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# A conceptual framework on the role of magnetic cues in songbird migration ecology

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## ABSTRACT

Migrating animals perform astonishing seasonal movements by orienting and navigating over thousands of kilometres with great precision. Many migratory species use cues from the sun, stars, landmarks, olfaction and the Earth's magnetic field for this task. Among vertebrates, songbirds are the most studied taxon in magnetic-cue-related research. Despite multiple studies, we still lack a clear understanding of when, where and how magnetic cues affect the decision-making process of birds and hence, their realised migratory behaviour in the wild. This understanding is especially important to interpret the results of laboratory experiments in an ecologically appropriate way. In this review, we summarise the current findings about the role of magnetic cues for migratory decisions in songbirds. First, we review the methodological principles for orientation and navigation research, specifically by comparing experiments on caged birds with experiments on free-flying birds. While cage experiments can show the sensory abilities of birds, studies with free-flying birds can characterise the ecological roles of magnetic cues. Second, we review the migratory stages, from stopover to endurance flight, in which songbirds use magnetic cues for their migratory decisions and incorporate this into a novel conceptual framework. While we lack studies examining whether and when magnetic cues affect orientation or navigation decisions during flight, the role of magnetic cues during stopover is relatively well studied, but mostly in the laboratory. Notably, many such studies have produced contradictory results so that understanding the biological importance of magnetic cues for decisions in free-flying songbirds is not straightforward. One potential explanation is that reproducibility of magnetic-cue experiments is low, probably because variability in the behavioural responses of birds among experiments is high. We are convinced that parts of this variability can be explained by species-specific and context-dependent reactions of birds to the study conditions and by the bird’s high flexibility in whether they include magnetic cues in a decision or not. Ultimately, this review should help researchers in the challenging field of magnetoreception to design experiments meticulously and interpret results of such studies carefully by considering the migration ecology of their focal species.

*Key words*: bird migration, orientation, navigation, geomagnetic map, migration ecology, magnetoreception, magnetic compass.

## CONTENTS

## I. INTRODUCTION

Migration is a worldwide and widespread phenomenon in animals, which may travel up to tens of thousands of kilometres and connect different continents and oceans during their seasonal movements (Milner-Gulland, Fryxell & Sinclair, 2011). Migratory birds perform these movements with astonishing orientation and navigation capabilities, including returning to specific locations after a journey of several thousands of kilometres (Mouritsen, 2018). For example, pied flycatchers (*Ficedula hypoleuca*) return to the same forest patch in Europe, often to the same nest box, every breeding season after overwintering in the same trees in sub-Saharan Africa year after year (Salewski, Bairlein & Leisler, 2002; Harvey *et al.*, 1984). Similarly striking side fidelity has been observed in other songbird species (Salewski, Bairlein & Leisler, 2000; Price, 1981). This accuracy has fascinated people for centuries (Bairlein *et al.*, 2014) and may be even more astonishing when considering that many songbird migrants travel at night and reach their population-specific wintering grounds without parental or social guidance during the autumnal inaugural migration. This requires an innate migratory program which determines, at its most basic, how long to migrate for and in which direction (clock-and-compass orientation) (Berthold, 1991; Mouritsen & Mouritsen, 2000; Mouritsen, 1998*a*) and how to respond behaviourally and physiologically to variation in environmental conditions *en route* (Jenni & Schaub, 2003; Schmaljohann, Eikenaar & Sapir, 2022).

Next to ‘orientation’, i.e. use of a compass to determine the direction of movement, migratory birds can also ‘navigate’, i.e. determine their location on a ‘map’ and use this information to decide on a compass direction towards the migratory destination (Griffin, 1952). The latter includes ‘true navigation’, i.e. returning to a known location from an unknown place (Holland, 2014). Available cues for orientation and navigation are celestial cues (star patterns, the sun's position and the sun's polarisation pattern), the Earth's magnetic field, landmarks and olfactory cues (reviewed in Mouritsen, 2018). The Earth's magnetic field provides two major information types: first, its dipolar magnetic characteristic provides information about direction for compass orientation (Fig. 1A). Second, its specific properties, namely intensity, inclination angle and declination angle, provide predictable geographical gradients around the globe, serving as map information for navigation (Fig. 1B–F).

With regards to the perception and use of these magnetic cues, songbirds are the most studied taxon among vertebrates and have been key model organisms for over half a century (Merkel & Wiltschko, 1965; Emlen, 1970*b*). This might be explained by songbirds having several characteristics that make them especially suited for orientation and navigation research. Many songbird species, especially long-distance migrants, predominantly migrate at night and independently of other individuals (Papi & Wallraff, 1982; Newton, 2008). As most juveniles are not guided by parents, siblings or conspecifics during their first migration to the unfamiliar wintering grounds (Newton, 2008; Pulido, 2007), they provide excellent naïve experimental units for studying orientation, while the study of adults allows investigation of experienced birds with successful previous migrations. Additionally, most songbirds follow a stop-and-go strategy during migration (Åkesson & Hedenström, 2007; Delingat *et al.*, 2006) with migratory flights during the night (Alerstam, 1990; Schmaljohann, Liechti & Bruderer, 2007), and stopover periods to accumulate energy, rest and recover during the day (Schmaljohann *et al.*, 2022). This allows researchers to separate migratory activity during the night from other activities at the stopover site during the day. Their small size further requires less space in an experimental setup, e.g. in orientation cages (Emlen & Emlen, 1966; Merkel, 1958), and allows adequate caging facilities for large sample sizes. Advantageously, even under caged conditions many songbirds show key behavioural characteristics that can be directly linked to migration behaviour in the wild. Specifically, orientation behaviour in funnel cages correlates with their vanishing bearing in free flight (Mouritsen, 1998*b*). Further, the amount of migratory restlessness (*Zugunruhe*), i.e. nocturnal movements in caged birds during migration season, predicts the actual departure motivation in the wild on a night-to-night level (Eikenaar *et al.*, 2014; Berthold, 1973) and the start of migratory restlessness correlates positively with departure timing within the night (Schmaljohann *et al.*, 2015).

