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Using high-resolution geospatial datasets to investigate the role of geomagnetic cues during long-distance bird migration

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Abstract

The Earth's magnetic field is an orientation and navigation cue for migratory animals, especially birds. However, current experiments used to test this hypothesis are limited. In my thesis, I compare different methods for combining animal tracking data with high-resolution satellite geomagnetic data by using an open-source software called MagGeo. I use the best-performing MagGeo algorithm to investigate if white storks *Ciconia ciconia* use geomagnetic cues to cross the eastern Sahara. Crossing this inhospitable and featureless habitat has likely selected for unique strategies that facilitate successful bird navigation during migration. I show that MagGeo can reliably be used to annotate animal movement tracks with geomagnetic data with high global accuracy. I find that white storks may use geomagnetic cues and prevailing wind conditions to cross a landscape barrier. Collectively, my work encourages further development, testing, and application of open-source data and tools to uncover relationships between migratory animals and geomagnetic data.

Keywords

Animal migration, bird navigation, orientation cues, geomagnetic field, prevailing winds, remote sensing, movement ecology

Summary for Lay Audience

Electric currents in the Earth's molten outer core generate a magnetic field that extends out into space and protects the Earth from incoming solar particles. The geomagnetic field also has regular patterns which may be helpful for migratory birds crossing featureless landscapes like deserts and oceans. Like how we use a map and compass, birds with internal maps and compasses could use geomagnetic information to make movement decisions like "Which direction should I migrate?"

I test and apply a new open-source software tool called MagGeo that connects satellite geomagnetic data with location data collected by animals wearing "GPS backpacks". I use these fused datasets to understand how animals may be experiencing and using geomagnetic information to perform long-distance migration spanning thousands of kilometers.

I first do an error analysis for MagGeo by creating and testing different versions. The goal is to ensure that the software outputs are an accurate representation of how migratory animals experience the geomagnetic field. Once I identify the best MagGeo version, I use it to annotate GPS tracks of 68 white storks *Ciconia ciconia* crossing the eastern Sahara. I transform MagGeo outputs into values that represent 4 different ways that these birds could be making movement decisions based on geomagnetic information.

I show that we can reliably use MagGeo to study long-distance animal migration anywhere on Earth. When I apply MagGeo to study bird migration, I find that white storks migrating over the eastern Sahara use geomagnetic cues for orientation information. They could also be relying on wind patterns to make movement decisions since selecting for certain wind conditions would help these bulky birds cross this risky landscape faster.

My research adds to the growing body of work that birds use multiple strategies to migrate long distances. My work also encourages development and application of new, open-source datasets and software. These tools can help explore age old questions about how animals interact with the natural world to perform the magnificent, unbelieve feat that is long-distance migration.

Co-Authorship Statement

Both chapters in this integrated-article thesis are co-authored with Dr. Jed Long as the senior author. He provided and facilitated funding for all projects and all work was done under his supervision in addition to his generous contributions to methodology, analysis, writing, and revising.

A version of the first chapter has been submitted for publication to Ecological Informatics.

AI performed the analysis and wrote the initial draft of the manuscript. FBP and VBB provided data sources and coding assistance. JAL conceptualized the initial research objective and design. VBB, CDB, UD, JAL provided insightful input during group discussions about results. All co-authors provided revisions for the final draft of the manuscript.

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A version of the second chapter is being prepared for publication to Movement Ecology.

AI performed the analysis and wrote the initial draft of the manuscript. BZ, UD and JAL conceptualized the initial research objective and design and provided insightful input during group discussions about methodology and results. BZ provided coding and analysis assistance. KS and MW facilitated data collection.

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Chapter 1

1 Introduction

Billions of birds make incredible migratory journeys, safely navigating across barren lands, endless oceans, and concrete jungles to travel between their breeding and wintering grounds. Evolutionary pressures selecting for traits and behaviors that lead to successful long-distance migration balance trade-offs that are likely unique to species (Åkesson et al., 2016; Åkesson & Hedenström, 2007; Alerstam et al., 2003) and perhaps even populations within a single species (Flack et al., 2016; Schmaljohann et al., 2007a). Constantly changing external conditions also require individuals to adapt their migration strategies and routes (Bishop et al., 2015; Gill et al., 2014; Vansteelant et al., 2017, 2021). Even so, birds can find their way back to the same nesting grounds with stunning fidelity year after year (Bollinger & Gavin, 1989; Komolkin et al., 2017; Lindberg et al., 1995; Winkler et al., 2004). While lines of inquiry around this navigation ability have universally fascinated humans for centuries, contemporary tools and frameworks to understand the underlying mechanisms have been trailing behind those used to uncover the energetics of migration. Navigation and orientation are however arguably equally important since both accuracy and precision are required for a successful migration. For bar-tailed godwits *Limosa lapponica* directional miscalculations in longitude by even 5^{o} in their oversea migration between Alaska and New Zealand could lead to certain death, even if they have sufficient energy stores to make this unbelievable journey (Battley et al., 2012).

The recent development and miniaturization of biologging tools has allowed researchers to fit even small birds safely with devices that record information like position, temperature, and speed (Bograd et al., 2010; Guilford et al., 2011; Nathan et al., 2008). These tools help discover basic facts about migration ecology such as wintering ground locations and overall connectivity (DeLuca et al., 2015; Hallworth et al., 2015, 2021; Ng et al., 2018; Tøttrup et al., 2012), and even causes of death during migration (Jobson et al., 2021). For example, GPS tags confirmed that bar-headed geese *Anser indicus* do indeed fly over the Himalayas (Hawkes et al., 2011) and birds fitted with temperature and pressure loggers provide further insight for how this amazing flight may be physiologically possible (Bishop et al., 2015). We can also fuse environmental attributes to a simple combination of longitude, latitude, and timestamp of a moving animal to then create movement models to uncover if an individual is selecting for specific habitats and conditions (Brum-Bastos et al., 2021; Dodge et al., 2013; Kays et al., 2022). Previous work shows how woodland caribou *Rangifer tarandus caribou* in Yellowstone National Park prefer conifer stands as it helps avoid predatory-prey interactions with gray wolves *Canis lupus* (Fortin et al., 2005). Models parameterized with sufficient biological information can further be used to predict how animals may react to changes in their environment (Avgar et al., 2016; Fieberg et al., 2021; Long & Nelson, 2013; Peck, 1999). As a result, there is a necessity to develop and apply such tools to model how an animal is influenced by its surroundings, both in the present and future.

How animals interact with their environment at the scale of landscapes and habitats has always been a fundamental pillar of ecology (Boyce, 2006; Levin, 1992; Lima & Zollner, 1996; Long & Nelson, 2013; Mueller et al., 2008; Peck, 1999). Earlier studies were comprised of direct and indirect observations of animal behavior in key habitats. Over time, studies have expanded in scale and scope with increasing access to diverse remote sensing datasets and tools which facilitate the study of bird migration across multiple continents (Jetz et al., 2022; Tucker et al., 2018). Studies have previously connected atmospheric data to GPS location data of migratory birds to then investigate how wind and weather shape movement decisions and migratory routes (Curk et al., 2020; Gill et al., 2014; Hawkes et al., 2011; Jobson et al., 2021; Safi et al., 2013). For example, Nourani et al. (2021) show how current and historical wind conditions shape sea-crossing of thermal soaring migratory raptors like buzzards. Movement ecologists have also used optical satellite imagery and meteorological data to study resource selection during migration to examine factors like quality of stopover choice (Buler et al., 2007; Cohen et al., 2021; Dossman et al., 2016). There is less emphasis however on using remote sensing data to understand how external cues may influence the navigation and orientation decisions of long-distance migratory birds (Wiltschko & Wiltschko, 2022).

Navigation and orientation have been largely studied in controlled laboratory settings (Chernetsov et al., 2017; Kishkinev et al., 2015; Schwarze et al., 2016). These experiments have been instrumental in devising a framework to explore possible mechanisms for a solar compass (Guilford & Taylor, 2014), a stellar compass (Foster et al., 2017), a geomagnetic compass (Pakhomov & Chernetsov, 2020), and olfactory navigation (Gagliardo, 2013). These experiments are necessary for outlining the physical, chemical, and even neurophysiological mechanisms that underlie long-distance bird migration (Holland, 2014). Advanced equipment and techniques have recently facilitated study of topics like quantum biology especially as it relates to geomagnetic orientation and navigation (Hiscock et al., 2016; Hore & Mouritsen, 2016). Recent experiments have suggested how certain visual pathways may be connected to a geomagnetic sense that could allow birds to use geomagnetic information to perform long-distance migration (Mouritsen & Heyers, 2016; Zapka et al., 2009). Outside of laboratory settings however, physical displacement experiments have provided contradictory evidence (Benhamou et al., 2003). For example, when gray catbirds *Dumetella carolinensis* with an impaired olfactory sense were displaced 1000 km east of their original position, they were not able to reorient towards the correct initial destination (Holland et al., 2009). Birds of the same species with an impaired geomagnetic sense did however reorient correctly towards the original wintering ground destination. These results suggest that migratory birds may rely on olfactory cues instead of geomagnetic cues to perform navigation (Bingman & MacDougall-Shackleton, 2017; Buehlmann et al., 2020; Holland, 2014; Pollonara et al., 2015; Wikelski et al., 2015).

A key gap in understanding geomagnetic orientation and navigation is how migratory birds experience the geomagnetic field in the wild, outside of laboratory settings (Benitez-Paez et al., 2021; Zein et al., 2022). Part of this knowledge gap is due to lack of access to remotely sensed geomagnetic data. While the geomagnetic community has been a leader in open-source data products and models (Chulliat et al., 2015; Finlay et al., 2020; Friis-Christensen et al., 2008), these datasets have complex formats and are therefore more difficult to manipulate. Some studies have used the more easily accessible model estimates to test theories of geomagnetic navigation. Komolkin et al. (2017) used in part the World Magnetic Model data to explore how migratory birds could theoretically use geomagnetic information to navigate with high accuracy and precision back to their breeding grounds. Model estimates however may not be the best available datasets to represent how animals in the wild experience the dynamic geomagnetic field (Benitez-Paez et al., 2021; Zein et al., 2022). The overarching objective of this thesis is to develop, test, and apply geomagnetic datasets and contribute to the growing cross-disciplinary effort that seeks to understand how birds use geomagnetic information to migrate long distances.

To achieve this objective, we use GPS tracking data from white storks *Ciconia ciconia* migrating between their breeding grounds in northeastern Europe and their wintering grounds in sub-Saharan Africa. Lab experiments have previously worked with nocturnal, long-distance migratory birds like passerines to test the role of geomagnetic cues during migration (Åkesson et al., 2005; Chernetsov et al., 2017, 2020; Kishkinev et al., 2015; Schwarze et al., 2016). Data collected remotely by individual songbirds and shorebirds fitted with loggers have also been used to create movement models to study ex-situ geomagnetic orientation and navigation (Åkesson & Bianco, 2016, 2017; Muheim et al., 2018; Sokolovskis et al., 2018). The bias towards these two avian groups is in part tied to the rationale that nocturnal migratory songbirds and shorebirds likely depend on geomagnetic cues to make movement decisions as other reliable cues, like landmarks, are unavailable (Wiltschko & Wiltschko, 1972). Additionally, the smaller size of species within these groups facilitates laboratory studies given that fewer resources are required for animal trapping, care, and handling. However, open-source GPS tracking data for these species is limited because lightweight loggers that do not negatively impact migratory performance are either unavailable, imprecise, or expensive (Bograd et al., 2010; Criscuolo & Sueur, 2020; Kay et al., 2019; Lisovski et al., 2020). Instead, larger birds like storks and raptors are overrepresented in biologging datasets, especially data collected by heavier GPS loggers that also provide more accurate and precise location information (Kays et al., 2022). There is currently no literature about the magnetoreception pathways and sensitivities for white storks. We assume that white storks are capable of magnetoreception given that structures for this sensory ability are pervasive and have been identified across different many species, including turtles, fish, marine mammals, and non-migratory birds (Heyers et al., 2017; Holland, 2014; Lohmann et al., 2007, 2008; Nyqvist et al., 2020). While it is possible white storks use other cues, like landmarks and olfaction, geomagnetic cues may also be part of the multi-factorial system necessary for successful migration (Mouritsen, 2018; Mouritsen & Heyers, 2016; R. Wiltschko & Wiltschko, 2013). Thus, given these biological considerations alongside the robust biologging dataset, white storks are a suitable candidate species for the analysis required for this thesis.

1.1 Background

1.1.1 The geomagnetic field

The Earth’s magnetic field is notionally a bar magnet with field lines exiting the geomagnetic south pole and entering the geomagnetic north pole (Campbell, 2003). In addition to polarity, the geomagnetic field has various properties that can be calculated from the field vector (Figure 1-1A). Total field intensity (F) and the horizontal component of the field intensity (H) measure the strength of the geomagnetic field vector in nanoteslas (nT). The global range of the Earth's geomagnetic field is from 20,000 nT to 60,000 nT which is roughly 1/20th of the strength of a common refrigerator magnet. Inclination is measured in degrees and refers to the angle between the field vector and the Earth's horizon. Given that the field lines enter the Earth at the poles, inclination is 90° at the poles and 0° at the geomagnetic equator which is at roughly the same location as the geographical equator. Declination is also measured in degrees and is the angle between the magnetic and geographic pole.

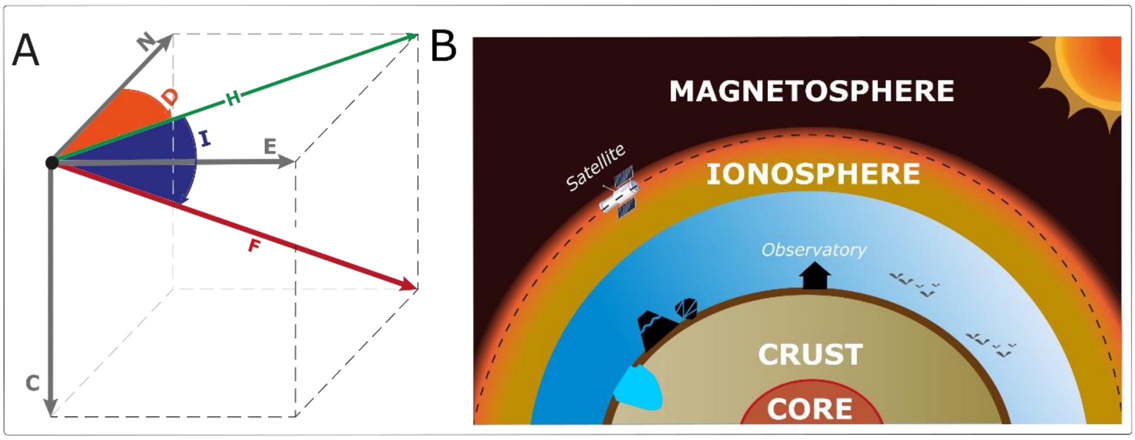

Figure 1-1. The main components of the geomagnetic field. A. The geomagnetic coordinate system is in the North-East-Centre (NEC) coordinate frame shown in gray with the four geomagnetic components highlighted in color: declination (D) in orange, inclination (I) in blue, horizontal intensity (H) in green, and total intensity (F) in red. **B.** The four main contributors to the geomagnetic field from innermost to outermost: core, crust, ionosphere, and magnetosphere. Examples of geomagnetic anomalies due to lithosphere composition represented by symbols for water body, volcano, and exposed magnetic rock. Satellite orbiting in the ionosphere and the geomagnetic observatory are representations for the two main geomagnetic data sources. Image inspiration from Benitez-Paez et al. (2020).

There are multiple sources of the Earth's geomagnetic field, the principal being the geodynamo in the liquid outer core, followed by magnetic minerals in the local subsurface (crust), then electrical currents in the ionosphere at approximately 100-1000 km from the Earth's surface, and finally the magnetosphere which extends even further into outer space (Figure 1-1B). Human activities like mining also expose geomagnetic materials that can influence the local geomagnetic field values. Geomagnetic values will also vary based on space weather like solar activity which influences geomagnetic activity. During periods of high solar activity such as geomagnetic storms, values of the geomagnetic field can change rapidly particularly at the mid to high latitudes. It is also at these locations where a combination of high solar activity, geomagnetic field lines and gasses in the Earth’s atmosphere interact to create beautiful auroral light displays.

1.1.2 The geomagnetic field as an orientation cue

Humans have used the reliable geomagnetic field patterns for navigation and orientation for centuries. The polarity of the field is detected by basic compasses and can be used to identify the four cardinal directions. Declination maps have helped sailors and colonizers navigate across open oceans (Hulot et al., 2010; Johnsen et al., 2020). Given the adequate anatomy and physiology to sense one or more of the geomagnetic field components, animals could use geomagnetic information to make movement decisions (Deutschlander et al., 1999; Johnsen & Lohmann, 2005; Mouritsen & Heyers, 2016). It is widely accepted that animals do not use polarity and it is heavily debated if all animals use total intensity, inclination, and/or declination values as part of a migratory strategy (Åkesson & Bianco, 2016; Boström et al., 2012; Chernetsov et al., 2020; Kiepenheuer, 1984; Wiltschko & Wiltschko, 1972b).

The current leading hypothesis is that some animals, like migratory birds, may sense the geomagnetic field through pathways related to photoreception (Deutschlander et al., 1999; Mouritsen, 2014). The exact anatomy and neurological pathways are still being discovered though a mechanism involving quantum particles called radical-base pairs seems plausible given the current evidence (Hore & Mouritsen, 2016). Like animal eyes that can detect only a portion of the electromagnetic field to see the visual spectrum of colors, some birds may also have the capacity to sense a range of values in the geomagnetic field spectrum (Åkesson et al., 2005; Schwarze et al., 2016; Semm & Beason, 1990). Magnetoreception could also vary drastically by animal. For marine animals, the pathways could be closely linked with electromagnetic induction (Keller et al., 2021; Nyqvist et al., 2020). If animals do possess the ability to sense this invisible but reliable cue, they could use it to make accurate and precise decisions that lead to successful migration.

The “map-and-compass” theory suggests that both navigation and orientation are necessary for successful migration (Kramer, 1961). Navigation in this context refers to activities commonly associated with maps that facilitate position finding relative to other locations (like a bi-coordinate latitude and longitude grid) (Åkesson & Hedenström, 2007;

Kishkinev, 2015; Phillips et al., 2006; R. Wiltschko & Wiltschko, 2022). Orientation refers to activities commonly associated with the compass which facilitates direction-finding (north, south, east, west) (Chernetsov, 2016; Muheim et al., 2006, 2018). For animals, the geomagnetic field could provide either map-based navigation information or compass-based orientation information though the pathways may not be as clearly distinct in animals as presented here (Holland, 2014). Additionally, it is likely that migratory animals are not using one but instead many cues to make their long migratory journeys.

1.1.3 Other possible cues

Linear visual features like coastlines, mountain ranges and roadways, can serve as orientation cues if they reliably direct the bird towards its destination for some part of its trajectory (Eisaguirre et al., 2020; Lipp et al., 2004; Wallraff, 2005). Birds can also use linear cues to maintain a constant heading after initially making a movement decision based on another cue. Pigeons *Columba livia* have been noted to follow the same linear roadways back to their home lofts after multiple displacements (Biro et al., 2007; Guilford & Biro, 2014). Distinct features in heterogenous landscapes like major cities or forest patches can also serve as orientation cues for birds following a “piloting” compass strategy (Biro et al., 2007; Holland, 2003). For this strategy, birds can sequentially use key landscape features to decide movement direction.

During the day, the sun and associated polarization patterns could also provide directional information. To account for the sun’s movement across the sky, sun compasses need to be calibrated against an internal clock to maintain constant migratory heading (Guilford & Taylor, 2014; Pakhomov & Chernetsov, 2020). Experiments with monarch butterflies *Danaus plexippus* have demonstrated that this two-compass system is required to maintain movement in a constant direction during their fascinating long-distance migration (Mouritsen & Frost, 2002). For nocturnal migrants, stars and their movement during the night (rotation) could also serve as an orientation cue (Foster et al., 2017). Early experiments with indigo buntings *Passerina cyanea* demonstrate that long distance migratory birds can also use the relative position of stars (star patterns) for directional information (Emlen, 1967, 1975). For either solar or stellar compasses, exposure to these patterns during key developmental stages is necessary for juvenile and adult birds to correctly use these cues for orientation during migration.

When visible cues are not applicable or reliable, some birds may use olfactory cues. Gradients of smells from different locations could signal to the bird a certain direction (Gagliardo, 2013; Jacobs, 2012). Seabirds particularly can use their sense of smell to seek out food sources during foraging trips in the open ocean (Bonadonna & Gagliardo, 2021). Some seabirds can also use smells to locate their home loft after a foraging trip. After being displaced from their nests, Cory's shearwaters *Calonectris borealis* with an impaired olfactory sense struggle more than birds with functional olfactory senses (Gagliardo et al., 2013; Pollonara et al., 2015). It is likely that there are spatial limitations to this cue since unique smells (unlike geomagnetic or celestial cues) are not omnipresent (Bingman & Cheng, 2005). Smells can also provide incorrect information if the direction of the smell is impacted by landscape features like mountain ranges that can deflect the wind and subsequently smells in unpredictable ways (Gagliardo et al., 2021; Holland, 2014; Holland et al., 2009).

Wind is another invisible cue that could facilitate orientation (Agostini et al., 2012; Schwarze et al., 2016; Vansteelant et al., 2017). Prevailing winds are winds that continuously blow in one direction within a geographical region (Mohamed Hereher, 2014). This reliable pattern could provide birds with directional information since the bird would only experience wind support (subsidized flight) if it was moving along the prevailing wind vector (Chevallier et al., 2010). However, it is difficult to distinguish if a bird is using the wind as a resource for energy subsidies or orientation or both. It is especially difficult to distinguish between these motivations for bulkier birds like storks or eagles who depend on energetic subsidies from the wind for migratory movement (Becciu et al., 2020; Biebach et al., 2000; Mandel et al., 2008; Nourani et al., 2018, 2021). Other orientation cues could also have energetic implications. As demonstrated by models created with data from tagged golden eagles *Aquila chrysaetos* in the Pacific Northwest, linear features can function as an orientation cue or as a site of energy resources such as roadkill (Eisaguirre et al., 2020).

