COGNITIVE ECOLOGY: ANIMAL MOVEMENT AND THE EFFECT OF EXPERIENCE ON COLLECTIVE DECISION-MAKING

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A Thesis Submitted to the School of Graduate Studies in Partial Fulfillment of the Requirements for a Master of Science

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Descriptive Note

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Lay Abstract

Cognition is the process of attaining, processing, and using information. Perception, learning, and memory are the main cognitive processes that are responsible for how we understand the world around us. In my thesis, I first review the cognitive processes involved in short-distance and long-distance animal movements. Secondly, I examine how a specific type of cognition, collective decision-making, improves with experience. Together, I reflect on various pillars of animal cognition, discuss my contributions to the field, and suggest further research ideas.

Abstract

Cognition shapes how we perceive and react to our environment. Throughout my Master of Science, I have studied two major fields of animal cognition. My thesis first reports on the cognitive aspects of animal navigation in home ranging and seasonal migration, then I explore the development of group expertise through extensive experience with collective decision-making. The key contributions of the first manuscript (Chapter 2) are a condensed yet detailed summary of the behaviours involved in individual and collective animal movement, followed by research ideas to fill the gaps of the current literature. The key contribution of the second manuscript (Chapter 3) is developing an experiment to study group expertise, a topic that currently lacks controlled experiments, via testing the effect of experience on collective decision-making. This thesis expands the existing knowledge on animal movement and collective decision-making.

Acknowledgments

Accomplishing a MSc is difficult, especially when a global pandemic began soon after I moved to a new city. Firstly, I would like to thank my parents, Faith and Herzl, and my sister, Nadia, for the encouragement and support throughout my MSc. I thank my supervisor, Reuven, who has taught me so much about research and integrity during my 28 months at McMaster. I would like to thank the Dukas Lab members who have helped me with questions I had about my project, department, or city, and who became my good friends throughout my time in Hamilton. Lastly, I would like to thank my friends who kept me sane during lockdown and were always willing to listen to me talk about my ants.

Preface

This thesis is composed of two independent manuscripts. I am the sole author of the general introduction (Chapter 1) and general conclusion (Chapter 4). I chose to take the lead authorship of the first manuscript (Chapter 2) because Dr. Dukas had presented me with this intriguing proposal on a fascinating topic. This first manuscript is called "The Cognitive Ecology of Animal Movement: Evidence from Birds and Mammals", and was published in Frontiers in Ecology and Evolution in September of 2021. I am the primary author, so in partner with my co-authors, Reuven Dukas and Tal Avgar, I researched, wrote, and edited this manuscript. The focus of my Master of Science was the second manuscript (Chapter 3), in which I established ant colonies in the Dukas lab, developed a new experimental protocol, executed the experiments, analyzed the data, and have written the manuscript. This second manuscript is called "Group Expertise: The Effect of Experience on Collective Decision-Making", which is currently in progress and intended for publication. I am the primary author, while my co-author Reuven Dukas assisted in editing the manuscript, and the other three co-authors, Janice Yan, Grant Doering, and Tricia Skelton, assisted with experimental design and video scoring.

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CHAPTER 1

General Introduction

Throughout my Master of Science, I have written two manuscripts on diverse topics that explore fundamental information relating to animal cognition. These manuscripts examine relevant to animal movement and collective decision-making, important for understanding the success of solitary and social living, and the development of group expertise.

Chapter 2 explores the newly emerging field of cognitive movement ecology. Cognitive movement ecology is a combination of two fields: Movement ecology, the study of animal movement throughout landscapes, has only recently began incorporating cognitive ecology, the study of animal cognition and behaviour. This extensive review serves as an empirical foundation for the cognitive movement ecology and summarizes existing evidence of cognition in movement ecology while inviting future research in specific areas.

Chapter 3 builds on the small existing pool of research testing how experience affects collective decision-making—a topic currently lacking in research. Group expertise, the ability for groups to master complex tasks with experience, is fundamental to social living. The success of social groups depends on their ability to make quick, effective decisions. Yet, it is unknown if collective decision-making performance improves with experience. To test this, we establish a new model for studying group expertise under controlled contributions.

CHAPTER 2

The Cognitive Ecology of Animal Movement: Evidence from Birds and Mammals

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ABSTRACT

Cognition, defined as the processes concerned with the acquisition, retention and use of information, underlies animals' abilities to navigate their local surroundings, embark on long-distance seasonal migrations, and socially learn information relevant to movement. Hence in order to fully understand and predict animal movement, researchers must know the cognitive mechanisms that generate such movement. Work on a few model systems indicates that most animals possess excellent spatial learning and memory abilities, meaning that they can acquire and later recall information about distances and directions among relevant objects. Similarly, field work on several species has revealed some of the mechanisms that enable them to navigate over distances of up to several thousand kilometers. Key behaviors related to movement such as the choice of nest location, home range location and migration route are often affected by parents and other conspecifics. In some species, such social influence leads to the formation of aggregations, which in turn may lead to further social learning about food locations or other resources. Throughout the review, we note a variety of topics at the interface of cognition and movement that invite further investigation. These include the use of social information embedded in trails, the likely important roles of soundscapes and smellscapes, the mechanisms that large mammals rely on for long-distance migration, and the effects of expertise acquired over extended periods.

Keywords: cognition, decisions, expertise, movement ecology, navigation, perception, philopatry, spatial learning, spatial memory, social learning, trails

INTRODUCTION

The factors necessary for maximizing growth, survival and reproduction vary in time and space. To accommodate this temporal and spatial variation, most animals possess the physical means for moving towards beneficial resources and away from harm. In addition to the ability to move, however, animals must frequently decide about the timing, direction and duration of movement as well as its final destination. To make such decisions, animals rely on their cognitive system, which consists of the structures and processes concerned with the acquisition, retention and use of information (Dukas, 2004, 2017). Research in the past few decades has integrated mechanistic information on animal cognition with functional knowledge on animal ecology and evolution (Dukas, 1998; Dukas & Ratcliffe, 2009; Morand-Ferron et al., 2016; Ratcliffe & Phelps, 2019). Our contemporary understanding of animal cognitive ecology, however, is still not well incorporated within the field of movement ecology.

Scientists across a wide range of disciplines have engaged in insightful research on organismal movement for a long time. Examples range from laboratory analyses of movement in bacteria at the micrometer scale (Adler, 1976; Koshland, 1980; Eisenbach & Lengeler, 2004) to field work on whale migration over thousands of kilometres (Pike, 1962; Rasmussen et al., 2007). The young field of movement ecology adds to this knowledge by relying both on new technologies for monitoring natural animal movement over vast areas, and on modern computational tools for analyzing the large data sets acquired through automated tracking (Nathan et al., 2008; Abrahms et al., 2021). Only recently, however, movement ecology has increased the consideration of animal cognition (Fagan et al., 2013, 2017; Avgar et al., 2015; Lewis et al., 2021), an approach that typically requires controlled experimental settings.

Animal cognition can be divided into a few interconnected categories. The first component is perception, which involves capturing information from the environment and converting it into internal representations retained by neuronal networks. Information acquisition is carried out by receptors specialized to capture cue attributes emitted by or associated with relevant objects including patterns of reflected light, sound, odors, flavours and texture. Newly acquired information may either fade away immediately, remain for brief periods, or consolidate into long lasting internal representations that can persist for many years. The process of adding new representations into neuronal networks is termed learning, and the information retained is referred to as memory. The only utility of information acquisition and retention is to determine and execute action. To this end, individuals have to continuously assess relevant environmental features and their experience to decide about their subsequent action (Anderson, 2015; Dukas, 2017; Rolls, 2014).

The framework of movement ecology laid out by Nathan et al (2008) clearly recognized the crucial role of cognition in general and navigational abilities in particular for the obvious reason that cognition underlies all animal decisions regarding when and where to travel. Although one can study movement while ignoring its underlaying internal mechanisms, a thorough understanding of individuals' movement decisions requires us to quantify the cognitive processes that drive them. Chief among the cognitive abilities relevant to animal movement are the mechanisms that enable spatial orientation. Such mechanisms allow individuals to both navigate their local surrounding while engaging in their daily routines, and to undertake long-distance seasonal migrations.

To keep our review within the space constraints, we will focus here on experimental research in birds and mammals as these groups have been the subject of most studies in movement ecology. While we will aid our analyses with a few examples from insects, we cannot encompass here the rich body of research on insect navigation (Dyer, 1998; Collett & Collett, 2002; Wehner, 2020). Our review has five parts. In the first two sections, we focus on individual cognition and ignore social influences. First, we discuss the roles of learning and memory in movements within the local settings of one's home range. Second, we take the broader perspective of the innate mechanisms, learning and memory involved in long-distance movements typically associated with seasonal migration. Most birds and mammals have parental care, many species live in groups (Clutton-Brock, 2016; Wilson, 1975), and even the ones classified as solitary show rich social interactions (Caro, 1994; Elbroch et al., 2017). Hence, our third section assesses the multiple effects of the social environment on the cognitive features that guide movement. The fourth part briefly integrates the previous three sections to address the understudied topic of animal expertise, defined as the traits that enable individuals to show superior performance after a long period of individual and social learning (Dukas, 2019). Finally, our prospects section focusses on a few suggestions for promising research at the interface of cognition and movement.

INDIVIDUAL LEARNING AND MEMORY WITHIN THE HOME RANGE

Most animals can benefit from learning about the attributes of relevant environmental settings, resources and individuals. Examples include food sources, shelters, temperature, predators and other hazards, kin, social partners, competitors, and prospective mates. Key features associated with such variables include unique, identifying cues such as odor, color, sound, taste, size and shape, and their location in space and time. It is thus not surprising that all animals subjected to critical experimental tests show learning when tested under the controlled conditions designed to distinguish learning from relevant alternatives (Dukas, 2008a, 2017). Critical evidence for learning, however, requires strict experimental protocols because learning can only be inferred indirectly through a change in behavior. This means that one has to carefully rule out non-learning alternatives including changes in perception, satiation, physiology, and motivation. For example, while GPS movement data on a single mule deer (*Odocoileus hemionus*) suggested reliance on spatial memory (Jakopak et al., 2019), the study could not critically rule out alternatives including the use of trails or other cues, or following other individuals. Nevertheless, evidence such as the ability of an individual to return to its summer range after moving about 100 km away is instructive regardless of the mechanism employed. That is, we encourage researchers to modulate their vocabulary based on their evidence where the settings and priorities do not allow for critical tests of learning. Additionally, future research may continue to develop protocols that allow critical tests of cognitive abilities in the field (Morand-Ferron et al., 2016). We provide examples of such field tests throughout our review.

Most relevant for movement ecology is animals' abilities to learn and remember the spatial locations of resources and individuals. Spatial learning and memory merely means having the ability to acquire and later recall information about distances and directions among relevant objects. This allows individuals to navigate, i.e., find their way among these objects. Controlled laboratory studies indicate robust spatial learning and memory in key model systems including fruit flies (*Drosophila melanogaster*) (Ofstad et al., 2011) and rats (*Rattus norvegicus*) (Moser et al., 2008; O'Keefe & Dostrovsky, 1971). Many field studies over the past several decades, which included controlled experiments as well as observations using individually tagged individuals, have revealed exceptional navigational abilities in honey bees (*Apis mellifera*) (Dyer, 1998; Menzel et al., 2005; Riley et al., 2005; Seeley, 1996; von Frisch, 1967). In addition to routinely traveling to flower patches up to several km away from their nests, honey bees communicate to nestmates the direction and distance to both flower patches and prospective new nests (Dyer, 2002;

Visscher, 2007). These skills allow honey bees to dynamically adjust to changes in the spatial and temporal distribution of floral rewards, and to locate the best locally available tree cavities for new nests (Beekman & Ratnieks, 2000; Seeley, 2010; Steffan-Dewenter & Kuhn, 2003; Visscher & Seeley, 1982).

It is fair to assume that all birds and mammals possess spatial learning and memory as good as or better than that experimentally demonstrated for honey bees in the field. Controlled laboratory and enclosure studies typically confined to up to several meters indeed demonstrate excellent spatial learning and memory in a variety of birds and mammals (e.g., Balda & Kamil, 1992; Morris, 1981; Sherry, Krebs, & Cowie, 1981). Much of the field work is either limited or suggestive owing to the lack of a large body of controlled experiments. A notable exception is the homing pigeon (*Columba livia domestica*) discussed in the cognition and long-distance movement section below (Wallraff, 2005; Wiltschko & Wiltschko, 2015).

Consider the following example for study design that has enabled strong inference on cognitive processes. A well controlled field study (Edwards et al., 1996) tested spatial memory in domestic sheep (*Ovis aries*) in a 30 by 45 m pasture. There was a grid of 4 by 8 plastic bowls with randomly chosen 4 bowls containing food pellets (Fig. 1a). The food could not be seen until a sheep was within 0.5 m from the bowl. Each sheep was tested individually 11 times over about a week. In trials 1-6, the position of the bowls containing food remained constant, and sheep reduced the number of bowl visits required to locate the four bowls containing food (Fig. 1b). In trial 7, half the sheep had no food in any bowl, and half the sheep had food in four new randomly chosen bowls. This probe trial tested whether sheep relied on spatial memory or on cues emanating from the food. The sheep in both groups mostly searched first in the four bowls that had previously contained food and then searched randomly among the other bowls. This resulted in no change in the number of visits needed to locate the previously food-containing bowls in the no-food group, and in a large increase in the number of visits needed to locate the four new food containing bowls in the location-switching group (Fig. 1b). Trials 8-10 consisted of retraining, where the no-food group from trial 7 received food again in the same bowls as in trials 1-6, while the location-switching group received food at the same bowls as in trial 7. Sheep from the previously no-food group maintained their small number of visits required to locate the four food bowls, while sheep from the location-switching group reduced again the number of visits required to find the new locations of the four food bowls (Fig. 1b). Trial 11 tested spatial memory after longer than the retention period of 12 h used previously. Here half the sheep were tested after 24 h while the other half were tested after 72 h. Both groups showed the same high performance as in the earlier trials (Fig. 1b). The sheep study illustrates how one can critically assess spatial memory in the field. Similar work may be conducted at larger spatial scales with a variety of wild animal populations that are habituated to feeding near humans.

INNATE BEHAVIOUR, INDIVIDUAL LEARNING AND MEMORY IN SEASONAL MIGRATION

Seasonal migration occurs in nearly all major animal groups. Traveling to exploit favourable conditions (e.g., food, warmth, or mates) and escaping adverse conditions (e.g., parasitism, predation, or competition) is a beneficial strategy that many animals adopt (Avgar et al., 2014; Somveille et al., 2015). To make navigational decisions during migration, animals use a combination of innate instructions, information they have previously learned either individually or gleaned from others, and cues they currently perceive (Spiegel & Crofoot, 2016). Seasonal migration consists of three phases in which animals use different cues to navigate (Mouritsen, 2018) (Fig. 2). During the long-distance phase, animals navigate using innate and learned information, and global/regional cues (Schmidt-Koenig, 1990; Gwinner, 1996). In the narrowing-in/homing phase, animals use compasses and landscape information (O'Keefe & Nadel, 1978; Toledo et al., 2020). For the pinpointing-the-goal phase, animals follow specific landmarks near the goal or the goal itself. We will focus on species that live long enough to partake in multiple migrations throughout their lives, providing good opportunity to discuss cognitive processes beyond innate instructions.

The vast literature on animal migration has revealed a multitude of innate mechanisms and learned features that guide individuals towards their long-distance goals. The number and complexity of processes involved as well as the variation among species precludes simple generalizations. We thus detail below several key elements. We will first assume no social interactions and focus on the combination of innate mechanisms and individual learning that guide navigation. Then we will discuss in the subsequent section social influences and social learning, which are prevalent in many species.

Compass Orientation

In many cases, orientation towards a long-distance goal can be aided by a compass mechanism. The three compasses—magnetic, sun, and stars—provide simple directional information regardless of the current location (Wiltschko & Wiltschko, 2015). Migratory birds, especially inexperienced individuals, rely on compasses during the long-distance and homing phases of long-distance movement (Mouritsen, 2018). The avian magnetic compass is primarily innate (Wiltschko and Gwinner, 1974), while celestial compasses are primarily learned (Michalik et al., 2014; Wiltschko & Wiltschko, 1980). Birds typically use one compass mechanism to calibrate another (Pakhomov & Chernetsov, 2020). For example, night-migratory songbirds update their star compass using their magnetic compass as a reference (Wiltschko & Wiltschko, 1975). Subsequently, the calibrated star compass can be used independently (Wiltschko & Wiltschko, 2015).