Despite an extensive literature on magnetoreception in songbirds, we still lack a clear understanding of when, where and how songbirds use magnetic cues for their migratory decisions in the wild. This becomes particularly obvious when considering the low repeatability, reproducibility and replicability in magnetic-cue-related studies, which show very high variability in the birds' behavioural responses to similar experimental manipulations [e.g. compare Cochran, Mouritsen & Wikelski (2004) with Chernetsov *et al.* (2011); Chernetsov *et al.* (2017) with Chernetsov *et al.* (2020); or Fransson *et al.* (2001) with Bulte *et al.* (2017)]. One reason for the high variability might lie in the fact that behavioural decisions of songbirds are based on a complex interplay of intrinsic (e.g. age, energy stores) and extrinsic (e.g. wind conditions, time of season) factors (Müller *et al.*, 2016; Schmaljohann *et al.*, 2022; Jenni & Schaub, 2003). Considering the decision-making processes of the birds and how they might differ depending on the migration ecology of the species could help to design more meaningful experiments and thus increase the probability of obtaining more repeatable, reproducible and replicable results. We therefore encourage researchers of magnetoreception and readers of the animal orientation and navigation literature to consider the migratory ecology of the study species when exploring how songbirds use magnetic cues for their migratory decisions.

The first objective of this review is to summarise the methodological approaches for assessing magnetic-cue-related hypotheses in migratory songbirds and evaluate their contribution to understanding these processes in the wild. Our second objective is to review the specific roles of magnetic cues in the context of migration ecology by focussing on the decision-making processes of songbirds in the wild. For this, we summarise how birds might perceive directional compass information and geographical map information. We then provide a conceptual framework investigating how magnetic cues might affect migratory decisions from stopovers to active migratory flight towards their destination. Additionally, we provide as supporting information (Table S1) a comprehensive list of the primary literature for each magnetic-cue-related hypothesis. Finally, we hope that our conceptual framework will be an important step to proper evaluation of the findings of future cage and free-flight studies in the field of magnetoreception in an ecological context.

## II. METHODOLOGICAL APPROACHES

To study the significance of magnetic cues for orientation- and navigation-related hypotheses in migratory songbirds, most experimental approaches follow a common structure incorporating two steps. The first step involves a manipulation altering the information provided by a magnetic cue that the bird might access (Fig. 2A). In the second step, the response of the bird to this manipulation is recorded, often in restricted environments, i.e. cage experiments, but also in free flight (Fig. 2B). Table S1 provides a list of magnetic-cue-related orientation and navigation hypotheses for migratory songbirds.

### (1) Manipulation of perceived magnetic information

An altered magnetic information perception for the bird can be achieved either by (*a*) manipulating the cue itself, or by (*b*) manipulating the (hypothesised) biological sensor for magnetic perception (Fig. 2A).

#### (*a*) *Magnetic cue manipulation*

Strategically selected study sites and times can provide natural ‘near-experimental’ setups to study magnetic orientation and navigation behaviour, e.g. natural magnetic anomalies caused by magnetic minerals in the Earth's crust (Alerstam, 1987; Skiles, 1985) or weather events (Able, 1982*a*). As the Earth's magnetic field varies constantly with patterns occurring on a scale from decades (secular variation) to days (Bloxham & Gubbins, 1985), one can also use this natural variation for correlative studies (Benitez-Paez *et al.*, 2021; Wynn *et al.*, 2020, 2022*a,b*).

Besides natural changes in the magnetic field, its three major components (Fig. 1) can be changed artificially: (1) intensity (Fig. 1B); (2) inclination (e.g. Wiltschko *et al.*, 1993; Fig. 1C, D), including the (horizontal) direction of field lines (e.g. Cochran *et al.*, 2004; Fig. 1A; see Section III); and (3) declination (e.g. Chernetsov *et al.*, 2017, 2020; Fig. 1E, F). The magnetic field can also be cancelled out, i.e. true-zero magnetic fields (Mouritsen, 1998*b*), or constantly moved, providing a non-specific magnetic stimulus (Elbers *et al.*, 2017). Further, one can imitate the magnetic field of other locations by specifically changing the components of the magnetic field, which is called 'virtual (magnetic) displacement'. Virtual magnetic displacement can be applied either instantaneously (Kishkinev *et al.*, 2015) or continuously over several days/weeks, simulating a slow migration through space (Fransson *et al.*, 2001; Bulte *et al.*, 2017). Nevertheless, care should be taken to select a magnetically unequivocal virtual location, as certain combinations of magnetic properties may be repeated across the globe (Schneider *et al.*, 2023). Helmholtz-coils (e.g. in Wiltschko, 1968) and three-dimensional Merritt-coils (Merritt, Purcell & Stroink, 1983) are used most frequently, but other coil arrangements (e.g. Alldred & Scollar 4-Coil, Lee-Whiting 4-Coil, Rubens 5-Coil) have been used as well (Kirschvink, 1992). As the magnetic field is only manipulated in a restricted space within the coil system (usually <1 $m^3$), birds have to be caged.

Alongside virtual displacement, actual physical displacement has been used for decades for navigational studies (e.g. Perdeck, 1958; Thorup *et al.*, 2007; Holland *et al.*, 2009; Mewaldt, Cowley & Won, 1973; Mewaldt, 1964; Chernetsov, Kishkinev & Mouritsen, 2008*b*). With a physical displacement, the magnetic cues also change, but interpretations of behavioural responses related to the location change must be made carefully, as other cues, such as landscape and odour, will likely alter as well. During transportation, the birds may experience a gradual shift in the magnetic cues or other environmental conditions, such as timing of sunrise and sunset events. If they consider these shifts, they may gradually adjust their behaviour to the new conditions, so that the effects of the displacement might be less than expected.

The most non-specific method to manipulate the perceived magnetic field for a bird is by attaching magnets to the bird. This method was first applied to pigeons (e.g. Larkin & Keeton, 1976; Keeton, 1971), and later to seabirds (e.g. Mouritsen *et al.*, 2003; Massa *et al.*, 1991), but only recently to songbirds (Packmor *et al.*, 2021).

Further conclusions about the use of the magnetic field by birds can be drawn from manipulation of other cues that are hypothesised to interact with and complement magnetic cues, such as location of sunset (e.g. Moore, 1985), polarisation pattern (e.g. Muheim, Phillips & Åkesson, 2006*b*; Schmaljohann *et al.*, 2013*b*), and stellar cues (e.g. Mouritsen & Larsen, 2001).