1.1.4 Studying movement ecology of migratory animals

Biologging data has enabled testing of navigation and orientation hypotheses for birds while they are in their natural surroundings, especially during migration. GPS tags can then help facilitate what has recently been termed as "laboratories in the wild" where cleverly designed experiments can help us understand how animals relate to dynamic surroundings instead of in carefully controlled laboratory settings. Displacement experiments including birds with impaired senses (through modifications like ablations) can help untangle the possibilities and limitations of how different birds sense, perceive, and integrate orientation cues (Benhamou et al., 2003; Holland et al., 2009; Pollonara et al., 2015). Movement trajectories of displaced common cuckoos *Cuculus canorus* show that both adult and juvenile individuals can reorient towards the original destination (Thorup et al., 2020). This suggests that at least in some birds, there might be an innate map that allows them to navigate accurately even on their first migration.

In addition to studying the movement patterns of displaced birds, we can attach remotely sensed environmental data to biologging data to represent the landscape as experienced by an individual at a specific point in space and time. After this data fusion, we can build mathematical models to test if individuals are selecting for specific environmental resources or conditions (Fieberg et al., 2021; Kölzsch et al., 2019; Thurfjell et al., 2014; Zein et al., 2021). Movement models, like all models, do have their limitations such as requiring accurate parameterization based on species-specific biological information which is often very difficult to acquire (Holland, 2003; Holloway & Miller, 2014; Muff et al., 2020). By diligently addressing and accounting for these limitations, movements models can provide rich insight about animals' preferences and decision-making processes.

1.2 Research objectives and questions

There is a notable research gap for combining high-resolution satellite geomagnetic data to animal movement tracks. This limitation has possibly hindered our understanding of how this environmental cue impacts an animal's movement decisions. MagGeo is an open-source software that was specifically developed to address this technological gap (Benitez-Paez et al., 2021). While MagGeo has been tested for 3 locations in Europe, a global analysis is necessary to ensure that this tool can be reliably used to study long-distance migration outside of Europe. Furthermore, some of the underlying assumptions of the algorithm have not been rigorously challenged and it is possible that alternative versions may produce results that better represent how migratory animals experience the geomagnetic field. Once the best performing MagGeo algorithm is identified, this tool can be used to address the knowledge gap of how geomagnetic cues can influence a bird's movement decision during long-distance migration. I work towards addressing these technological and knowledge gaps in my thesis through the following two data chapters.

In chapter 2, my objective is to test current and modified versions of the MagGeo algorithm by performing a global error and accuracy analysis for this open-source software. To do this, I first combine high-resolution satellite geomagnetic data and geomagnetic model estimates. I then use data from a global network of geomagnetic observatories to ground truth different MagGeo algorithms. Through this chapter, I seek to answer:

RQ1: What is the best spatiotemporal interpolation method for attaching high-resolution satellite geomagnetic data to a moving animal?

RQ2: Is a combination of geomagnetic model estimates and satellite data more accurate than only model estimates to represent geomagnetic values as experienced by migratory animals near the Earth's surface?

In chapter 3, my objective is to apply the results and methodology from chapter 2. I fit movement models to test four geomagnetic orientation strategies for white storks crossing the eastern Sahara. This species is a thermal-soaring long-distance migratory bird and relies on wind patterns to subsidize flight costs. In this chapter, I explore:

RQ3: Can geomagnetic orientation cues facilitate successful bird migration across a featureless, energetic barrier?

RQ4: How do prevailing winds influence biannual migration decisions for thermal soaring migrants crossing an energetic barrier?

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Chapter 2

2 Spatial-temporal interpolation of satellite geomagnetic data to study long-distance animal migration

2.1 Introduction

Understanding how migratory animals navigate the landscape is challenging not least because of the spatiotemporal range of some migrations (Wilcove & Wikelski, 2008). Access to remote sensing imagery has influenced our understanding of how and why an animal interacts with its environment (Pettorelli et al., 2014). However, the predominant use of optical remote sensing imagery often restrains how we model an animal's relationship to its surroundings. Alternatively, Synthetic Aperture Radars (SARs) and Light Detection and Ranging (LiDAR), offer opportunities for novel lines of questioning in wildlife movement ecology. Satellites with geophysical sensors measuring the Earth's magnetic field are another underexplored non-optical resource that can bring new insights, especially with regards to the magnetic map hypothesis (Lohmann et al., 2007; Mouritsen, 2014; Naisbett-Jones et al., 2017; Wiltschko & Wiltschko, 2013).

Electric currents in the Earth's molten outer core generates a magnetic field that extends out into space and provides protection from incoming solar particles (Campbell, 2003). Large scale geomagnetic patterns vary predictably across space and time, thus allowing humans to reliably use geomagnetic information for wayfaring for many centuries. Animals who are capable of sensing and perceiving the geomagnetic field may also use geomagnetic patterns to make movement decisions during migration (Lohmann et al., 2007; Mouritsen & Heyers, 2016; Wiltschko & Wiltschko, 2021). The underlying mechanisms of geomagnetic navigation strategies vary between species and are highly debated in the literature. Specifically, navigation consists of two tasks: 1) knowing the current location (geographic positioning) and 2) knowing in which direction to go (compass orientation). Some research suggests that animals use geomagnetic information for orientation, and it is also possible that animals use two or more geomagnetic values to build cognitive maps for positioning, although this has not been proved.

Physiological capabilities to sense geomagnetic values have been tested in laboratory experiments, alongside physical or virtual displacement that demonstrates how a bird's migratory direction oscillates with changes in a magnetic environment (Kishkinev, 2015). The exact sensitivity range to changes in absolute geomagnetic values is unclear and likely varies by species, internal states, and external conditions. Some experiments suggest ranges from 15 nT to 200 nT for total intensity (Beason & Semm, 1987; Semm & Beason, 1990), 2° to 5° for inclination (Schwarze et al., 2016) and at least 8° for declination (Chernetsov et al., 2017). There are even fewer experiments that have explored how wild migrants respond to the geomagnetic field while migrating and what strategies they use for orientation and positioning. To understand what happens outside of controlled laboratory settings, there has been a push to test geomagnetic strategies from a data-driven, geospatial perspective by taking advantage of open-source geomagnetic models and satellite data (Zein et al., 2021, 2022).

To look at this, previous studies have successfully combined geomagnetic model estimates with animal tracking data (Åkesson et al., 2016; Åkesson & Bianco, 2017; Sokolovskis et al., 2018; Zein et al., 2021). Model estimates are typically geomagnetic field values predicted using a set of coefficients that are informed by satellite geomagnetic data collected during periods of low geomagnetic activity otherwise known as quiet-time (Chulliat et al., 2015; Matzka et al., 2010; Olsen et al., 2006). Model estimates are continuous across time allowing estimates for any latitude, longitude, and altitude combination (location in 3D space). As such, estimates are useful for movement ecologists trying to understand how geomagnetic information can influence animal behavior across the entire migratory trajectory. For example, Åkesson & Bianco (2016, 2017) used the 11th Generation International Geomagnetic Reference Field (IGRF-11) model to create simulated migratory paths built from model estimates. They compared these trajectories with observed paths recorded by migratory birds carrying GPS trackers. Zein et al. (2021) used IGRF-12 to combine migratory bird tracks with model estimates to test different geomagnetic navigation strategies. Studies concluded that a geomagnetic compass is possible though further exploration about an animal's instantaneous response to actual geomagnetic conditions during migration was restricted due to limitations of model estimates (Zein et al., 2022).

Model estimates capture much of the variability in the geomagnetic field, but not all and especially not the dynamics that may affect an animals' instantaneous responses to the contemporaneous geomagnetic conditions. The geomagnetic field varies across space and time at different scales. Across space, there are both large planetary variations of the field generated by Earth's core and small-scale changes related to crustal field generated by magnetic rocks in the Earth's crust. Temporally, the crustal field changes slowly over millions of years, while the core field changes over years to decades – this is called secular variation. However, the field also changes over the course of the day in response to the variable solar wind, which generates fluctuations in the ionosphere and magnetosphere (Courtillot & Le Mouel, 1988). Solar storms and large solar flares can further lead to disturbances over much shorter temporal scales (seconds to hours) known as geomagnetic storms, whose effects can range from benign and beautiful auroral light displays to technological disruptions, such as satellite anomalies and power blackouts (Babayev et al., 2006; Hapgood, 2012; Kikuchi, 2003; Lanza & Meloni, 2006). Specifically, model estimates omit fine-scale spatial variability created by very local but acute geomagnetic anomalies in the crustal field, and they also do not represent the short-term temporal dynamics of the field, as the models are derived from data largely measured during quiet-time conditions. This means that model estimates do not wholly represent the geomagnetic landscape as experienced by animals.

Raw geomagnetic data collected continuously by sensors on-board satellites are a source of localized higher spatial and temporal resolution geomagnetic information. The most comprehensive example is the European Space Agency's (ESA) recent mission of Swarm satellites (European Space Agency, 2020; Friis-Christensen et al., 2006; Olsen et al., 2013). Since 2014, two satellites in near-polar parallel circular orbits and a third in a drifting local time circular orbit, are continuously collecting geomagnetic data as they move over the Earth's surface at an altitude of 450-510 km. Unlike model estimates, satellites measure the actual magnetic conditions, which include contributions from all major magnetic sources (core, crust, ionosphere) as well as the real-time effects of the interaction with the solar wind. Swarm data are openly available through the VirES interface (European Space Agency, 2021; Kloss, 2021).

MagGeo is an open-source tool that takes advantage of the high resolution of Swarm data and combines it with model estimates to create an accurate representation of magnetic conditions at a specific location and moment in time (Benitez-Paez et al., 2021), thus enabling linkage of satellite geomagnetic data with animal tracking data (such as trajectories collected by GPS tags). MagGeo gets model estimates from the 7th Generation of the CHAMP, Ørsted and SAC-C (CHAOS-7) model of the Earth's magnetic field (Finlay et al., 2020). A major challenge when combining animal tracking data with environmental variables like geomagnetic data is matching the spatial and temporal resolution of different datasets (Brum-Bastos et al., 2021). Interpolation methods are required to overcome these differences because it is rare that a measured environmental variable and a moving animal coincide perfectly in space and time. After correcting for the difference in altitudes between satellite orbits and animals moving near the Earth's surface, MagGeo uses an inverse-distance weighting interpolation method to combine Swarm satellite data with GPS tracking data to allow movement ecologists to test hypotheses about geomagnetism and animal movement from a geospatial data-driven perspective.

Benitez-Paez et al. (2021) performed an initial error and accuracy analysis of MagGeo though, it was limited to 3 test locations in Europe for six days of variable geomagnetic activity. A more thorough error and accuracy analysis is required to ensure MagGeo's useability for locations outside of Europe and across various time periods. Furthermore, MagGeo assumes that (1) inverse-distance weighting and (2) a combination of model estimates and satellite data are the most likely interpolation method and data structure respectively to accurately model the geomagnetic field as experienced by animals. These assumptions have not been tested.

I perform a global error and accuracy analysis for MagGeo by testing more than 100 locations across 7 years (2014-2020) and following common practices outlined by the geophysical community (Beggan et al., 2021; Chulliat et al., 2015; Macmillan & Olsen, 2013). I evaluate accuracy measures across four spatiotemporal interpolation methods: (1) inverse-distance weighting, and three nearest-neighbor methods for (2) space, (3) time and (4) spacetime. Next, I compare the accuracy between model estimates (from CHAOS-7) and a fused model estimate and satellite data (combining CHAOS-7 and Swarm satellite data). I highlight important considerations for researchers hoping to model the geomagnetic field through MagGeo to ask questions about animal navigation. I also demonstrate the benefits of performing error and accuracy assessments of remotely sensed environmental data that are applicable to movement ecologists. I believe that studies like mine encourage cross-disciplinary collaboration and will become increasingly important with the current trends in technology evolution and data accessibility (Guilford et al., 2011; Kays et al., 2022; Nathan et al., 2022).

2.2 Background

2.2.1 Earth’s geomagnetic field

The Earth’s magnetic field is notionally like a bar magnet on a large scale with field lines exiting the geomagnetic south pole (near Antarctica) and entering the geomagnetic north pole (near the Arctic Circle). In detail, the geomagnetic field is far more complex and has various components apart from polarity (Figure 2-1A). Total field intensity (F) and the horizontal component of the field intensity (H) are two scalar quantities that measure the magnitude of the geomagnetic field vector in nanoTeslas (nT). Inclination (I) and declination (D) are angular components of the geomagnetic field vector measured in degrees. Inclination refers to the angle between the field vector and the Earth’s horizon whereas declination is the angle between the magnetic and geographic pole. Declination is used to align the geomagnetic field on the Earth and is not a natural property of the field since it requires additional knowledge of the relative position of the geographic North and South poles. Geometrically, these components (FHDI) can be calculated from values collected by geomagnetic sensors which are measured in the North (N), east (E) and center (C) cartesian coordinate system (Figure 2-1A).

There are multiple sources of Earth’s geomagnetic field, the principal being the geodynamo in the liquid outer core which accounts for around 98% of the total field and has a surface strength of between roughly 20,000 to 60,000 nT. Next, the magnetic minerals in the local subsurface (crust) varies between 10-1000 nT depending on location. Electrical currents in the ionosphere at approximately 100-1000 km from the Earth’s surface and followed by the magnetosphere which extends even further into outer space are the two final sources of the geomagnetic field (Figure 2-1B). Different altitudes at the same geographic coordinate will have different geomagnetic values depending on the proximity to the geomagnetic sources (Campbell, 2003; Hulot et al., 2010; Thébault et al., 2010). The typical strength of the external field in magnetically quiet conditions is 20-50 nT but rises to >1000 nT in active periods. Geomagnetic field activity is quantified on a quasi-logarithmic scale called the Kp index (with values of 0-9) which often accompanies open-source geomagnetic data (Matzka et al., 2021). During periods of high solar activity such as geomagnetic storms, values of the geomagnetic field can change rapidly particularly at the mid to high latitudes.

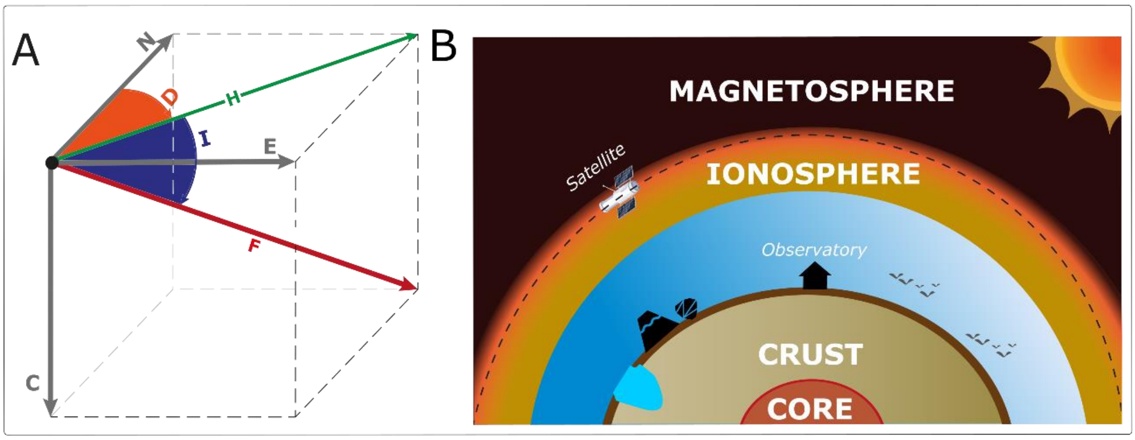

Figure 2-1. The main components of the geomagnetic field. A. The geomagnetic coordinate system is in the North-East-Centre (NEC) coordinate frame shown in gray with the four geomagnetic components highlighted in color: declination (D) in orange, inclination (I) in blue, horizontal intensity (H) in green, and total intensity (F) in red. **B.** The four main contributors to the geomagnetic field from innermost to outermost: core, crust, ionosphere, and magnetosphere. Examples of geomagnetic anomalies due to lithosphere composition represented by symbols for water body, volcano, and exposed magnetic rock. Satellite orbiting in the ionosphere and the geomagnetic observatory are representations for the two main geomagnetic data sources. Image inspiration from Benitez-Paez et al. (2020).

2.2.2 Geomagnetic data sources

Geomagnetic data are traditionally collected at ground-based observatories. The INTERMAGNET network of observatories (Figure 2-2) currently has 126 operational stations across the world that collect geomagnetic data (INTERMAGNET, 2020) available at second-, minute- and hour frequencies. Since observatories are located at ground level, their data are heavily influenced by the core and crustal components of the geomagnetic field (Thébault et al., 2010). While they have high temporal resolution, data from INTERMAGNET observatories are limited to their locations which are irregularly distributed (Hulot et al., 2010). For example, there are only six stations in Africa and six stations in South America. The low station density impairs study of long-distance animal migration that can span multiple continents.

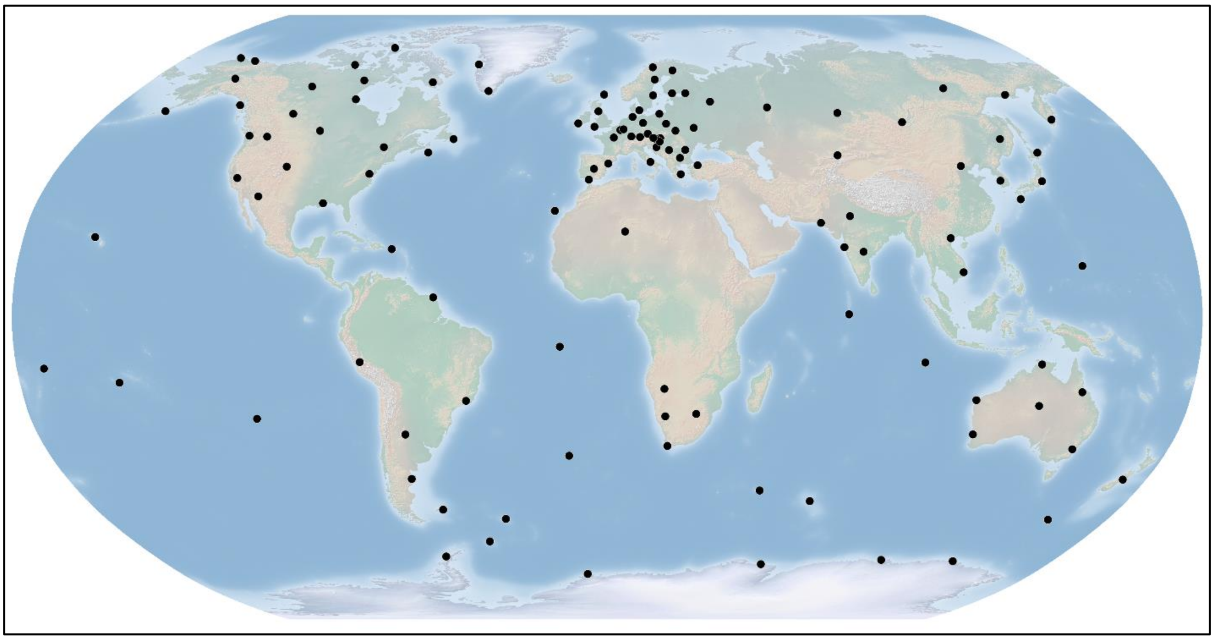

Figure 2-2. Global distribution of INTERMAGNET observatories (n=126).

In contrast to ground stations, polar-orbiting satellites with on-board magnetometers collect globally distributed data on the geomagnetic field for locations on their orbit. These satellites collect data at high altitudes (400-500 km) and are strongly influenced by the ionosphere (Benitez-Paez et al., 2021; Campbell, 2003) (Figure 2-1B). An ongoing mission to gather satellite geomagnetic data is operated by the ESA with their launch of three Swarm satellites in late-2013 (Friis-Christensen et al., 2006; Olsen et al., 2013). One-second resolution data from these satellites are available within 96 hours of collection and can be accessed through the VirES platform (European Space Agency, 2021).

A combination of observatory data, satellite data, and ground data are used to inform creation of geomagnetic models which are often spherical harmonic models determined by a set of coefficients (Chulliat et al., 2015; Olsen et al., 2006; Sabaka et al., 2020). Geomagnetic values are then estimated from these model coefficients and are used for geophysical studies, long-term monitoring, resource exploration and extraction. Models are updated periodically to account for the non-linear continuous changes in the geomagnetic field (secular variation). Due to the ease at which model estimates data can be accessed for each unique location in 3D space, they are often used in non-geophysical field applications, and have previously been used in the analysis of animal migrations (Boström et al., 2012; Komolkin et al., 2017). Due to the complexity of the field, model estimates alone however cannot capture the spatial and temporal variability outside of quiet-time and at the scale that animals moving near the Earth's surface might experience the geomagnetic field.

2.3 Data and methods

MagGeo is an open-source tool that combines model estimates and satellite data and attaches it to wildlife tracking data anywhere on the Earth's surface from November 2013 to present. Model estimates are available for any 3D location and timestamp of an animal tracking fix. MagGeo uses the CHAOS-7 model to estimate the core, crustal and magnetosphere contributions of the geomagnetic field (Figure 2-1B). CHAOS-7 model estimates do not estimate ionospheric contributions. There are other models, such as the Swarm Comprehensive models (Sabaka et al., 2020), which provide estimates for the ionosphere. The flexibility of the MagGeo framework can allow for replacing the CHAOS-7 values with other data sources that provide complete model estimates of the geomagnetic field based on user preference and research objectives. Model estimates however will include only averaged quiet time values for the ionosphere and subsequently will not capture the local, real-time variation. I include the Swam satellite data to introduce this local and temporal variability to CHAOS-7 model estimates.

