience and these may or may not correlate with their social dominance rank. It remains to be explored how navigational performance changes in mixed-experienced groups with underlying social structures.

I also examined the effect of varying the weighting each individual places on its own information about the preferred target in relation to the weighting it places on social interactions, which can also be referred to as individual “assertiveness”. In general, as assertiveness increased, navigational error decreased for groups both with and without underlying social structure. However, when each member of the group was heavily influenced by its own preferred direction while attending less to the movements of conspecifics, preferred attachments became insignificant factors. High assertiveness can be observed in animals for which reaching the target is most crucial (e.g. food-deprived animals Krause et al. 1992, or lactating females Fischhoff et al. 2007). Nonetheless, groups with unassertive members benefited more from hierarchical organisations than from no or random networks. Groups in which social interactions are highly influential can gain navigational benefits from a transitive social structure. Past work has suggested that a higher weighting on the preferred direction can result in more efficient navigation. Furthermore, individuals can increase their influence on the group’s movements by changing their assertiveness, or weighting factor (Conradt et al. 2009). Here I found that groups in which the individuals with the most social-followers were also highly assertive navigated most accurately. Interestingly, hierarchical organisation became ineffective when highly followed individuals paid less attention to their target information (unassertive social-leaders). King et al. (2008) found that groups of chacma baboons *(Papio ursinus)* failed to visit food patches when the dominant male was guarding oestrus females. The priority of the male changed from foraging to mate-guarding – a phenomenon which can be compared with the unassertive social-leader scenario in the present simulation.

Empirical studies have shown that individuals' movement decisions are strongly influenced by their social relationships (Sueur et al. 2009; Jacobs et al. 2011b). In species with strong dominance hierarchies such as mountain gorillas (*Gorilla beringei beringei*) or wolves (*Canis lupus*), the alpha male consistently determines the group's movements (Schaller 1963; Peterson et al. 2002). Similarly, theoretical work has shown that collectively migrating groups can consist of a small group of actively navigating individuals while the greater part of the group adopts socially facilitated movement behaviour (Guttal & Couzin 2010). However, the current chapter shows that if those individuals that have many social-followers pay less attention to their preferred directions, the group does not gain any navigational benefits from underlying social structures. Hence, we can assume that if group performance is to be maximised, individual assertiveness and position within the social network should correspond to each other.

The risk of group fragmentation increases with individual assertiveness, as reaching the target becomes a higher priority than staying in a group (Conradt et al. 2009). As all individuals in my groups were informed about the target goal, I observed fragmentation only in groups with random network structures and only when the weighting factor was low (when individuals put more weight on social interactions). Randomly generated networks can allow the formation of several unconnected subgroups, which in turn may decrease the group's overall navigational performance. Such sub-groups seem highly likely in animal groups, because many preferred interactions may be between pairs of individuals (e.g. sexual partners, parents-offspring). Hence, we can assume that the performance of moving animal groups is critically affected by the group's structure.

Nagy et al.'s (2010) study examining pigeon flock dynamics not only found a well-defined leadership hierarchy among flock members in terms of the initiation and copying of small-scale directional changes, but also that individuals' spatial positions within the flock correlated with their place in the hierarchy. Although I did not test this, theory predicts that an individual's spatial position within the group is linked to its position in the underlying social structure (Hemelrijk 2000; Bode et al. 2012b). Here I observed that that the social structure of the groups – as determined by the underlying network – is mirrored in the group dynamics. Information on movement decisions flows from the more socially connected individuals to those with fewer or no connections. However, which aspect of an individual determines the type and number of its preferential attachments may vary between species and depend on many different features. For example, in this thesis I have shown that frequent encounters between pairs of pigeons can influence their behaviour in a group (see Chapter 3). In line with that, a very recent study on mixed-species flocks of jackdaws (*Corvus monedula*) and rooks (*Corvus frugilegus*) showed that birds preferentially associate with conspecifics (Jolles et al. 2013).

In summary, my results confirm theoretical predictions that the navigational error of a group will depend strongly on its specific social organisation, and furthermore suggest which of several alternatives produces the best performance in small navigating groups. My results have broader implications for studies on collective navigation and motion because they show that only by considering a group's social system can we fully comprehend the dynamics and advantages of joint movements.

Chapter 7

Conclusions and future directions

This thesis provides new insights into conflict resolution and collective decision-making in co-navigating homing pigeons. As proposed in my opening chapter, it explored both the relationship between individual and group performance during homing, and the influence of the group members' past individual experience on group decision-making by combining empirical and theoretical approaches. In this final chapter, I shall summarise and link together the main findings from each chapter, and provide an outline of potential future directions on the basis of my work.