### (*b*) *Magnetic sensor manipulation*

Instead of manipulating the cues, manipulations can also take place on the level of the biological (magnetic) sensor (Fig. 2B). Currently, there are three sensor types proposed: (1) the radical-pair-based mechanism in the eye (Hore & Mouritsen, 2016); (2) a magnetic-particle-based mechanism (Wiltschko *et al.*, 2006), likely located in the upper beak and innervated by the ophthalmic branch of the trigeminal nerve (Beason & Semm, 1996; Heyers *et al.*, 2010; Kishkinev *et al.*, 2013); and (3) a magnetoreceptor in the inner ear, either based on magnetite (Wu & Dickman, 2011; but see Malkemper *et al.*, 2019) or on electromagnetic induction (Nimpf *et al.*, 2019; Jungerman & Rosenblum, 1980). Electromagnetic induction was first described for aquatic animals (Lohmann & Johnsen, 2000; Paulin, 1995) and was recently suggested to be the basis of a magnetic compass and/or map sense in pigeons (Nimpf & Keays, 2022). Experimental proof for a role of electromagnetic induction in songbird navigation is currently lacking, hence we focus herein on the first two mechanisms.

Formerly, it was assumed that there is a clear functional separation of the two sensors proposed for songbirds: the radical-pair-based sensor in the eye provides compass information, i.e. magnetic direction, and the magnetic-particle-based sensor in the upper beak provides geomagnetic map information, i.e. magnetic location (see Section III). However, recent findings question this strict separation, as the radical-pair-based sensor might contribute to the geomagnetic map by providing information on declination (Chernetsov *et al.*, 2017) and/or inclination (Fig. 1C–F).

The radical-pair-based mechanism has been experimentally disturbed by electromagnetic radiation in the ~0.1 to ~100 MHz frequency range (e.g. Leberecht *et al.*, 2023; see Table S1 for more references) or by inactivating the putatively corresponding brain region, named Cluster N (Zapka *et al.*, 2009). Manipulation of the putative magnetic-particle-based mechanism has been attempted either by nerve section or anaesthesia of the trigeminal nerve to disable neuronal transmission (Kishkinev *et al.*, 2013; Beason & Semm, 1996) or by modifying the mechanism by remagnetisation of the assumed magnetic particles using magnetic pulses (Holland & Helm, 2013; see Table S1 for more references, e.g. Wiltschko *et al.*, 1994; Karwinkel *et al.*, 2022*a*).

A general problem with disrupting the hypothesised magnetic sensors is that some manipulations, like surgery, electromagnetic radiation exposure or magnetic pulsing, affect the whole organism. Therefore, such manipulations can potentially impact multiple non-target areas of the body, such as other sensory organs or even physiological traits, both of which could unintentionally cause the observed behaviour. For such manipulations, convincing sham, i.e. control, groups are difficult to achieve, as they do not necessarily impact non-target traits to the same extent as the treatment manipulation. In particular when birds show disorientation after manipulation, it is difficult to assign this with certainty to an effect on magnetic navigation/orientation behaviour, rather than to a non-magnetic-cue related unspecific effect, as indicated in other species groups. For example, a magnetic pulse was found to alter gene expression in rainbow trout (*Oncorhynchus mykiss*) (Fitak *et al*., 2017). Furthermore, the effects of low-level electromagnetic radiation appear to be more complex in other species groups (e.g. murine rodents, turtles, newts) than reflected in the songbird literature. There it alters the direction, rather than only increase the scatter in directional responses. Additionally, the directional response in the laboratory in the non-songbird taxa seems to be dependent on the similarity of the electromagnetic environment to the natural, i.e. capture, location (Landler *et al*., 2015; Phillips *et al*., 2022; J.B. Phillips, personal communication). These examples outside the songbird literature highlight that magnetic treatments may lead to unintended and unexpected responses of the study animal and that we, consequently, must always question critically whether alternative reasons may explain the results of a study.

### (2) Recording the bird's behavioural response

The second part of the methodological approaches involves measurements of the birds' behavioural responses to the manipulations described above, from which conclusions about their use of the magnetic field can be drawn. In general, these studies can be divided into two categories: (*a*) experiments with caged birds, often performed in laboratory environments and (*b*) experiments with free-flying birds in their natural environment (Fig. 2B, Table S1).

#### (*a*) *Recording behaviour in caged environments*

In captive birds, responses regarding orientation and navigation abilities are typically tested in small funnel-shaped orientation arenas called Emlen-funnels (Emlen & Emlen, 1966)

(Fig. 2B). During the night in the migration period birds hop in a preferred direction in these circular funnel arenas, leaving footprints and/or scratches on the inclined funnel wall that are assumed to reflect their preferred migratory direction. Although other methods (e.g. videotaping with automated image analysis; use of electric signals triggered when a bird perches in different positions in a cage) have been developed to record the bird's preferred direction digitally (Merkel & Fromme, 1958; Mouritsen *et al.*, 2004; Mouritsen & Larsen, 2001; Muheim *et al.*, 2014), many researchers still prefer to record manually the scratches on paper produced by the bird on the funnel wall, and this method remained unchanged for decades (e.g. Emlen & Emlen, 1966; Leberecht *et al.*, 2023). One reason for this is that electrical devices emit electromagnetic radiation that could disrupt the magnetic compass in songbirds (Engels *et al.*, 2014), perhaps making it impossible to study magnetic responses of birds using electronic methods.

Other migratory traits studied less frequently in relation to the Earth's magnetic field in caged birds include migratory restlessness (*Zugunruhe*; the amount of nocturnal movement) (Bulte *et al.*, 2017) and physiological responses such as accumulation of energy (Bulte *et al.*, 2017; Fransson *et al.*, 2001; Kullberg *et al.*, 2007) or hormone responses (Henshaw *et al.*, 2009).

### (*b*) *Recording behaviour in free flight*

Behavioural responses to manipulations can be also recorded in free flight (Fig. 2B), but one has to consider carefully the temporal resolution of the method used. For example, ring recoveries can provide sufficient behavioural data to answer research questions, but often require long study periods (usually >10 years) and large sample sizes (Perdeck, 1958; Wynn *et al.*, 2020, 2022*b*). For an immediate response, i.e. within a day of treatment, a simple method is to observe visually the vanishing bearings of migratory songbirds at night by attaching a light stick to the bird and tracking its flight direction using binoculars. The spatial resolution of this method is limited to about 0.7–2 km (Mouritsen, 1998*b*; Dierschke & Delingat, 2003). Radio tracking can substantially extend this range to ~ 5–20 km, with researchers manually tracking radio-tagged birds with handheld antennas over time (Holland, 2010; Schmaljohann *et al.*, 2013*b*) and space (Cochran *et al.*, 2004; Holland *et al.*, 2009). In recent years, automated radio-receiving arrays (e.g. Smolinsky *et al.*, 2013; Müller *et al.*, 2018; Brown & Taylor, 2017) advanced this technique by excluding observer biases inherent in manual tracking and integrating single radio-receiving stations to continental-wide networks (Taylor *et al.*, 2017). The lightest available radio tags are only 0.13 g and provide signals for a few weeks with a time resolution of a few seconds. Recent advances in satellite tracking techniques allow recording the behaviour of migrating birds at a higher spatial resolution, but even the lightest tags are at present too heavy for most songbird species (McKinnon & Love, 2018; Bridge *et al.*, 2011) and therefore satellite tags tend to be used for non-passerine orientation and navigation research (e.g. Wikelski *et al.*, 2015; Mouritsen *et al.*, 2003; Gagliardo *et al.*, 2013; Thorup *et al.*, 2020).