For the CHAOS-7 model, the contributions from the core, lithosphere and magnetosphere are added to create an estimate of geomagnetic values at the ground level:

$$CH_g = CH_g^C + CH_g^L + CH_g^M \qquad [1]$$

Where CH represents the CHAOS-7 model estimates, the subscript g represents geomagnetic estimates at ground level altitude and the superscripts represent the different geomagnetic source components (C = core, L = lithosphere, M = magnetosphere). As the model estimates are designed to be continuous in space, they do not require spatial interpolation.

Raw geomagnetic data collected by satellites from the ESA's Swarm constellation (European Space Agency, 2021; Friis-Christensen et al., 2006) are also freely available. It is unlikely however that geomagnetic values at satellite altitude will represent the geomagnetic field as experienced by an animal at the ground level. To correct for this altitude difference, I calculate satellite residuals by subtracting CHAOS-7 model estimates at satellite altitude for the core, lithosphere, and magnetosphere contributions.

$$SW_s^{Res} = SW_s - CH_s^C - CH_s^L - CH_s^M \qquad [2]$$

Where SW represents raw geomagnetic data collected by Swarm satellites, the subscript s represents values collected or estimated at satellite altitude and the superscripts represent the different geomagnetic source components (C, L, or M) or the satellite residuals (Res). The Swarm satellite residuals (SW_s^{Res}) primarily represent ionosphere contributions at satellite altitude though they are ultimately a combination of ionosphere, magnetosphere, crust, and other smaller influences on the geomagnetic field. SW_s^{Res} introduces temporal variability with fine resolution to capture the dynamic nature of the geomagnetic field outside of quiet-time values as estimated by geomagnetic models.

Given the satellite orbit however, it is unlikely that the satellite will be directly above a location on Earth for a specific timestamp. Therefore, geomagnetic data collected by satellites require interpolation to attach to an animal tracking fix. SW_s^{Res} can be interpolated to the animal tracking point by creating a space-time kernel. This kernel is a space-time cylinder where the radius of the cylinder has spatial dimensions, and the height has a temporal dimension (Figure 2-3A). Based on the Swarm satellites' polar orbits, the kernel's spatial boundary (the size of the cylinder's base, R in Figure 2-3A) varies with latitude, with smaller spatial boundaries at higher latitudes (approximately 900 km) compared to equatorial latitudes (approximately 1800 km). The kernel's temporal boundary (the height of the cylinder) is +/- 4 hours (ΔT) from the tracking fix, again based on the properties of the polar orbit and to ensure that sufficient satellite data are present at lower latitudes (Benitez-Paez et al., 2021).

SW_s^{Res} within the space-time kernel are then linked to the animal tracking fix using a spatiotemporal interpolation method (Figure 2-3B). Benitez-Paez et al. (2021) proposed inverse distance weighting (IDW) where the space-time distance (dST) is calculated to account for both the distance in space (measured in km; dS) and time (measured in seconds; dT) between the satellite residual and the tracking fix. Data points closest in space-time distance (lowest dST) are weighted higher than those farther away and the sum of all weights in each spacetime kernel is 1. I propose three alternative nearest neighbour methods that are both simpler, and potentially more accurate for spatiotemporal interpolation of satellite residuals with wildlife tracking fixes.

The nearest neighbour in space (NNS) interpolation method uses the residuals from the satellite data point closest in space (lowest dS within the space-time kernel) (Figure 2-3C).

It follows that to create the nearest neighbour in time (NNT) and space-time (NNST) interpolation, I use residuals of the satellite point closest in time and spacetime to the point of interest (lowest dT and dST within the space-time kernel respectively; Figure 2-3D, Figure 2-3E). Finally, after interpolation to the animal tracking fix, I then add the satellite residuals with the CHAOS-7 model estimates at ground altitude for the core, lithosphere, and magnetosphere contributions to get the final MagGeo output.

$$MG = SW_s^{Res} + CH_g \qquad [3]$$

Thus, to create a complete model of the geomagnetic field for a 3D location and timestamp of an animal tracking fix which includes core, crustal, ionospheric and magnetospheric contributions, MagGeo combines model estimates and satellite residuals. For simplicity, I will refer to the fused model estimate and satellite residual outputs as MG and the CHAOS-7 model estimates at ground altitude as CH for the remainder of the paper. I can use MG and CH values measured in the North-East-Centre (NEC) coordinate system to calculate the four components of the geomagnetic field that are relevant for animal migration (F, H, D, and I). I perform the error analysis on these components as their values are more applicable to MagGeo users whose primary objective will likely focus on movement ecology research questions. For a similar geophysical-centered error analysis on the orthogonal components of geomagnetic model estimates, readers can refer to Beggan (2022).

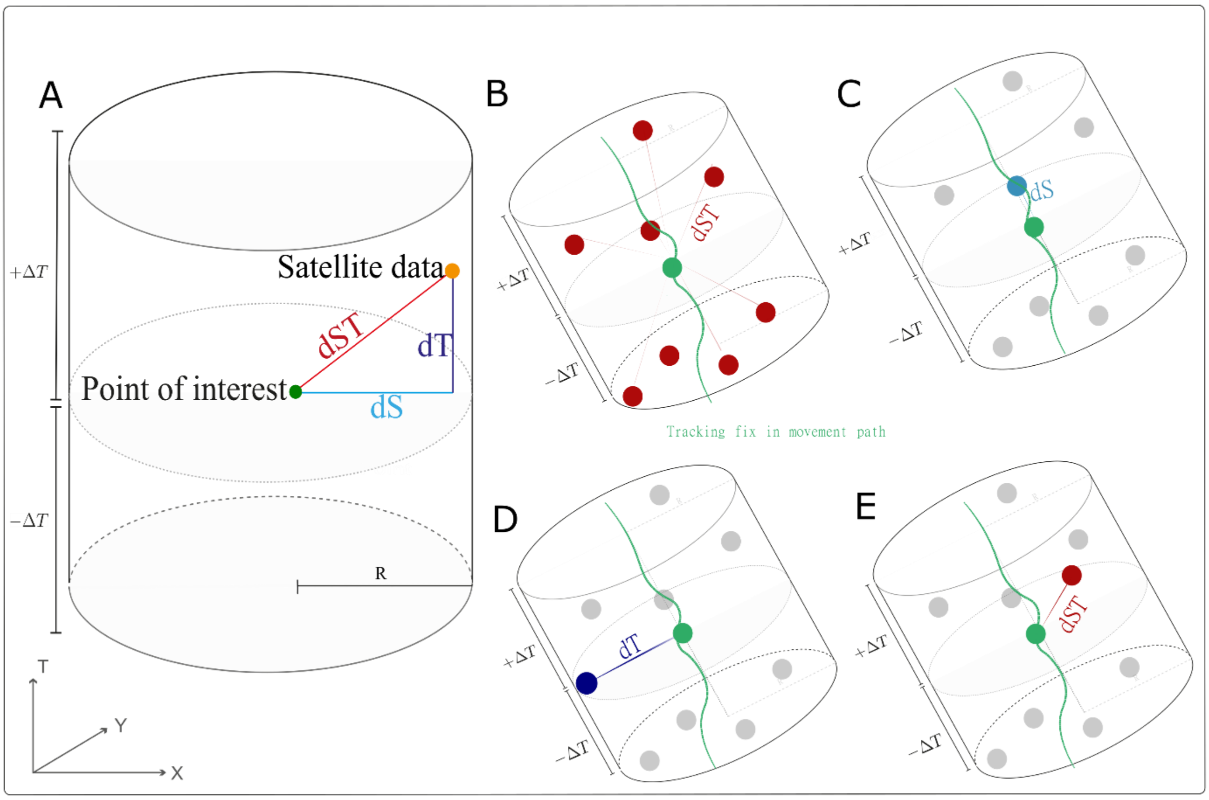

Figure 2-3. Current and modified spatiotemporal parameters of the spacetime cylinder used by MagGeo. A. The space-time cylinder calculating the distance in space (dS; light blue), time (dT; dark blue) and spacetime (dST; red) between point of interest (green) and satellite point (orange). X and Y axis represent spatial dimensions whereas the Z-axis represents temporal dimension. Figures **B-D** represent the four spatiotemporal interpolation methods used to attach satellite residuals to an animal tracking fix (such as movement path of a migratory bird collected by a GPS tag). Figure **B** represents the concept of inverse-distance weighting and Figures **C-E** represent nearest neighbour iterations for satellite points closest to the animal tracking fix in space (**C**), time (**D**) and spacetime (**E**).

2.3.1 Data preparation

My analysis centers on the assumption that data from INTERMAGNET observatories represent the best available measurement of the geomagnetic field at their location on the Earth’s surface (Beggan, 2022; Kerridge, 2001). Data from these terrestrial observatories are acutely influenced by the local crustal field, which is not captured by either model estimates or satellite data but might be detected by animals moving at this local spatial scale. Additionally, INTERMAGNET observatories collect high temporal resolution geomagnetic data and are rigorously calibrated (Kerridge, 2001). I compare geomagnetic values from INTERMAGNET observatories (OBS) against MG outputs interpolated to the station location for the same timestamp. The objective is to compare MG and OBS values for the four geomagnetic components (F, H, D, I) to assess MagGeo accuracy at ground altitude. My analysis is conceptually consistent with geophysical studies that test, calibrate, and validate satellite (Beggan et al., 2013; Macmillan & Olsen, 2013; Ridley & Macmillan, 2014) and model data (Chulliat et al., 2015; Finlay et al., 2020).

I acquired minute-mean observatory geomagnetic data for all available stations for seven years (2014-2020). I compiled a dataset to test MagGeo under the full range of geomagnetic activity levels (i.e., Kp 0 – 9). I term this dataset "All Kp." I included data from 60 days a year uniformly sampled across all twelve months for seven years resulting in a total of 420 days of data. I obtained geomagnetic data at three time points each day equally spaced 8 hours apart (Table 2-1). I had fewer INTERMAGNET stations for later years as there is usually a delay between station measurements and access to the final geomagnetic dataset.

To test MagGeo specifically during periods of high geomagnetic activity, I compiled a "High Kp" dataset. To build the High Kp dataset, I acquired data for all days in 2014-2020 with high geomagnetic activity (Kp > 6 for 6 or more hours) (Space Weather Live, 2021). I subset this dataset to include only data where the satellite recorded Kp > 6 to further filter out quieter periods even during a day classified as having overall high geomagnetic activity. The High Kp dataset (n = 393,054) was substantially smaller than the All Kp dataset (n = 6,327,537). There were fewer days with High Kp in 2014 and in 2018 to 2020. These periods were less geomagnetically active as they were in the quieter part of previous solar cycle (Kakad et al., 2020)

Table 2-1. Datasets used for MagGeo error and accuracy analysis. All data are minute-mean for 2014 to 2020. "All Kp" includes data from all Kp levels whereas "High Kp" includes only data from geomagnetically active periods (Kp>6).

Year	All Kp	High Kp	INTERMAGNET stations
2014	899 967	8 602	109
2015	950 346	206 448	111
2016	1 044 477	78 467	103
2017	1 023 750	65 259	100
2018	892 808	26 363	95
2019	888 681	7 915	97
2020	627 508	8 602	88
n total	*6,327,537*	*393,054*	

2.3.2 Accuracy assessment

To test the performance of the different spatiotemporal interpolation strategies and data structures relative to one another I used two accuracy measures. The first is the absolute difference (*d*) between MG and OBS values for each timestamp:

$$d = |MG - \mathrm{OBS}| \qquad [4]$$

Lower values of absolute error correspond to better agreement between the MagGeo output and the INTERMAGNET data.

The second measure (alpha; α) is the absolute difference between the standardized MagGeo output and the standardized observatory output for each timestamp (Ridley & Macmillan, 2014):

$$\alpha = \left|\left(\frac{MG-\overline{X}_{MG}}{\sigma_{MG}}\right) - \left(\frac{OBS-\overline{X}_{OBS}}{\sigma_{OBS}}\right)\right| \qquad [5]$$

Where $\overline{X}_{MG}$ and σ_{MG} are the mean and standard deviation respectively for the interpolated MagGeo values at a station while $\overline{X}_{OBS}$ and σ_{OBS} are the mean and standard deviation respectively of the geomagnetic values at the same INTERMAGNET station. As with the absolute difference measure, lower alpha values correspond to better agreement between the MagGeo output and observatory values. The alpha measure is useful for identifying how well MagGeo captures relative patterns in the geomagnetic data instead of just the absolute difference. For example, during a geomagnetic storm, both MG and OBS are very different from their respective means ($\overline{X}_{MG}$ and $\overline{X}_{OBS}$). While the absolute difference between $X_{MG}$and X_{OBS} might be large during these storms, if the sudden change in geomagnetic value is captured by both sources, the α value will be low thus making it possible for MagGeo outputs and observatory outputs to have high absolute difference error but low alpha values. In this case, the pattern would suggest that MagGeo is able to capture the temporally dynamic nature of the geomagnetic field like the observatory data irrespective of any consistent offsets between the two sources.

We removed data from 8 stations (Appendix 1) because their absolute difference error was consistently greater than 2 standard deviations (95% quantile) for any three of the orthogonal components (eg., DIF, XYZ or DHZ) for more than 6 months' worth of data (Beggan, 2022). We also removed data from 3 days (2017-09-08, 2018-08-26, and 2018-

08-27) which had high daily error across all stations reflecting the impact of very strong geomagnetic storms on these days.

I calculated the error measures (d and α) for MagGeo values for each spatiotemporal interpolation method (IDW, NNT, NNS, and NNST) and underlying data structure (model estimates and model estimate and satellite residuals). I compare across interpolation methods and data structure using summary statistics, but also by recording the proportion of data records where each interpolation method and data structure had the lowest error values (“best performance”).

I fit generalized linear mixed-effect models (GLMMs) with the dependent variable as either error metric (d and α) and by using MagGeo outputs from the best performing interpolation method and data structure combination. To reduce temporal autocorrelation, I created hourly averages from my minute-mean data. For fixed effects, I included three variables to account for geomagnetic field behaviour: Kp, time of day, and latitude. For simplicity, I categorized time-of-day into two categories: day as 7:00AM to 7:00PM local time and night as 7:00PM to 7:00AM local time to allow sufficient variation in sunset and sunrise times for stations differing by latitude. Solar wind influences the geomagnetic field activity and is reflected as a high Kp value which is more likely during the day and at polar latitudes (Campbell, 2003; Hulot et al., 2010; Lanza & Meloni, 2006). I also included two additional fixed effects in my model that address how MagGeo space-time kernel parameters may influence error: the geographical distance between the INTERMAGNET station and the satellite data point (km) and the temporal difference (minutes) between the timestamp at the INTERMAGNET station data and the nearest Swarm satellite pass.

I used station ID as a random effect for all models as it is likely that values from individual ground stations are heavily influenced by local crustal field conditions (Beggan, 2022; Lesur et al., 2016). Additionally, each station has subtle differences in collection and reporting of geomagnetic data (St-Louis, 2012). I tested all possible combinations of the fixed effects and chose the best model for each geomagnetic component based on the lowest Akaike information criterion (AIC) values. I calculated the marginal and conditional R^2 values for the best performing models, where the marginal R^2 (R^2m) is the proportion of the variance explained by the fixed effects, and the conditional R^2 (R^2c) is the overall proportion of the variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013). I report the model coefficient (β), standard error (SE) and p-values for the intercept and all fixed effects for the best model.

To demonstrate the difference between the geomagnetic data sources for studying long-distance animal migration, I used GPS tracking data from one white stork *Ciconia ciconia* individual from the 2017 spring migration period (Carlson et al., 2021). I resampled the tracking data to hourly intervals when the bird was in flight (speed > 5 km/h) as this state likely reflects when birds are using geomagnetic field values to make movement decisions (Acácio et al., 2022; Chernetsov, 2017). I attached geomagnetic values from the nearest INTERMAGNET station to the bird's location. I compared these observatory values with the MG outputs from the best performing interpolation method and data structure for the same location.

2.3.3 Tools and data availability

MagGeo is available as a GitHub repository (Benitez & Long, 2022). For my analysis, I modified scripts from MagGeo 1.0 (Feb 2021). MagGeo uses two Python packages for geomagnetic data acquisition. The ESA-VirES Client package connects to the VirES servers to acquire satellite residuals (Smith, 2020) whereas the chaosmagpy package accesses the CHAOS-7 estimates through the VirES server (Kloss, 2021). I used the Swarm Magnetic Earth Jupyter notebooks to fetch geomagnetic data from ground observatories which we accessed via the British Geological Survey FTP server, though a VirES-based access method is currently available as well (https://github.com/Swarm-DISC/Swarm_notebooks). To fit my general linear mixed-effect models, I used the "lme4" R package (Bates, 2010). Finally, I used the "dredge" function from the "MuMIn" R package to test all possible combinations of fixed effects (Bartoń, 2022). I accessed white stork GPS data from Carlson et al. (2021) which are available on Movebank (Kays et al., 2022).

2.4 Results

For each of the four spatiotemporal interpolation methods, there was little variation in the median, mean, standard deviation, or skew across all geomagnetic components, for both accuracy measures and during variable (All Kp) and high geomagnetic activity (High Kp) (Table 2-2). The variation in mean absolute difference between the four interpolation methods was within 10 nT for scalar intensity geomagnetic components (F and H) and within 1° for angular directional geomagnetic components (D and I) (Table 2-2).

Furthermore, almost all categories showed positive skew (with median <mean), suggesting that mean values may be influenced by a few data points with unusually high error. For both scalar components, while values between the interpolation methods were similar, NNT often had the highest median and mean values. Across each data record (unique location and timestamp) however, the NNT always had the highest occurrence (%) of lowest error ("best performance") for all components during periods of variable and high geomagnetic activity (Table 2-3). This distinction was more evident during variable geomagnetic activity where NNT had the lowest error about 40% of the time among the four interpolation methods compared to periods of high geomagnetic activity where NNT on average had the lowest error 30% of the time (Table 2-3). Thus, all interpolation methods had similar central tendencies (Table 2-2), but NNT consistently had the best performance (Table 2-3). Therefore, I used the NNT interpolation method to subsequently test the difference between CH and MG datasets.

When separated by station and arranged by latitude, I found that certain stations have greater variation in error than others (large interquartile range for individual station box plot) (Figure 2-4 and Appendix 2). In general, stations at higher latitudes have a greater variation in absolute differences compared to stations closer to the equator. I also observe that these error patterns are consistent between the four interpolation methods such that if a station has high error variability for total intensity, this pattern will be replicated across all interpolation methods (Figure 2-4 and Appendix 2).

Between the two data structures, there was little variation in the median, mean, standard deviation, or skew across all geomagnetic components, for both accuracy measures and during variable (All Kp) and high geomagnetic activity (High Kp) (Table 2-4). With a few exceptions, difference between CH and MG for the mean and median absolute difference error was approximately within 10 nT for the scalar components and within 1° for the angular components (Table 2-4). For the absolute difference error metric, apart from horizontal intensity, CH has equal or lower median and mean error than MG (Table 2-4). During both variable and high geomagnetic activity however, MG has either equal or lower mean and median alpha values. Positive skew during variable geomagnetic conditions is also higher for MG alpha values suggesting that the reported mean is being skewed by a few instances of very high error (Table 2-4).

For 11 out of 16 categories based on geomagnetic components and activity, MG has slightly better performance than CH (Table 2-5). However, there is little difference in performance across all geomagnetic components, activity and accuracy measures since the overall average performance is 48% for CH and 52% for MG. The average alpha error per station is also around 1 unit during variable geomagnetic activity and slightly higher during high geomagnetic activity (Figure 2-5 and Appendix 3). Except for declination, MG has lower station-wide alpha error than CH (Figure 2-5 and Appendix 3). Additionally, there is a log-linear increase in Swarm satellite contribution to the MG output (e.g., increasing residual values) associated with an increase in geomagnetic activity (Appendix 4).

Table 2-2. Median, mean, standard deviation and skew of error for current and modified MagGeo spatiotemporal interpolation methods: IDW, NNS, NNST and NNT. Results are for all geomagnetic components (FHID) with minute-mean data from 2014-2020. “All Kp” includes data from all Kp levels whereas “High Kp” includes only data from geomagnetically active periods (Kp>6). Results are presented for both accuracy measures: absolute difference (*d*) and alpha (*α*).

	d								***α***							
	All Kp				**High Kp**				**All Kp**				**High Kp**			
Component	*Median*	*Mean*	*± SD*	*Skew*	*Median*	*Mean*	*± SD*	*Skew*	*Median*	*Mean*	*± SD*	*Skew*	*Median*	*Mean*	*± SD*	*Skew*
Total intensity																
IDW	79.2	127.4	135.4	2.1	101.5	258.8	592.3	6.0	0.5	0.7	0.8	2.4	0.8	1.0	0.8	2.6
NNS	79.4	127.4	135.0	2.1	101.6	259.7	593.2	5.9	0.5	0.7	0.8	2.3	0.8	1.0	0.9	5.2
NNST	79.4	127.6	135.3	2.1	100.8	258.6	592.5	5.9	0.5	0.7	0.8	2.4	0.8	1.0	0.9	4.2
NNT	79.7	128.0	135.7	2.1	108.4	267.3	591.3	5.9	0.5	0.8	0.8	2.7	0.8	1.0	0.9	4.0
Horizontal intensity																
IDW	211.3	211.2	133.1	1.0	284.4	371.1	393.2	4.1	0.6	0.9	0.9	2.8	0.9	1.1	0.9	2.0
NNS	211.5	211.7	134.0	1.1	284.3	374.1	401.3	4.0	0.6	0.9	0.9	2.9	0.8	1.0	0.9	4.5
NNST	211.7	212.0	134.2	1.1	285.5	375.6	401.7	4.0	0.6	0.9	0.9	2.9	0.9	1.0	0.9	3.6
NNT	211.5	211.9	133.4	1.0	298.0	382.8	392.6	4.0	0.6	0.9	0.9	2.9	0.9	1.1	0.9	3.6
Inclination																
IDW	0.3	0.3	0.2	2.6	0.4	0.5	0.5	4.0	0.6	0.8	0.9	2.9	0.9	1.1	0.9	2.0
NNS	0.3	0.3	0.2	2.6	0.4	0.5	0.5	4.0	0.6	0.8	0.9	3.0	0.8	1.0	0.9	4.7
NNST	0.3	0.3	0.2	2.6	0.4	0.5	0.5	4.0	0.6	0.8	0.9	3.0	0.8	1.0	0.9	3.6
NNT	0.3	0.3	0.2	2.6	0.4	0.5	0.5	4.0	0.6	0.8	0.9	2.9	0.9	1.1	0.9	3.6
Declination																
IDW	0.1	0.4	0.6	3.8	0.3	0.9	2.4	13.2	0.7	0.9	0.8	2.2	0.9	1.0	0.9	2.3
NNS	0.2	0.4	0.7	3.6	0.3	0.9	2.4	12.1	0.7	0.9	0.9	2.3	0.8	1.0	0.9	5.4
NNST	0.2	0.4	0.7	3.6	0.3	0.9	2.4	12.2	0.6	0.9	0.8	2.4	0.8	1.0	0.9	4.1
NNT	0.2	0.4	0.7	3.7	0.3	1.0	2.5	10.9	0.7	0.9	0.9	2.7	0.8	1.0	0.9	4.2

Table 2-3. Percent of lowest error between four MagGeo spatiotemporal interpolation methods: IDW, NNS, NSST, and NNT. Bolded rows represent the interpolation method that had the overall highest frequency of lowest error (best performance). Results shown for all geomagnetic components (FHID) with minute-mean data from 2014-2020. "All Kp" includes data from all Kp levels whereas "High Kp" includes only data from geomagnetically active periods (Kp>6). Results are for both accuracy measures: absolute difference (*d*) and alpha (α).