Information from multiple compasses is usually available concurrently, depending on the season, time of day, weather, and magnetic anomalies. Currently, there are various conflicting theories regarding the hierarchy of the compasses used for orientation (Johnsen et al., 2020; Pakhomov & Chernetsov, 2020). When multiple cue types are available, birds likely have preferences for which one to follow based on individual experience, current environment, and distance to their goal (Chernetsov, 2017; Munro & Wiltschko, 1995; Wiltschko & Wiltschko, 2015). If an in-use compass becomes unreliable, birds switch to cues with more accurate readings. For example, pigeons initially rely on magnetic cues, then attempt to compensate for disorientation during magnetic anomalies or experimental disturbance using celestial cues (Ioalé, 1984; Keeton, 1971; Schiffner et al., 2011; Wiltschko & Wiltschko, 2001).

Magnetic Compass. Geomagnetic fields stretching from poles to equator remain relatively consistent over animals' lifetime, making them informative for determining direction. Birds may rely on a few features of magnetic fields including intensity (strength of the magnetic field), inclination (the angle between the magnetic field and earth surface), direction (polarity), and declination (the difference between true north and magnetic north) (Mouritsen, 2018; Wallraff, 2005; Wiltschko & Wiltschko, 2015; Wiltschko & Wiltschko, 2005). While much of the research on magnetic compasses has been done in birds, there is growing evidence that mammals, specifically rodents and bats, also possess a magnetic compass (Finn, 2021; Holland et al., 2010; Holland et al., 2006; Oliveriusová, et al., 2014; Oliveriusová et al., 2012). Some large terrestrial mammals can spontaneously align their bodies with magnetic fields (Begall et al., 2013; Červený et al., 2017; Obleser et al., 2016; Painter et al., 2016), but it is unclear if they use an established magnetic compass for navigation.

Birds inherit their ability to sense magnetic inclination (Wiltschko & Gwinner, 1974; Wiltschko & Wiltschko, 1972, 2005). In some cases, they must calibrate this compass using celestial cues (Able & Able, 1990; Cochran et al., 2004), or vice versa (Muheim et al., 2007; 2009). Magnetic compass orientation is dependent on the presence and wavelength of light (Muheim et al., 2002; Wiltschko & Wiltschko, 1981b), although night-migratory songbirds require less light than diurnal birds (Wiltschko & Wiltschko, 2015). The avian magnetic compass works in a functional magnetic intensity window; increasing or decreasing the magnetic strength by 25-30% is disorienting, until birds establish a separate functional window (Wiltschko & Wiltschko, 2015; Wiltschko, 1978). Because magnetic field intensity changes through space, an adjustable compass is advantageous for long-distance movements (Wiltschko & Wiltschko, 2015).

<u>Solar Compass</u>. The temporal cycles and perceived movement of the sun make it an excellent guide for orientation (Guilford & Taylor, 2014). Solar cues are valuable during the long-distance phase of movement (Mouritsen, 2018; Wiltschko & Wiltschko, 2015). Birds may use polarized light cues or the azimuth of the sun itself (Munro & Wiltschko, 1995; Wiltschko & Wiltschko, 2015; Muheim et al., 2016). The sun compass requires learning in juvenile birds. Pigeons establish their sun compass before they are 12 weeks old, while early experience flying can accelerate learning to 8-10 weeks (Wiltschko & Wiltschko, 1981a).

Birds must integrate the sun's movements into their internal clock to orient themselves based on their perceived time-of-day (Wiltschko & Wiltschko, 1980, 1981a; Schmidt-Koenig, 1990; Schmidt-Koenig et al., 1991; Åkesson et al., 2017). The integrated sun compass and internal clock must constantly be updated to account for daily and seasonal changes in the perceived location of the sun (Wiltschko & Wiltschko, 2015). Improper synchronization between the internal and sun compass is disorienting. For example, pigeons under experimental settings in which the light-dark cycles were shifted 6 hours ahead flew 90 degrees counter-clockwise compared to control pigeons (Schmidt-Koenig, 1958). Once individuals recognize that their compass is shifted, they resynchronize their sun compass and internal clock. Such synchronization occurs naturally when birds travel to different locations (Schmidt-Koenig, 1958; Wiltschko et al., 1998). Yet in some cases, following the sun compass without updating it can be advantageous. Arctic shorebirds such as the American golden plover (*Pluvialis dominica*), semipalmated sandpiper (*Calidris pusilla*), pectoral sandpiper (*C. melanotos*), and the white-rumped sandpiper (*C. fuscicollis*) migrate without synchronizing their internal clock and sun compass. At high altitudes, nonstop flights attuned to the sun compass result in orthodomes, travelling the shortest distance between two points on a sphere (Alerstam et al., 2001).

Star Compass. The other celestial compass, which is based on stars, provides direction for nighttime navigation. Night-migratory songbirds learn to locate a north-south directional axis based on the fact that stars closer to the celestial axis move through smaller arcs (Emlen, 1970). In order for night-migratory songbirds to learn the compass, they require 2-3 weeks of exposure to a rotating star pattern (Able & Able, 1990; Michalik et al., 2014). Learning occurs during the pre-migratory period before autumn (Emlen, 1972, 1970), but can take place the following spring if needed (Zolotareva et al., 2021). Star patterns change seasonally because of the earth's rotation around the sun, so migrating birds must regularly update their celestial information (Wiltschko & Wiltschko, 2015). On the other hand, because birds learn the celestial axis rather than the time-dependent celestial location of stars, shifting birds' internal clock does not affect their star compass orientation (Emlen, 1970; Mouritsen & Larsen, 2001; Pakhomov et al., 2017). Once a star compass is established, it can be used independently of magnetic and solar cues.

Vector Navigation

Long-distance movement poses a considerable challenge for young, inexperienced individuals. First year avian migrants either follow experienced individuals (see Social Learning section below) or use vector navigation (Gwinner, 1996; Bingman & Cheng, 2005; Mouritsen, 2018). Vector navigation, also called the clock-and-compass strategy, uses at least one compass and a set of genetically encoded instructions for direction and distance rooted in their internal clock (Mouritsen et al., 2016). Garden warblers (*Sylvia borin*) deprived of any seasonal cues for a year displayed migratory restlessness only at the appropriate temporal windows for spring and fall migrations (Gwinner, 1996). The inherited migratory instructions are population specific. Crossbreeding individuals from separate populations with distinct migration routes results in hybrid offspring with intermediate migration patterns (Berthold & Querner, 1981; Helbig, 1991).

Circadian and circannual clocks are responsible for the onset, distance (duration), and direction of migration (Gwinner, 1996). Before learning alternative navigation strategies, naïve individuals rely on genetic instructions, effectively demonstrated by displacement experiments. Experienced birds can correct for displacement over extraordinary distances, while inexperienced juveniles typically fail to do this (Perdeck, 1958). For example, in an experiment involving the displacement of juvenile and adult white-crowned sparrows (*Zonotrichia leucophrys gambelii*), adults corrected for displacement by adjusting their route towards their usual wintering grounds. Juveniles neglected to reorient themselves, flying in the direction of the expected migration route (Fig. 3) (Thorup et al., 2007). Juveniles fail to correct for displacement not because they lack that ability, but because they lack information required for compensation (Wiltschko & Wiltschko, 2015).

In some instances, juveniles can correct for displacement. Surprisingly, juvenile blackcaps (*Sylvia atricapilla*), willow warbles (*Phylloscopus trochilus*) and garden warblers could reorient themselves after experimental or natural displacement during their first migration to an unfamiliar goal (Thorup et al., 2011). Likewise, some juvenile common cuckoos (*Cuculus canorus*) corrected for experimental displacement at the same level as adults, travelling towards their expected wintering grounds (Thorup et al., 2020). These compensation mechanisms towards an unfamiliar goal remain unclear—juveniles may be following magnetic cues or using inherited signposts, which are discussed next (Thorup et al., 2011, 2020).

Signposts

Signposts are markers that trigger specific responses that aid in navigation (Freake et al., 2006; Wiltschko & Wiltschko, 2005). Behavioural responses to signposts can be genetically encoded or imprinted. Various species respond to signposts. These include birds (Beck & Wiltschko, 1988; Fransson et al., 2001), turtles (Lohmann et al., 2001), eels (Schabetsberger et al., 2016; Naisbett-Jones et al., 2017), salmon (Putman, 2015; Scanlan et al., 2018) and lobsters (Boles & Lohmann, 2003). Signature magnetic and physical properties act as signposts. Examples include region-specific magnetic intensity, temperature, odor, water salinity or currents (e.g., Fransson et al., 2001; Schabetsberger et al., 2016). For example, particular magnetic intensities can trigger animals to change directions during migration (Naisbett-Jones et al., 2017; Putman, 2015; Scanlan et al., 2018), reorient themselves to avoid ecological barriers and dangerous conditions (Beck &

Wiltschko, 1988; Lohmann et al., 2001), or land at stopover sites for refueling (Fransson et al., 2001).

True Navigation

True navigators are individuals that can navigate to a goal after being displaced to an unknown location, at an unknown distance and direction (Able, 2001; Griffin, 1952; Keeton, 1974; Kishkinev et al., 2021; Kramer, 1953; Thorup et al., 2007, 2020; Wikelski et al., 2015). True navigation allows individuals to reach their goal when familiar landscape information is absent. Animals must determine their geographic location, then orient themselves toward the goal using a compass (Griffin, 1952). As mentioned in the vector navigation section above, displaced adult white-crowned sparrows flew towards their usual wintering grounds, exhibiting true navigation, while inexperienced juveniles relied on vector navigation, flying according to genetically encoded instructions (Thorup et al., 2007). Bi-coordinate position fixing, that is, navigation using at least two gradients, is a prerequisite for true navigation (Griffin, 1952; Freake et al., 2006). True navigation involves at least one compass and gradient-based or location-based navigation discussed in the section below.

Navigation Based on Learning and Memory

Animals may learn distinct information for guiding their navigation. Such learning may be egocentric, meaning that it is based on the animal’s own movement, or exocentric, implying that it is based on features of the landscape (Klatzky, 1998). Based on the type of information learned, one can distinguish among four non-mutually exclusive navigation strategies (Fagan et al., 2013) detailed in the four sub-sections below (Fig. 4).

Route-based navigation. During route-based navigation, also called path integration (Fig. 4A), individuals record their movements relative to the starting point using a compass and return by reversing their net outward movements (Bidder et al., 2015; Fagan et al., 2013; Schmidt-Koenig, 1975; Wallraff, 2005; Wiltschko & Wiltschko, 2000, 2015). Learning is egocentric and structured around self-movement, thus the individual does not need to be familiar with the landscape because landmarks are not required (Kimchi et al., 2004; Wehner et al., 1996). Route-based navigation is a cognitively simple strategy that requires little memorization (Fagan et al., 2013; Mittelstaedt &

Mittelstaedt, 1982; Wehner & Wehner, 1986). Additional distance and turns increase the cognitive demand of keeping track of the route, leaving more room for mistakes. Thus, we can expect route-based navigation to be used at smaller scales. During route-based navigation, individuals acquire information of the unfamiliar area *en route* to build their exocentric navigation strategies (Wiltschko & Wiltschko, 2015).

Location-based navigation. In location-based navigation (Fig. 4B), one learns the spatial relationships between landmarks and goals (O'Keefe & Nadel, 1978; Bingman & Cheng, 2005; Wallraff, 2005; Fagan et al., 2013; Wiltschko & Wiltschko, 2015; Toledo et al., 2020). This strategy may use simple memory snapshots (Alert et al., 2015; Cartwright & Collett, 1982) or complex cognitive representations of space (Bingman & Cheng, 2005). A compass is required for learning geographical directions in relation to landmarks (Wiltschko & Wiltschko, 2015, 1982). Although learning spatial relationships between landmarks and goals can produce a heavy memory load, repeated experience moving throughout the landscape should reinforce these memories, reducing cognitive load. Migratory animals probably learn spatial information at a larger scale but lower acuity compared to non-migratory navigators (Bingman & Cheng, 2005). This navigation technique is valuable during the homing phase of long-distance movement.

Beacon-based navigation. Individuals using the beacon-based strategy (Fig. 4C) are guided to their goal by at least one familiar beacon, which is a landmark near the goal (Biro et al., 2004; Fagan et al., 2013; Papi, 1992; Wallraff, 2005; Wiltschko & Wiltschko, 2015). This includes traveling towards the goal itself or following a series of landmarks to reach the goal (Collett et al., 1986, 1992; Steck et al., 2009; Guilford & Biro, 2014; Yovel & Ulanovsky, 2017). While exploring unfamiliar areas, individuals use a compass to navigate until they learn which landmark(s) lead them to their goal. Once they have established a route, compasses become unnecessary as they can follow the landmark(s) directly (Biro et al., 2007; Guilford & Biro, 2014; Papi, 1992). Beacon-based navigation is most applicable during the homing and pinpointing phases of long-distance movement, as landmarks are typically too small to perceive at long distances, with the exception of massive geographical features such as coastlines or mountains.

Gradient-based navigation. Individuals that rely on gradient-based navigation (Fig. 4D) have to learn perceptual signatures of at least one feature that changes gradually over space (e.g., magnetic or olfactory gradients) (Bingman & Cheng, 2005; Fagan et al., 2013; Wallraff, 2005; Wiltschko & Wiltschko, 2015). Navigating using gradients requires a compass (Wiltschko & Wiltschko, 2015). Magnetic cues provide both compass orientation and gradient-based navigational information through different perceptual mechanisms—interfering with magnetic cues for one does not impair the other (Chernetsov et al., 2017; Deutschlander et al., 2012; Holland & Helm, 2013; Munro et al., 1997). Gradients are functional during the homing phase and can be projected to longer distances beyond an individual's experience (Gagliardo et al., 2013; Wikelski et al., 2015). For example, birds learn the features of the magnetic field throughout their home or migratory range, then extrapolate that information to spatial scales beyond what they have experienced (Fig. 5) (Thorup et al., 2007; Kishkinev et al., 2021). Extrapolated gradients are not always accurate representations of nature (Wallraff, 2005). Individuals extrapolate to unknown locations based on memory of familiar gradients, leaving unfamiliar anomalies and gradient changes unaccounted for, which could result in navigation miscalculations. For instance, individuals displaced to the northwest corner of Fig. 5A would move away from their true home because their extrapolated gradient is signalling them to fly in the opposite direction (Wallraff, 2005).

Selecting a navigation strategy. Strategies of navigation vary among species. In species that employ multiple strategies, their use depend on individual experience, preference, available information, distance from the goal, and energy expenditure (Filannino et al., 2014; Green et al., 2020). Furthermore, animals may use multiple navigation strategies simultaneously (Wiltschko & Wiltschko, 2015). Navigation strategies driven by landscape familiarity (location-, beacon- or gradient-based, Fig. 4) are generally preferred over route-based navigation (Wiltschko & Wiltschko, 2015), likely because these strategies are less prone to errors, and allow for short cuts and course corrections. Pigeons using gradient-based navigation modified their route depending on their current motivational state. Food deprived pigeons released at an unknown location flew to a known food source, while satiated pigeons released at the same location flew to their home loft (Blaser et al., 2013). Contrarily, route-based navigation does not allow individuals to revise their goal, and displacing individuals is disorienting, as their reversed net outwards movements no longer lead to the return point (Müller & Wehner, 1988; Andel & Wehner, 2004). If information necessary for a preferred strategy is unavailable, animals revert to a simpler feasible navigation technique. For instance, rats revert to route-based navigation when beacons are unavailable (Shettleworth & Sutton, 2005).

Synthesis

Notwithstanding our precautionary note that both the multitudes of complex processes involved in navigation and the variation among species preclude simple generalizations, we wish to end this section with a synthesis. In many species, naïve individuals traveling alone can successfully execute long-distance migration based on innate instructions and one or more compasses. All three compasses typically include innate as well as learned information. Overall, navigation is greatly enhanced by learning, which may be solely based on an individuals' own movement, but typically also on a variety of environmental features including landmarks and gradients. Furthermore, individuals in many species acquire information related to navigation from others, a topic we discuss next.