7.1 The experiences of pigeons

Experience – either actively participating in certain activities or more passively observing them – leads to the accumulation of knowledge or skills. Throughout their lives, homing pigeons, like other animals, can gain experience concerning many different aspects of their existence. For example, their navigational experience can be influenced by repeated homing flights from the same or different release sites. Their social experiences will be structured by frequent encounters with conspecifics. In group-living animals, such as pigeons, we can further assume that individual experiences will vary widely across group members, which in turn might have an influence on group decision-making tasks. The experiments in this thesis manipulated the experience of homing pigeons in various ways in order to observe the effect of those different treatments on their group behaviour.

7.1.1 How does navigational experience influence leading/following behaviour?

The spatial knowledge of pigeons is built up through their spontaneous exploratory, foraging and homing experiences within a certain area around the loft. To these can be added experimental manipulations where birds are artificially displaced to familiar and unfamiliar locations that they subsequently home from. In Chapter 2 I examined factors contributing to the establishment of leadership/followership during joint travel by pairs of individuals, focusing on the role of previous navigational experience, generated through individual homing flights. The results illustrate that the larger the difference in experience between two partners, the higher the likelihood the more experienced bird will emerge as leader. My findings also suggest that there is a short sensitive period in the development of a route, during which pigeons are more likely to respond to conspecifics by following the latter's route. In several different species, it has similarly been shown that more knowledgeable individuals can have more influence on group movements (Reebs 2000; Lusseau & Conradt 2009; Bousquet & Manser 2011). However, other types of individual variation among group members, such as dominance (Sueur & Petit 2008), or satiation (Nakayama et al. 2012b) have been shown to determine leadership across a range of species. In general, group movements are directed by those specific individuals for whom reaching the goal is most crucial (Conradt et al. 2009). Further research is necessary in order to established whether there are other individual features in pigeons – such as breeding state, motivation, or hunger – that can influence leadership and collective decision-making.

Furthermore, many migratory species rely on social cues during their long-distance trips, which provide juveniles with the possibility to learn routes from more experienced adults (Schüz 1949; Hochbaum 1955; Chernetsov et al. 2004). Although on a smaller spatial scale compared to long-distance migrants, homing pigeons provide a unique semi-natural system to explore the vertical transfer of route information. Pigeons start to fly when they are approximately six weeks old. They will perform spontaneous exploratory flights around the loft, and will gradually build up a memory of the landscape surrounding their home. Most studies on pigeon navigation have used experienced birds, and have focused on homing flights on a large spatial scale. Far less work has been done on how spatial memory develops in juveniles as they begin to gain experience in the areas around their loft and of more distant sites they spontaneously visit alone or in the company of others. By tracking youngsters on their first flights around the loft, we might gain insights into how a young bird acquires spatial information about its environment. Furthermore, extending the tracking to the parents, other experienced loft members, and, eventually, the entire loft will inform us about the extent to which the social setting in which a bird matures is involved in the development of its knowledge about the environment.

7.1.2 How do socially shared experiences influence leading/following behaviour?

The experiment in Chapter 3 was inspired by two distinct previous findings. First, I aimed to examine further the phenomenon of the short sensitive period in route learning during which birds are more likely to follow the movements of partners (see Chapter 2) by testing whether such following behaviour also represents a learning opportunity. I found that, like individually trained birds, pairs develop idiosyncratic routes, which they recapitulate together faithfully. Although the results indicate that partners profited from their joint flights by acquiring route knowledge faster, the experimental design did not allow formal comparisons between pair and solo training. Further experiments are necessary to discover the potential benefits of conspecifics on route learning. Second, I aimed to examine whether the outcome of paired decision-making experiments (Biro et al. 2006) scales up to larger groups. The experiment showed that pair-routes can prevail during the homing flights of quadruples, but compromise routes can also be observed, depending on the spatial relationship between the previously established joint routes of the pairs. This finding is in agreement with what has been observed in individually trained birds, although pairs do seem to tolerate a greater range of disagreements prior to the transition than do single birds. I concluded that pairs develop into a “behavioural unit” through their shared experience of repeated joint flights, and that these flights can also subsequently affect collective decision-making in larger flocks. A valuable next step would be to examine the influence of naturally occurring social bonds, like sexual partners or parents and their offspring, on group behaviour. Moreover, I would encourage future investigation into the social aspects of foraging flights. Homing experiments necessarily involve a level of artificiality to provide experimental control, but it seems likely that the findings found in this thesis can also be observed in more natural situations like, for example, during foraging flights. It would require experiments in which pigeons are trained to feed at a distant site away from their loft to examine whether information about foraging locations will spread socially across the group. If it does, then the direction and speed characterising diffusion could be compared to social relationships that exist between individuals, to examine how underlying social organisation can structure the spread of information through a group.