	Percent (%) with lowest error			
	All Kp		**High Kp**	
Component	*d*	α	*d*	α
Total Intensity				
IDW	17.8	18.5	22.0	**27.8**
NNS	31.4	19.3	33.4	22.7
NNST	8.4	22.5	5.6	22.4
NNT	**42.4**	**39.7**	**39.1**	27.2
Horizontal intensity				
IDW	19.4	18.6	21.5	22.6
NNS	30.8	20.4	34.2	24.8
NNST	8.9	19.9	5.3	22.4
NNT	**40.9**	**41**	**39.1**	**30.2**
Inclination				
IDW	19	19.5	20.9	23.2
NNS	30.6	19.9	34.1	24.5
NNST	8.7	21.1	5.0	22.9
NNT	**41.7**	**39.4**	**39.9**	**29.5**
Declination				
IDW	21.3	20.3	26.8	25.8
NNS	30.5	19.5	32.9	24.6
NNST	8.2	20.7	5.1	21.7
NNT	**40.1**	**39.5**	**35.2**	**27.9**

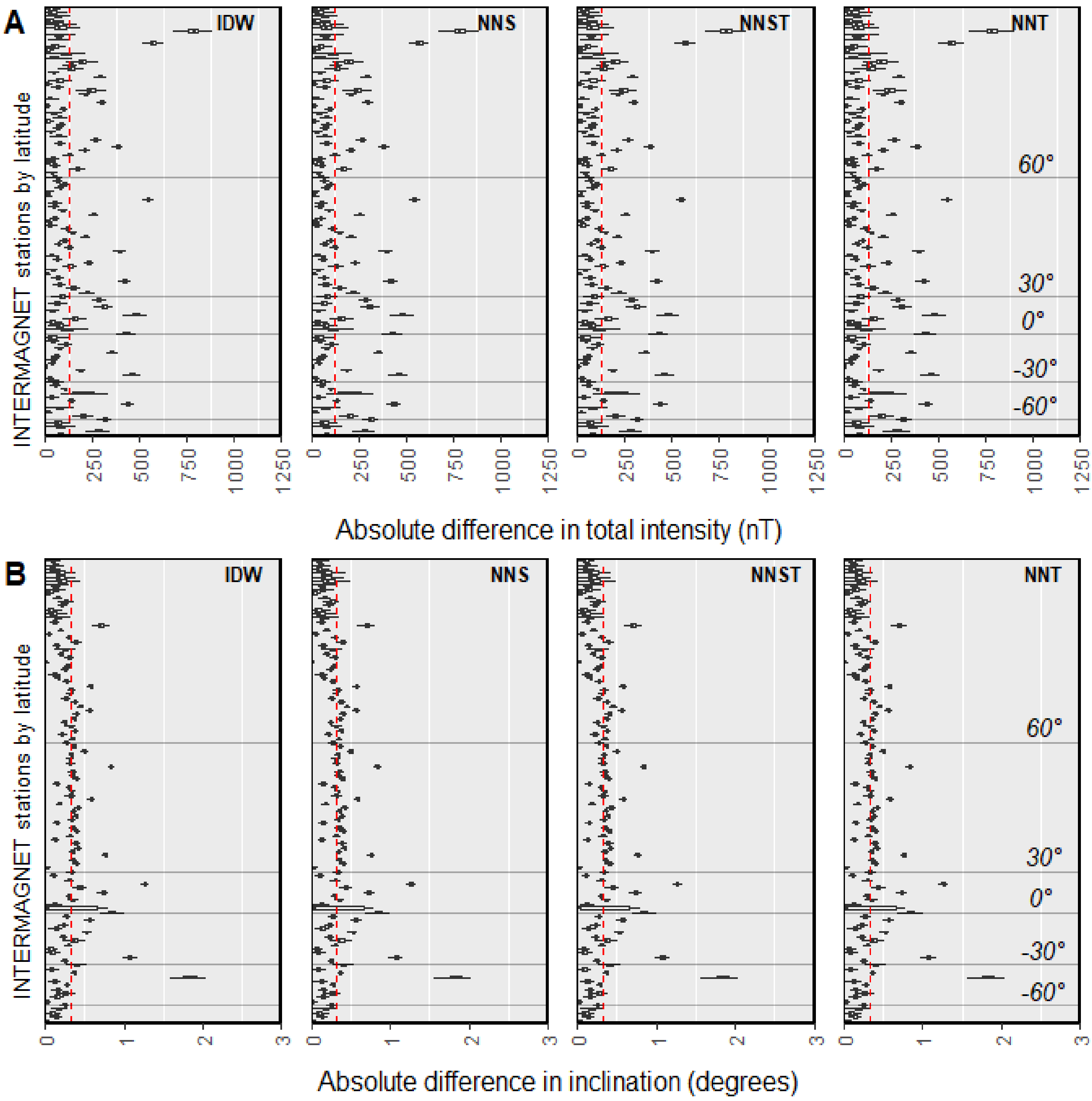

Figure 2-4. Absolute difference metric (d) for each individual INTERMAGNET station arranged by latitude from northernmost (top) to southernmost (bottom). Each panel represents one of the four possible MagGeo spatiotemporal interpolation methods: IDW, NNS, NNST and NNT. Dotted red lines represent overall average absolute difference. Figures are arranged by geomagnetic component: total intensity **(A)** and inclination **(B).** For similar figures for horizontal intensity and declination, see Appendix 2.

Table 2-4. Median, mean, standard deviation and skew of error for current and modified MagGeo data structures: CH (CHAOS-7) and MG (CHAOS-7 estimates and Swarm residuals). Results are for all geomagnetic components (FHID) with minute-mean data from 2014-2020. “All Kp” includes data from all Kp levels whereas “High Kp” includes only data from geomagnetically active periods (Kp>6). Results are for both accuracy measures: absolute difference (*d*) and alpha (*α*).

	d								***α***							
	All Kp				**High Kp**				**All Kp**				**High Kp**			
Component	*Median*	*Mean*	*± SD*	*Skew*	*Median*	*Mean*	*± SD*	*Skew*	*Median*	*Mean*	*± SD*	*Skew*	*Median*	*Mean*	*± SD*	*Skew*
Total intensity																
CH	78.6	126.9	135.3	2.1	105.0	261.8	595.3	5.9	0.6	0.8	0.8	2.1	1.0	1.1	0.8	0.9
MG	79.7	128.2	153.8	65.8	108.4	267.3	591.3	5.9	0.5	0.8	0.2	3.7	1.0	1.1	0.8	1.0
Horizontal intensity																
CH	212.0	211.1	131.7	1.0	297.8	365.9	379.6	4.5	0.8	1.0	0.8	2.1	1.0	1.1	0.9	1.0
MG	211.7	212.4	134.9	2.1	298.0	382.8	392.6	4.0	0.6	0.9	1.0	3.7	0.9	1.1	0.9	1.3
Inclination																
CH	0.3	0.3	0.2	2.6	0.4	0.5	0.5	4.1	0.7	0.9	0.8	2.2	1.0	1.1	0.8	1.0
MG	0.3	0.3	0.2	3.7	0.4	0.5	0.5	4.0	0.6	0.8	0.9	3.7	0.9	1.1	0.9	1.2
Declination																
CH	0.1	0.3	0.6	3.9	0.2	0.8	2.3	13.8	0.7	0.9	0.8	1.8	1.0	1.1	0.8	1.0
MG	0.2	0.4	0.7	4.1	0.3	1.0	2.5	10.9	0.7	0.9	0.9	3.3	0.9	1.1	0.9	1.2

Table 2-5. Percent of lowest error between two MagGeo data structures: CH (CHAOS-7) and MG (CHAOS-7 and Swarm). Bolded rows represent the data type that had the highest percentage of lowest error for each category (best performance). Results are for all geomagnetic components (FHID) with minute-mean data from 2014-2020. “All Kp” includes data from all Kp levels whereas “High Kp” includes only data from geomagnetically active periods (Kp>6). Results are for both accuracy measures: absolute difference (*d*) and alpha (α).

Component	**Percent (%) with lowest error**			
	All Kp		**High Kp**	
	d	α	*d*	α
Total Intensity				
CH	**52.8**	41	**50.8**	48.9
MG	47.2	**59**	49.2	**51.1**
Horizontal intensity				
CH	47.9	40.8	47.6	48.6
MG	**52.1**	**59.2**	**52.4**	**51.4**
Inclination				
CH	**50.7**	41.4	47.3	48.1
MG	49.3	**58.6**	**52.7**	**51.9**
Declination				
CH	**55.6**	48	**58.2**	45.3
MG	44.4	**52**	41.8	**54.7**

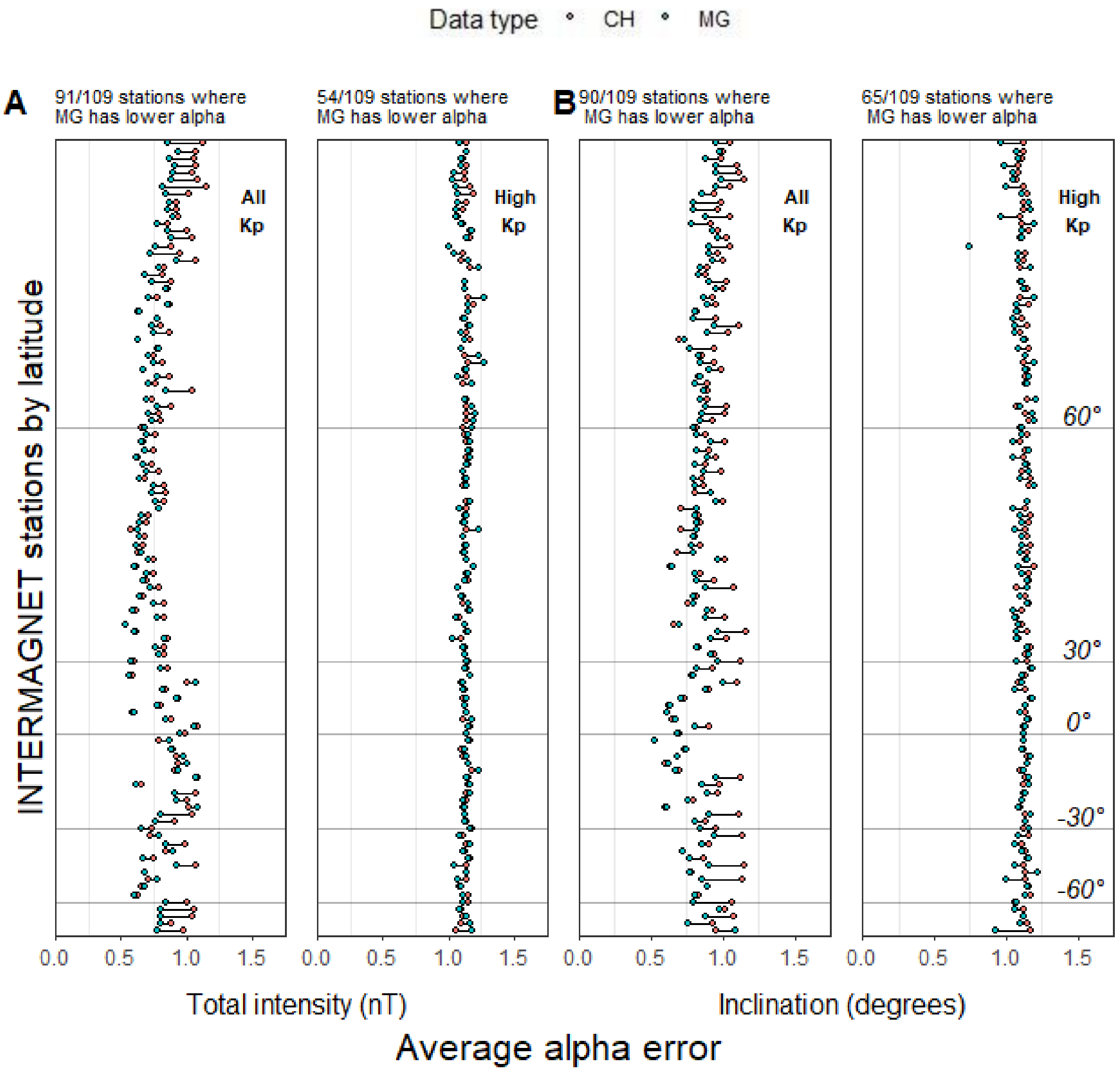

Figure 2-5. Comparison of average alpha measure (α) between CH (red dots) and MG (blue dots) for each individual INTERMAGNET station arranged by latitude from northernmost (top) to southernmost (bottom). "All Kp" includes data from all Kp levels whereas "High Kp" includes only data from geomagnetically active periods (Kp>6). Individual plot titles indicate count of stations where MG had lower alpha error. Figures are arranged by geomagnetic component: total intensity (**A**) and inclination (**B**). For similar figures for horizontal component of intensity and declination, see Appendix 3.

2.4.1 Factors influencing error and accuracy structure

For distance in space, most satellite data points are between 1000-1250 km away from the INTERMAGNET station (Figure 2-6). This pattern might be a result of the clustering of stations at mid-latitudes in Europe (Figure 2-2 and 2-6B) who will have similar space-time kernel parameters and subsequently error. The low hourly error at smaller distances might reflect that MagGeo can accurately capture geomagnetic patterns if the satellites are close in space to the INTERMAGNET station (Figure 2-6A). Conversely, the low hourly error at high distances might be indicative of stations near the equator who have larger space-time kernels but are also found at latitudes where there is lower geomagnetic activity (Figure 2-6B).

There is little variation in the distance in time between the INTERMAGNET station and satellite data point though there are two peaks at 0-30 minutes and 190-220 minutes (Figure 2-7). This clustering is likely related to the +/- 4-hour parameter of the space-time kernel where the nearest satellite data point is either directly above the INTERMAGNET station (0-30 minutes) or will just meet the +/- 4-hour cut-off by either passing over the INTERMAGNET station 4 hours before or after the timestamp (190-220 minutes).

Random effects (individual stations) and fixed effects (geomagnetic activity and time of day) together explain most of the absolute difference between geomagnetic values collected at INTERMAGNET stations and outputs from MagGeo (conditional R^2 is close to 0.9-1.0 for all geomagnetic components, Table 2-6). Apart from inclination (marginal R^2 is 0.5), variation at individual stations (random effects) explains most of the difference (marginal R^2 is equal to or below 0.1). Generally, INTERMAGNET data from stations at higher absolute latitudes are consistently different from MagGeo outputs, especially for the angular directional geomagnetic components such as inclination and declination (Table 2-6, Figure 2-4B).

Random and fixed effects do not explain most of the variation in the alpha error (conditional $R^2$is equal to 0.11, Table 2-7). For these models however, fixed effects explain all the difference between MagGeo outputs and INTERMAGNET values (marginal R^2 equal to conditional R^2, Table 2-7). For example, for all geomagnetic components, high geomagnetic activity leads to higher error (Table 2-7). These models also suggest that alpha error is higher during the day compared to nighttime. Distance in space and time between satellite pass and INTERMAGNET station have a statistically significant impact on error such that an increase in distance leads to larger error.

Table 2-6. Results of the generalized linear mixed-effect models with absolute difference as dependent variable. Individual station as a random effect and fixed effects as Kp, absolute value of latitude, time of day and distance in space and time between satellite and point of interest. R^2m and R^2c refer to marginal and conditional R-squared respectively. A new model was fit for each geomagnetic component (FHID). Models are fit with combined model estimate and satellite residual data and NNT interpolation during periods of variable geomagnetic activity (All Kp). Minute-mean data are averaged into hourly values, and empty rows indicate that the fixed effect did not contribute to the final model (based on lowest AIC) for that geomagnetic component.

	Total intensity			**Horizontal intensity**			**Inclination**			**Declination**		
	β	**SE**	**p**	**β**	**SE**	**p**	**β**	**SE**	**p**	**β**	**SE**	**p**
Intercept	71.3	36.3	0.05	245.6	32.6	<0.01	-33.0	1.3	<0.01	-0.2	0.1	0.2
Kp	1.6	0.1	<0.01	5.5	0.1	<0.01	0.007	1.3E-04	<0.01	0.02	5.9E-04	<0.01
Absolute Latitude	1.4	0.8	0.07	-1.1	0.7	0.1	0.7	0.01	<0.01	0.01	0.003	<0.01
Time of day (Ref: Day)												
Night	0.8	0.2	<0.01	4.7	0.3	<0.01	0.008	3.3E-04	<0.01	-0.004	0.001	0.01
Distance (km)												
Time difference (min)	-0.003	0.0	0.03				-3.8E-06	2.4E-06	0.1			
R^2m	0.03			0.02			0.5			0.1		
R^2c	1.0			0.9			1.0			0.9		
n	107116											
INTERMAGNET stations	114											

Table 2-7. Results of the generalized linear mixed-effect models with alpha measure as dependent variable. Individual station as a random effect and fixed effects as Kp, absolute value of latitude, time of day and distance in space and time between satellite and and point of interest. R^2m and R^2c refer to marginal and conditional R-squared respectively. A new model was fit for each geomagnetic component (FHID). Models are fit with combined model estimate and satellite residual data and NNT interpolation during periods of variable geomagnetic activity (All Kp). Minute-mean data are averaged into hourly values, and empty rows indicate that the fixed effect did not contribute to the final model (based on lowest AIC) for that geomagnetic component.

	Total intensity			**Horizontal intensity**			**Inclination**			**Declination**		
	β	**SE**	**p**	**β**	**SE**	**p**	**β**	**SE**	**p**	**β**	**SE**	**p**
Intercept	0.5	0.1	<0.01	0.5	0.03	<0.01	0.3	0.06	<0.01	0.8	0.01	<0.01
Kp	0.2	0.002	<0.01	0.2	0.002	<0.01	0.2	0.002	<0.01	0.1	0.002	<0.01
Absolute Latitude	-9.1E-04	6.4E-04	0.2				0.003	5.5E-04	<0.01			
Time of day (Ref: Day)												
Night	-0.1	0.005	<0.01	-0.2	0.005	<0.01	-0.1	0.005	<0.01	-0.3	0.01	<0.01
Distance (km)	4.4E-05	2.8E-05	0.1	4.2E-05	2.5E-05	0.1	4.4E-05	3.0E-05	0.1			
Time difference (min)	3.3E-04	3.4E-05	<0.01	1.8E-04	3.8E-05	<0.01	2.0E-04	3.6E-05	<0.01	2.5E-04	3.7E-05	<0.01
R^2m	0.1			0.1			0.1			0.1		
R^2c	0.1			0.1			0.1			0.1		
n	107116											
INTERMAGNET stations	114											

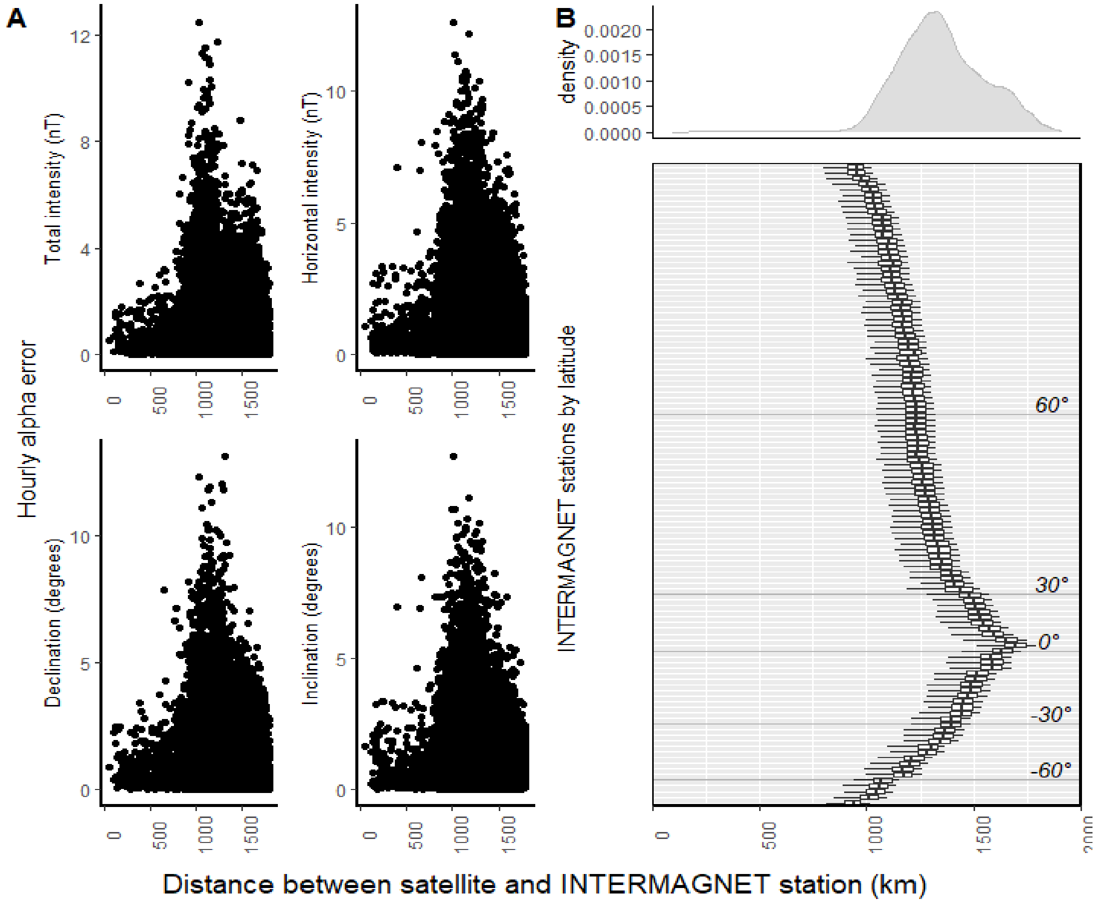

Figure 2-6. Distance in space between satellite pass and INTERMAGNET station (km) where (A) shows the distribution of hourly alpha error for each geomagnetic component (FHDI) and (B) shows the spread of the distance values for each individual station arranged by latitude from northernmost (top) to southernmost (bottom). Density plot in (**B**) mirrors the pattern seen in (**A**) where most distance values are between 1000-1500 km. Data are combined model estimate and satellite residual and interpolated to the station location using a NNT method during periods of variable geomagnetic activity (All Kp).