Data from a wide spatial range derived from radio-receiving networks and satellite tracking is valuable because vanishing bearings of free-flying birds for the first few kilometres must be interpreted carefully, as the initial direction does not necessarily represent the preferred migratory direction (Brown & Taylor, 2015; Sjöberg & Nilsson, 2015). Vanishing bearings may also reflect movements within a stopover landscape (Schmaljohann & Eikenaar, 2017; Taylor *et al.*, 2011), depend on energy stores and weather conditions (Schmaljohann & Naef-Daenzer, 2011) or might simply reflect escape behaviour after handling.

Species that may breed or winter in the vicinity of the experimental site may already be at their migratory destination. In this case, their behaviour, including vanishing bearing, are not necessarily related to orientation or navigation. Therefore, researchers using vanishing bearings must ensure that experimental birds are still on active migration, do not perform landscape movements and have not reached their migratory destination. Comparison with known species- or population-specific routes from ring recoveries (Spina *et al.*, 2022) can increase confidence in the validity of vanishing bearings.

Besides tracking directional responses, other behavioural responses, such as the day-to-day and within-the-night departure decisions (Müller *et al.*, 2016), could also be affected by experimental manipulations but are often not considered in orientation and navigation studies.

Other methods to monitor the flight directions of free-flying nocturnal migrants include radar (e.g. Nievergelt, Liechti & Bruderer, 1999), infrared-cameras (e.g. Mirzaei *et al.*, 2012) and the moon-watching method (Liechti, Bruderer & Paproth, 1995; Liechti, 2001), but these are not suited to observing individuals after an experimental manipulation. Such observation methods therefore require 'near-experimental' designs by using natural variation of environmental cues, such as magnetic anomalies (Alerstam, 1987), ecological barriers (Fortin, Liechti & Bruderer, 1999) or specific landmarks, such as mountain ridges (Liechti *et al.*, 1996; Hilgerloh, Weinbecker & Zehtindjiev, 2006), different timings within the year (Zehtindjiev & Liechti, 2003) or natural variation in cloud cover (Able, 1982*a*).

### (*c*) *Comparison of caged* versus *free-flight experiments*

In comparison with free-flight experiments, cage experiments have the advantage that the surrounding environment can be controlled for confounding effects, enabling a causal link to the experimental manipulation. A disadvantage is that the caged environment is highly unnatural in many respects (restricted space, feeding conditions, intensity of natural radiation, light, etc.), which might reduce the bird's motivation or even its ability to show natural behaviour. Further, the experimental manipulation of environmental cues in laboratories, especially of landscape or celestial cues, might not be sufficiently realistic to elicit natural behaviour. Consequently, results obtained in the laboratory do not necessarily reflect responses to the same treatment in the wild, where other cues than the manipulated one are available. For example, birds might ignore a manipulated magnetic cue when other important cues for their decision are present. Thus, the assumption that results obtained in artificial environments predict birds' behaviour in the wild is not inevitably correct and should be made with caution (see Table S1 for contrasting results). Therefore, any hypotheses generated in the laboratory should be re-examined with free-flying birds to assess their ecological relevance.

When researchers temporarily house wild-caught migratory birds for either cage-based or free-flight experiments upon release, they need to consider how the feeding conditions may have changed from the natural to the artificial environment. On the one hand, birds with low levels of fuel (body fat) that continue to lose body mass during stopovers (i.e. are in low-quality food conditions), will continue to exhibit migratory restlessness the next night and continue migration. By contrast, birds that gain fuel during stopovers (i.e. are in high-quality food conditions, e.g. with *ad libitum* food), may suppress restlessness until they have replenished their fuel levels. Thus, a counterintuitive suppression of migratory motivation of apparently fat birds might be misinterpreted as an effect of the experimental manipulation. Therefore, in cage studies, an interplay of food availability, changes in food availability and the current energy stores of an individual bird is likely to affect its decision-making process significantly (Biebach, 1985; Biebach, Friedrich & Heine, 1986; Klinner *et al.*, 2020; Gwinner, Schwabl & Schwabl-Benzinger, 1988). Further, birds that show little restlessness, i.e. little migratory motivation, but move for instance within an Emlen funnel in a certain direction could be misinterpreted as intending to migrate in that direction, even though they have a low probability of resuming migration towards the seasonally appropriate destination (Eikenaar *et al.*, 2014). While in many studies the activity of the birds needs to exceed a certain level before their orientation is taken into account (Leberecht *et al.*, 2023), any decrease in migratory restlessness and related behaviour could be wrongly interpreted if the ecology of the individual bird is not taken into account.

Studying free-flying songbirds comes with several limitations. First, it is difficult to manipulate the birds during flight because the low body mass of many songbird species (< 100 g) restricts the total mass of devices for manipulation and tracking to a maximum of 3–5 g (Casper, 2009). Manipulations involving changes to the polarisation pattern (Schmaljohann *et al.*, 2013*b*; Muheim *et al.*, 2006*b*), exposure to electromagnetic radiation (Schwarze *et al.*, 2016*a*; Engels *et al.*, 2014) or the properties of the magnetic field (Mouritsen, 1998*b*) have so far not been applied in free flight. Consequently, to study the birds' behavioural responses to these manipulations in free flight, it is currently only feasible to manipulate the birds on the ground and then release them. As the points in time at which songbirds make their decision to resume migration from stopover and to determine their flight direction remain unclear, it is not straightforward to determine when to manipulate the birds optimally to potentially affect their migration decisions. There is correlative evidence for one night-migratory songbird species, the northern wheatear (*Oenanthe oenanthe*), suggesting that the departure decision is made at least several hours before sunset (Eikenaar *et al.*, 2020*b*), but this might vary among species dependent on their specific migration ecology. This timing issue can be overcome by using long-lasting or permanent manipulations of free-flying birds, such as magnetic pulsing (with effects found up to 10 days; e.g. Holland & Helm, 2013), attaching magnets (lasting days to weeks, depending on attachment; Packmor *et al.*, 2021) or nerve sections (probably permanent; Kishkinev *et al.*, 2013). However, such permanent manipulations pose an ethical challenge and the low recapture probability of wild birds on migration makes it almost impossible to reverse the manipulation after the end of the experiment.