SOCIAL INFLUENCES AND SOCIAL LEARNING

The traditional separation of animals into solitary and social species is rapidly fading as we learn to appreciate the sophisticated social skills of animals historically classified as non-social (Costa, 2006; Durisko & Dukas, 2013; Elbroch et al., 2017). It is fair to assume that individuals in most species can gain from information gleaned from conspecifics, and that such information may guide their movements. Social influence merely means that a focal's behavior is affected by the presence, activity, or cues left by other individuals. Social learning means that a focal acquires novel information based on the presence, activity, or cues left by other individuals. As we discuss below, a dominant source of information that young individuals should attend to is parents and other old individuals. While we focus here on species with parental care, direct or indirect cues left by parents are highly relevant in species in which young do not encounter their parents (Dukas, 2010). We begin by discussing philopatry and the importance of trails. We then review collective navigation, and the use of social learning for decisions regarding home range and migratory movement.

Philopatry

In birds and mammals, newborn rely on their parents for food and protection. When young are sufficiently mature, they typically travel farther from their nest or shelter and often follow their parents. The duration of parental feeding of fledgling varies widely among birds and is positively associated with the duration of practice required for reaching some threshold of foraging proficiency (Ashmole & Tovar, 1968; Heinsohn, 1991; Hunt et al., 2012). In mammals, post-weaning maternal care is brief in short-lived species but can last for years in long lived species (Clutton-Brock, 2016). At least in carnivores, the long duration of post-weaning maternal care is related to the low learning rate associated with challenging hunting skills (Caro, 1994; Wachter et al., 2017). While there is wide variation among species, in the vast majority of birds and mammals, young have ample opportunities to learn many features of their natal environment including the food types preferred by their parents, foraging skills, and the spatial locations of food, shelters and hazards (Slagsvold & Wiebe, 2007, 2011).

In most species, a large proportion of individuals do not reach reproductive maturity. Of those that reproduce, a large proportion of parents fail to lead their offspring to independence owing to either predation or starvation (Clutton-Brock, 1988). Hence the fact that young have reached independence is a solid evidence that their parents have chosen well their natal environment. Given their likely lack of knowledge about alternative sites and the costs of acquiring such information, the young should copy their parents' choice and show philopatry where possible (Stamps et al., 2009). Several other factors that promote philopatry include advantages of familiarity with biotic and abiotic features of the natal habitat, improvements to the environment by previous generations such as reusable burrow systems, tree cavities and trails, and the mortality risk associated with exploration of novel areas (Waser & Jones, 1983). Indeed, philopatry is prevalent in both birds and mammals (Greenwood, 1980; Waser & Jones, 1983).

A large cross fostering study tested the effects of early social experience on natal habitat preference in pied flycatchers (*Ficedula hypoleuca*) in Spain. Pied flycatchers are long-distance migrants who breed throughout Europe but spend the winter south of the Sahara. The experiment involved cross fostering nestlings between nests in a coniferous habitat and nests in a deciduous habitat one km away and, as a control, cross fostering nestling within each of the two distinct habitats. Most returning young birds came to the forest patch from which they had fledged, regardless of whether they had been cross-fostered within or between patches (Fig. 6a). These results indicate a strong effect of early experience on habitat choice (Camacho et al., 2016), which is consistent with many other bird studies (Greenwood, 1980; Weatherhead & Forbes, 1994). The results also illustrate remarkable navigational and spatial memory abilities, which allowed one year old birds to relocate the small patch of their natal forest after a round trip migration of thousands of km. While the young birds receive no guidance from their parents (Mouritsen & Larsen, 1998), some reliance on social information cannot be ruled out.

Similar effects of early social influence were observed in a study involving 57 radio-collard moose (*Alces alces*) in Sweden, which revealed strong philopatry by calves. Ten of the 14 radio collard calves returned with their mothers to their summer range, and 9 out of the 10 subsequently separated from the mothers but remained within 2 km from them. The female offspring kept returning to that range in subsequent summers (Cederlund et al., 1987).

In both birds and mammals, site fidelity is even stronger in breeding adults than in young. The same reasons listed above can readily explain why adults remain in their current home range, or keep returning to it in species that show seasonal migration. Indeed, adult philopatry tends to increase with the temporal consistency in conditions, risks, and resources, and particularly their predictability from year to year (Riotte-Lambert & Matthiopoulos, 2020; Morrison et al., 2021). The factor of experience becomes stronger over time, because individuals can keep learning site-specific relevant information as discussed in the expertise section below (Dukas, 2019). Individuals, however, can rely on their experience to decide whether it pays to show site fidelity. Indeed in many bird species, individuals are more likely to show site fidelity if they succeed than fail in reproduction (Greenwood & Harvey, 1982). For example, an elegant experiment manipulated the nesting success of prothonotary warblers (*Protonotaria citrea*) that used nest boxes in southern Illinois (Hoover, 2003). Birds were randomly assigned into rearing zero, one or two successful broods within a season, with the failures manipulated via predation. Success rates strongly affected the return rates of birds in the following season, after their long-distance migration to Central or South America (Fig. 6b). Intriguingly, males whose nesting attempts failed were three times more likely to show site fidelity if they had successful rather than unsuccessful neighbors. Because the males can monitor and even father offspring in neighbouring territories through extrapair copulations, it is likely that neighbors' success affected their subsequent site fidelity (Hoover, 2003). In addition to their remarkable navigational and spatial memory abilities, the prothonotary warblers also showed sophisticated skills in optimizing decisions affecting future reproductive success based on both their own and their neighbors' experience.

To synthesize, while there are clear benefits to philopatry and obvious costs to dispersal, the social and genetic trade-offs vary among species, leading to a large within and between species variation in the overall and sex-specific patterns of philopatry (Clutton-Brock, 2016; Greenwood, 1980; Morrison et al., 2021; Smale et al., 1997; Waser & Jones, 1983). There are many unresolved issues ripe for investigation, which can take advantage of modern movement ecology tools. Specifically, the causes and consequences of within species variation in philopatry provide intriguing questions. On the cognitive ecology side, in species where one sex remains and the other sex disperses, are there between sex differences in cognitive traits such as spatial abilities, tendencies to explore, attachment to kin, and openness to new experiences? On the movement ecology side, current tracking techniques can help us quantify the sex-specific trade-offs that underlie philopatry versus dispersal.

Trails

Trails can be perceived as social information left from previous generations owing to their usefulness in connecting multiple sites containing resources such as food, water, minerals and shelters while minimizing effort and perhaps danger. Similarly, trails may be used for migratory movement. Trails are also a rich source of contemporary social information, as olfactory and visual cues left by previous trail users can provide information on their identity, number, reproductive state, condition, and the time and direction of travel (Mutinda et al., 2011). Finally, established and well maintained trails allow fast, efficient travel between feeding areas, and between feeding patches and shelters. Indeed, as noted above, an established trail system is one factor that can promote site fidelity in walking species. For example, elephant shrews (*Elephantulus rufescens*) restrict much of their travel to a network of trails from which they regularly remove plant material and other obstacles. It has been suggested that their rapid running along these trails is an effective anti-predatory strategy (Rankin, 1965; Rathbun, 1979). In larger animals, trails have been studied primarily in elephants (*Loxodonta africana*) (Vanleeuwe & Gautier-Hion, 1998; Mutinda et al., 2011) and mentioned in a few other studies (Di Fiore & Suarez, 2007; Noyce & Garshelis, 2014; Trapanese et al., 2019). Despite the prevalence and potential importance of animal trails in shaping animal movement, however, they remain understudied.

Aggregations, information, and individual movement

A fair number of animals live their whole or part of their lives in aggregations. Examples include bird and bat roosts, and nesting aggregations in solitary bees and birds (Allee, 1931; Beauchamp, 1999; Fenton & Simmons, 2015; Michener et al., 1958; Rolland et al., 1998). Philopatry, discussed above, can readily lead to aggregation. Additional factors include the rarity of appropriate sites, anti-predatory advantages and social information about food and predators (Danchin et al., 2004; Galef & Giraldeau, 2001; Evans et al., 2016). The most likely effect of social information on movement is via local enhancement, whereby individuals searching for food join others whom they observe feeding (Krebs et al., 1972; Thiebault et al., 2014; Thorpe, 1963). Another possibility is that individuals from the aggregation follow departing, apparently informed individuals to food patches. Some field observations agree with this possibility while others do not (Brown, 1986; Danchin & Richner, 2001; Harel et al., 2017; Marzluff, Heinrich, & Marzluff, 1996; Mock et al., 1988; Sonerud et al., 2001; Urmy, 2021). It is fair to assume, however, that socially biased movement occurs in many species.

Both philopatry and the rarity of satisfactory aggregation sites should lead to large spatial variation in the distribution of aggregating species. Because members of the aggregation can save time and energy as well as incur lower mortality by foraging closer to the aggregation, one would expect lower individual densities farther from the aggregation (Fig. 4 in Dukas & Edelstein-Keshet, 1998). Bumblebees in the field indeed showed such pattern of spatial distribution (Fig. 3, 4 in Osborne et al., 2008). Reliance on social information would further increase the spatial variation in individual densities. This can lead to cascading spatial effects on other trophic levels. For example, bumblebee wolves (*Philanthus bicinctus*), sphecid wasps that prey on bumblebees, nest in rare, large aggregations that persist over decades as indicated by the fact that an aggregation studied in the early 1960s (Armitage, 1965) still existed in 2004 (Dukas, 2005). Bumblebee densities at flowers were much lower within 4 km than farther than 5 km from the bumblebee wolf aggregation (Fig. 7a). Consequently, fewer flowers of the bumblebee pollinated plant, western monkshood (*Aconitum columbianum*), set fruit within a few hundred m from the bumblebee wolf aggregation than 6 km away from the aggregation (Fig. 7b) (Dukas, 2005).

Collective Navigation and Social Learning

Group-living animals balance individually acquired information with social information to make navigational decisions for home range and migratory movement. When individual information is insufficient, social information can reduce uncertainty (Bergman & Donner, 1964; Hamilton, 1967; Grünbaum, 1998; Couzin, 2018). As we discuss below, collective decision-making mechanisms consist of sharing information among group members or following a subset of directed individuals. Concurrently, knowledge regarding movement patterns can propagate within the group, reducing individual learning costs and improving movement efficiency (Mueller et al., 2013; Sasaki & Biro, 2017; Jesmer et al., 2018).

Collective Navigation Using Shared Information

Collective navigational accuracy can be increased by comparing information through social cues (emergent sensing), pooling information (many wrongs), or communicating preferences (voting).

Emergent sensing. In emergent sensing (Fig. 8A), group members respond to environmental gradients. This results in collective navigation even if all individuals are naïve (Berdahl et al., 2018; Couzin, 2018). Theoretical models suggest that this is a simple collective decision-making strategy that does not require either memory or complex cognition (Berdahl et al., 2013; Hein et al., 2015; Torney et al., 2009). Individuals within the group respond to environmental information and subsequent social cues. For example, golden shiners (*Notemigonous crysoleucas*) were tested in environments with varying light patches. Golden shiners prefer dark environments and increase swimming speed as a function of light, causing individuals to reduce speed in dark patches, resulting in the group collectively navigating towards dark areas (Berdahl et al., 2013). There is a trade-off between sensitivity to environmental gradients and social information. Greater ability to perceive environmental gradients lessens the need for social interaction, which could decrease group cohesion (Puckett et al., 2018). Therefore, an appropriate balance between environmental cues and social information can be achieved by weighing incoming information (Puckett et al., 2018).

Many wrongs. The many wrongs principle (Fig. 8B) emerges from individuals pooling each imperfect estimate of direction to improve accuracy, in which group cohesion suppresses individual noise (Berdahl et al., 2018; Bergman & Donner, 1964; Biro et al., 2006; Codling & Bode, 2014; Nesterova et al., 2014; Simons, 2004; Tamm, 1980). For example, homing pigeons released with a small flock flew faster and more direct routes compared to their routes when released alone, even in familiar areas (Fig. 9) (Dell'Ariccia et al., 2008). When individuals are uncertain about navigational decisions, averaging group information reduces error. However, if the difference between individual estimates becomes too large, the group may split or adopt a leader (Biro et al., 2006; Nesterova et al., 2014). For example, homing pigeons with distinct individually established route preferences were released in pairs. When the distance between the two routes was small, pairs typically averaged their paths. But if the distance between each individual's established route grew beyond a threshold, pigeons either followed one of the established routes or split to pursue their own route (Biro et al., 2006). For both emergent sensing and many wrongs, directional accuracy increases as group size increases, notably in groups with few individuals (Berdahl et al., 2013; Bergman & Donner, 1964; Wallraff, 1978). We can expect these strategies to be especially advantageous when knowledge among the group members is low and homogeneous, e.g., a group moving through a novel landscape or consisting of inexperienced juveniles.

Voting. During the voting strategy (Fig. 8C), individuals advertise their preference and then the group selects the majority or averages the choices (Black, 1988; Norton, 1986; Sueur, Deneubourg, & Petit, 2011; Sueur et al., 2010; Walker et al., 2017). For example, it has been suggested that adult female African buffalo (*Syncerus caffer*) indicate their preferred foraging patch by orienting themselves towards a certain direction while grazing. The herd then departs in the average direction of individual preferences (Prins, 1996). This widely cited example requires critical tests. Similarly, individuals in troops of Olive baboons (*Papio anubis*) propose a movement path. If the difference between the various prospective paths is above a threshold, the group follows the majority. But, when the angle between proposed routes is below the threshold, the group compromises to average the paths (Strandburg-Peshkin et al., 2015). Emergent sensing, many wrongs, and voting are not mutually exclusive. Furthermore, they are frequently combined with leadership and social learning discussed in the next sections.

Leadership

Group members can have varying degrees of influence on navigational decisions. Commonly, animal groups consist of a subset of individuals called "leaders" which guide the remaining group members deemed "followers" (Chance, 1967; Squires & Daws, 1975; Wallraff, 1978; Wilson, 2000; Van Vugt, 2006). Leadership can be distributed among multiple animals or centered around a sole individual (Garland et al., 2018; Strandburg-Peshkin et al., 2018). Leaders may be aware of their status, are recognized by the group as leaders, and can even produce overt signals to lead their group (Boinski & Campbell, 1995; Lusseau & Conradt, 2009; Poole et al., 1988; Raveling, 1969). Alternatively, leaders could be anonymous and unaware of their influence, thus followers rely on passive cues, such as the orientation of neighbours (Couzin et al., 2005; Rosenthal et al., 2015). The terms leader and follower are relative, as a leader in one situation may be a follower in another. For example, leadership may vacillate depending on the area. Homing pigeons can take turns leading during different segments of the same route (Biro et al., 2006). Additionally, leadership status depends on the identity of others in the group. For example, pigeons have leader hierarchies: if individual A leads B, and B leads C, A will also lead C (Biro et al., 2006; Nagy et al., 2010).

In some groups, knowledge or experience determines leadership. Leaders may possess and act on information that followers do not have, such as knowledge of a migratory route (Chernetsov et al., 2004; Jesmer et al., 2018; Olsen, 2001a, 2001b; Reebs, 2000). However, followers are not always naïve. Followers may hold the same knowledge as leaders, but are more agreeable (Arnold, 1977; Smith et al., 2016), have lower route fidelity (Freeman et al., 2011), or are more receptive to social information (Guttal & Couzin, 2010). In homing pigeons, experience increases the chance of becoming a leader, but does not predict it (Flack et al., 2013; Flack et al., 2012; Watts et al., 2016). Factors such as social status (King et al., 2008), sex (Lusseau & Conradt, 2009), or age can also drive leadership. For example, pods of killer whales (*Orcius orca*) are led by postreproductive females (Brent et al., 2015). Likewise, V-formations in families of greater white-fronted geese (*Anser albifrons*) are primarily led by the father (Kölzsch et al., 2020).

Old individuals may possess information on the most efficient migratory route or the location of a rarely visited site that provides limited resources such as food or water. Such a site may be crucial for the group's success during either a local food shortage or drought. It has been suggested that old elephant matriarchs possess exclusive spatial information crucial to group fitness (Foley et al., 2008; Mutinda et al., 2011). There is indeed evidence for a positive association between matriarch age and her social knowledge, which translates into superior leadership by older matriarchs (McComb et al., 2001, 2011; Mutinda et al., 2011). The role of spatial information in that superior leadership, however, is unknown.