7.1.3 How do more challenging navigational experiences influence leading/following behaviour?

Chapter 4 continued to examine the idea that lower levels of experience predispose birds to becoming followers, and that as a result group travel can potentially compensate less experienced birds for their relative deficiency in navigational information when they fly with better informed partners. I further investigated this finding by manipulating birds’ experiences through training from multiple release sites, which I hypothesised may lead to homing becoming a more challenging task. Developing the idea that earlier established routes are comparable to less well developed routes (due to memory decaying over time as well as to interference from later experiences at different sites), I examined whether I could detect differences in the leading/following behaviour of birds from three treatment groups, each exposed to a different training regime from three different sites. Pigeons were more likely to follow others when they were forced to home from earlier – potentially less well remembered – routes. I discussed that the recency of spatial memories may alter an individual's propensity to initiate or follow movements. Leading/following behaviour emerges from the interplay between the strengths of a pigeon's route memories, which can vary depending on time or intensity of training, and its tendency to rely on cues from conspecifics. The finding of this chapter opens new possibilities for manipulating the capacities and the robustness of pigeons' spatial memory to explore the effect of individual differences on collective decision-making. For example, one can compare differences in leader-follower relationships of birds that received the same number of training flights over different time scales, so as to measure the extinction of route memories.

The experiment also revealed for the first time a pigeon's capacity to store, recall and eventually apply spatial memories from multiple routes in parallel. Route memories can be seen as a sequence of landmark snapshots, which might provide information about directions to take and distances to travel next. This has been observed in ants that use landmarks not only when pinpointing their nest entrance (Knaden & Wehner 2005), but also when following stereotypical foraging paths (Collett et al. 1992; Kohler & Wehner 2005). Additionally, it has been shown that they can store and later successfully retrieve up to three different foraging routes (Sommer et al. 2008). Examining such phenomenon requires displacing ants that have completed a training run to the start of their inbound route. These so-called zero-vector ants can only rely on landmark-based route information because their path-integration vector has been reset to zero-state. A zero-vector ant is comparable to a displaced homing pigeon, as both have no access to information from the outbound trip. However, it would be interesting to examine whether those route memories are bi-directional, which has been suggested for honeybees (Zhang et al. 1999). If this were the case, pigeons would be able to fly from the loft to a release site despite the fact that they have learned the inbound routes only.

7.1.4 How does navigational experience influence leadership hierarchies?

In pigeon flocks some individuals contribute with higher weights to the movement decisions of the group than others, which results in hierarchical networks of transitive leader-follower relationships (Nagy et al. 2010). The findings of Chapters 2 and 4 raised new questions about whether and how variations in flock members' individually held navigational knowledge can influence the dynamics of the entire group. Chapter 5 reveals that leadership hierarchies in pigeon flocks appear resistant to changes in the navigational knowledge of a subset of their members, at least when these changes are relatively small in magnitude. I discussed that the advantage of hierarchical group structures might lie in the stability of the structure itself, rather than arising from particular features of its leader(s). The modelling work of Chapter 6 then developed this idea further by testing the navigational performance of simulated flocks with various underlying social structures, and discusses the potential benefits of structural stability in decision-making networks.

7.1.5 Are there advantages to hierarchical social structures?

In my penultimate, theoretical chapter, I incorporated social preferences into a model of collective motion to investigate the role of social connections on group navigation. Groups with hierarchical social structures navigated most accurately, especially when the number of preferred attachments per individual was small. Additional strong connections which led to more influential interactions seemed to distract from the target thereby decreasing the group's accuracy. I also observed that the group's leader-follower dynamics, which were determined by the members' movement decisions, closely mirrored the underlying social structure of the same group. Highly socially connected individuals were more influential when it came to movement decisions than those with fewer or no followers. Furthermore, my results suggested that position in the social network must correspond with individual assertiveness to allow maximum group performance. However, which aspect of an individual determines the type and number of its preferential attachments may vary between species and depend on many different features. The findings of this chapter contribute to a better understanding of the potential payoffs of collective travel in species that possess a range of different social associations. Yet, the question *why* groups navigate more accurately when they are hierarchically organised remains open. I suggest that this type of social relationships optimize collective decisions in that they allow a faster transfer of information between individuals. Groups will have few individuals that are central to the social network because of their number of affiliations to others. Following those individuals will be faster and therefore more beneficial than following those that are peripheral to the group (i.e. poorly affiliated), since information has to pass through only a few links to reach every member of the group (King & Sueur 2011). In many primate species, social relationships determine the movement decisions of the group. Preferred or connections between individuals can develop based on dominance levels or kinship. For example, rhesus (*Macaca mulatta*) and Japanese macaques (*Macaca fuscata*) are more likely to follow the movements of their relatives (Sueur & Petit 2008; Jacobs et al. 2011a). Furthermore, multi-female groups of Hamadryas baboons (*Papio hamadryas*) are directed by the single male of the group, a central individual which is highly connected to each group member (Kummer 1968). Yet, those social networks cannot only be found in primate groups. (Lusseau & Newman 2004) showed that groups of bottlenose dolphins contain individuals that are highly associated to other members of the group (i.e. high centrality). Interestingly, those central individuals also have a greater knowledge about the environment, and are more likely to initiate group movements (Lusseau & Conradt 2009) thereby reinforcing fast and most accurate decisions.