## III. MAGNETIC CUES IN SONGBIRD MIGRATION ECOLOGY

### (1) Perception of directional information

The magnetic field of the Earth roughly resembles the magnetic field of a bar magnet centred in the axis between the poles (Skiles, 1985) (Fig. 1A). This arrangement provides directional magnetic characteristics for orientation on the Earth's surface. The horizontal (parallel to the Earth's surface) component of the magnetic field line can be used for orientation, as it always points towards one magnetic pole. The human-made compass is based on this polarity characteristic of the magnetic field, whereas birds use an inclination compass. They compare the magnetic vector, i.e. the axial direction of the magnetic field line in space, with the gravity vector (orthogonal to Earth's surface) to determine a poleward and equatorward direction (Wiltschko & Wiltschko, 1972). Inclination, defined as angle of the intersection between the magnetic field lines and the Earth's surface (Fig. 1C), varies between 90° at the magnetic poles and 0° at the magnetic equator (Skiles, 1985) (Fig. 1D). In contrast to the horizontal compass, i.e. human-made compass, the inclination compass does not discriminate between north and south but instead provides information about polewards and equatorwards directions. It was shown that songbirds can use inclination angles for orientation up to 85–87° (Åkesson *et al.*, 2001; Lefeldt *et al.*, 2015) and down to at least 5° (Schwarze *et al.*, 2016*b*), meaning that the magnetic compass is not functional in the close vicinity of the magnetic poles (inclination angle 90°) and the magnetic equator (inclination angle 0°), respectively.

Alongside the magnetic field, other cues have also been shown to provide directional information: the sun or its skylight polarisation pattern (Able & Able, 1993; Muheim *et al.*, 2006*b*; Phillips & Moore, 1992), sunrise and sunset direction (Moore, 1987*b*; Schmidt-Koenig, 1990) and the positions of the stars (Emlen, 1970*a*; Wagner & Sauer, 1957; McLaren, Schmaljohann & Blasius, 2022) (Fig. 3A), but not the moon (Moore, 1987*a*). Notably, songbirds seem to use the different compass systems flexibly and switch between them depending on their availability, as shown by compass redundancy in experiments with caged birds (Mouritsen, 1998*b*; Sandberg, Uttosson & Pettersson, 1991; Packmor *et al.*, 2021) (Table S1). Observations from free-flying birds that orient appropriately even when certain cues are not available, e.g. during overcast skies or at magnetic anomalies, also suggest redundancy of the star and magnetic compass in the wild (Alerstam, 1987; Griffin, 1973; Able, 1982*a*) (Table S1).

The relative importance of the different directional compass cues, their hierarchy and calibration, and their use in the wild is still subject to debate. For the magnetic compass, three hypotheses for compass calibration have been proposed: (1) the magnetic compass is calibrated by sunset cues; (2) the magnetic compass is calibrated by polarisation cues; and (3) the star compass is calibrated by the magnetic compass (Table S1). Notably, cue-conflict experiments have revealed contrasting results under free-flight conditions (Schmaljohann *et al.*, 2013*b*; Sandberg *et al.*, 2000; Cochran *et al.*, 2004; Chernetsov *et al.*, 2011; Sjöberg & Muheim, 2016) and cage experiments where compass cues were meticulously controlled for (Muheim *et al.*, 2006*b*; Sjöberg & Muheim, 2016; Moore, 1985; Phillips & Moore, 1992) (Table S1). The topic of cue hierarchy and compass calibration is intensively discussed in Sjöberg & Muheim (2016), Pakhomov & Chernetsov (2020) and Liu & Chernetsov (2012). Here, we briefly summarise the two contrasting opinions: Sjöberg & Muheim (2016) present a structured flow chart for daily decisions of cue integration during migration devised to explain the contradictory results of the cue-conflict experiments under different conditions. By contrast, Pakhomov & Chernetsov (2020) and Liu & Chernetsov (2012) stress the natural high variability of cue integration of birds and do not try to propose a consensus concept.

### (2) Perception of geographical location

In addition to directional information where information for a bearing is obtained independent of the actual location, the arrangement of the Earth's magnetic field can also provide positional information. This is possible due to its parameters changing in a predictable way over most parts of the globe (Fig. 1). They are commonly referred to as 'geomagnetic map cues' (but with inconsistent use in the literature) and we refer to this term herein when positional rather than directional information from the Earth's magnetic field is discussed, whether in one or two dimensions.

The intensity of the magnetic field shows a gradient from the equator towards the poles (Fig. 1B) (Skiles, 1985) and can therefore be used for latitude determination. Due to natural fluctuations in magnetic intensity, the accuracy of this component for navigation of fast-moving animals is limited to 10–30 km (Mouritsen, 2018). Magnetic inclination also shows a gradient from the equator to the poles (Skiles, 1985) and thus can provide latitudinal information for most parts of the world (Fig. 1D). Consequently, magnetic inclination might provide two sources of information for migrating songbirds: (1) as an orientation, i.e. compass, cue (see Section III.1), and (2) as a navigation, i.e. positional, cue. While there is evidence for the use of inclination (Wiltschko & Wiltschko, 1992; Wynn *et al.*, 2022*b*) as a geomagnetic map cue, convincing evidence for the biological importance of magnetic intensity for songbird navigation, similar to that shown for sea turtles (Lohmann & Lohmann, 1996), is currently lacking. Notably, as magnetic navigation might be easier when isolines are orthogonal, a bi-coordinate map of magnetic intensity and inclination for position determination may be less useful for navigation in many parts of the world (compare Fig. 1B and 1D) (Schneider *et al.*, 2023; Boström, Åkesson & Alerstam, 2012*a*; Wynn *et al.*, 2022 *a,b*).