In some cases, leadership is much less systematic. For example, individuals that travel at high speeds (Pettit et al., 2015) or near the front of the group (Pettit et al., 2013b) can emerge as leaders. Further, group members may rotate leadership roles frequently. Alternating leadership roles is fittingly seen in juveniles with similar demographics and experience (Nesterova et al., 2014). For example, flocks of juvenile northern bald ibis (*Geronticus eremita*) take turns leading their V-formation during migration (Voelkl & Fritz, 2017; Voelkl et al., 2015). Additionally, leaders can emerge through simple behavioural rules by followers following the movements of their neighbours (Herbert-Read et al., 2011; King et al., 2011; Rosenthal et al., 2015; Sankey et al., 2021; Torney et al., 2018). Thus, the individuals that initiate movement may have a large influence on group navigation.

Although followers are less influential than leaders, followers can participate in and even initiate decisions. However, the threshold to reach a quorum is higher when followers propose decisions compared to leaders (Bousquet et al., 2011; Kummer, 1968; Walker et al., 2017). For example, families of Canada geese (*Branta canadensis*) perform vocalizations and head-tossing to evoke movement in the group, which ensures cohesion for take-off. If the calls are initiated by a family member other than the father, the number of calls required to elicit movement increase, as well as the period of time before departure (Raveling, 1969).

Cognitive abilities are not identical across group members, leaving some individuals predisposed to become leaders or followers. The shy–bold dimension of animal personality posits that bold individuals have a consistent tendency to explore unfamiliar areas and objects (Gosling & John, 1999; Réale et al., 2007; Sih et al., 2004). Bold individuals are more likely to be leaders than shy individuals (Found & St. Clair, 2016; Kurvers et al., 2009). Compared to shy individuals, leaders are more likely to explore while navigating (Flack et al., 2018), travel at faster speeds, and lead in both familiar and unfamiliar locations (Sasaki et al., 2018). In some cases, leaders may be responsible for immense changes in collective migratory behaviour. For example, in elk (*Cervus canadensis*), bold individuals are three time less likely to migrate than shy individuals from the same population (Found & St. Clair, 2016), likely because they better adapt to changing environments (Found & St. Clair, 2019). Another dimension of personality, sociability, can also produce leaders. Chacma baboons (*Papio ursinus*) follow the movements of individuals that they are socially affiliated with (King et al., 2011). Thus, individuals that are highly social are more influential than their less social peers.

Social Learning

Information can diffuse throughout a population and across generations via social learning. Accumulated knowledge can act as a second, nongenetic, inheritance system (Jesmer et al., 2018; Tennie et al., 2009; Whiten, 2005). Many animals learn migratory behaviour from their parents or older conspecifics in their population (Agostini, 2004; Chernetsov et al., 2004; Harrison et al., 2010; Olsen, 2001a, 2001b; Palacín et al., 2011; Urbanek et al., 2005). Social influences may even override genetic instructions (Schüz, 1951; Perdeck, 1958; Ferrari et al., 2009; Mellone et al., 2016). Old individuals possess valuable information that has helped them survive thus far. Hence, juveniles profit by learning from old, experienced members of their group, even if juveniles possess adequate migratory information. For example, juvenile whooping cranes (*Grus americana*) migrate using more direct routes when flying with older individuals compared to groups consisting only of young birds (Fig. 10) (Mueller et al., 2013). It is unclear, however, if juveniles deviate from direct routes because of either error or exploration of unfamiliar territory (Mueller et al., 2013; Wolfson et al., 2020). Additionally, learned migratory behaviours are more flexible than genetic instructions, allowing changes in migratory patterns to spread through populations within the lifetimes of individuals. For example, populations containing older whooping cranes were more likely to modify their migratory routes by establishing new wintering grounds closer to their breeding grounds (Teitelbaum et al., 2016).

Individuals can update socially transmitted information to filter out inefficient routes. While homing, pigeon followers actively participate in navigation, learning more direct routes than that of their leader (Pettit et al., 2013). Additional individuals incorporating their own information into the collective pool of knowledge can further improve group performance. An experiment by Sasaki and Biro (2017) investigated the effects of social learning and cumulative improvement. The experimental group consisted of chains of homing pigeon pairs, beginning with a single pigeon that had developed a homing route after 12 releases. The pigeon was then paired with a naïve individual for another 12 releases. The naïve individual learned the route throughout those trials, becoming experienced, then was paired with a new naïve individual for another 12 releases. This process of pairing a newly experienced pigeon with a naïve pigeon was repeated an additional two times for a total of 60 releases per chain. One control group consisted of solo pigeons and the other control group consisted of fixed pairs of pigeons. Pigeons in both control groups were released 60 times from the same site as the experimental group. By the end of the experiment, the experimental group outperformed both solo and fixed pair controls, which plateaued in efficiency. This suggests that naïve individuals learn route information via social learning and contribute to cumulative improvements in route efficacy, more so than solo or fixed pairs with the same total amount of experience.

Synthesis

Social groups adopt various strategies, typically coinciding, to move within and throughout a landscape. Groups can share information to improve navigational accuracy, during which opinions from some individuals have more influence than others, while valuable information can diffuse throughout the group via social learning. For example, leadership and voting coincide in packs of African wild dogs (*Lycaon pictus*) during pre-departure social rallies. Pack members increase the amount of abrupt nasal exhales (sneezes) prior to departure. Any pack member can propose a departure by initiating sneezing, although individuals other than the highest ranking dominant dogs must have higher signal frequency in order to succeed (Walker et al., 2017). Collective navigation, leadership and social learning are difficult to assess in nature through observation alone. Without controlled experiments, we can only estimate which process is occurring without firm conclusions.

EXPERTISE AND MOVEMENT

Individual learning, social influence and social learning are ubiquitous among animals. Their long term, combined effects lead to expertise, defined as the features that allow individuals with extensive experience on a given complex task to show superior performance on that task compared to novices (Dukas, 2019). While expertise has been studied primarily in humans (Ericsson & Lehmann, 1996; Ericsson et al., 2006; Strittmatter et al., 2020; Vaci et al., 2019), it is highly relevant for other species as it can manifest in many behaviors including movement. Two domains pertinent to movement ecology are first, mastery of an individual’s habitat, which may include a vast memory about the identity, location and occurrence of a variety of relevant items, events and individuals. Examples include the location of seasonal food plants, shelters, territorial neighbors, and predators. Second, individuals can improve their movement speed and efficiency with practice. This may be owing to motor learning within a small territory (Stamps, 1995), adopting optimal routes that avoid challenging terrain in a large home range (Green et al., 2020), or learning to better handle a variety of challenges throughout a long travel route. For example, a within individual comparison in black kites (*Milvus migrans*) indicated improvement in migratory performance with age. Part of this improvement was due to birds enhancing their abilities to exploit tailwinds and cope with wind drift (Sergio et al., 2014). Other studies also indicate that birds improve their abilities to handle winds and rising air currents with experience (Harel et al., 2016; Wynn et al., 2020).

Critical research on expertise is currently scarce as it requires comparisons of the same individuals over time while controlling for relevant alternatives that affect performance. These include correlated changes in anatomy, morphology, physiology and effort (Dukas, 2019). Furthermore, between individual analyses are insufficient as they commit selection bias owing to the likely higher mortality rates of inferior individuals. As far as we know, only a single program, which combined observations and controlled experiments in the field, has considered all factors by quantifying within individual foraging performance in natural settings, muscle physiology, and effort as functions of experience (Dukas, 2008b, 2008c; Dukas & Visscher, 1994; Schippers et al., 2010; Schippers et al., 2006). Many other species are amenable for long term research programs that add controlled experiments to information about within individual changes in performance with age (Clutton-Brock, 2016; Clutton-Brock, 1988; Daunt et al., 2007a; Daunt, et al., 2007b; Leach & Sedinger, 2016; Sand et al., 2006; Wooler et al., 1990).

CONCLUSIONS AND PROSPECTS

Our three main conclusions are first, that birds and mammals possess good spatial learning and memory, which enable them to find their way while engaging in their daily activities. Second, we have good understanding of the cognitive mechanisms that allow many species to navigate successfully over distances spanning up to thousands of km. Third, the movement ecology of many birds and mammals is heavily determined by social influence and social learning. While there is large variation among animals, researchers initiating work on a lesser studied species may assume that it has good spatial cognitive abilities that are influenced by social observations. Nevertheless, the strength of evidence for our three conclusions is rather mixed. Very few controlled experimental studies assessed spatial learning and memory in birds and mammals over a large area. On the other hand, owing to the conspicuousness and ubiquity of animal migration, we have known for a long time about animals’ abilities to orient well between their winter and summer grounds. Some of the mechanisms underlying these navigational skills are mostly understood, at least for a small selection of species, primarily birds. Finally, we know that social information influences some aspects of bird and mammal movement including, for example, philopatry and migration in some species. There are probably, however, many other aspects of movement that are under social influence but understudied. Examples include trails, long-lasting scents, and cues that indicate recent activity or successful reproduction by conspecifics.

While we focused on relatively well studied topics, our review can readily reveal subjects that invite future research. Most notably, we have not critically addressed specific issues of both perception and decisions even though they likely have strong effects on animal movement (Avgar et al 2013). Some studies have addressed issues of perception relevant to movement ecology. For example, the topic of perceptual range, defined as the maximum distance from which one can detect relevant landscape features, has been recognized for some time (Zollner, 2000; Schooley and Wiens, 2003), but we still know relatively little about it. Similarly, while decisions have been implicitly included within the overall study of animal movement, there has not been a focus on the exact decision rules employed by individuals when considering, for example, when and where to go (Bauer et al., 2011). Finally, our review primarily encompassed issues related to movement either within a home range or during seasonal migration. We have not addressed the two other relevant categories of dispersal and nomadism (Baguette et al., 2014; Teitelbaum & Mueller, 2019) even though they can gain from a synthesis that takes a cognitive ecology approach.

There are various areas that would gain from further integration of methods and insights from cognitive ecology into the study of animal movement. First, there is a strong research bias towards the visual domain. It is thus crucial that we devote more research effort to the effects of understudied sensory domains on animal movement. Such domains include olfaction, electromagnetic radiation beyond the human perceptual range, and night vision. For example, we perceive the landscape primarily in the visual domain, but soundscape (Pijanowski et al., 2011; Van Oosterom et al., 2016) and smellscape (Ackels et al., 2021; Buehlmann et al., 2015; Gagliardo et al., 2013; Henshaw, 2013; Nevitt, 2008; Wallraff & Andreae, 2000) may be as or more important for many species. Particularly promising is the likely possibility that many animals perceive a rich scene of long-lasting olfactory cues, which inform them about the location, condition, age and sex of conspecifics, competitors and predators. Second, enlightening information gathered from GPS-collard animals has inspired increased interest in the spatial information that animals learn about, remember and employ to guide their movement. The GPS data, however, are merely observations on individuals' locations over time. Hence they must be supplemented with controlled field studies that critically test for the spatial learning and memory of species of interest. Such work may modify protocols previously employed for critical tests of spatial memory in the field, such as the one detailed in Fig. 1 (Edwards et al., 1996). Third, a few studies indicate that the large-scale spatial structure of animal movement affects species at other trophic levels through competition, predation, herbivory, pollination and seed dispersal (e.g., Dukas, 2005; Kohl et al., 2018). We think that further research on the effect of the movement patterns of one species on other species can be highly illuminating. Fourth, understandingly, a large share of movement ecology research has been devoted to large mammals. However, we have little experimental data on the mechanisms underlying seasonal migration in these species. For example, do they rely on all three compasses as birds do? Fourth, mechanisms of time keeping both within day and throughout the year have received significant attention in both animal cognition and physiology (Gallistel, 1989; Shettleworth, 2009; Kumar et al., 2010). While we know that animals possess excellent biological clocks that guide their short and long term movement decisions, we know less about how animals time their revisits to familiar places within and between days and years (Janmaat et al., 2013, 2014; Berger-Tal & Bar-David, 2015). Finally, there is growing appreciation that non-humans show long-term improvements in performance similar to those studied in human experts (see Expertise and Movement section above). Mechanisms contributing to the superior performance of experts include greater working and long-term memory, better allocation of attention among co-occurring tasks, and quicker and refined decisions (Dukas, 2019). Decisions regarding movement can benefit from expertise and should be subjected to future research. Similarly, evidence from humans indicates that people working together for a long time develop group expertise primarily owing to enhanced social dynamics (Argote & Epple, 1990; Tindale & Winget, 2017). Similar group expertise likely occurs in animal groups and probably contributes to superior movement performance.

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Figure Captions

Figure 1. (a) The layout of food bowls in the sheep spatial memory experiment. Open circles illustrate empty bowls while filled circles depict the four bowls containing food. (b) The mean ± SE number of visits required to locate all food bowls. In trials 1-6, the food was always in the same 4 bowls. In trial 7, half the sheep encountered food in 4 new bowls (▫) and these bowls also contained food in trials 8-11. The other half of the sheep encountered no food in any bowl in trial 7 (▪) and had food in the same bowls as in trials 1-6 in trials 8-11. In trial 11, half the sheep were tested 24 h after trial 10, and the other half were tested 72 h after trial 10. The asterisks indicate visit numbers statistically different from random search in tests conducted in trials 1, 2 and 8. Data from Edwards et al. (1996).

Figure 2. Illustrated phases of long-distance navigation. (A) During the long-distance phase, individuals rely on celestial and magnetic cues as well as on large landmarks such as mountains, lakes and coastlines. (B) During the homing phase, gradients, landmarks, and compasses are important. (C) During the pinpointing-the-goal phase, residential cues including beacons and the goal itself are valuable. Figure from Mouritsen (2018) with permission.

Figure 3. Last observed direction of white-crowned sparrows after experimental displacement east of their location. Adults (blue, large arrow is the average) correctly reoriented southwest towards their original wintering grounds, exhibiting true navigation. Juveniles (red, large arrow is the average) failed to reorient, continuing southward using vector navigation. Based on Thorup et al., (2007).

Figure 4. Types of memory-based navigation. (A) In route-based navigation, the individual sums the distance and direction of its outward movements to estimate its current position and take a direct path to its starting point. (B) In location-based navigation, the individual memorizes spatial relationships between landmarks and goals. (C) In beacon-based navigation, specifically pilotage, the individual follows sequential landmarks leading to the goal. (D) In gradient-based navigation, the individual navigates with memorized gradients. In this illustration, both gradients are magnetic

(solid and dash lines), with a magnetic anomaly in the southeast corner, which could initially disorient the individual. The scale of D is over 1000 km. Created with BioRender.com.

Figure 5. An example of true and extrapolated magnetic gradients. A single gradient is showed for simplicity with positive (dashed line) and negative (solid line) values, on a scale over 1000 km. (A) True magnetic gradient values surrounding the individual's home (black dot) and its familiar range (red circle). (B) The individual extrapolates gradients based on experience, and incorrectly anticipates the gradient in the northwest and southeast corners. Based on Wallraff (1985).

Figure 6. (a) The proportions of pied flycatcher nestlings that returned to breed in the same patch where they had fledged after being cross-fostered within or between habitats containing either pines or oaks. Data from Camacho et al. (2016). (b) Territory fidelity of female and male prothonotary warblers that were experimentally manipulated to have 0, 1 or 2 successful broods in the previous year. Data from Hoover (2003).

Figure 7. (a) The mean ± SE number of bumble bees observed at six matched pairs of coneflower (*Rudbeckia occidentalis*) and goldenrod (*Solidago* spp.) within 4 km and farther than 5 km from a large bumble bee wolf aggregation. (b) Fruit-set in the bumble bee pollinated flower, western monkshood (*Aconitum columbianum*), within 0.5 km and farther than 5 km from a large bumble bee wolf aggregation. Left bars: the percentage (mean ± SE) of marked monkshood flowers that produced fruits. Right bars: the total number (mean ± SE) of fruits on haphazardly chosen monkshood plants. Data from Dukas (2005).

Figure 8. Illustrated examples of collective decision-making strategies. (A) Emergent sensing in which individuals respond to environmental gradients (e.g., golden shiners increase swimming speed as a function of light) and social cues (e.g., responding to movement of neighbours). This results in collective navigation towards favourable dark areas. (B) Many wrongs in which the collective pooling of estimates supresses individual error (e.g., indirect homing routes in pigeons; dashed arrows) and increases collective navigational accuracy (large arrow). (C) Voting occurs when individuals express their preference for initiation or direction of movement (e.g., African buffalo orienting towards a proposed movement path; small blue and red arrows). Voting prompts

the group to choose the majority (large red arrow) or average the proposed paths. Created with BioRender.com.