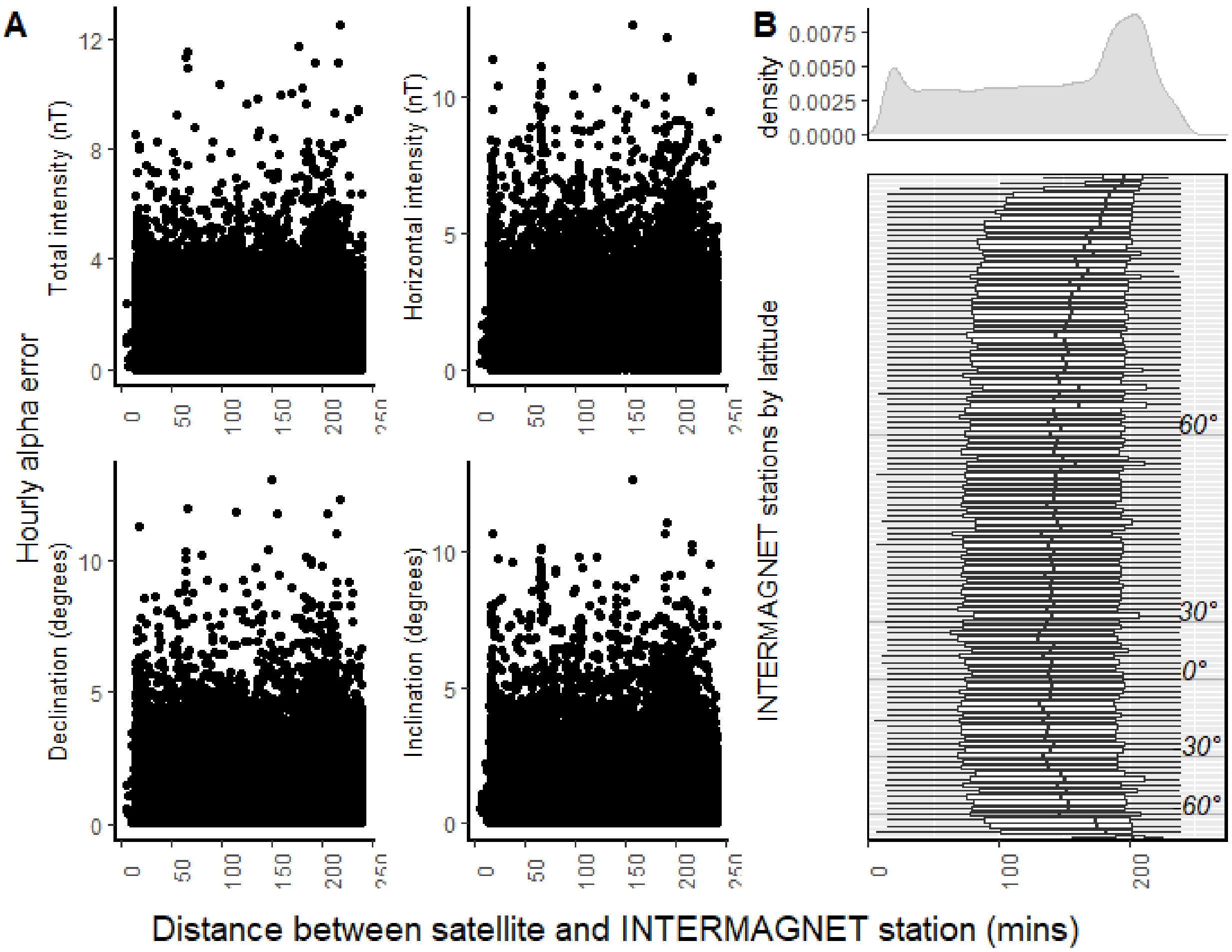

Figure 2-7. Time difference (mins) between satellite pass and INTERMAGNET station timestamp where (A) shows the distribution of hourly alpha error for each geomagnetic component (FHDI) and (B) shows the spread of time difference for each individual station arranged by latitude from northernmost (top) to southernmost (bottom). Data are combined model estimate and satellite residual and interpolated to the station location using a NNT method during periods of variable geomagnetic activity (All Kp).

2.4.2 Attaching geomagnetic data to a migratory bird movement track

I used movement data collected by a GPS tag attached to one white stork individual during spring migration as it moves from its wintering grounds in sub-Saharan Africa to its breeding grounds in northeastern Europe by crossing the Sahara Desert (Figure 2-8). Due to the limited number of stations in Africa, the distance between the bird's location and the nearest INTERMAGNET station is high. This distance decreases as the bird nears its breeding grounds in Europe where there is high station density. In this region, attaching data from the nearest INTERMAGNET station to the bird's location effectively mirrors a continuous geomagnetic data surface. For example, in the later stages of the bird's migration (after Day of Year 90), the curved lines at the northern latitudes using observatory values appears like the curved lines using MagGeo outputs. MagGeo outputs however use continuous model estimates across the world and can represent the changes in geomagnetic values at every location as the bird moves across large distances. Even when including the interpolated satellite residuals required to create the MG data framework, the farthest distance between a satellite pass and a bird's location is still lower than the farthest distance between an INTERMAGNET station and a bird's location.

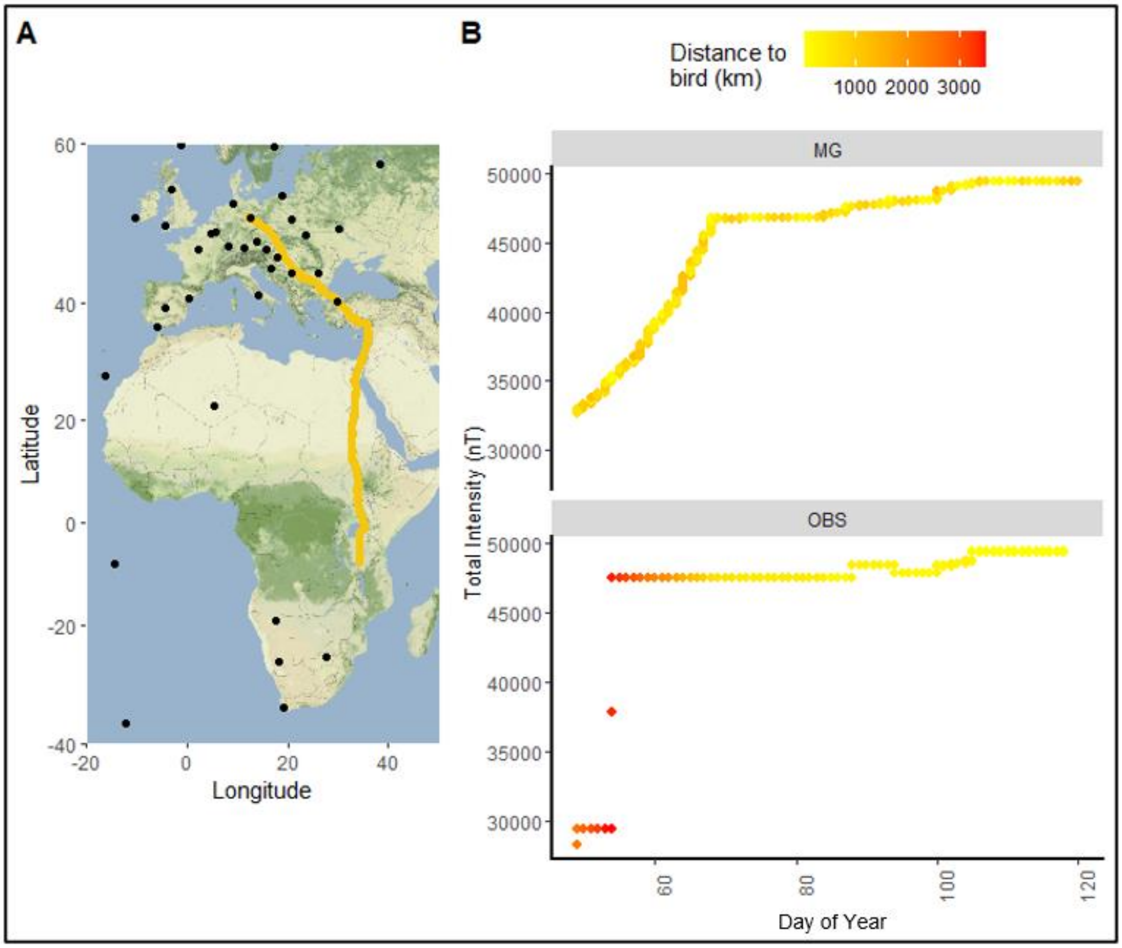

Figure 2-8. Comparison of geomagnetic data sources for attaching total intensity (nT) values to a movement track of a migratory White stork individual travelling between its wintering ground in sub-Saharan Africa and its breeding ground in northeastern Europe in spring. A. The migratory track (yellow) of a White stork individual carrying a GPS tag. INTERMAGNET stations are identified with black dots. **B.** Difference between using geomagnetic data from nearest INTERMAGNET station (OBS) compared to the MagGeo tool (MG) is more evident in locations where there is a lower density of stations (areas outside of Europe). The fused model estimates and satellite residual data framework alongside the nearest neighbour interpolation method of MagGeo ensures a high likelihood of representing the gradient of values experienced by the bird as it moves across long distances.

2.5 Discussion

The overall absolute difference error was less than 1% of the possible range of values for all geomagnetic components. For example, globally, the total intensity ranges from 20,000 nT to 60,000 nT and the mean and median error were 128 nT and 80 nT respectively when using the fused model estimate and satellite residual data (MG) framework and NNT interpolation method. Absolute difference stayed below 1% for all geomagnetic components despite changes to the underlying spatiotemporal interpolation method or geomagnetic data structure. NNT did consistently capture the values and patterns observed at ground observatories better than all other interpolation methods thus having the best overall performance. Generally, MG also captured the patterns observed at stations better than just model estimates (CH) especially during high activity levels. Overall, MagGeo accuracy is lower at higher latitudes and during geomagnetically active periods where there is greater influence of solar activity. In comparison to the Benitez-Paez et al. (2021) who test MagGeo at three INTERMAGNET stations for 6 days in a single year, I test an average of 105 geomagnetic observatory locations across 7 years. My results suggest that changing MagGeo’s underlying spatiotemporal interpolation method from IDW to NNT while continuing to use fused model estimate and satellite residual data will likely represent values experienced by animals near the Earth’s surface; thus, proving useful for movement ecology studies that test unique research questions regarding the navigational abilities of migratory animals anywhere in the world.

2.5.1 Interpolation methods

A persistent challenge for the field of remote sensing and movement ecology is how to annotate dynamic environmental covariate data to a moving object (such as a migratory animal) to best model the landscape in a way that accurately represents the animal’s experience (Brum-Bastos et al., 2021). This question is addressed by platforms like Movebank (Kays et al., 2022; Kranstauber et al., 2011) and Env-DATA (Dodge et al., 2013) that annotate a movement track with dynamically changing covariates like wind. Env-DATA offers the user with some flexibility for how to interpolate covariate data to the location and timestamp of interest. While the Env-DATA database currently stores information for many different environmental covariates useful for movement ecologists, it does not provide an avenue for attaching geomagnetic data to a movement track.

When Benitez-Paez et al., (2021) developed MagGeo to address this technological gap, they implemented an IDW method to interpolate satellite residuals to an animal tracking fix in addition to using model estimates. The assumption was that an average geomagnetic value for satellite residuals will reduce the influence of any outlier value on the final geomagnetic outputs (Benitez-Paez et al., 2021). However, compared to any nearest neighbour algorithm, averaging the geomagnetic values through IDW may smooth over the very fluctuations MagGeo hopes to capture. I tested this assumption by testing three simpler nearest neighbour interpolation techniques within the MagGeo framework. I found that the NNT had the best performance since it had the highest percent occurrence of lowest error when compared to values and patterns observed at terrestrial geomagnetic stations part of the INTERMAGNET network. Attaching satellite residuals closest in time to the point of interest like an animal tracking fix will increase the likelihood of capturing the temporal dynamics of the geomagnetic field. The NNT method is also computationally simpler than the IDW algorithm. Based on these results and rationale, there is a strong argument for changing MagGeo's underlying spatiotemporal interpolation from IDW to NNT.

It is important to highlight that while I tested different interpolation methods, I maintained the time and space parameters of the existing MagGeo kernel. Benitez-Paez et al. (2021) selected these parameters based on the structure of the polar-orbiting Swarm satellites that pass near a location every four hours with higher clustering of data points at polar latitudes compared to equatorial latitudes due to the radius of the Earth (Friis-Christensen et al., 2006; Olsen et al., 2010). It is important to maintain some function that ensures that temporally contemporaneous geomagnetic data are within a certain spatial distance of an animal tracking fix. Future research may look at what this optimal distance may be to maximize performance, but it is likely that it will vary by latitude like the current implementation.

2.5.2 Data structure

I found that using a combination of CHAOS-7 model estimates and Swarm satellite residuals (MG) can capture relative geomagnetic patterns (lower alpha) observed on the Earth's surface better than using only CHAOS-7 (CH) model estimates. Interestingly, while the satellite residual contribution increased as geomagnetic activity increased, this additional data did not significantly improve accuracy when comparing with INTERMAGNET stations values (average performance around 50%). This result is surprising since Benitez-Paez et al. (2021) proposed the MG data structure with the expectation that the addition of satellite residuals would capture the temporal variability of the geomagnetic field during periods of higher geomagnetic activity.

Model estimates, which are built primarily from quiet-time data, do not represent geomagnetic values during periods of higher activity such as daytime fluctuations outside of quiet-time or discrete events like geomagnetic storms (Finlay et al., 2020; Thébault et al., 2010). Interpolation of residuals from satellites is then likely to add some of the temporal variability not captured by models (Benitez-Paez et al., 2021). My results indicate however that overall mean MagGeo error increases during periods of higher geomagnetic activity though a positive skew index suggests that mean error may be influenced by a few exceptionally high error data points. Indeed, a double exponential (Laplacian) distribution with a sharp peak around zero and long tail is expected when comparing geomagnetic model data with ground-based measurements (Walker & Jackson, 2000). For example, when comparing IGRF-13 values against ground-based measurements, Beggan (2022) reported absolute difference error values closely mirroring my results alongside the expected Laplacian distribution.

Additionally, high geomagnetic activity may impact satellite data collection which will consequently impact the satellite residuals used for the MG structure (Babayev et al., 2006; Lanza & Meloni, 2006). For example, I had to remove data from days during known solar storms as the error was particularly high. Additionally, though I used the NNT interpolation method, the residuals from satellite data may reflect values almost 4 hours before or after the geomagnetic storm due to the MagGeo's space-time cylinder parameters (Benitez-Paez et al., 2021). As a result, while the INTERMAGNET station may have recorded geomagnetic values during the geomagnetic storm, MagGeo outputs may not have captured the localised storm at such a fine temporal resolution given a possible lagged satellite residual.

When combining satellite data and model estimates (MG), I corrected for the difference between satellites collecting geomagnetic data at orbit altitudes and animals experiencing the geomagnetic field at ground altitudes by using model estimates for ground altitudes. The satellite residuals I used however still represent values at orbit altitude and neither my current MagGeo data framework nor interpolation method cannot address this limitation. It is possible to access other geomagnetic model data which, unlike the CHAOS-7 model, provides estimates for all sources of the geomagnetic field. These models do not require correction for the altitude difference (Chulliat et al., 2020; Sabaka et al., 2018, 2020). These values however will not accurately represent the instantaneous and local variability of the geomagnetic field as may be experienced by migratory animals. Incorporating satellite data at satellite altitude will capture some of this variability, and such local variations, especially during geomagnetic storms, are likely to impact orientation by animals using the geomagnetic field. Further work will be necessary to compare error and accuracy of different models with the MG data framework.

During most time periods, my results suggest that MG data can consistently capture geomagnetic patterns well. Indeed, while geomagnetic storm events are uncommon, my results suggest that MG still captures geomagnetic patterns slightly better than CH. Additionally, my accuracy analysis uses data from INTERMAGNET stations collected by well calibrated instruments that have high accuracy and precision. This sensitivity may not be necessary when studying animals who sense the geomagnetic field for navigation and orientation purposes Furthermore, one of the leading hypotheses for animals using the geomagnetic field is the gradient hypothesis, where relative patterns in geomagnetic intensity or inclination might be more useful for migratory animals than absolute values (Boström et al., 2012; Kishkinev et al., 2015; Wiltschko & Wiltschko, 2021). Based on these considerations, the algorithm from MagGeo I implement provides a highly useful and robust framework for combining geomagnetic data with animal tracking data.

2.5.3 Outliers

I found outliers to be particularly informative as they highlighted spatial nuances of the geomagnetic field. Most outliers in my dataset represent locations with unique geomagnetic signatures due to local geophysical properties not captured by model estimates at such an acute scale (e.g. Beggan, 2022). Many of the stations highlighted in Appendix 1 are volcanic islands with basaltic composition including high concentrations of ferromagnetic minerals (Johnston, 1989; Thébault et al., 2010). Others like the Bangui magnetic anomaly relate to deep geological structures (Girdler et al., 1992). Such lithospheric anomalies have a large local influence on geomagnetic values which may subsequently impact an animal moving through this geomagnetic landscape. For example, birds passing over the geomagnetic anomaly in Sweden have been previously noted to change their behavior suggesting that animal movement may in fact be influenced by local anomalies (Alerstam, 1987). Similar analyses can be conducted by using open-source resources like the World Digital Magnetic Anomaly Map (WDMAM) which allows users to easily extract anomaly information from a raster layer (Lesur et al., 2016).

As expected, stations located at high northern latitudes consistently exhibit outliers. In general, all geomagnetic components have a larger range of error at the polar latitudes since charged particles ejected from the sun more readily enter the Earth's atmosphere in the auroral zones at the poles (Campbell, 2003). Model estimates, created from quiet-time data, do not capture these changes for any geomagnetic component. However, for long-distance migrants especially near polar latitudes, geomagnetic strategies may not be useful for navigation or orientation as values can be unreliable in both magnitude and sign. The lack of predictability would thus provide little useful information, especially for migratory animals who have high site fidelity (Lohmann et al., 2008; Wynn, Padget, et al., 2020). Nevertheless, MagGeo's high global accuracy can still be a valuable tool to reliably attach geomagnetic data to animal tracks for studies wishing to test hypotheses specific to this geographic region.

2.5.4 Limitations

Geomagnetic sensitivity and perception ranges are unknown for most species and to my knowledge, there are no instruments that accurately record geomagnetic conditions as experienced by migratory animals, though there are species-specific estimates (Åkesson et al., 2005; Beason & Semm, 1987; Chernetsov et al., 2017; Schwarze et al., 2016; Semm & Beason, 1990). The most suitable candidate for attaching geomagnetic data to animal movement data would be INTERMAGNET stations which collect high-temporal resolution geomagnetic values at ground altitudes. These stations however do not have a high global density and thus cannot be used to accurately capture the range of geomagnetic values experienced by an animal during long-distance migration. Using GPS tracking data of a white stork individual, I demonstrate how attaching geomagnetic data from the nearest station to a migratory bird's location might be ideal for locations in Europe. Outside of Europe however, there would likely be a large mismatch between the geomagnetic values experienced by a bird and a station collecting geomagnetic data more than 2,000 km away. Instead, using a combination of model estimates and interpolated satellite residuals could serve as a sufficient alternative that captures high spatiotemporal resolution geomagnetic data for all locations on Earth.

I do use INTERMAGNET station data as the ideal standard to perform my error and accuracy analysis to test the MagGeo tool. I did not however anticipate the level of uncertainty introduced by the station data themselves though this is primarily explained by local crustal fields (Beggan, 2022). My analyses suggest that MagGeo outputs and observatory values are offset by a unique amount specific to each INTERMAGNET station and my linear mixed-effect models reveal that the majority of the error structure for absolute difference can be explained by these random, location-specific effects (St-Louis, 2012). In addition to geomagnetic activity as a fixed effect, these models explain most of the variation in the error structure for differences between MagGeo outputs and observatory values. These results highlight the limitation of my structural set-up as this station-specific offset skews the absolute difference by a consistent amount for each data record. The alpha measure partly addresses this issue by subtracting the standardized MagGeo outputs from the standardized observatory values (Ridley & Macmillan, 2014). My linear mixed-effect models fit with alpha as the dependent variable suggest that random, location-specific effects explained much less of the error structure. It is noteworthy however that Kp and time of day influenced the error structure in predictable ways such that periods of high geomagnetic activity led to higher error (Campbell, 2003; Lanza & Meloni, 2006).