The third spatial component of the magnetic field is declination, which describes the angular deviation between magnetic and geographical North at a specific location (Fig. 1E). This is not a purely magnetic cue because it relies on a geographical compass derived from other cues (e.g. celestial cues). Declination angle has a pronounced east–west gradient between approximately –20 and 20° in North America and between around –10 and 20° in Europe (Skiles, 1985) (Fig. 1F). A study in Europe suggested that reed warblers (*Acrocephalus scirpaceus*) use declination for navigation (Chernetsov *et al.*, 2017), while another study failed to show this for songbirds such as the European robin (*Erithacus* *rubecula*) and the garden warbler (*Sylvia borin*) (Chernetsov *et al.*, 2020) (Table S1). Combination of declination information with magnetic intensity or inclination information could provide a reliable bi-coordinate map across much of the Earth (Wynn *et al.*, 2022*b*), but whether songbirds make use of this is still unclear.

Although the magnetic field is present globally, it is currently unknown whether birds use or rely on it universally. There are possibilities (and some evidence) for alternative cues from which birds might perceive information about location: for example, photoperiod (Kishkinev, Chernetsov & Mouritsen, 2010), celestial rotation (Pakhomov, Anashina & Chernetsov, 2017), olfactory cues [Holland *et al.*, 2009; reviewed in Kishkinev (2015) and Gagliardo (2013)], infrasound (Patrick *et al.*, 2021) and landmarks (Holland, 2003) (Fig. 3B). These cues may be used exclusively or in combination, with magnetic cues for example [see extensive review in Holland (2014) and Mouritsen (2018)].

### (3) Magnetic cues during stopover

During stopover, birds take on fuel, rest and recover (Linscott & Senner, 2021; Schmaljohann *et al.*, 2022). Depending on their requirements at the stopover site, songbirds may resume migration shortly (a few hours) or several weeks after arrival (Packmor *et al.*, 2020; Schaub & Jenni, 2001*a*). Since birds spend more time and energy during stopovers than during migratory flights (Wikelski *et al.*, 2003; Schmaljohann, Fox & Bairlein, 2012; Green *et al.*, 2002; Alerstam & Lindström, 1990), variation in total stopover duration will affect total speed of migration (Schmaljohann & Both, 2017; Schmaljohann, 2018; Nilsson, Klaassen & Alerstam, 2013). Studying stopover and the parameters that affect departure and landing decisions is crucial for understanding a species' migration ecology. In this section, we review when, where and how birds might use magnetic cues for migratory decisions in the wild.

#### (*a*) *Fuelling*

The innate migration programme controls seasonal changes in the energy stores of migrants (Bairlein & Gwinner, 1994; Totzke & Bairlein, 1998). At stopover, the amount of energy accumulated is affected by biotic factors, such as food availability (Bayly, 2007), competition (Moore & Yong, 1991) and predation risk (Schmaljohann & Dierschke, 2005; Fransson & Weber, 1997), as well as abiotic factors, such as weather and climate (Schaub & Jenni, 2001b; Bairlein, 1993). Virtual displacement experiments showed a tight interaction between the amount of accumulated energy and virtual position on a geomagnetic map [Fransson *et al.*, 2001; but see Bulte *et al.* (2017) for a counter-example; Table S1). Those experiments were conducted with naïve juvenile birds with no prior experience of the natural changes in geomagnetic map cues along their migratory route. This suggests that the innate migration programme for fuelling not only contains a temporal (circannual) component, but also a flexible/adaptable spatial component, triggered by geomagnetic map cues. Notably, the temporal component might override the effect of geomagnetic map cues on fuelling both early (Kullberg *et al.*, 2007) and late in the season (Kullberg *et al.*, 2003). Moreover, the altered geomagnetic map cues do not have to be coherent with cues from travelling time, as experiments with abrupt virtual magnetic displacement and stepwise virtual displacements along the route triggered the same fuelling response (Henshaw *et al.*, 2008), suggesting the presence of inate (heritable) geomagnetic signposts for stopovers, probably similar to inherited magnetic signposts for a migratory shift (*Zugknick*), i.e. the abrupt change of migration direction on the route (McLaren, Schmaljohann & Blasius, 2023).

Studies on free-flying birds show that birds undergo extensive fuelling in front of major ecological barriers like the Atlantic Ocean or the Sahara Desert (Dierschke, Mendel & Schmaljohann, 2005; Delingat, Bairlein & Hedenström, 2008; Bayly, Gómez & Hobson, 2013; Bairlein, 1991; Odum, 1963). Thus, the natural fuelling patterns might be, at least in part, induced by geomagnetic map cues.

### (*b*) *Physiological recovery*

The physiological processes involved in recovery during stopover are poorly understood (Eikenaar *et al.*, 2023, 2020*c*; Eikenaar, Hessler & Hegemann, 2020*a*; Schmaljohann *et al.*, 2022), and even less is known about the roles of geomagnetic map cues in recovery. Speculatively, they might be important for stimulating recovery periods in preparation for ecological barrier crossings or exceptionally long migratory flights. The only study investigating links between physiological parameters and magnetic cues described a reduced adrenocortical hormone response after experiencing a virtual magnetic displacement towards an ecological barrier (Henshaw *et al.*, 2009). A reduced adrenocortical hormone response is proposed to be a physiological adaptation to migration for preventing detrimental effects of high corticosterone hormone levels. Wild migrants, by contrast, did not show this effect during stopover at an ecological barrier (Schwabl, Bairlein & Gwinner, 1991) (Table S1). The few studies available and the variability in their results make it difficult to draw conclusions regarding the biological importance of magnetic cues for recovery.

### (*c*) *Departure decisions*

The decision to depart from a stopover site consists of three interlinked components, which we term the 'departure triangle' (Fig. 3C): (*i*) the daily bimodal decision to depart or not to depart from the stopover site, i.e. day-to-day departure decision (reviewed in Jenni & Schaub, 2003); (*ii*) the departure time within the night (reviewed in Müller *et al.*, 2016); and (*iii*) the departure direction from the stopover site.

#### (*i*) *Day-to-day departure decision*

The general motivation to migrate is genetically encoded in the innate migration programme (Berthold, 1973) and then modified by intrinsic and extrinsic factors (Müller *et al.*, 2016). Bulte *et al.* (2017) demonstrated that a virtual geomagnetic map displacement along the migration route decreased the amount of migratory restlessness expressed as birds virtually approached their migratory goal. Thus, geomagnetic map cues might be an extrinsic factor modifying the departure probability from stopover. By contrast, Henshaw *et al.* (2010) did not observe this pattern. As their virtual magnetic displacement was marginal compared to the total migration distance of their focal species, the lesser whitethroat (*Sylvia curruca*), we speculate that this displacement was too short to observe any relevant effect (Table S1). It therefore seems possible that geomagnetic map cues are used to calculate the remaining distance to the migratory destination and thereby influence migratory motivation, i.e. day-to-day departure decisions.