Figure 9. GPS-tracked pigeon routes between a release location (R) and home loft (H). Six pigeons were released six times individually (blue), then six times as a flock (red; one track per flock release), then pigeons were released another six times individually (green). Pigeons released with a small flock flew faster and more direct routes compared to their routes when released alone. Figure from Dell'Ariccia et al., (2008) with permission.

Figure 10. Groups of whooping cranes containing old individuals migrate using more direct paths compared to groups consisting of only juveniles. (A) Telemetry and visually observed locations of whooping cranes throughout their migratory journey. (B) Examples of migratory routes that juveniles performed with (blue) and without (red) the presence of older individuals. (C) Distance from straight line paths during migration of juvenile groups with and without older individuals. Figure from Mueller et al., (2013) with permission.

Figures

Fig 1

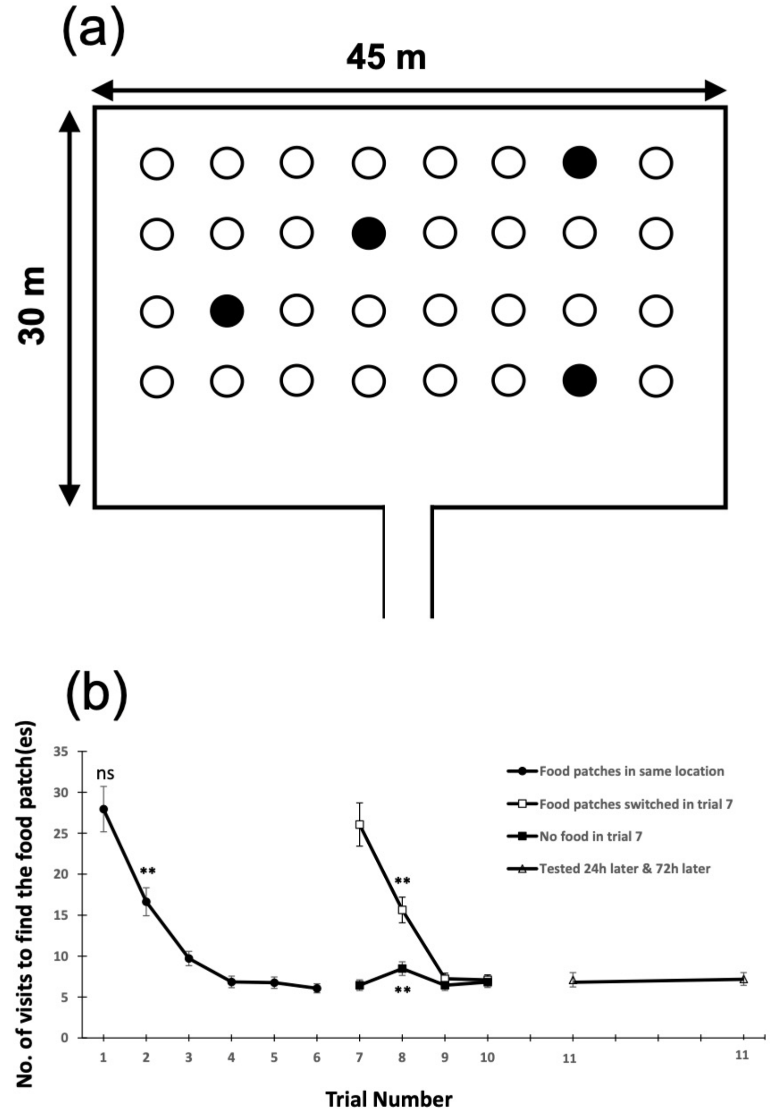


Fig 2

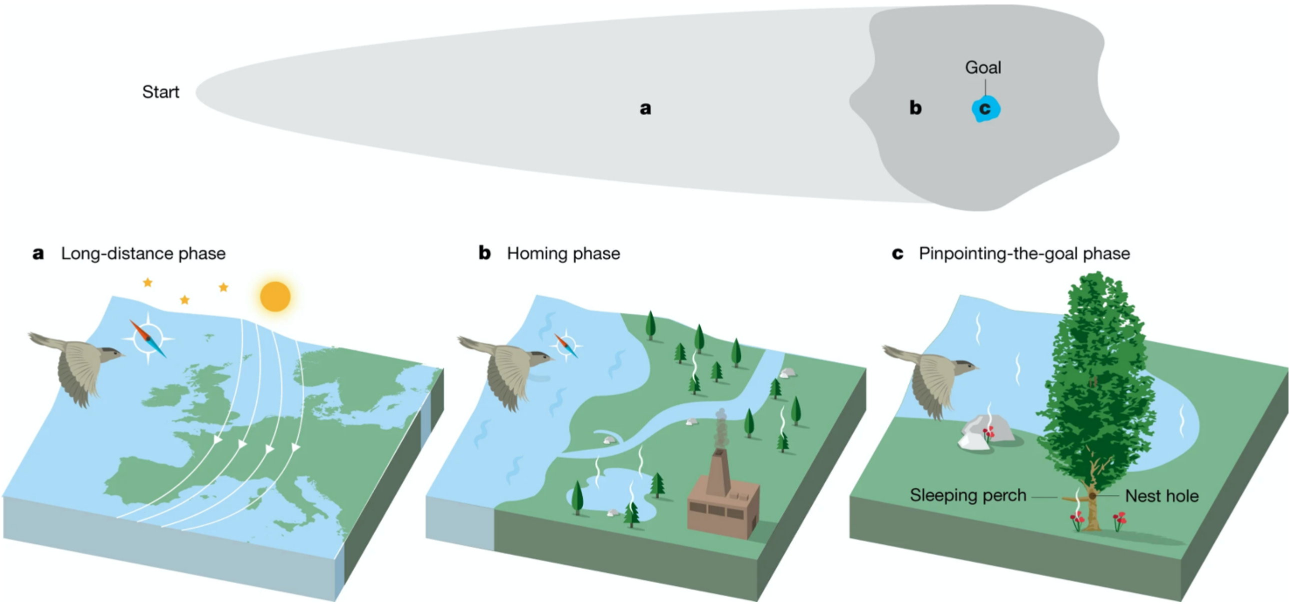

Start
a
b
Goal
c
a Long-distance phase
b Homing phase
c Pinpointing-the-goal phase
Sleeping perch
Nest hole

Fig 3

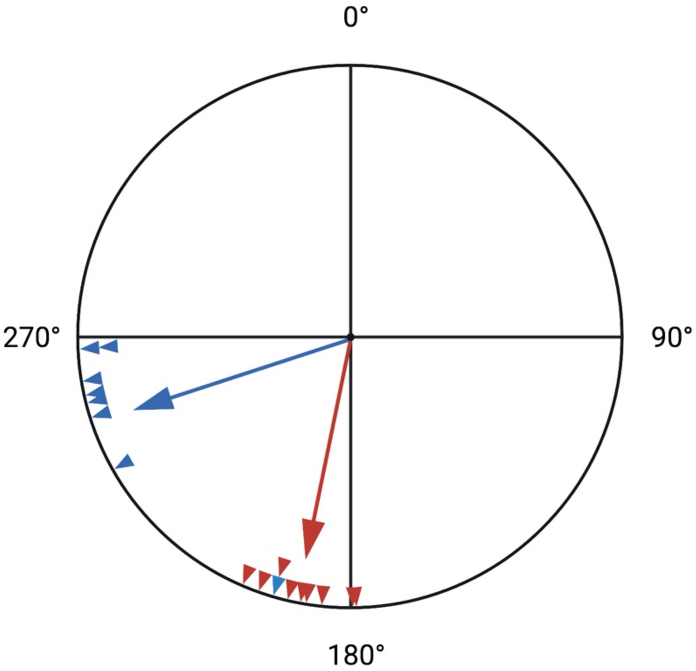
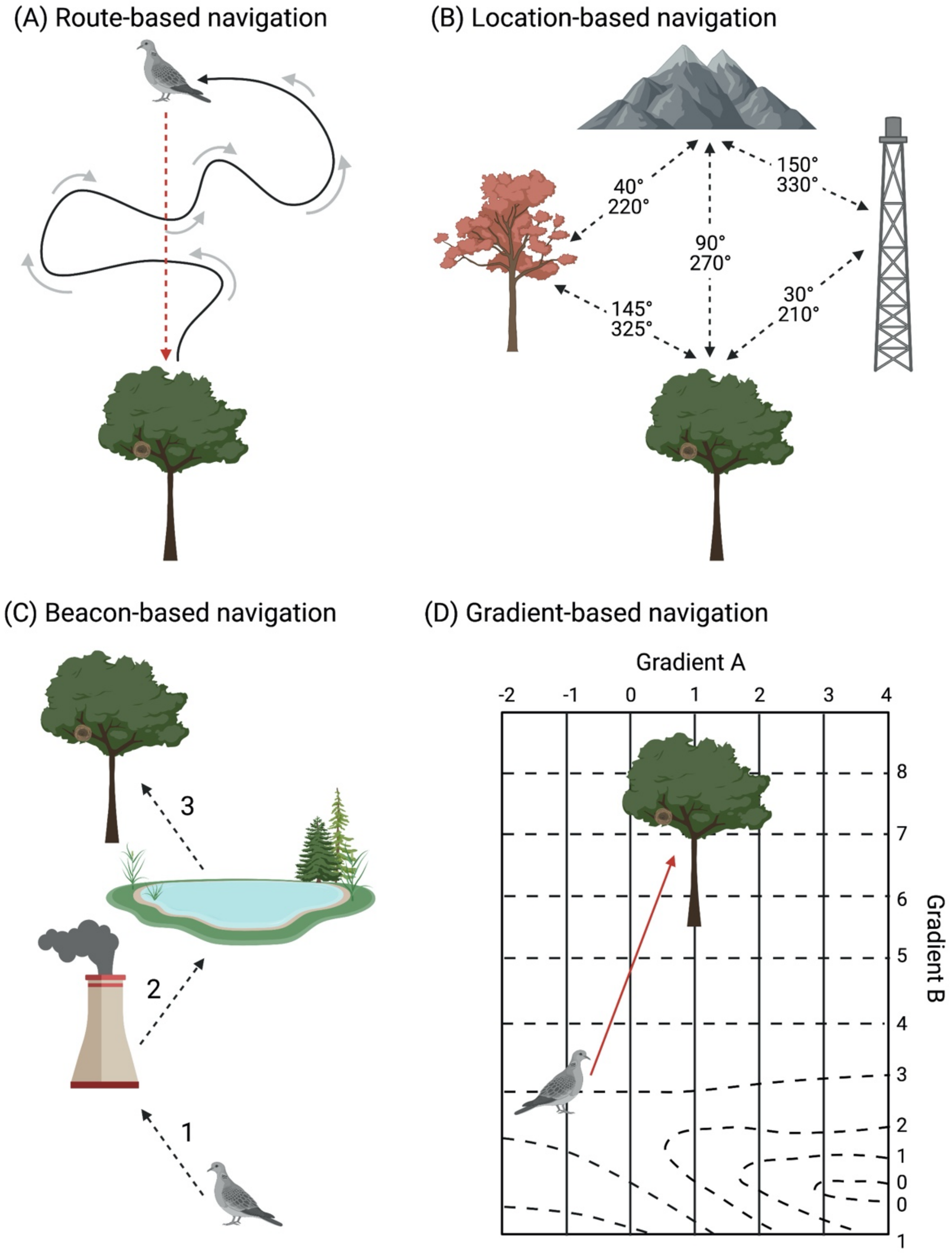