2.5.5 Applications and open questions

Most of my analysis is from data collected in the last 7 years (2014-2020) which is largely during the quieter period of the solar cycle (Li et al., 2011). The 11-year and 22-year solar cycle has a significant influence on geomagnetic field activity since years of high solar activity correspond to higher occurrence of geomagnetic storms (Cliver, 1994; Li et al., 2011; Thébault et al., 2010). Given that CHAOS-7 model estimates contribute three of the four geomagnetic sources (core, lithosphere, and magnetosphere) in MagGeo's framework, I can assume that MagGeo will capture long term changes in the geomagnetic field so long as the CHAOS-7 estimates inputs are updated. Models only capture temporal changes related to secular variation, which arises from changes in the geomagnetic field over a few years due to the motion in the Earth's liquid outer core (Campbell, 2003). The slow solar cycle variation of the magnetospheric field is also represented though the unpredictable effects from geomagnetic storms are not completely captured.

Currently, I am using the CHAOS-7 model estimates (Finlay et al., 2020) but MagGeo's algorithm allows for integration of any other geomagnetic data sources within the VirES platform and may be modified as per the user's need. Specifically, the next couple years of high geomagnetic activity might be of interest to researchers studying the impact of geomagnetic activity on animal behavior. High geomagnetic activity events present a natural occurrence of an experimental extreme that could answer fundamental questions about animal behavior outside of laboratory settings through new "laboratories-in-the-wild" experimental approaches (Nathan et al., 2022). For all above scenarios, the MagGeo tool can facilitate exploration of these research questions.

2.6 Conclusion

With its relatively low error and flexible framework, MagGeo is a promising tool for movement ecologists and biologists who want to test animal navigation hypotheses about geomagnetism using open, high spatiotemporal resolution geomagnetic datasets. In addition to highlighting the strengths of MagGeo, my study also showcases the importance of error and accuracy tests for environmental covariate data that can be attached to animal movement data. As access to remotely sensed environmental data increases, it will be imperative to enlist cross-discipline expertise to maximize a dataset's full potential and understand the respective strengths and weaknesses of different datasets. Further, my research highlights the need for continued development of analytical tools for combining animal tracking with environmental data. As a research community, I can continue to learn how to better integrate multiple data sources to understand how an animal interacts with its environment thereby contributing to better knowledge of an animals' inevitable ties to the living world.

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Chapter 3

3 Geomagnetic orientation cues facilitate biannual migration across the eastern Sahara for thermal soaring birds

3.1 Introduction

Across all major flyways in the world, billions of long-distance migratory birds must traverse landscape barriers such as oceans, mountains, and deserts to successfully reach breeding and wintering grounds (Åkesson & Hedenström, 2007; Hahn et al., 2009; Hawkes et al., 2011). Bird migration strategies are likely a result of evolutionary pressures that balance trade-offs for each species (Åkesson et al., 2016; Alerstam et al., 2003) and even for certain populations within a species (Bairlein et al., 2012; Cheng et al., 2019; Flack et al., 2016; Schmaljohann et al., 2007b). Specifically, there is likely selection for orientation mechanisms that facilitate multiple, successful return migrations across landscapes that lack both energy-rich resources for refueling and characteristic visual markers for orientation. Patterns in the Earth's magnetic field could serve as a reliable orientation cue in an otherwise visually featureless landscape (Hore & Mouritsen, 2016; Lohmann et al., 2007; Mouritsen, 2014). In my study, I test four geomagnetic orientation strategies while accounting for the influence of wind conditions for 68 white stork *Ciconia ciconia* individuals crossing the eastern Sahara.

I make a clear distinction between navigation and orientation for the purpose of my study. I associate navigation with a map-based strategy where birds can position their current location relative to a destination (Holland, 2014; Lohmann et al., 2007; Tsoar et al., 2011; Zein et al., 2021). For long-distance migratory birds, this destination is a location thousands of kilometers away. I associate orientation with compass-based strategies where birds can determine direction of travel based on external cues (Chernetsov, 2017; Hiscock et al., 2016; Sokolovskis et al., 2018). For an environmental condition to function as an orientation cue, it needs (1) to vary reliably in space and time and (2) the animal using the cue needs appropriate anatomical structures and physiological pathways to sense, perceive, and integrate patterns to make movement decisions. It is generally accepted that birds and other long-distance migrants use a combined map-and-compass strategy to navigate between summer and wintering grounds with high site fidelity (Komolkin et al., 2017; Kramer, 1953; Toledo et al., 2020).

An innate geomagnetic compass in animals has been proposed and tested (Kishkinev et al., 2021; Lohmann et al., 2007; Wiltschko & Wiltschko, 1972b, 1988) though the exact mechanisms and overall feasibility are heavily debated (Gagliardo, 2013; Pollonara et al., 2015; Wikelski et al., 2015). Popular theories based on quantum biology suggest a radical base-pair mechanism where some birds sense and integrate geomagnetic field information connected to a visual system (Hiscock et al., 2016; Holland, 2014; Johnsen & Lohmann, 2005; Mouritsen & Heyers, 2016). Virtual displacement studies also record changes in the bird's movement direction that align with how individuals would be expected to re-orient if they used geomagnetic information during migration (Chernetsov et al., 2017, 2020; Kishkinev et al., 2015). Strong counterarguments arise primarily from studies where displaced birds with impaired geomagnetic sensory abilities (treated birds) have similar return rates to birds with intact abilities (control birds) thereby suggesting that geomagnetic information may not be necessary for navigation and orientation (Benhamou et al., 2003; Holland et al., 2009; Keeton, 1971; Pollonara et al., 2015; Wikelski et al., 2015; W. Wiltschko et al., 2007).

Studies using geospatial data to create movement models largely provide support for the geomagnetic navigation and orientation hypothesis. Åkesson & Bianco (2016) found that simulated trajectories based on geomagnetic inclination ended in theoretical destinations that closely matched observed wintering ground locations of individuals fitted with GPS tags, especially when accounting for wind patterns (Åkesson & Bianco, 2016, 2017). Recently, Zein et al. (2022) tested 19 different geomagnetic navigation and orientation strategies with tracking data from greater white fronted geese *Anser albifrons* moving from western Europe to the Russian Arctic. They specifically tested two geomagnetic orientation strategies called taxis and constant heading (sometimes called menotaxis). Taxis is the movement towards or away a geomagnetic extreme along an environmental gradient whereas constant heading is movement at a consistent angle from an environmental cue (Togunov et al., 2021; Zein et al., 2021). Models based on taxis and constant-heading for total intensity and inclination consistently performed better than any other combination of strategy and geomagnetic component (Zein et al., 2021, 2022).

It is likely however that multiple factors influence movement decisions during migration. Muheim et al. (2018) performed simulation studies to test sun and geomagnetic compasses for

3 species that have vastly different migration routes. They found that the feasibility of compasses depends on species, migratory destinations, and external conditions. Wind, weather, and other atmospheric variables are often included in most movement models as these conditions strongly dictate behaviour like flight (Becciu et al., 2020; Bishop et al., 2015; Blas et al., 2020; Eisaguirre et al., 2020). Rising pockets of hot air called thermals are often exploited by larger birds like storks and raptors to subsidize flight costs (Chevallier et al., 2010; Curk et al., 2020; Flack et al., 2018; Nourani et al., 2021). Birds first gain altitude by remaining at the edge of the thermal and then glide towards the next thermal, typically in the direction of their destination (Thorup et al., 2003; Togunov et al., 2021; Wynn, Collet, et al., 2020). While thermal development and wind patterns can be unpredictable, prevailing wind conditions are reliable in certain regions of the world. For example, in the eastern Sahara, winds continuously blow from the northeast to the southwest and are called north-easterly trade winds (Mohamed Hereher, 2014; Loonstra et al., 2019; Vansteelant et al., 2017). These reliable patterns may have a significant role in shaping migratory routes and behaviours especially when crossing energetic barriers (Nourani et al., 2021; Vansteelant et al., 2017).

In my study, I test geomagnetic taxis and constant heading orientation using total intensity and inclination for white storks crossing the eastern Sahara. White storks are large wetland birds with an expansive range (Becciu et al., 2020; Flack et al., 2016; Rotics et al., 2016). I focus on white storks in the Asian-East African Flyway who have breeding grounds in northeastern Europe and wintering grounds in sub-Saharan Africa (Berthold et al., 2002). The size of these birds necessitates thermal-soaring behaviour which provides energetic subsidies by minimizing flapping flight (Chevallier et al., 2010; Flack et al., 2018; Nourani et al., 2018; Van Loon et al., 2011). Prevailing wind conditions may provide further support during the fall when migratory movement direction is aligned with the north-easterly trade winds (Moreau, 1972; Schmaljohann et al., 2007a, 2007b). Given the life history traits of the study species alongside previous geomagnetic orientation model results, I predict that (1) wind conditions will have a strong impact on a white stork's movement decisions and that (2) out of the four possible combinations for geomagnetic orientation cues, the best performing movement models will be taxis based on total intensity (Zein et al., 2021, 2022).

3.2 Data and methods

3.2.1 GPS tracking data

I compiled GPS tracking data from Movebank of white storks from 12 different studies between years 2014 to 2021. To address discrepancies between the different datasets, I pre-processed the data to ensure a minimum level of data quality required for my investigation (Figure 3-1). Specifically, I filtered points by keeping only tracking fixes based on a unique combination of tag identifier, latitude, longitude, and timestamp. Furthermore, white storks are social birds and migrate in flocks, and it is likely that individuals in the same flock adhere to flock-wide decisions (Flack et al., 2016). I defined flock overlap between two individuals using spatial-temporal contact analysis (Long et al., 2022), where contacts were defined as having tracking fixes within 5 km of each other in the space of an hour. I then defined two individuals as being in the same flock if individuals had greater than 80% contact rate based on my spatial and temporal thresholds of 5 km and 1 hour (Long et al., 2022). I retained only one individual from each flock. This filtering step ensures that no two individuals within my dataset are close enough in spatial-temporal proximity to follow the same flock-wide decisions.

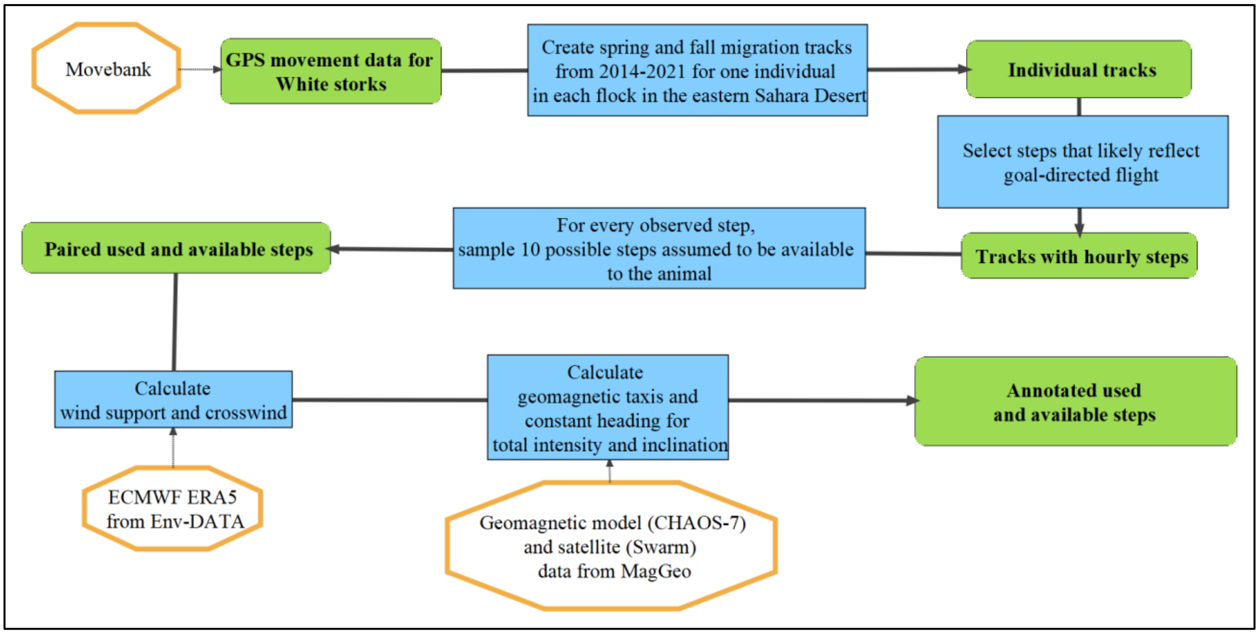

Figure 3-1. Process for how GPS movement data are converted to hourly used and available steps for input into the step selection framework to study geomagnetic orientation for white storks crossing the eastern Sahara. Orange hexagons with dotted arrows represent data sources, green rounded rectangles represent data outputs and blue rectangles represent methods for the processing steps.

I defined a study area comprising arid regions of the eastern Sahara after crossing the Gulf of Suez (bounding box: E 5°-60°, N 17°-30°) (Figure 3-2A). I then only use points during spring (Day of Year 27 to 124) and fall (Day of Year 203 to 335) migration from 2014 to 2021 (Reed & Lovejoy, 1969). For my study, a track begins when an individual enters the study area and finishes when the bird exits the study area. Alternatively, I cut off tracks 15 days after an individual initially entered the bounded region as it would be energetically unviable for migrating white storks to spend more than 2 weeks in the desert. Longer durations within the bounded region might indicate tag failure, bird death, extended stopover periods near the Nile or movement at wintering sites near the Sahel. For my dataset, 95% of the tracks (258/270 tracks) passed through and beyond the study area in less than 15 days. Additionally, to have sufficient data to build robust statistical models, I removed any migration tracks that had fewer than 25 GPS tracking points. For my study, one individual could have multiple tracks if I had an individual's movement data from more than one season. In total, I captured n=144 migrations in spring and n = 126 migrations in the fall.

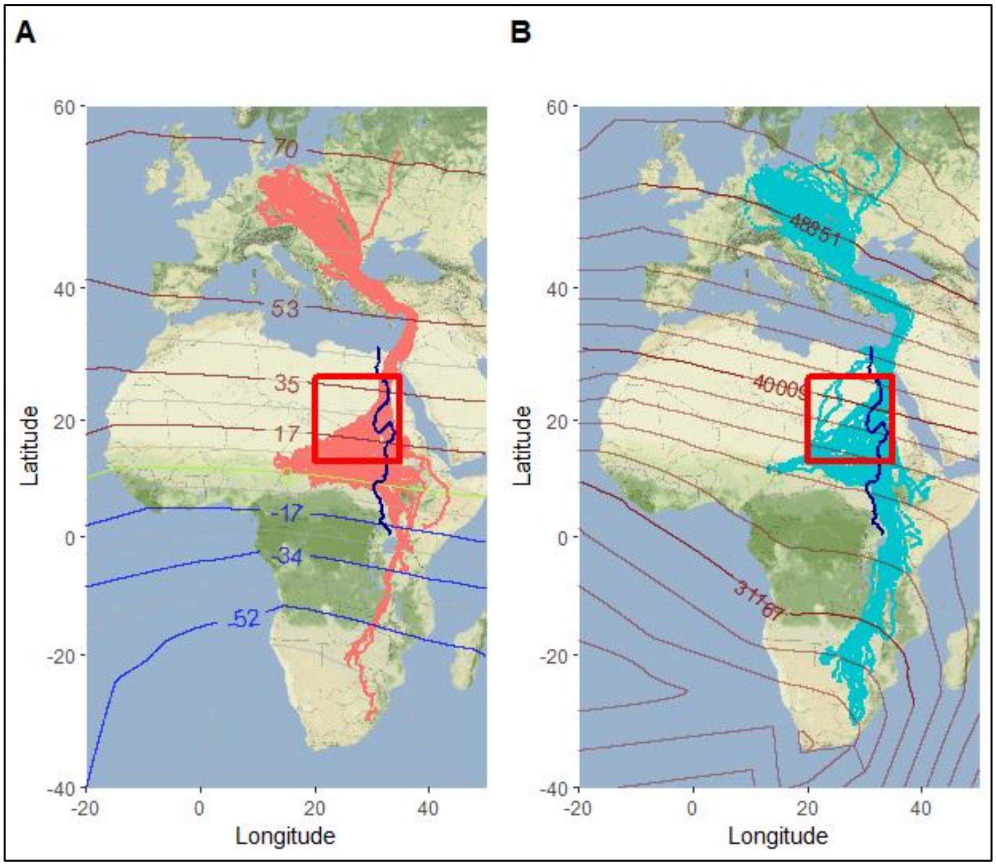

Figure 3-2. Biannual migration for 68 white stork individuals from 2014-2021 through the eastern Sahara with the Nile highlighted in dark blue. Base map includes geomagnetic isolines. A. 126 fall migration tracks with birds moving from breeding grounds in northeastern Europe to wintering grounds in sub-Saharan Africa. Birds move from positive inclination values (red isolines) towards the geomagnetic equator (green isoline) in the fall and some individuals continue their migration to South Africa (negative inclination values, blue isolines) **B.** 144 spring migration tracks with birds moving towards their breeding grounds. Birds move from areas of low geomagnetic total intensity in sub-Saharan Africa to high geomagnetic total intensity in northeastern Europe.

Within each track, I select for periods when birds are performing goal-directed flight (GDF). In this state, birds are more likely to use environmental cues, like the geomagnetic field, to make orientation decisions (Chernetsov, 2017). First, I select for GDF based on the overall and daily displacement within the region by focusing on days when the birds moved at least 100 km within a 24-hour period. Within these selected days, I resample tracks to have regular hourly temporal relocations, henceforth described as “steps” in the movement track. Finally, I select only hourly steps with speeds ≥5 km/h as that is when birds are most likely in-flight and moving towards a goal (Acácio et al., 2022).

White storks are diurnal migrants which implies that most hourly steps with speeds ≥5 km/h would occur during the day (Reed & Lovejoy, 1969). During evenings and nights, birds are likely resting or foraging at stopover sites which are both activities that have slower flight speeds (< 5 km/h). Stopover sites are typically located in habitats that provide protection and food though this may not be entirely possible when birds are travelling in the eastern Sahara (Efrat et al., 2019; Schmaljohann et al., 2007a). Outside of chance oases in the desert, only habitat around the Nile and nearby development have reliably high ecosystem productivity in the study region (Sergio et al., 2022).

In total, I had 270 migration tracks for 68 unique individuals and 19,560 hourly steps. To understand seasonal differences in movement, I applied a Wilcoxon test to compare the fall and spring values for track duration, number of stopovers, movement path distance, daily speed, and proportion of steps near the Nile.

3.2.2 Step-selection functions

Step selection functions (SSFs) are a statistical framework that compare environmental conditions experienced by an animal at each observed step (sometimes called “used step”) with environmental conditions assumed to be available to the animal at theoretically possible, alternative steps (Figure 3-3). To investigate an animal’s habitat selection pattern, environmental variables at observed and possible steps are inputted into a case-control design within a conditional logistic regression model which can be found in most common software programs. Traditionally, SSFs have been applied to understand patterns in habitat selection for terrestrial animals (Fortin et al., 2005; Oliveira-Santos et al., 2016; Roever et al., 2010). Recently, SSFs have also been used to investigate selection for wind and weather conditions during raptor migration (Curk et al., 2020), especially for thermal-soaring raptors (Eisaguirre et al., 2020; Nourani et al., 2018, 2021). I fit SSFs to understand how white storks may use geomagnetic orientation to cross a major energetic barrier while controlling for the impact of wind conditions.