### (*ii*) *Departure timing within the night*

After the decision to resume migration, the next decision is when to depart within the night (Fig. 3C). Müller *et al.* (2016) predict that species/populations with longer remaining migration distances will depart earlier within the night and/or show less variation in timing than birds with shorter remaining distances, for which there is supporting evidence (Schmaljohann *et al.*, 2013*a*). Using a similar argument to that above for location determination using geomagnetic map cues (Section III.3.*c.i*), we predict that geomagnetic map cues might, at least to some extent, affect departure timing within the night. To investigate experimentally whether such a causal relationship exists, one would need to disentangle the effect of geomagnetic map cues from seasonal, night length and body condition effects, among others (reviewed in Müller *et al.*, 2016). It currently remains unclear whether and how magnetic cues influence songbird migrant decisions of when to resume migration at night.

### (*iii*) *Departure direction*

Songbirds can use the magnetic compass, among other systems, to detect directional information (see Section III.1). The departure direction decision in many songbird migrants will involve an interplay between the innate migration direction (Helbig, 1991; Wynn *et al.*, 2023) and the current intrinsic and extrinsic conditions, such as fuel load (Sandberg & Moore, 1996; Sandberg *et al.*, 2002; Sandberg, 2003, 1994), hormone levels (Schneider *et al.*, 1994; Lõhmus *et al.*, 2003), weather (Schmaljohann & Naef-Daenzer, 2011; Müller *et al.*, 2018), and time of year (Chernetsov *et al.*, 2008*a*) (Fig. 3C). In addition, experienced migrants seem to integrate their actual location within the decision-making process to determine their departure direction from stopover. Studies with physical or virtual magnetic displacement demonstrate that birds are able to correct their migratory direction to reach their intended destination, i.e. perform true navigation (Thorup *et al.*, 2007, 2011; Kishkinev *et al.*, 2015, 2020; Chernetsov *et al.*, 2008*b*; but see Kishkinev *et al.*, 2016; Table S1). Therefore, it is generally accepted that the directional departure decisions of migration-experienced songbirds include geomagnetic map cues and involve map-based true navigation (Mouritsen, 2018; Berthold, 1996).

Juveniles on their first migration mainly fail to compensate for such displacements (Thorup *et al.*, 2007; Mouritsen & Larsen, 1998; Perdeck, 1958) (Table S1), probably because they have not yet generated a corresponding geomagnetic map and thus rely on clock-and-compass orientation during inaugural migration (Mouritsen, 1998*a*; Mouritsen & Mouritsen, 2000). Intriguingly, there is evidence that some free-flying juvenile birds [including common cuckoos (*Cuculus canorus*), whose migration ecology is similar to that of songbirds] were able to correct for displacements (Thorup *et al.*, 2011; Thorup & Rabøl, 2007; Thorup *et al.*, 2020). Potential explanations for this phenomenon are that juveniles might have learned parts of the geomagnetic map beforehand by exploring their home range (Züst *et al.*, 2023) or during transportation to the displacement location (Åkesson *et al.*, 2005). Alternatively, they could follow a time-compensated sun-compass, which is partially self-correcting for displacements (McLaren *et al.*, 2022), or possess inherited magnetic map information, comparable to fish and sea turtles (Lohmann *et al.*, 2022).

The hypothesis that migration-experienced but not juvenile birds possess and use a geomagnetic map is further supported by magnetic pulse experiments. Currently, it is assumed that migratory songbirds navigate by sensing geomagnetic map cues using a magnetic-particle-based receptor. Exposing birds to a strong but brief magnetic pulse should remagnetise the magnetic particles and this would alter how the birds perceive local geomagnetic map cues, which in turn should alter the orientation direction in caged birds or departure direction in free-flying birds (Holland & Helm, 2013; see Table S1 for further references, e.g.Wiltschko *et al.*, 1994). However, not all studies show this (Karwinkel *et al.*, 2022*a*,*b*). The observation that the orientation/departure direction of only migration-experienced but not juvenile songbirds was affected by a magnetic pulse (Holland & Helm, 2013; Munro *et al.*, 1997*b*; Munro, Munro & Phillips, 1997*a*), supports the hypothesis that only in experienced birds, but not in juveniles, are geomagnetic map cues involved in the decision-making process.

### (4) Magnetic cues during migratory flight

Investigating the role of magnetic cues during migration also requires understanding decision-making processes during the migratory endurance flight (Fig. 3C). Two crucial stages include (*a*) updating and maintaining the flight direction, including possible directional adjustments and (*b*) deciding when to interrupt the flight, i.e. the landing decision.

#### (*a*) *Updating and maintaining flight direction*

After they have departed in a specific direction, bird migrants generally maintain this direction during the endurance flight (e.g. Karwinkel *et al.*, 2022*a*; Fortin *et al.*, 1999; Bruderer & Liechti, 1998; Bruderer, 1994), but not all birds necessarily fly in the same direction throughout the night (Sjöberg & Nilsson, 2015). Magnetic cues could play two major roles for updating and maintaining the flight direction. First, the magnetic compass could be used for direction determination in flight, as described in Section III.1. Second, geomagnetic map cues could be used to make decisions about changing their flight direction.

Radar studies provide supportive evidence that magnetic cues are perceived and used during the migratory flight, as birds orient towards the seasonally appropriate direction under full overcast conditions (Able, 1982*a*; Griffin, 1973), although landmarks cannot be excluded as additional or alternative orientation cues. Further support that migrants regularly assess magnetic cues during flight and update their flight behaviour accordingly is provided by reports that birds change their flight altitude when passing a magnetic anomaly (Alerstam, 1987).