0°
90°
180°
270°

Fig 4

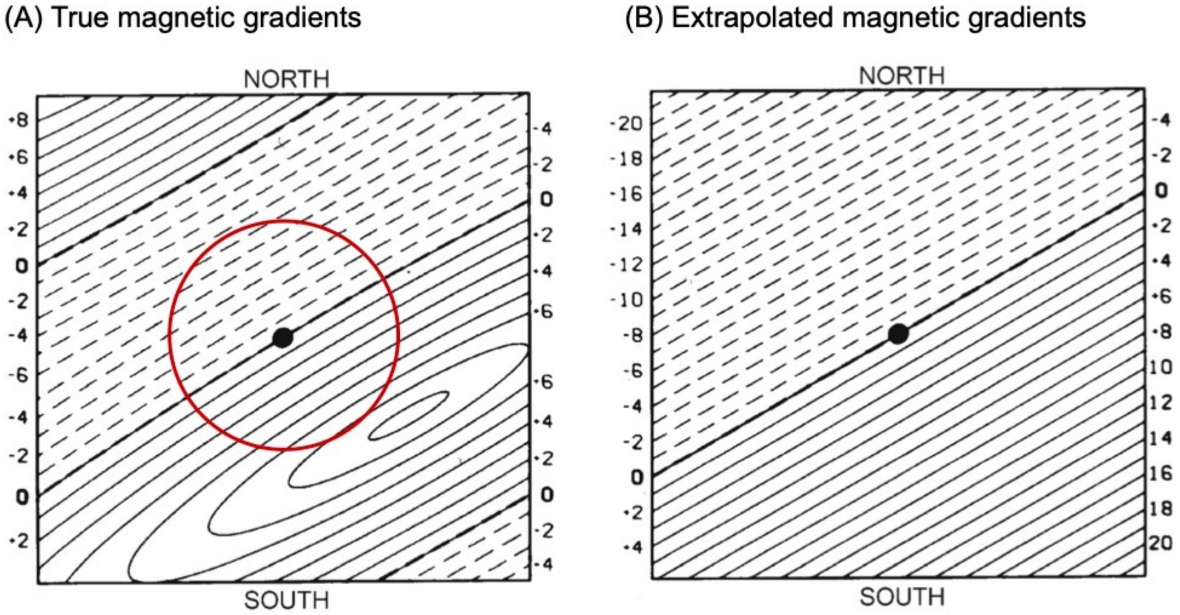

(A) Route-based navigation

(B) Location-based navigation

(C) Beacon-based navigation

(D) Gradient-based navigation

Fig 5


(A) True magnetic gradients

(B) Extrapolated magnetic gradients

Fig 6

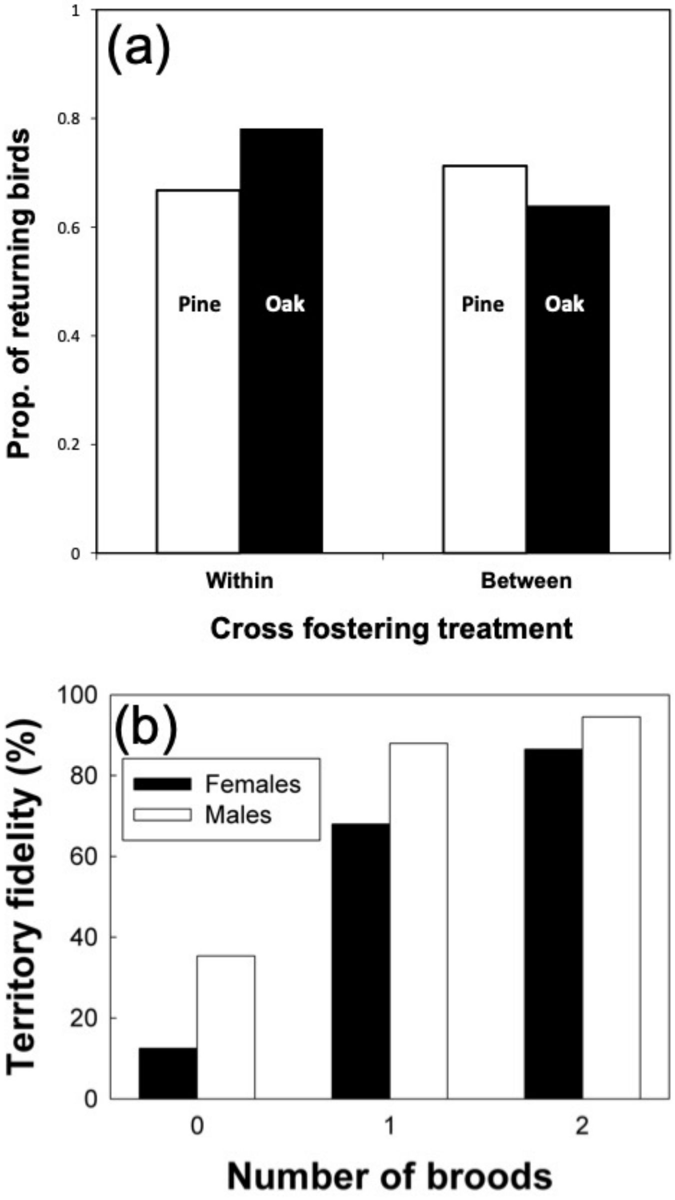
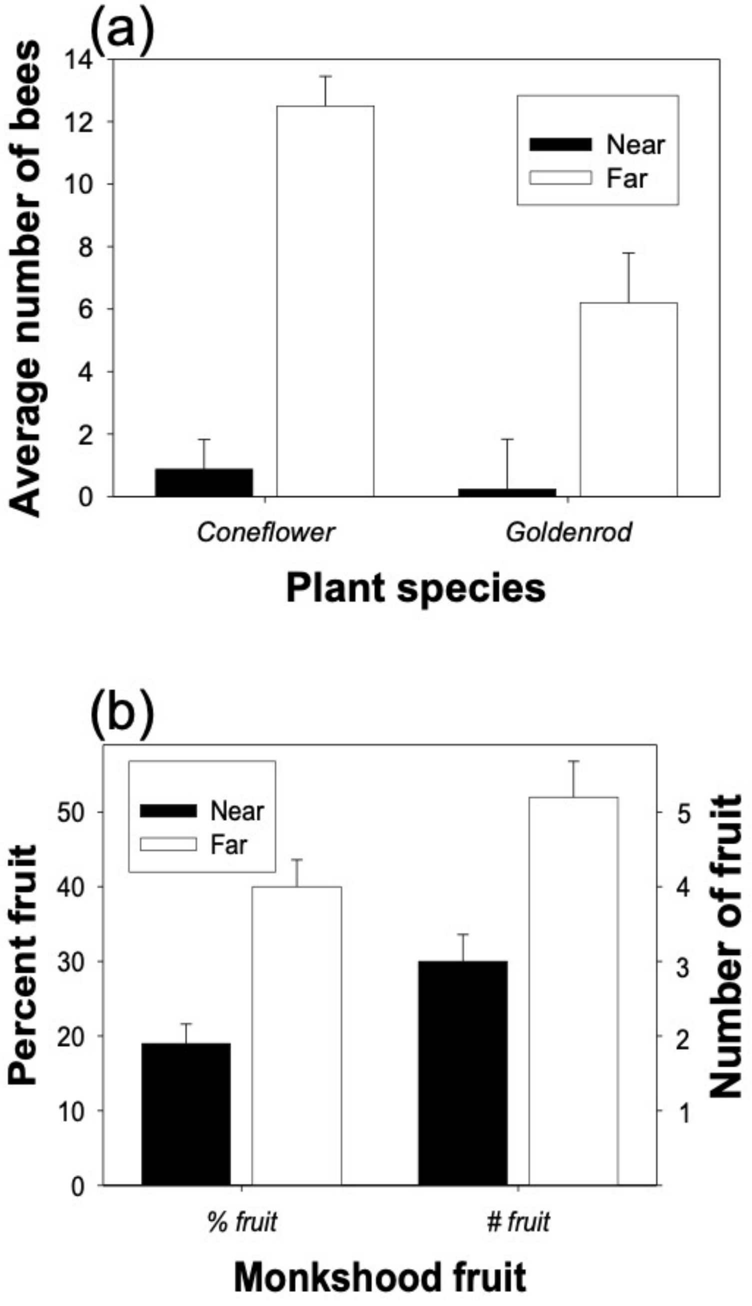

(a)
1
0.8
0.6
0.4
0.2
0
Prop. of returning birds
Pine
Oak
Pine
Oak
Within
Between
Cross fostering treatment
(b)
100
80
60
40
20
0
Territory fidelity (%)
Females
Males
0
1
2
Number of broods

Fig 7



(a)
Average number of bees
14
12
10
8
6
4
2
0
■ Near
□ Far
Coneflower
Goldenrod
Plant species
(b)
Percent fruit
50
40
30
20
10
0
■ Near
□ Far
Number of fruit
5
4
3
2
1
% fruit
# fruit
Monkshood fruit

Fig 8

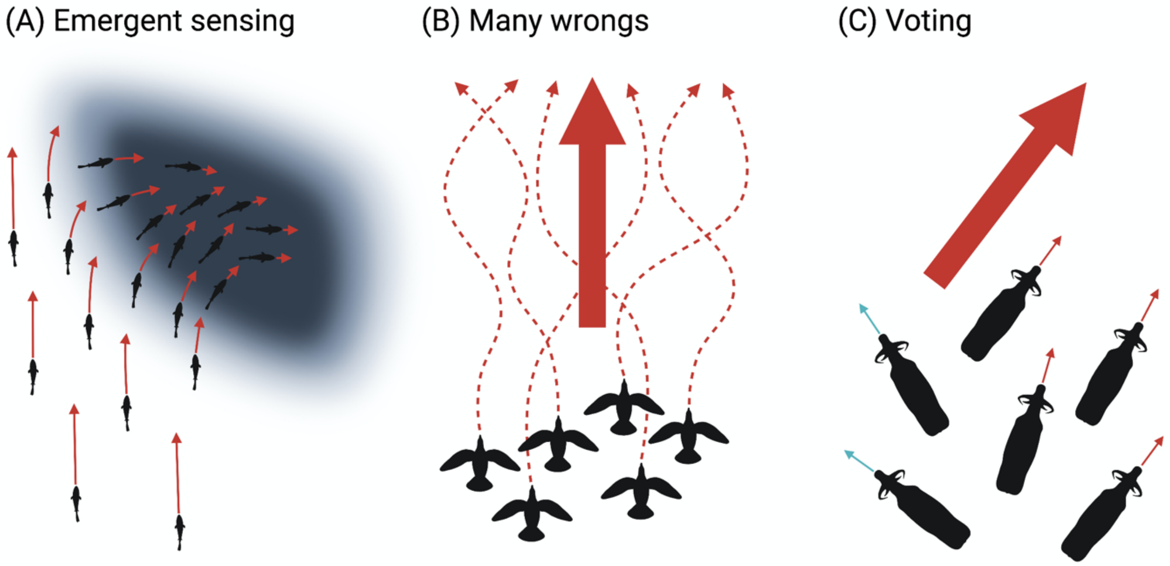


Fig 9

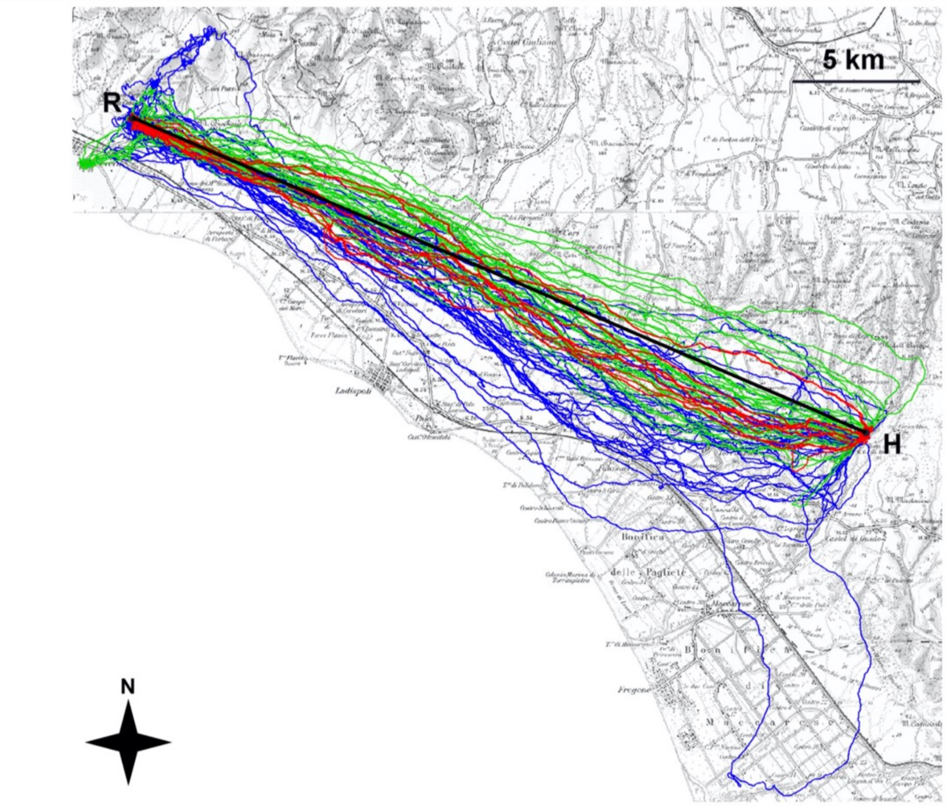
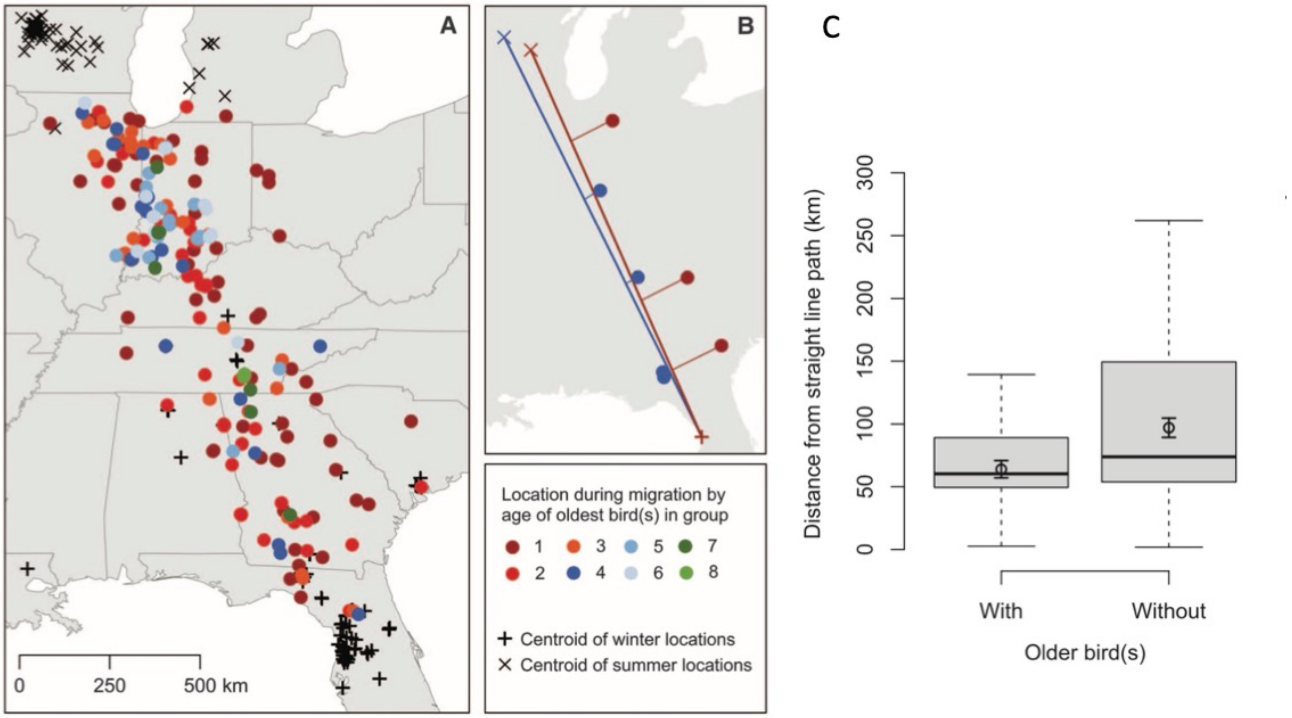


Fig 10


A
0
250
500 km
B
Location during migration by age of oldest bird(s) in group
1
2
3
4
5
6
7
8
+ Centroid of winter locations
× Centroid of summer locations
C
Distance from straight line path (km)
0
50
100
150
200
250
300
With
Without
Older bird(s)

CHAPTER 3

Group Expertise: The Effect of Experience on Collective Decision-Making

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In progress, intended to be published

ABSTRACT

Expertise allows individuals to perform significantly better than novices on a complex task. Social groups can also develop expertise from extensive collective experience. Within group expertise, collective decision-making is crucial for maintaining cohesion, but it is unknown whether a group's collective decision-making skills can improve with experience. To investigate this, we tested whether repeated experience choosing between two nests during emigration in acorn ants (*Temnothorax ambiguus*) would improve the speed and efficiency with which colonies reach consensus. We predicted that experience with collective decisions improves colony decision-making efficiency and speed. We first ran preliminary experiments to quantify nest features that colonies prefer in order to establish good-quality and mediocre-quality artificial nests. Twenty colonies belonging to the choice treatment emigrated six times with a choice between a good- and mediocre-quality nest. Another 20 colonies belonging to the no-choice treatment emigrated six times with no choice, as they were provided with a single nest. Then, we tested both treatments with the choice between a good- and mediocre-quality nest during a final emigration. We found that colonies with experience on a binary decision-making task were more efficient, but not faster, at reaching consensus than colonies without binary experience in decision-making. Additionally, we found that decision-making speed did not differ when choosing between two nests compared to one. We conclude that previous experience making decisions can improve subsequent decision-making. Studying decision-making in ants will allow us to achieve an improved understanding of the development and mechanisms behind group expertise.

INTRODUCTION

Experts possess exceptional skills and knowledge allowing them to consistently outperform novices within their domain (Ericsson and Charness, 1994; Ericsson et al., 2006; Dukas, 2017, 2019). Developing expertise requires extensive practise, leading to changes in decision-making ability (Randel et al., 1996; Eisele, 2004; Dew et al., 2009), memory capacity (Allard and Burnett, 1985; Ericsson and Kintsch, 1995), motor skills (Cauraugh et al., 1999), brain activity (Yang, 2015; Wimshurst et al., 2016), and the volumes of brain parts (Elbert et al., 1995; Woollett and Maguire, 2011). A classic example is how master chess players gain expertise with extensive practise (Charness et al., 1996). Within the specific domain of chess, master chess players have remarkably greater working memory capacity, memory recall, larger visual search spans, and better decision-making skills under pressure compared to less skilled chess players (Gobet and Charness, 2007). For centuries, expertise has played a crucial role in human societies, relating from necessities for survival such as hunting (Gurven et al., 2006) and medicine (Norman et al., 1989; Vickers et al., 2008), to entertainment like sports (Allard and Burnett, 1985; Wimshurst et al., 2016), games (Charness, 1991; Gobet and Charness, 2007), and art (Starkes et al., 1987; Hopper et al., 2018).

Humans live in social groups where we must collectively solve complex tasks repeatedly throughout our lives, creating the potential for group expertise to develop. Social groups can learn from accumulated experience working together on a task (Dutton and Thomas, 1984). For instance, factory workers in an assembly line improve their performance over time by increasing their speed of production and reducing their error rate as they gain experience (Argote and Epple, 1990). This collective improvement is the result of both individual-level and group-level learning, with collective improvements in communication and developing more efficient routines (Argote, 2013). The stability of individuals within the group is an important consideration. Stable groups improve their performance more so than groups consisting of individuals that are less familiar with each other (Reagans et al., 2005; Huckman et al., 2009). Furthermore, the experience of individuals working in consistent roles is positively related to collective performance (Huckman et al., 2009). Despite the importance of group expertise, little research has critically tested the development of group expertise.

Understanding the developmental mechanisms of group expertise is an enticing scientific challenge. Observational data provide good evidence for group expertise (Argote and Epple, 1990; Tindale and Winget, 2017), but lack controlled experiments. Laboratory studies provide good headway (Watson et al., 1991; Littlepage et al., 1997). For example, groups of 5-6 graduate students worked throughout a 4-month semester for at least 30 hours. At the beginning, middle, and end of the course, students completed an independent test, which they compared with their group afterwards, and submitted their group's final answer. Group performance improved over the three time periods, suggesting that collective decision-making improves with experience (Watson et al., 1991). However, laboratory studies typically use small, simple tasks over a relatively short period. Modelling approaches are a useful tool for studying group expertise (Ficapal-Cusí et al., 2021; Turalska et al., 2021). For example, Turalska et al., (2021) created an agent-based model considering how problem complexity, social structure, and search strategies contribute to optimizing the efficiency of collective decision-making. They found that performance decreases as problem complexity increases, interaction rules between individuals are more important for collective performance than network structure itself, and favouring the search for new information as opposed to using known solutions improves collective performance. Nonetheless, group expertise needs to be supported by well-controlled experimental data. We can gain a better understanding of group expertise by running controlled experiments using a nonhuman animal model system. Nonhuman animals can master complex tasks with experience at an individual or group level. For example, with age and experience, honey bees improve individual foraging efficiency (Dukas and Visscher, 1994) and wolf packs increase hunting success (Sand et al., 2006). Expanding expertise research to nonhuman animals allows us to study a natural behaviour in animals living in long-lasting social groups. This form of system provides the necessary ability and timescales for group expertise to develop.