Pigeon groups are not only hierarchically organised when flying in flocks, but they also possess strong dominance hierarchies in the loft. Their definite, constant social organisation, which is determined by repeated pecking interactions (Masure & Allee 1934), is beneficial since it reduces aggressive interactions within the group. Once group members established their dominance rank relative to others, there are less aggressive interactions among group members (Lorenz 1935). Individuals only fight with those few others that possess similar rankings within the group, so as to maintain or improve their status (Heinroth & Heinroth 1956). Hence, without changes from the outside (e.g. addition or removal of group members), the overall organisation of the group is relatively robust and undergoes few changes. The results of Chapter 5 indicate that similar principles account for flight hierarchies. Stability in hierarchical networks may be beneficial if the process of changing from an existing, nearly optimal hierarchical structure to a potentially better one is likely to proceed through arrangements that are much less efficient than the original and the final state. Interestingly, dominance hierarchies go through extensive changes and fights when high ranked individuals are taken out of the group. Whether flight hierarchies are going through similar reorganisation processes when leaders leave the flock is an open – and highly interesting – question that will be the basis of future work.

7.2 Concluding remarks

When I began working on my thesis, most studies on group navigation and collective motion assumed that each individual behaves according to essentially identical interaction rules. With every chapter of this thesis however, the diversity of the individual features influencing group-movements and decision-making became ever more apparent. The experiments of this thesis provide a wealth of information on how pigeons' solo and group performance are influenced by social and navigational experiences.

The results of this thesis allow some reflections on the movements and organisation of naturally occurring pigeon flocks travelling in familiar area. A flock most likely consists of individuals with different ages that vary in their navigational experience. Some of the members might be sexual partners, siblings or parents and offspring. I now know that the flock will move along paths that the older and more experienced members have flown before. Young and inexperienced pigeons will benefit by following the movements of their conspecifics. By doing so, they will learn new routes or refresh obliterated memories. Those individuals that are more familiar to each other might fly in discrete dyads, closely coordinating each other's movements. The flock's leader/follower dynamics will be hierarchical and may depend strongly on its members' social relationships. In summary, I can say that movement decisions of pigeon flocks arise from specific interactions between members whose outcome is determined by individual behavioural features.

Modelling work can formulate mathematically the mechanisms underlying general biological principles but, in the end, there is always need for testing those potential mechanisms through experimental work. I hope with my work I have shown that this holds true for collective movements and decision-making, and that I have made some significant steps towards understanding how distinct individual features, experience and social links to others can influence conflict resolution and collective decision-making in co-navigating group of animals.

Glossary

Collective behaviour	Mechanistic aspect of grouping; mainly used for self-organised grouping behaviour that is usually characterised by synchronised individuals (Krause et al. n.d.)
Conflict resolution	Mutually exclusive preferences for homing routes
Consensus decision	Members of a group choose between two or more mutually exclusive actions with the specific aim of reaching a consensus (Conradt & Roper 2005)
Follower	An individual that follows/joins the initiator/leader for a certain activity (Pyritz et al. 2011)
Group	Two or more interdependent individuals who influence each other through social interaction (Dyer et al. 2009)
Leader	Individual eliciting following behaviour/exerting social influence on others, by its rank into the progression, its behaviour, or its social status (Petit & Bon 2010)
Leadership rank	A bird's ordinal position when flock members are ranked according to the average time differences with which they lead or follow others

Homing efficiency	The ratio between the straight-line distance between the release site and the loft, divided by the sum of the direct distances between the neighbouring fixes
Mimetism	The probability that an individual performs an behaviour depends on the number of individuals already performing this behaviour (anonymous mimetism), or the social relationships the individual has with group members already displaying the behaviour (selective mimetism) (King & Sueur 2011)
Navigational experience	Accumulated knowledge about certain locations and their relative position to the loft
Navigational information	Sum of all sensory inputs perceivable at a certain location
Leadership	The initiation of new directions of locomotion by one or more individuals, which are then readily followed by other group members
Route fidelity	Accuracy with which a bird reproduces the same route repeatedly

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