Free-flying birds change their flight direction when facing barriers depending on, among other factors, time within the night or fuel load (Nilsson & Sjöberg, 2016; Åkesson *et al.*, 1996; Fortin *et al.*, 1999; Bruderer & Liechti, 1998; Zehnder *et al.*, 2002; Komenda-Zehnder, Liechti & Bruderer, 2002; Schmaljohann & Naef-Daenzer, 2011). Similar patterns were found in caged birds (Sandberg, 2003; Sandberg *et al.*, 2002). Whether geomagnetic map cues play a role in recognising these barriers and thus contribute to changes in flight directions is still unknown. However, as geomagnetic map cues are involved in the determination of migratory bearings (e.g. Kishkinev *et al.*, 2021, 2015), it seems plausible that they might also affect changes in flight direction in free flight. However, very little is known about how songbirds update and maintain flight direction during migration.

### (*b*) *Landing decision*

For landing decisions within a migratory endurance flight, it is likely that similar extrinsic and intrinsic factors play a role as for the departure decision (Müller *et al.*, 2016) (Fig. 3). However, since we are only just beginning to study and understand when, where and how birds decide to land (e.g. Rüppel *et al.*, 2023), our current knowledge on the biological importance of magnetic cues on these decisions is very limited. We speculate that geomagnetic signposts may contribute to identifying crucial stopover landscapes before crossing ecological barriers, although evidence for this hypothesis is not yet available.

## IV. UNSOLVED QUESTIONS

Regarding the biological significance of magnetic cues for the decision-making process in songbirds, several significant knowledge gaps remain.

(1) How can juvenile migratory songbirds react to (fuelling, restlessness) and correct for (direction) virtual/physical geomagnetic map displacements, although they have never experienced those conditions before?

(2) How are the different compass systems (sun, polarisation pattern, stars, magnetic) calibrated and what is the hierarchy between the different compass systems (Table S1)?

(3) When, where, how and how often do birds use geomagnetic map cues during stopover and flight for their migratory decisions?

(4) How do birds use their compasses, including the magnetic compass, during active migratory flight?

(5) Do magnetic cues play a role in the birds' decisions to interrupt migratory endurance flights, i.e. in landing decisions?

## V. CONCLUSIONS

(1) Magnetic cues can significantly influence the decision-making processes of songbirds during migration. The innate migratory programme provides the basis for migratory decisions, which are modulated by an interplay of intrinsic and extrinsic factors, in which magnetic cues play a role.

(2) Magnetic cues are just one of many environmental cues, e.g. weather, stopover habitat, landmarks or celestial cues, that are available to birds. We should not overestimate the importance of magnetic cues in the wild, as songbirds may use other cues for their migratory decisions.

(3) Likewise, we know that in birds, redundancy may exist and several different systems may function flexibly for the same task (e.g. sun, stars, magnetic compass direction). This might explain some of the variation in results obtained following magnetic manipulations in orientation cage experiments *versus* free-flight tracking studies in the wild, where multiple cues are available (Table S1).

(4) Cage experiment studies are useful for demonstrating the sensory capabilities of birds, as the environment can be meticulously controlled. However, we should not infer that the sensory capability of a bird in a cage equals the bird's behaviour in the wild in an ecological context. In general, there is little evidence of magnetic disruption leading to deficits in orientation and navigation performance in field studies.

(5) There is high variability and inconsistency in the results of orientation and navigation studies in general, especially when using different species or at different locations. This low level of repeatability, reproducibility and replicability might largely be attributed to high natural variability in the use of magnetic cues among birds with different migratory strategies (e.g. short-distance migrants *versus* long-distance migrants), species, populations, locations, individuals, and even within an individual (e.g. due to experience, health status, etc.), or to subtle differences in experimental design or experimenters. This variability and the contradictory results found in many studies make it difficult to draw general conclusions regarding how wild songbirds use magnetic cues for their migratory decisions.

(6) We hope that this review encourages researchers to improve the design of future orientation and navigation experiments on all bird taxa by carefully considering the migration ecology of the focal species. Furthermore, we hope that we have illustrated how the

appropriate interpretation of orientation and navigation studies can only be made in the context of the species-specific migration ecology.

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## VII. AUTHOR CONTRIBUTIONS

T.K. wrote the initial draft of the manuscript with input from H.S. All authors provided substantial input to the content and edited the manuscript. H.S. supervised the process. All authors read and approved the final version.

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## VI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Overview of magnetic-cue-related orientation and navigation hypotheses for migratory songbirds from cage-based and free-flight studies.

## Figure legends

**Fig. 1.** Properties of the Earth's magnetic field. (A) The Earth's magnetic field behaves roughly as if there is a bar magnet in the centre of the Earth. This results in a horizontal

directional component with geographic North (gN) and magnetic North (mN) almost aligned. This property is known to most people through the use of a classical compass. (B) The magnetic field intensity varies around the globe and is highest at the poles (~60 µT) and lowest in the equator region (~30 µT). (C, D) The inclination angle is defined as the angle at which the magnetic field lines cross the Earth's surface. At the magnetic poles, the field lines are perpendicular to the surface (90°), whereas they are parallel at the magnetic equator (0°). This feature can be used by birds as a compass to identify poleward and equatorward directions. (E, F) The declination angle is defined as the angular difference between the geographic and magnetic North pole. It therefore displays the error of a magnetic compass compared to true geographical North at a given location. When both poles are aligned, the angle is 0°. Maps in B, D and F show selected isolines derived from NCEI (2019). Due to their projection, maps do not show the poles.

**Fig. 2.** Graphical summary of methods used to assess magnetic-cue related hypotheses in songbirds. (A) Experiments generally start with the manipulation of the perceived magnetic cue information. This can be done by manipulating the magnetic cue itself or the corresponding sensory structures of the bird. (B) This experimental manipulation is then followed by recording the bird's behavioural response. This can be done either in a caged setup or by recording the birds in free flight in the wild. See main text for detailed description of methods. 'Attaching magnets' adopted from Packmor *et al.* (2021); 'section trigeminal nerve' adopted from Kishkinev *et al.* (2013); 'brain lesion' adopted from Zapka *et al.* (2009); all graphics adopted with permission.

**Fig. 3.** Schematic conceptual framework demonstrating the role of magnetic cues in the migration ecology of songbirds during the long-distance phase (Mouritsen 2018). Factors involving cues from the Earth's magnetic field are highlighted in grey. (A) Possible factors

involved in perception of geographical location. (B) Possible factors involved in perception of directional information. See main text for further explanation. (C) Conceptual framework of the behaviour of a migrant following a stop-and-go strategy. The upper green box represents the behaviour during the stopover and decisions on the ground at the first stopover location (*i*). The lower blue box represents behaviour and decisions during the migratory flight. When the migrant reaches the next location (*i*+1), the scheme will repeat.