Here, we measure the development of group expertise by providing ants with extensive experience on a natural decision-making task. Ants live in stable colonies of familiar individuals with division of labour, making them a good model system for group expertise. House-hunting is a well-established behavioural system of collective decision-making in social insects (Seeley and Buhrman, 1999; Franks et al., 2003a; Visscher, 2007; Sasaki and Pratt, 2018). In *Temnothorax* ant colonies, individual scouts search for new nests when their current nest becomes inadequate (Möglich, 1978). Scouts assess nest quality based on characteristics such as darkness, cavity height, and entrance size, which are ranked in order of importance (Franks et al., 2003b). Nests are discovered independently, or through a recruiting behaviour called tandem running (Pratt, 2008), in which a knowledgeable leader teaches a naïve follower the route to a new nest or food source (Franks and Richardson, 2006; Sasaki et al., 2020). Once a quorum is achieved, scouts switch to transporting brood and nest mates into the new nest (Pratt et al., 2002; Pratt, 2005).

Surprisingly, little research has explored how previous experience affects collective decision-making during emigration (Biro et al., 2016; Sasaki and Pratt, 2018). Repeated experience emigrating increases overall speed of emigration when one nest option is available

(Langridge et al., 2004, 2008; Mitrus, 2016). Additionally, previous experience assessing nests can affect subsequent decision-making. For example, individual scouts that assessed nests in descending order of quality (excellent-, good-, then poor-quality) treated the good- and poor-quality nests similarly. Contrarily, scouts that assessed three nests in ascending order of quality (poor-, good-, then excellent-quality) spent increasingly more time assessing each nest of increasing quality (O'shea-Wheller et al., 2017). Additionally, colonies learn to assess specific nest qualities that have been informative of better-quality nests in the past (Sasaki and Pratt, 2013). Further, colonies that had explored a good and mediocre-quality nest a week before being induced to emigrate, thus possessing the knowledge of the nests, preferred emigrating to the better-quality nest whereas colonies naïve to both nests did not show a significant preference (Stroeymeyt et al., 2010). Taken together, these studies illustrate how prior experience can influence house-hunting. However, it remains unclear if the process of collective decision-making itself improves with groups' collective experience.

In this study, we tested if repeated experience with collective decision-making can improve the group's performance on a decision-making task. First, we provided *Temnothorax ambiguus* colonies with experience emigrating on six occasions during a training phase. In each training emigration, we provided colonies of the choice treatment with two nests of distinct qualities and colonies of the no-choice treatment with a single nest. While colonies of either treatment experienced the two nest qualities during the training phase, only colonies of the choice treatment had experience choosing collectively between the two nests. We then tested all colonies in a final test emigration in which we provided them with two nests of different qualities. We predicted that colonies from the choice treatment would be faster and more efficient at collective decision-making than colonies from the no-choice treatment. We defined efficiency as the proportion of ants transported directly from the old nest to the better of the two nests. In addition to our key prediction, we also made two secondary predictions regarding colony performance in the training phase. We predicted first, that colonies from both treatments would emigrate faster over the six emigrations of the training phase, similar to previous studies (Langridge et al., 2004, 2008; Mitrus, 2016). Second, we predicted that colonies from the choice treatment would become more efficient throughout training.

METHODS

Collection and Maintenance of Colonies

With written permission from the Heartland Forest Nature Experience in Niagara, Ontario, we collected 40 colonies of *T. ambiguus* from acorns during July 2020 and May 2021. Colonies were tested within nine months of collection, and contained between 12 to 107 adults (mean = 47.63), and 0 to 5 queens (mean = 1.75). We emigrated colonies into standard lab nests (Fig. 1a) made of balsa wood sheets 1.6 mm thick with a circular cavity 38mm in diameter, and an entrance 2 mm wide and 4 mm long (Franks et al., 2003b). We sandwiched the balsa wood between two glass slides (75 x 50 x 1 mm). We placed nests individually into plastic containers (110 x 110 x 38 mm) with dead *Drosophila*, honey, and water provided ad libitum except during emigrations. Colonies were kept in 12hr:12hr light:dark cycle at 22°C ± 2°C.

Experimental Design

Colonies lived in their experimental arena (290 x 160 x 112 mm) lined with Fluon (by Formica PTFE Insect Barrier) for the duration of the experiment. Two dissimilar landmarks (three black circles, one black triangle) remained in the same location throughout the experiment to aid in navigation (Mcleman et al., 2002; Hunt et al., 2018). We tested a total of 40 colonies in 4 replicates. Each replicate included 10 colonies, 5 in the choice treatment and 5 in the no-choice treatment. We randomly assigned colonies into treatments while matching colony size between the treatments.

Preliminary Trials

We performed a preliminary experiment to establish various nest qualities. *Temnothorax* ants prefer darker nests (Franks et al., 2003b; Dornhaus et al., 2004), so we varied visible light inside the nest cavity to create a good-quality and a mediocre-quality nest. Nests consisted of the same dimensions as the standard nest with an added light filter. Five additional colonies were used during preliminary experiment and not in the subsequent main experiment. Each colony emigrated twice, for a total of ten preliminary trials. Two nests were available each trial, one with a dark-grey filter (GAM GC1516 Cine ND .6), the other with a light-grey filter (GAM GC1515 Cine ND .3), which reduces half as much visible light as the dark-grey filter. Colonies on six occasions emigrated to the dark nest, one colony emigrated to the light nest, and three had split between the two. Thus, we deemed the preferred darker nest as the good-quality nest, and the dim nest was the mediocre-quality nest.

Training Emigrations

In the training phase, each colony had to emigrate 6 times. Each emigration, colonies of the choice treatment had a choice between one good quality nest and one mediocre-quality nest, while colonies of the no-choice treatment encountered only a single nest (Fig. 1). For the no-choice treatment, that nest was of the good quality in 3 emigrations and of the mediocre quality in the other 3 emigrations. We randomized and counterbalanced the order and placement of the nests in the arenas.

Prior to the first training emigration, we placed each colony into a clean experimental arena to acclimate overnight. We placed new nests facing the occupied nest, 90 mm away from the occupied standard nest (new entrance to old entrance; Fig 1). For the choice treatment, the two nests were side by side, 75 mm apart (new entrance to new entrance). To initiate emigration, we removed the roof and walls of the occupied nest to simulate natural, irreparable nest damage. We allowed ants to emigrate, which we video-recorded using eight 6th generation iPod touches (for 34 colonies), an iPhone 6S (for 4 colonies), and a Logitech HD Pro c920 webcam (for 2 colonies). We recorded for approximately four hours if the colony had moved into a single nest, or five hours if the colony had split between two. If colonies had brood remaining in the old nest past five hours, we continued recording until all brood items were moved into a new nest. If all brood items had not been moved by eight hours, we manually added brood to the new nest (this occurred only once in a no-choice colony). If the colony remained split between two nests after five hours, we briefly removed the light filters of each nest to take a photo to record the number of workers, queens and estimated brood count in each nest. Then we removed the roof of the nest occupied with the least number of queen and brood to force reunification. We removed the light filter for roughly the same time it would take to take a photo for colonies that did not split to ensure the same amount of disturbance. Afterwards, we removed the old nest and unused nest, and added food and water.

After colonies lived in their chosen experimental nest for 24 hrs, we removed the filter from the nest and shifted it to the center of the arena while remaining close to the landmark they had emigrated towards, converting it into a standard nest on the opposite side of the arena as their previous standard nest (Fig 1C). This resulted in colonies alternating between emigrating towards and away from the triangle landmark. Colonies remained in the standard nest for approximately 40 hours. We then moved colonies to clean arenas, allowing acclimation for 15 min prior to initiation emigration. We reused arenas, light filters, and glass slides by cleaning them with 70% ethanol to remove pheromones. Balsawood is too absorbent to clean, so we discarded each piece after use.

Test Emigration

The test emigration allowed us to examine how the distinct experiences of colonies from the choice and no-choice treatments affected their emigration decisions. We used a similar protocol to that of the training phase and initiated the test 40 hrs after the sixth training emigration of each colony. We placed in each arena one good and one mediocre nest (Fig. 1a) and initiated emigration by removing the roof and wall from the standard nest of each colony.

Scoring Video Recordings

We scored videos using Behavioural Observation Research Interactive Software (BORIS) (Friard and Gamba, 2016). Observers were blind to colony ID and trial number while scoring emigrations of the training phase and to colony ID and treatment while scoring the test emigrations. We recorded the beginning of each trial, the first discovery of each nest, and adult transports. We excluded brood transports because brood were too small to reliably detect. If transports originated inside one of the new nests, we noted their origin and considered it an indirect transport. Transports that originated from the old nest or arena were considered direct transports. We watched the whole duration of the videos, or until there was 60 minutes with no transports if the colony had moved into one nest (no-choice treatment and united colonies in the choice treatment).

Measures

We used two parameters to quantify emigration performance. Decision latency was the duration between discovering a nest until the first transport (Franks et al., 2003a). We chose this measure because it isolates the decision-making process by including the assessment of the new nest(s), and the choice to accept a nest. Transport efficiency was the proportion of direct transports into the good nest, i.e., the number of transports directly to the good nest divided by the number of direct transports to either new nest. We chose this measure because the most efficient emigration should consist of assessment of the alternative nests, choice of the best nest, followed by transports exclusively to the best nest. We had decision latencies for all test and training emigrations, and transport efficiency measures for all test emigrations as well as the training emigrations of the choice treatment.

Statistical Analyses

We analyzed the data using R Studio version 4.1.2 (R Core Team 2020), and used the tidyverse package version 1.3.0 (Wickham et al., 2019) to organize the data. For the test emigration, we used the lmer function from the lme4 package version 1.1-26 (Bates et al., 2015). We used generalized linear models (GLM) to compare the performance of the choice and no-choice treatments during the test emigration. To model transport efficiency, the arcsine square root of the proportion of transports directly to the better nest was the dependent variable and treatment and replicate were the fixed factors. To model decision latency, the duration between the first discovery and first transport was the dependent variable and treatment and replicate were the fixed factors. We used replicate as a fixed factor because it had too few levels to be a random factor. We excluded a clear outlier colony from the decision latency model and figure 2b. The outlier was a choice treatment colony with a decision latency of three hours and forty minutes, while the second highest value was one hour and eleven minutes in another choice treatment colony. We inspected dispersion and diagnostic plots for the models using the DHARMa package version 0.4.3 (Hartig, 2020). Then, we tested the significance of the effects using the Anova function from the car package version 3.0.10 (Fox and Weisberg, 2019), reporting the Wald χ^2 test statistic and p-value.

We used generalized linear mixed models (GLMM) to analyse the changes in performance over the course of the six training emigrations within each treatment. With the lmer function, we modelled transport efficiency for the choice treatment using the arcsine transformation of the proportion of transports directly to the better nest as the dependent variable, with trial and replicate as fixed factors, and colony as a random factor. We did not model transport efficiency for the no-choice treatment over the training phase, as there was only one nest option. We analysed decision latency during training phase for both treatments separately because the choice treatment had two nest options while the no-choice had one, thus directly comparing decision latency between treatments is inapt. We modelled decision latency separately for each treatment using the glmmTMB function from the glmmTMB package version 1.0.2.2 (Brooks et al., 2017). Duration between the first discovery and first transport was the dependent variable, and trial and replicate were the fixed factors, with colony as a random factor. For all three training phase models, we assessed dispersion and inspected diagnostic plots for the models using the DHARMa package. Then, we tested the significance of the fixed effects using the Anova function from the car package.

We excluded a clear outlier that occurred during the first emigration from the choice treatment decision latency model and figure 4a. The outlier was a colony with a decision latency of four hours and fifteen minutes, while the second largest value during training was another choice treatment colony with a decision latency of two hours and sixteen minutes. Additionally, we were missing one emigration from a choice treatment colony because the video was not saved, thus we did not include it in either the transport efficiency of decision latency choice treatment models. In the no-choice treatment, there was one colony consisting of twelve adults that performed no transports during their first emigration, thus they did not have a value in the no-choice decision latency model. We are still in the process of scoring the training phase videos, so there are seven emigrations missing for the choice treatment (from three colonies) and three emigrations missing for the no-choice treatment (from one colony).

RESULTS

During the test emigration, the choice treatment had significantly higher transport efficiency than the no-choice treatment ($\chi^2_1 = 3.92$, $p < 0.05$, Fig. 2a). However, we did not observe a significant effect of treatment on decision latency during the test emigration ($\chi^2_1 = 0.12$, $p = 0.73$, Fig. 2b).

We did not detect a significant change in transport efficiency throughout the training phase for the choice treatment ($\chi^2_1 = 0.14$, $p = 0.71$, Fig. 3). The choice treatment significantly decreased their decision latency throughout the training phase ($\chi^2_1 = 26.89$, $p < 0.0005$, Fig. 4a). Likewise, the no-choice treatment significantly decreased their decision latency throughout the training phase ($\chi^2_1 = 54.21$, $p < 0.0005$, Fig. 4b).

DISCUSSION

To summarize our key findings, transport efficiency during the test emigration was significantly higher in the choice treatment than no-choice treatment (Fig. 2a). However, we detected no difference in decision latency between treatments during the test emigration (Fig. 2b). For our secondary findings, we observed no significant change in transport efficiency throughout the training emigrations in the choice treatment (Fig. 3). Both treatments significantly improved their decision-making speed throughout the training emigrations (Fig. 4).

The effect of experience on collective decision-making remains poorly researched (Biro et al., 2016; Sasaki and Pratt, 2018). Our study provides additional evidence to expand on the existing knowledge for this topic. So far, research has tested how exposure to nests can affect subsequent choices (Stroeymeyt et al., 2010; Sasaki and Pratt, 2013; O'shea-Wheller et al., 2017) and how experience with successive emigrations increases speed (Langridge et al., 2004, 2008; Mitrus, 2016). Here, we show that the process of decision-making itself can improve with experience. To our knowledge, we are the first to document that the decision-making process itself improves with experience with both binary and singular decisions. Colonies with binary decision-making experience perform more efficiently during a binary choice compared to colonies with no experience making such choices. Additionally, colonies increase their speed of reaching decisions about emigration with experience in both choice and no-choice scenarios. This improvement in decision-making speed with experience is consistent with previous studies indicating that the total emigration speed increases when one nest option is available (Langridge et al., 2004, 2008; Mitrus, 2016).

Transport efficiency varied highly throughout the training emigrations for the choice treatment, although the choice treatment significantly outperformed the no-choice treatment during the test. The first plausible explanation for such high variation in transport efficiency throughout the choice training is that there was similar feedback for both qualities of nests. Feedback contributes to collective learning. Groups tend to improve performance when they receive feedback about their work (Van der Vegt et al., 2010; Greve and Gaba, 2020). The colonies in our experiment may have received relatively similar feedback for both nest qualities. Regardless of the quality chosen, we removed the light filters on the nests 24 hrs after emigration, then removed the roofs and walls to induce emigration 40 hrs afterwards. Perhaps if we varied the feedback between choosing the good-quality and mediocre-quality nest, there would have been a greater improvement in transport efficiency. For example, if the colonies received an extra day of rest if they chose the good nest, they may have learned to choose that nest more often. Another plausible explanation for the high variance in transport efficiency throughout training in the choice treatment, yet still a significant difference between treatments during the test emigration, is organizational depreciation. The no-choice treatment could have performed poorly during the test emigration because colonies had no recent experience deciding upon multiple nest options, deteriorating the colonies' ability to make binary decisions. In nature, numerous nest options with various qualities are available to emigrate to. Possibly, the unnatural task of deciding upon a single nest repeatedly caused their binary decision-making ability to decay by lack of use. This decay prediction is consistent with organizational depreciation in which the group's performance regresses due to interruptions in behaviour such as group turnover or a strike (Argote, 2013; Argote et al., 2021).