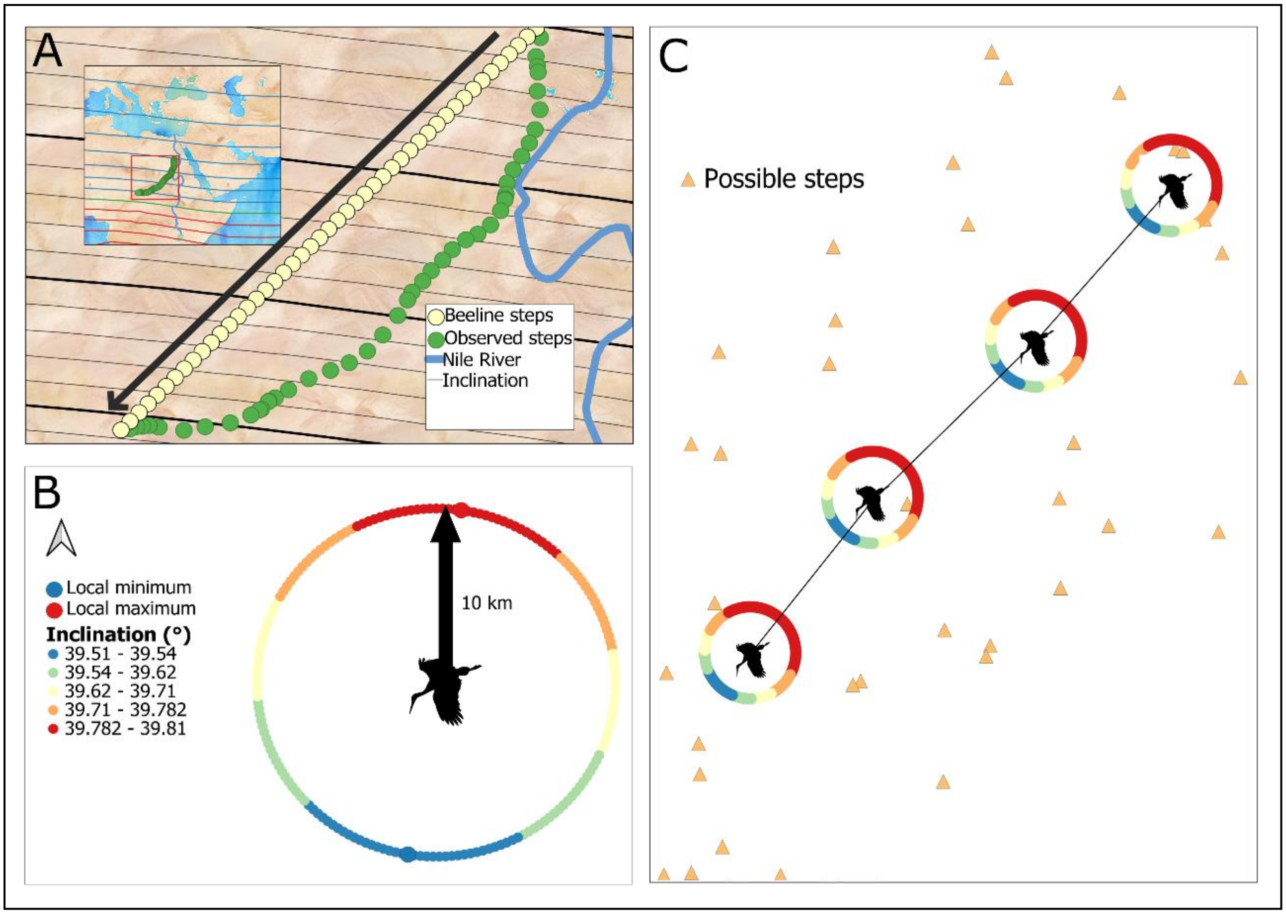

Figure 3-3.Conceptual overview of how I tested geomagnetic orientation for white storks crossing the eastern Sahara. A. Track of one bird during fall migration recorded with GPS loggers (observed steps in green) and the associated shortest path trajectory (beeline steps in yellow). Inset and base map have geomagnetic inclination isolines that show the bird moving down the inclination gradient towards a global geomagnetic minimum indicated by the green geomagnetic equator where inclination values are 0. **B.** A 360 º field of perception (FOP) created using 180 points in a radius of 10 km around the bird’s current position represented by the silhouette of white stork in flight. All points on FOP are annotated with raw geomagnetic inclination and total intensity values (only inclination values shown here). **C.** For the step selection analysis, every observed step (white stork with FOP) had 10 possible steps (orange triangles) that were assumed to be available to the bird. Step lengths for the possible steps are roughly the same length as the observed step whereas turn angles can range from 0 º to 360 º.

3.2.2.1 Geomagnetic orientation

I accessed geomagnetic data from the open-source MagGeo software (Benitez-Paez et al., 2021) which combines satellite data from the European Space Agency's Swarm satellites (Friis-Christensen et al., 2006) with geomagnetic model data from the 7th Generation of the CHAMP, Ørsted and SAC-C model (CHAOS-7) (Finlay et al., 2020). My version of MagGeo interpolates this fused geomagnetic data to the hourly steps using a nearest neighbour method. MagGeo outputs include high spatiotemporal resolution geomagnetic values for total intensity (F) and inclination (I). All steps are also annotated with a quasi-logarithmic metric for global geomagnetic activity called the Kp index (Matzka et al., 2021). Kp values greater than 5 are indicative of geomagnetic storms.

I used the total intensity and inclination values to test two geomagnetic orientation strategies: taxis (Figure 3-4) and constant heading (also called menotaxis) (Figure 3-5). Based on the geomagnetic values in the eastern Sahara and final seasonal destinations of white storks, I assumed that in the fall, the birds used the geomagnetic minimum as the extreme value (Figures 3-2A) whereas in the spring, they use the geomagnetic maximum (Figures 3-2B). I assume that individuals at each step must in general display movement towards, away or at a constant angle to the local extreme (step-level movement) to eventually display movement towards, away or at a constant angle to the global extreme (track-level movement within the study region).

For my study, I qualified the local, step-level movement based on a field of perception (FOP) which is a circle with a 10 km radius around the bird's current position (Figure 3-3B). This FOP is represented by 180 uniformly spaced points around a circle with a radius of 10 km from the central point (starting point in a step) (Figure 3-3B). I use the FOP to model taxis and constant heading. I used the MagGeo software to attach total intensity, inclination and Kp values to (1) all observed steps, (2) all 180 points in the FOP for every observed step, and (3) all 180 points in the FOP for every beeline step (see below for more information) (Figure 3-3).

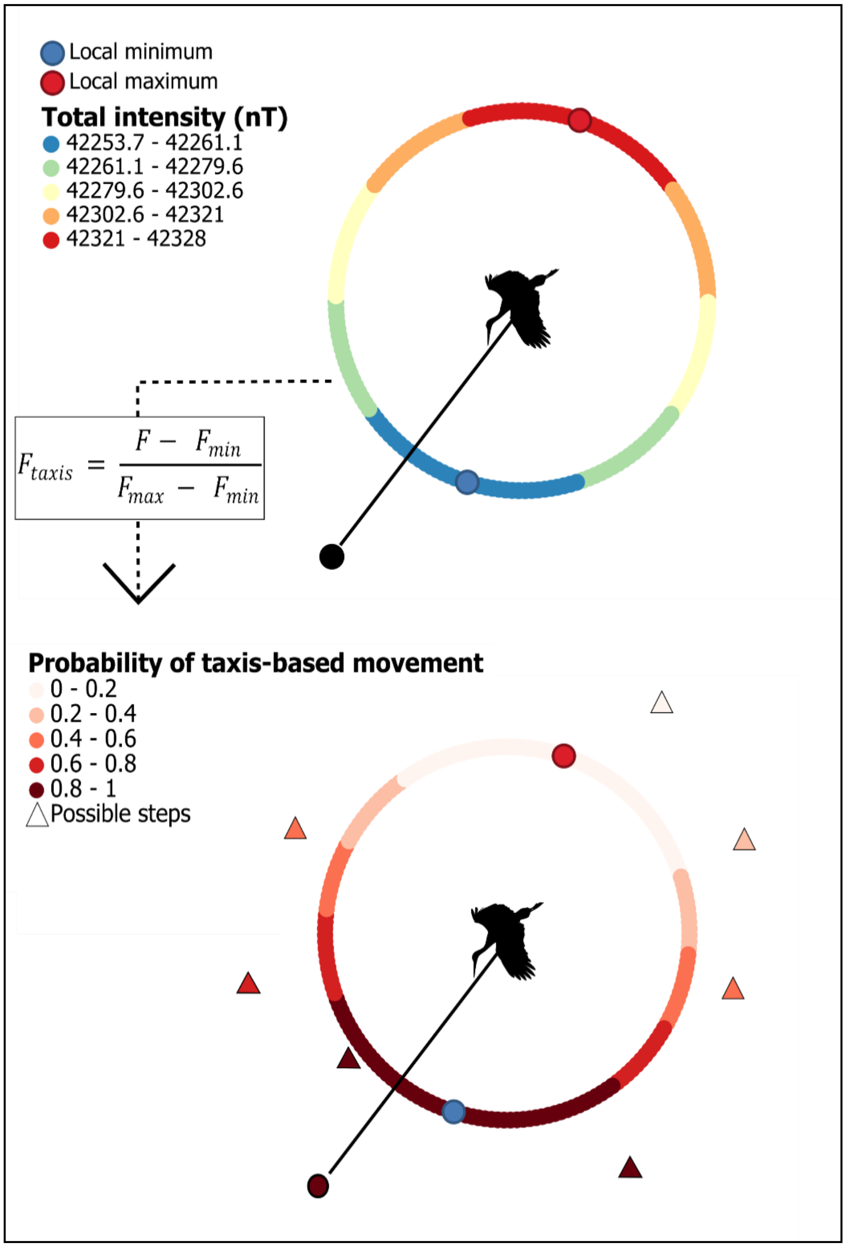

Figure 3-4. Conceptual overview of geomagnetic taxis orientation calculations using total intensity values. Example uses data from one step of one white stork individual moving southwest during fall migration. For every observed step, I created and annotated a FOP with raw geomagnetic values which I then converted to a probability value for taxis-based movement. In the fall, FOP points closest to the local minimum had normalized scores closer to 1 (dark red in bottom panel) indicating higher probability of taxis-based movement. Normalized scores on the FOP were attached to observed (circle symbols) and possible (triangle symbols) end points of each step based on the nearest neighbour method with probability values from points in the FOP.

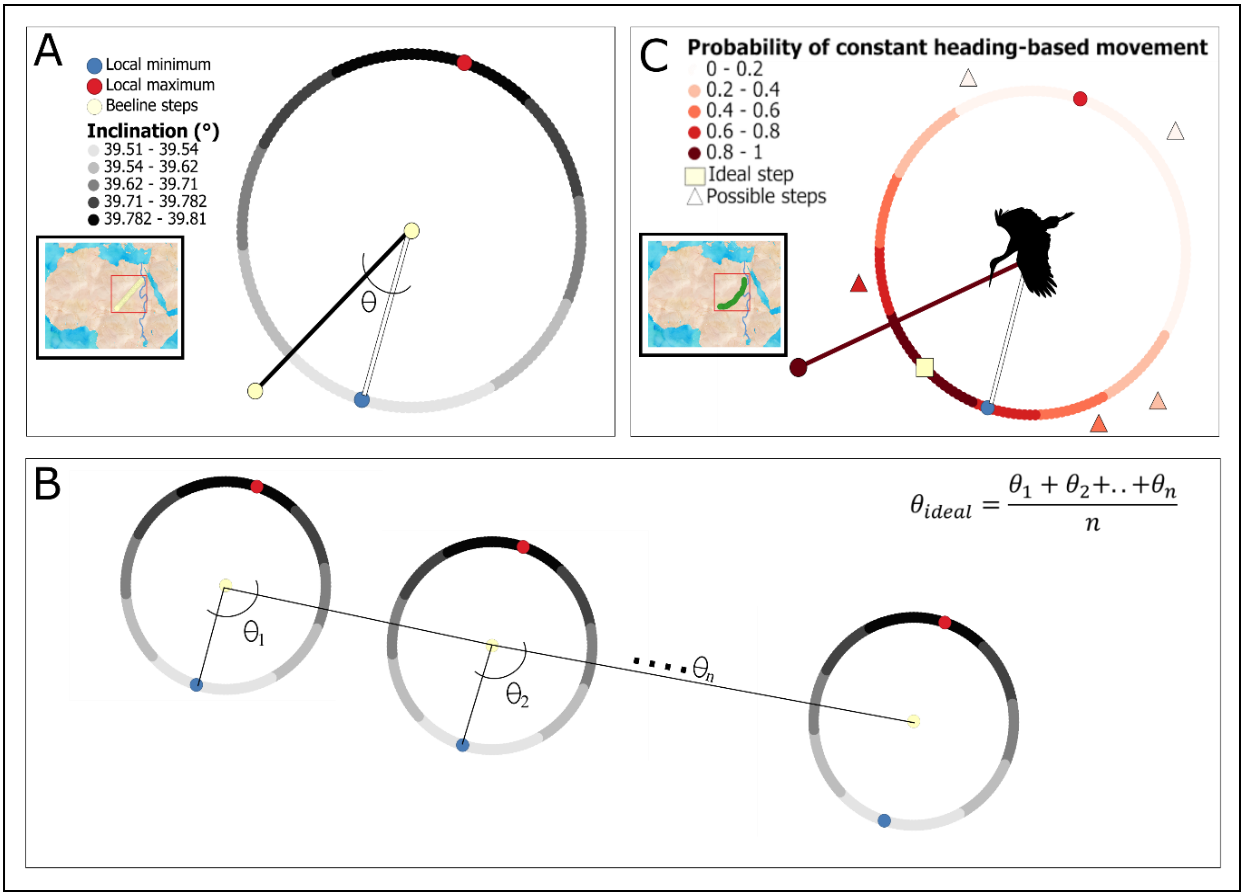

Figure 3-5. Conceptual overview of geomagnetic constant heading orientation calculations using inclination values. I first create a beeline trajectory (light yellow points in inset map in panel A) for every observed trajectory (bright green points in insert map in panel B). I create a FOP around every beeline step and annotate it with geomagnetic values. **A.** For fall, I calculate the angle (θ) between the local geomagnetic minimum on the FOP (blue circle) and the end point of the current step (yellow circle). **B.** I take the average angle of all beeline steps (yellow circle) to calculate an ideal angle ($\boldsymbol{\theta_{ideal}}$). $\boldsymbol{\theta_{ideal}}$ is the average angle to the geomagnetic extreme that the bird would have to maintain to migrate through the study region in the shortest distance. **C.** For the observed steps, I calculate a normalized score for constant heading relative to the ideal step based on $\boldsymbol{\theta_{ideal}}$. FOP points closest to the ideal step (light yellow square) have a higher probability of constant heading-based orientation (normalized scores closer to 1) and are represented by dark red colors. Like taxis, normalized scores for both observed (circle points) and possible (triangle points) end points of the step reflect probability values of the nearest point on the FOP.

3.2.2.1.1 Geomagnetic orientation: taxis

I annotate all observed steps and all 180 points in the FOP with total intensity and inclination values from MagGeo (Figure 3-4). For every point in the 180 points in FOP, I normalize the raw geomagnetic values on a scale of 0-1 using the formula:

$$F_{taxis} = \frac{F - F_{min}}{F_{max} - F_{min}} \quad [1]$$

Where F_{taxis} is the normalized score between 0 and 1 for total intensity values, F_{min} is the minimum total intensity value in the FOP (step-level minimum), F_{max} is the maximum total intensity value in the FOP (step-level maximum) and F is the total intensity value of the current point in the FOP (Figure 3-4). The same formula set-up is used for geomagnetic inclination values. For both components, normalized scores closer to 1 indicate higher probability of movement based on geomagnetic taxis whereas scores closer to 0 indicate lower probability of movement based on geomagnetic taxis. I use the nearest neighbour interpolation to annotate the used and possible end points of a step which then assume the normalized score of the nearest point in the FOP (Figure 3-4).

For example, in the fall, normalized scores closer to 1 (high probability of taxis) indicate movement towards the local minimum geomagnetic extreme value which would guide the white storks in the direction of local minimum geomagnetic extreme near the geomagnetic equator. Conversely, normalized scores closer to 0 (low probability of taxis) indicate movement towards the local maximum geomagnetic extreme value which would be in the direction of nearest global maximum geomagnetic extreme value near the North pole.

3.2.2.1.2 Geomagnetic orientation: constant heading

To calculate constant heading, I first create a beeline trajectory (shortest path) between the observed starting and ending point of each track (inset map in Figure 3-5A). Every beeline trajectory has the same number of intermediate steps as the original, observed track. For example, if a bird crosses the eastern Sahara within 45 steps, the beeline trajectory will also have 45 steps with the same starting and ending points as the true, observed trajectory.

I create and attach geomagnetic information to the FOP around every beeline point and calculate the angle between the end point of the beeline step and the extreme geomagnetic value in the FOP (Figure 3-5A). I call this angle "heading" (θ) and calculate a trajectory heading by using the average heading values of all points in the track. I term this average value "ideal heading" (θ_{ideal}) (Figure 3-5B) because it is the angle that the bird must maintain in reference to a geomagnetic extreme to cross the study region in the Sahara in the shortest distance.

I use θ_{ideal} from the beeline trajectory to calculate normalized scores for each step in the observed trajectory (inset map in Figure 3-5C) to determine the probability of constant heading-based movement. First, I create a FOP around each observed step and identify the point in the FOP corresponding to the θ_{ideal}. I calculate normalized scores based on proximity such that points in the FOP closest to the θ_{ideal} have values closer to 1 to indicate higher probability of constant heading-based movement. It follows that the values closer to 0 indicate lower probability of constant heading-based movement and are further away on the FOP from the θ_{ideal}. For example, if θ_{ideal} was 30^{o} from the geomagnetic extreme, FOP points roughly between $20 \leq \theta \leq 40$ would have normalized scores closer to 1 whereas FOP points roughly $\theta \geq 80$ would have normalized scores closer to 0 (Figure 3-5C). Again, I use the nearest neighbour interpolation to attach the FOP normalized scores to the observed and possible endpoints of each step.

3.2.2.2 Possible steps

I create a set of 10 possible steps associated with one used step (Figure 3-3C). I choose a normal distribution to sample step lengths (distance between start and end point of a step) and a uniform distribution to sample turn angles (angle between the previous step and new direction of movement). The selection for this sampling distribution is unusual compared to other studies using SSF, where it is more common to sample from a gamma distribution and Von Mises distribution for step length and turn angle respectively (Holloway & Miller, 2014; Thurfjell et al., 2014). However, most studies fit SSFs to investigate habitat selection for terrestrial animals whereas I am modeling orientation strategies for thermal soaring migratory birds. The minimal variation in movement steps paired with uniform directionality represents the assumed 360^{o} view of the landscape for thermal circling white storks during goal-directed flight (Mackintosh, 1949). I attach environmental variables to all possible steps following the same process for used end steps.

3.2.2.3 Wind support and crosswind

I annotate all observed and possible steps with wind data from the Env-DATA track annotation service associated with Movebank (Figure 3-1) (Dodge et al., 2013). Atmospheric models are from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 reanalysis database and have a spatial resolution of 0.25° and a temporal resolution of 1 hour. Data are linearly interpolated to the latitude, longitude, altitude, and timestamp of the tracking fix. I extracted both eastward (u) and northward (v) components of the wind at 850 mb (Shamoun-Baranes et al., 2003). I transformed these components to tailwind and crosswind variables following Safi et al. (2013). To understand seasonal differences for wind conditions experienced by the birds in the dataset, I applied a Wilcoxon test to compare the fall and spring values for wind support and crosswind values.

I scaled and centred tailwind and absolute crosswind values between 0-1 for each step (Curk et al., 2020; Nourani et al., 2018, 2021). Wind support values closer to 0 indicate headwind whereas values closer to 1 indicate tailwind. Crosswind values closer to 0 indicate that the horizontal component of the wind vector is parallel to the bird's direction of travel (bird is flying in direction of wind) whereas values closer 1 indicate that the horizontal component of the wind vector is perpendicular to the bird's direction of travel (bird is flying into the wind).

3.2.2.4 The Nile as a linear feature

The Nile is one of the most prominent landscape features in the eastern Sahara north of the Sahel. It is also one of the most productive areas in the desert. For wetland birds like white storks, the Nile and the surrounding developed habitat (agriculture and urban) would likely be a stopover site for resting and refuelling (Efrat et al., 2019). Additionally, though there are prominent bends in the Nile (like the aptly named "Great Bend"), the main tributaries are a linear feature on a north-south axis in an otherwise featureless landscape (Faccenna et al., 2019). As a result, the river could also function as a reliable orientation cue in the study region.

I create a 10 km buffer around the Nile vector shapefile from OpenEarth to compare what percentage of steps are near the Nile and surrounding habitat. I classify a step as being within the Nile habitat if both the starting and ending point of the step are within the 10 km buffer. Preliminary analyses revealed that steps in the buffer were largely restricted to the northern range of the study area (Figure 3-2). The lack of both possible and observed steps in the buffer in the remainder of the trajectory was not suitable for the step-selection framework. Therefore, while I did calculate track statistics using the Nile buffer to describe geographic patterns in the data, I did not include it as a variable in the final movement models.

I tested a total of six variables in the final models where two were derived from wind values (wind support and crosswind) and the remaining four were derived from geomagnetic values (total intensity and inclination).

3.2.2.5 Fitting step selection functions

I fit a core movement model using only wind variables (wind support and crosswind). I then append the core model with one of the four unique combinations for geomagnetic orientation strategies and component– specifically taxis-total intensity (TX-F), taxis-inclination (TX-I), constant heading-total intensity (CH-F), and constant heading-inclination (CH-I). For all models, wind and geomagnetic variables are included as fixed effects and individual steps are classified as stratum-level effects. All the fixed effect variables are normalized on a scale of 0 to 1 to allow for consistent and comparable interpretations across all models (Appendix 5).

I first fit the SSF models individually, for each of the 270 tracks (Fieberg et al., 2021). For each individual, I identify the movement model with the lowest Akaike Information Criterion score (AIC). I also fit random effect SSFs to capture individual-specific variation in a single model by including animal IDs as a random-intercept term (Muff et al., 2020). Again, I calculated an AIC score for each model. Finally, I calculated an adjusted McFadden’s pseudo-R^2 value for each mixed-effect model to compare the model likelihood (model with fixed and random effects) against a null model (model with only random effects). I interpreted the Pseudo-R^2 values between 0.2-0.4 to represent a good model fit and values above 0.4 to represent an excellent model fit (Hemmert et al., 2018; McFadden, 1977).

3.2.3 Tools and availability

All analyses were formed in R (version 1.4). Flock definition was conducted using the wildilfeDI R package (Long et al., 2014, 2022). The open-source program MagGeo is available through GitHub (https://github.com/MagGeo/MagGeo-Annotation-Program, continuously updated version) and was used to attach geomagnetic data to the migration tracks; additional information about system parameters can be found in Benitez-Paez et al. (2021). I used the “amt” R package to perform individual level SSF analysis (Fieberg et al., 2021) and used the “coxme” R package to fit the multilevel conditional logistic regression model (Muff et al., 2020; Therneau, 2022).

3.3 Results

3.3.1 Migration route and conditions across seasons

Within the study region during fall migration, most birds generally travelled in a southwest direction which took them farther away from the Nile (Table 3-1; Figure 3-6). In spring, birds maintained a general northeast heading which was largely parallel to sections of the Nile. Thus, the proportion of steps within the Nile buffer was twice as high in spring compared to the fall (Table 3-1), though still low overall. Birds spent a shorter time within the study area during fall migration (Figure 3-6B) even though they travelled longer distances (Figure 3-6C). Birds also had a larger daily displacement and a faster hourly step speed during goal-directed flight in fall compared to spring (Figures 3-6D and E, Appendix 6). Across both seasons, most of the goal-directed flight (speeds >5 km/h) occurred during the daytime (Figure 3-6F).

Table 3-1. Comparing spring and fall migratory conditions and behaviour for White storks crossing the eastern Sahara.