As mentioned in the methods, we performed two statistical analyses for decision latency throughout training because we expected the choice treatment to have a longer decision-latency than the no-choice treatment. Visual inspection of figure 4, however, suggested that there was no difference in decision latency during the training phase between the treatments. To confirm there was no detectable different between treatments, we ran a posteriori GLMM using the glmmTMB function with decision latency as the dependent variable, trial, treatment, trial by treatment interaction, and replicate as fixed factors, and colony as a random factor. Contrarily to our a-priori expectation, we did not observe a significant difference in decision latencies between treatments throughout training ($\chi^2_1 = 2.14$, $p = 0.14$, Fig. 4). The lack of difference between treatments could arise from both nest qualities meeting the acceptance threshold of the scouts. Although we confirmed with preliminary experiments that colonies prefer the good-quality nests, the mediocre-quality nests are also better quality than the standard nest. Both nests have reduced visible light in the nest cavity, which is the most important factor when choosing a nest (Franks et al., 2003b). If indeed the ants perceived both nest qualities as sufficiently high, we would expect no differences in decision latencies in trials of the no-choice treatment with either the good- or mediocre-quality nests (Mallon et al., 2001). We tested this prediction via the glmmTMB function with decision latency as the dependent variable, trial, nest quality, trial by nest quality interaction, and replicate as fixed factors, and colony as a random factor. We observed no significant difference in decision latency in no-choice colonies emigrating to either nest type ($\chi^2_1 = 1.27$, $p = 0.26$, mean ± SD, 2046.33 ± 1192.25, and 2026.27 ± 1523.57, for the good-quality and mediocre-quality nests respectively). This suggests that the ants given a choice between the mediocre- and good-quality nests have a lower tendency to reject the mediocre nests than we initially thought. The colonies could be favouring speed over efficiency. Although the darker nest is preferred, both nests are acceptable quality, thus the ants favour the speed of emigrating, not whether to emigrate to the best of two good options. This observation could also explain the high variation in transport efficiency in the choice treatment throughout the training phase. Similarly, *T. albipennis* ants favour speed over accuracy when environmental conditions are harsh (Franks et al., 2003a). In an experiment performed by Sasaki et al. (2018), colonies were faster at emigrating during a binary choice compared a singular choice. Our results were not consistent with this study, potentially because the standard nest in Sasaki et al., (2018) was an intermediate quality between the better- and lesser-quality nests. Accordingly, colonies may decide faster in a binary choice than a singular choice when the lesser-quality nest is inferior to the standard nest, promoting the decision to emigrate to the best-quality nest. In comparison, our standard nest was the lowest-quality nest. Colonies improved by emigrating regardless of their nest choice, thus there was no difference in decision-latency between a binary and singular choice.

We successfully used ant colonies as a model system to study the development of group expertise. Similarly to humans (Argote and Epple, 1990; Argote, 2013; Srour et al., 2016), colonies improve collective performance with experience. Parallel to humans, colonies may also rely on feedback (Van der Vegt et al., 2010; Song et al., 2018; Greve and Gaba, 2020), and abilities may decrepitate from lack of use (Levitt et al., 2013; Agrawal and Muthulingam, 2015; Argote et al., 2021). Further research studying the evolutionary mechanisms of group expertise can benefit from using ant colonies a model system. In conclusion, we demonstrate that previous experience making decisions can affect subsequent decision-making. Colonies with collective experience on a binary decision-making task were more efficient than colonies without experience. Additionally, colonies improved speed of reaching consensus while gaining experience in both the choice and no-choice conditions.

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Figures

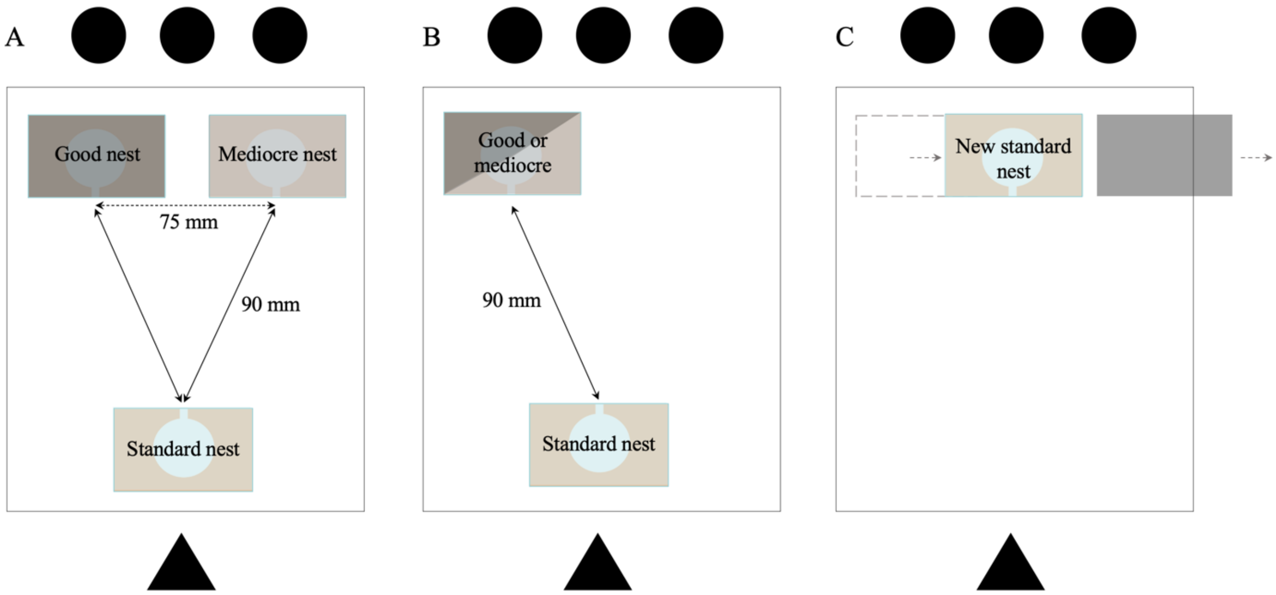

Figure 1: Experimental arena set up for: A) the training session of the choice treatment, and the test for both the choice and no-choice treatment, B) the training session for the no-choice treatment, C) the 40-hour rest interval where we remove the filter and position it in the center to convert the occupied experimental nest into the new standard. The black circles and triangles were landmarks glued to the walls of the arenas to enhance ant orientation.

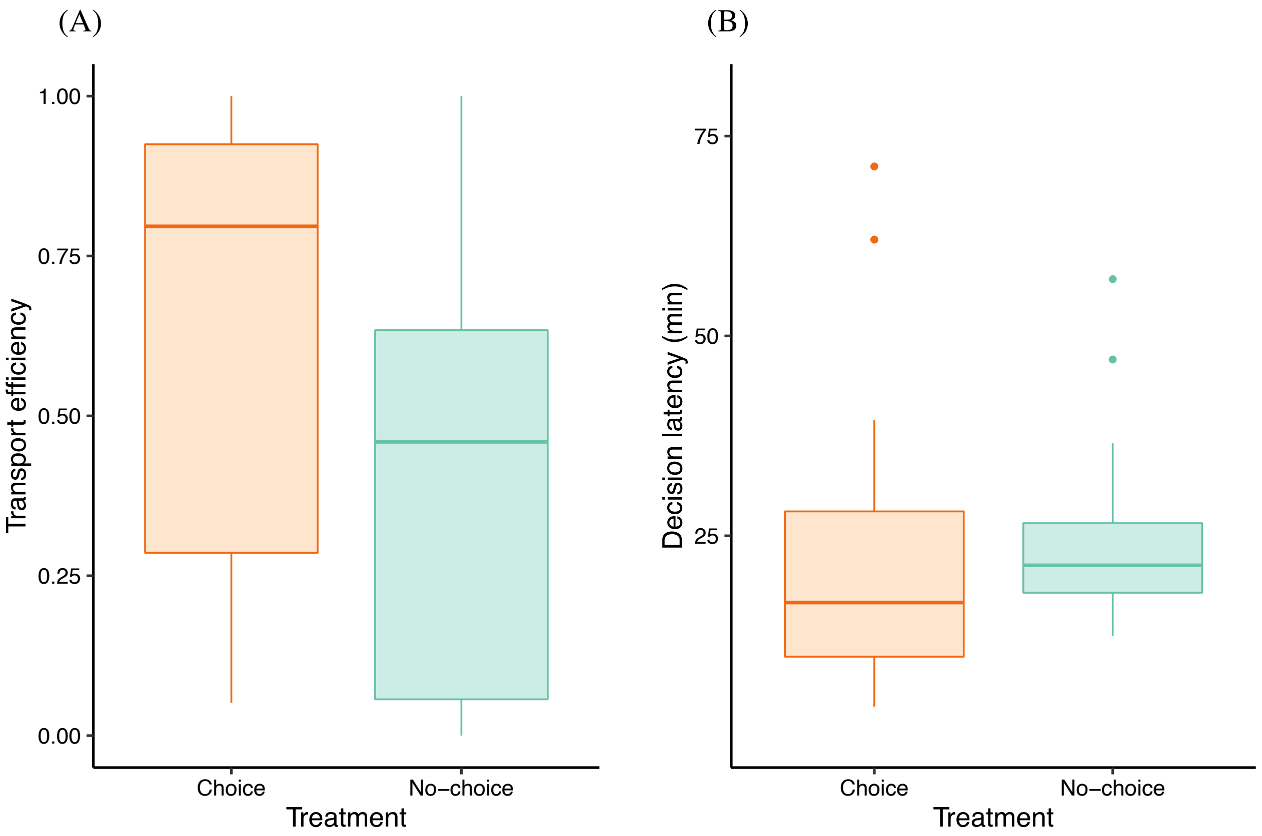

Figure 2: Performance during the test emigration. Boxplots show the 25th, 50th (median) and 75th percentiles, with whiskers showing the 1.5 IQR of the upper/lower quartiles. A) Transport efficiency of the choice and no-choice treatments, measured between 0 and 1. B) Decision latency of the choice and no-choice treatments.

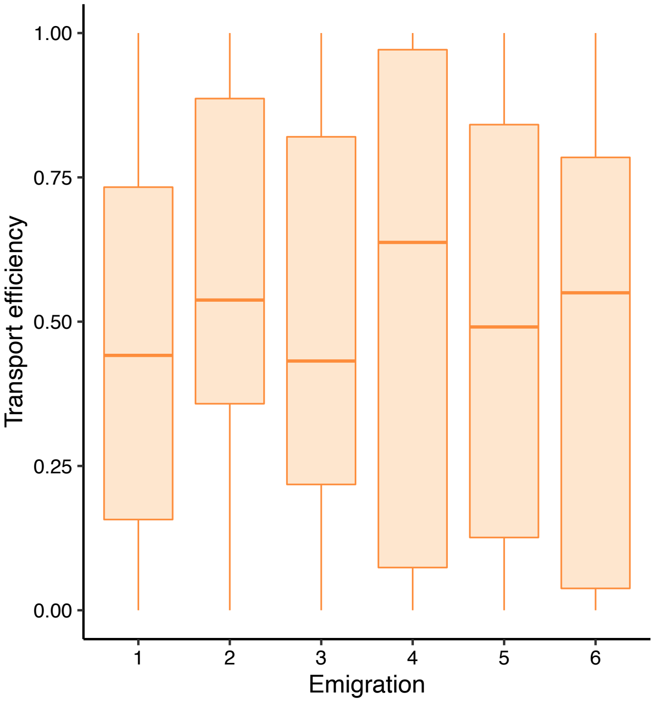

Figure 3: Transport efficiency of the choice treatment during the training emigrations, measures between 0 and 1. Boxplots show the 25th, 50th (median) and 75th percentiles, with whiskers showing the 1.5 IQR of the upper/lower quartiles.

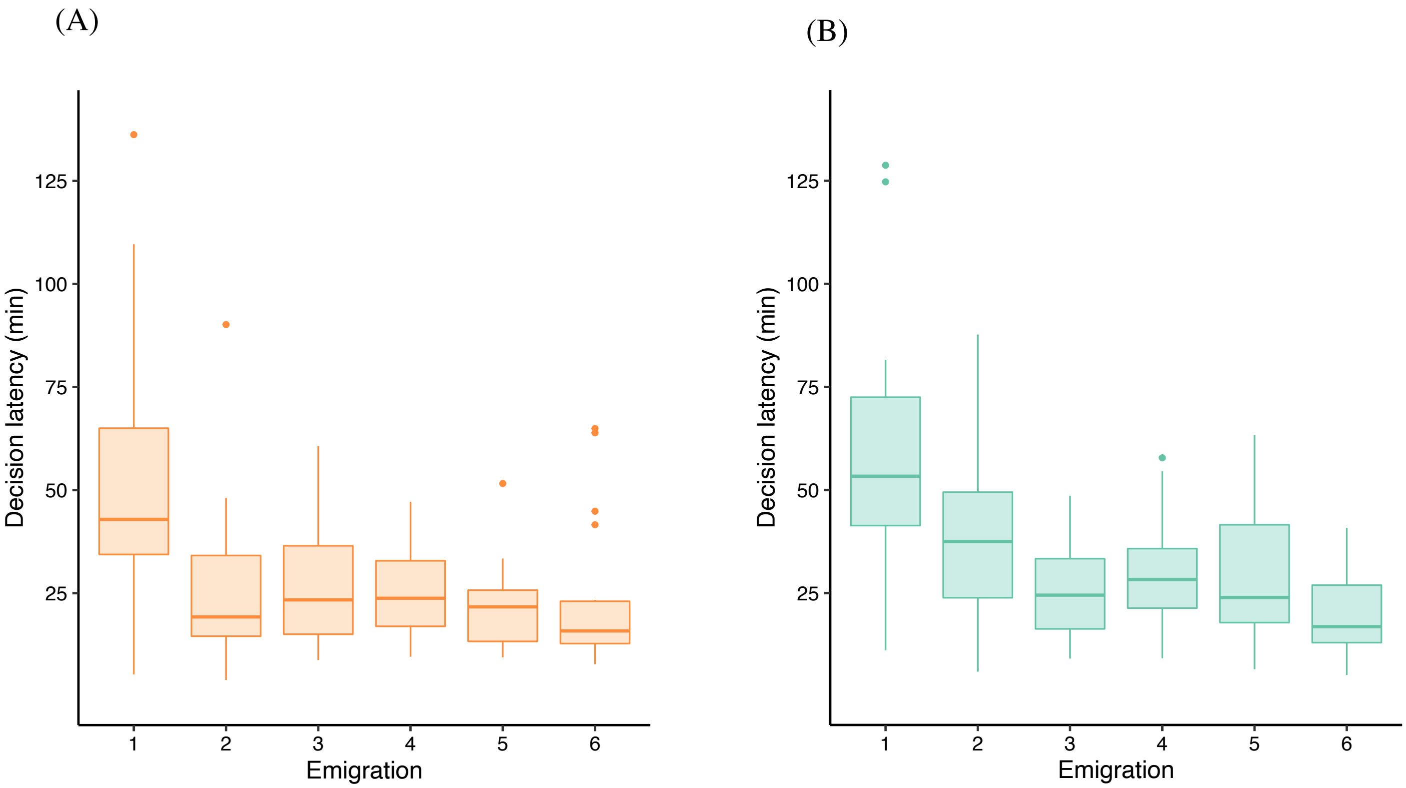

Figure 4: Decision latency of the (A) choice and (B) no-choice treatments throughout the training emigrations. Boxplots show the 25th, 50th (median) and 75th percentiles, with whiskers showing the 1.5 IQR of the upper/lower quartiles.

CHAPTER 4

General Conclusion

Combined, these manuscripts further our knowledge on various fundamentals of animal cognition. In chapter 2, we explored the considerably large field of cognitive movement ecology, finishing with overall conclusions and prospects. The implications of "The Cognitive Ecology of Animal Movement: Evidence from Birds and Mammals" include the extensive summary of existing evidence, acting as a one-stop tool for researchers to learn about the newly emerging field. Chapter 3 then examines the unanswered question of if collective decision-making improves with experience. We successfully demonstrated that collective decision-making does improve with experience, and we used the behavioural system of house-hunting to study group expertise. The implications of "Group Expertise: The Effect of Experience on collective Decision-Making" are to uncover fundamental mechanisms of group expertise and collective decision-making—a topic imperative to social living.