Variable	**Mean**		**Standard deviation**		**Wilcoxon value**	**p**
	Fall	***Spring***	***Fall***	***Spring***		
Track statistics						
Bearing	220.32°	61.83°	10.52°	124.06°	11716	<0.01
% of steps in Nile habitat	3.95	7.97	19.48	27.08	42863080	<0.01
Track duration (days)	6.65	3.10	9.31	3.62	3646	<0.01
Overall displacement (km)	1750.15	1332.63	170.66	197.62	12803	<0.01
Daily displacement (km)	184.54	132.83	160.87	77.48	1010813	<0.01
Step speed (km/h)	37.68	21.65	17.25	11.23	50454193	<0.01
Migration conditions						
Wind support (m/s)	0.79	-2.05	3.63	4.31	72459044	<0.01
Crosswind (m/s)	-1.21	-0.90	3.25	4.71	42841299	<0.01
Normalized scores for observed steps						
Wind support	0.73	0.32	0.32	0.33	71219130	<0.01
Crosswind	0.53	0.58	0.34	0.35	40107707	<0.01
Taxis – total intensity	0.81	0.87	0.26	0.20	38413673	<0.01
Taxis – inclination	0.80	0.87	0.26	0.20	34958347	<0.01
Constant heading – total intensity	0.69	0.71	0.27	0.23	43381801	<0.01
Constant heading – inclination	0.70	0.74	0.27	0.23	41141767	<0.01

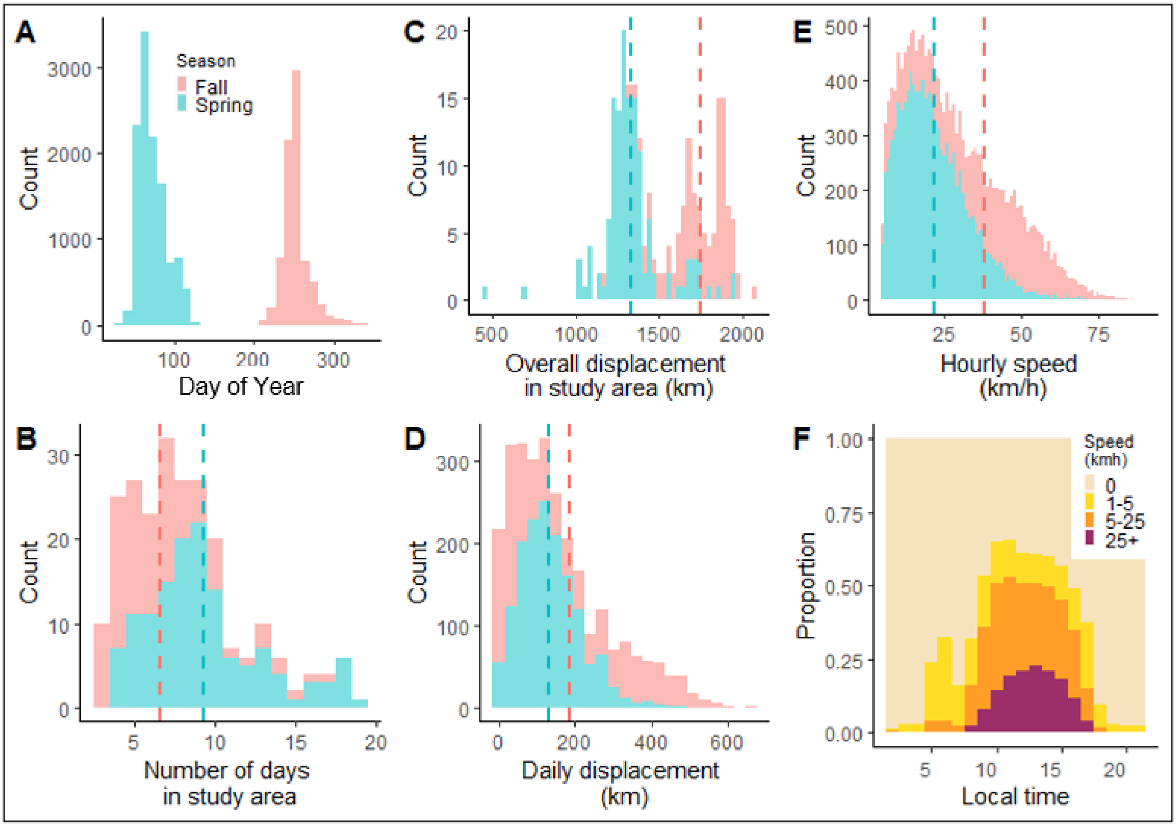

Figure 3-6. Migratory behaviour of white storks crossing the eastern Sahara. Dotted lines indicate the mean values for fall (orange) and spring (blue) migrations. (**A**) Day of year counts for movement within the study area show peaks in migratory activity for both seasons. Track level statistics indicate how long (days) (**B**) and how far (km) (**C**) a bird has travelled while crossing the study area. Values for daily displacement (km) (**D**) and hourly step speed during goal-directed flight (km/h) (**E**) suggest that in spring, birds travel a shorter distance but fly at slower speeds thereby spending a longer time in the region compared to the fall. (**F**) White storks are diurnal migrants, and their activity increases from daybreak until noon. Wind patterns and thermal formation during the day likely facilitate movement >25 km/h.

Birds experienced greater wind support and slightly lower crosswind (Figure 3-7A and B and Table 3-1) in fall compared to spring. Birds largely experienced the same geomagnetic values for total intensity and inclination during both seasons (Figure 3-7C). Within the study area, the total intensity and inclination values are highly correlated (r=0.996). Across both spring and fall migration over 7 years, the birds mostly encountered quiet geomagnetic conditions as only 2% of steps were during recorded during high geomagnetic activity.

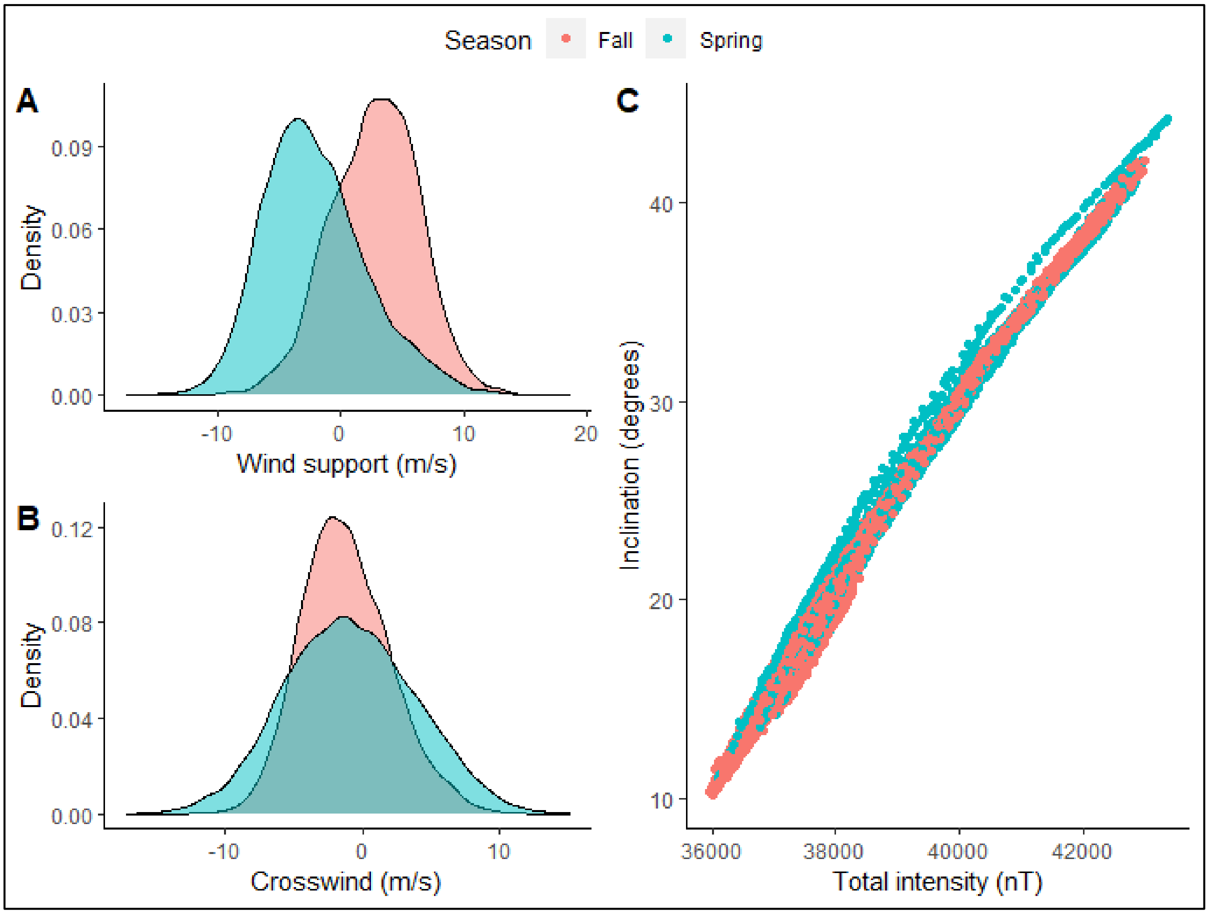

Figure 3-7. Wind and geomagnetic conditions experienced by birds during spring (blue) and fall (orange) migration. Wind support (**A**) and crosswind (**B**) values (m/s) differ by season where birds have less wind support and more varied crosswind conditions during spring compared to fall. Total intensity and inclination values (**C**) are highly linearly correlated (r=0.996) along all 270 tracks within the eastern Sahara.

3.3.2 Step-selection analysis: individual models

For most of the 126 fall tracks, I find that white storks are generally selecting for positive wind support (Figure 3-8A). Across both seasons, birds are selecting for moderate crosswind conditions. Wind support was a significant predictor in 50% of the best individual models in fall but only 39% in spring. Crosswind was a significant predictor in 23% of the best individual models in fall and 24% of the models in spring.

For all 270 tracks, birds are selecting for steps with a high probability of geomagnetic orientation since all geomagnetic orientation coefficient values are above 0. Overall, the median coefficient values for geomagnetic orientation are higher than coefficient values for wind support and crosswind conditions. Geomagnetic coefficients were a significant predictor in all models that included a geomagnetic coefficient in the best individual model.

For both seasons, constant heading-inclination (CH-I) models had the lowest AIC scores for most tracks (73% in fall, 56% in spring) based on the individual level step-selection analyses (Figure 3-8B). In the fall, constant heading-total intensity (CH-F) consistently had the second lowest AIC scores (15%) though, the ΔAIC was clustered around 0 suggesting that there might be little meaningful difference between these two constant heading models. In the spring, taxis-inclination (TX-I) had the second lowest AIC scores (32%). For both seasons, ΔAIC values between geomagnetic orientation models and core wind models had high positive values suggesting that including a geomagnetic orientation component was an improvement from models that had just wind support and crosswind values.

3.3.3 Step-selection analysis: random effect models

Results from the mixed-effect conditional logistic regression models aligned with the individual model results (Table 3-2). For example, mixed effect model results also reveal that birds are selecting for higher wind support in fall compared to spring. Additionally, the mixed-effect model results specifically indicate that birds are selecting for lower crosswind in fall compared to spring. Together, these results suggest that in spring, birds faced unfavorable wind conditions in the form of low wind support and higher crosswind. For both seasons, birds select for steps that are consistent with geomagnetic orientation across all unique combinations of orientation strategies though effect sizes for the coefficients are greater in spring compared to the fall.

Mirroring the individual model results, CH-I mixed-effect models had the lowest AIC score followed by CH-F in spring and TX-I in fall. Within each season, results for orientation strategies were more similar than results for geomagnetic components. For example, in fall, taxis models had similar AIC values even when modelled with different geomagnetic components compared to constant heading models with the same geomagnetic component. All core models had much higher AIC values compared to any geomagnetic model. Core models also had low model fit as indicated by the < 0.2 pseudo-R^2 values. In the fall, the constant heading models (pseudo $R^2 > 0.2$) were comparatively better than taxis models (pseudo $R^2 <$

0.2) though, the fit was still only moderately good. In the spring, all geomagnetic models had a decent fit (pseudo $R^2 > 0.2$). For both seasons, CH-I had the best model fit.

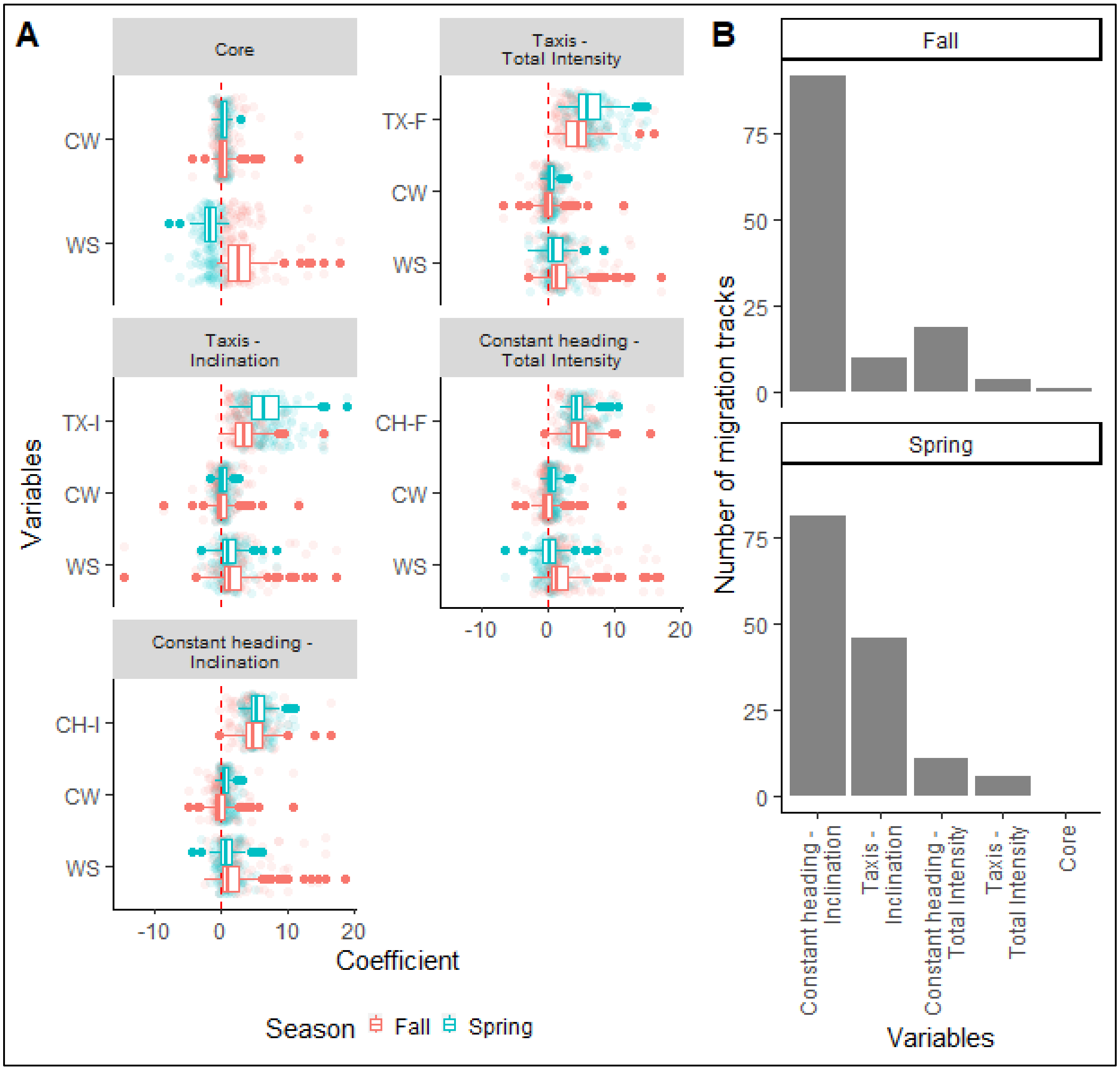

Figure 3-8. Individual conditional logistic regression model results for 270 white stork migration tracks separated by season. A. Coefficient values for every individual is represented by transparent dots and the boxplots represent overall patterns for fall (orange) and spring (blue). Variables are shortened for clarity (WS: wind support, CW: crosswind, TX: Taxis, CH: constant heading, F: total intensity, I: inclination). Core model includes only wind support and crosswind, and all geomagnetic models additionally included a unique geomagnetic strategy. Dotted red lines indicate where coefficient values are 0. **B.** Frequency of best model performance on an individual track-level indicates that the model with the highest frequency for having the lowest AIC was constant-heading inclination for both seasons.

Table 3-2. Mixed conditional logistic regression model results for 270 white stork tracks during spring and fall migration across the eastern Sahara. Core model includes only wind support and crosswind, and all geomagnetic models additionally include a unique combination of geomagnetic strategy and component. All coefficient values (β) are significant ($p<0.05$). The best performing model based on the lowest AIC score (indicated with *) was constant heading-inclination for both fall and spring and the ΔAIC values are calculated in reference to this model. Pseudo R^2 refers to adjusted McFadden's Pseudo R^2 where values between 0.2-0.4 represent good model fit and values about 0.4 represent excellent model fit.

Model	**AIC**	**ΔAIC**	**Pseudo R^2**	**WS**			**CW**			**Geomagnetic**		
Fall				β	SE	p	β	SE	p	β	SE	p
Core	34153	5827	0.08	1.78	0.04	0.00	-0.15	0.04	0.00			
Taxis - Total Intensity	30254	1928	0.18	1.12	0.05	0.00	-0.19	0.04	0.00	2.81	0.05	0.00
Taxis - Inclination	30782	2457	0.17	1.12	0.05	0.00	-0.18	0.04	0.00	2.58	0.05	0.00
Constant heading - Total Intensity	28702	376	0.22	1.28	0.05	0.00	-0.19	0.04	0.00	3.21	0.05	0.00
Constant heading – Inclination*	28326	0	0.23	1.16	0.05	0.00	-0.21	0.04	0.00	3.36	0.05	0.00
Spring												
Core	52922	12745	0.05	-1.44	0.03	0.00	0.18	0.03	0.00			
Taxis - Total Intensity	41904	1727	0.25	0.39	0.05	0.00	0.20	0.03	0.00	4.72	0.06	0.00
Taxis - Inclination	41897	1720	0.25	0.29	0.05	0.00	0.18	0.03	0.00	4.67	0.06	0.00
Constant heading - Total Intensity	42532	2355	0.23	0.25	0.05	0.00	0.45	0.03	0.00	4.10	0.05	0.00
Constant heading – Inclination*	40177	0	0.28	0.65	0.05	0.00	0.50	0.04	0.00	4.78	0.06	0.00

3.4 Discussion

3.4.1 Seasonal differences in migration route and conditions

Migration has one of the highest probabilities of mortality risk for birds (Bingman & Cheng, 2005; Hallworth et al., 2015; Winger et al., 2012). It is especially dangerous when crossing energetic barriers like the Sahara where chances to rest and refuel are limited (Biebach et al., 2000; Moreau, 1972; Strandberg et al., 2010). Energetic subsidies are therefore critical especially for larger birds like white storks where flapping flight is a costly behaviour (Efrat et al., 2019; Eisaguirre et al., 2020; Harel et al., 2016; Mackintosh, 1949; Nourani et al., 2021). Thermals are an important resource for white storks and likely influence movement decisions within (Kemp et al., 2010; Shamoun-Baranes et al., 2003; Van Loon et al., 2011) and outside of the study region (Becciu et al., 2020; Blas et al., 2020; Mestecăneanu & Mestecăneanu, 2011). Nevertheless, I did not test for white storks' selection of thermals since the flat landscape paired with the warm and dry atmospheric conditions likely provides adequate opportunities for relatively uniform thermal development for both seasons in the eastern Sahara (Chevallier et al., 2010; Mackintosh, 1949; Reed & Lovejoy, 1969).

I did test for selection of wind conditions since there is a strong seasonal effect. I found that in the fall, birds select for and thus experience high wind support in the form of tailwinds and low crosswinds with movement trajectories largely aligning with the prevailing wind vector (Bellrose, 1972; Biebach et al., 2000; M Hereher, 2011; Moreau, 1972). Though this results in a longer distance travelled in the eastern Sahara region in the fall, birds move at a faster hourly step speed and have a shorter overall trajectory duration through this region. Black kites, which are also thermal soaring migrants, experience similar conditions that result in equivalent trajectory characteristics when travelling through the western Sahara (Chevallier et al., 2010; Sergio et al., 2019, 2022).

In spring, the white storks in the study area are flying into the prevailing winds and I observed that these birds have slower speeds and spend a longer time in the region though they travel a shorter distance compared to fall. Longer duration could suggest that birds are waiting for better wind conditions before continuing their migration (Beauchamp et al., 2020; Weber et al., 1998) or longer stopovers in areas with higher ecosystem productivity (Chevallier et al., 2010; Sergio et al., 2022). I observed twice as many movement steps closer to the Nile habitat in spring which suggests that birds could be staying close to energy-dense habitats to refuel after flying in adverse wind conditions (Efrat et al., 2019). Migration routes along the Nile would also allow the birds to funnel towards the Gulf of Suez where they have been recorded to continue their over-land migration to avoid flying across the Red Sea (Efrat et al., 2019; Reed & Lovejoy, 1969). From an orientation perspective, birds may also be using the Nile as a static linear feature to maintain a constant direction of movement especially when they need to compensate for wind drift (Bingman et al., 1982). But I found relatively low rates of migration in very close proximity to the Nile during goal-directed flight in both spring and fall which may support that this linear feature is used in a relatively limited capacity for orientation (Eisaguirre et al., 2020).

On an evolutionary scale, routes and behaviours have been and continue to be shaped by global and regional wind patterns (Agostini et al., 2012; Kemp et al., 2010; Shamoun-Baranes et al., 2003; Vansteelant et al., 2017). At a local level, in addition to immediate energetic consequences, wind patterns may also influence orientation decisions (Bellrose, 1972; Sergio et al., 2022; Thorup et al., 2003). For example, in the study area, prevailing winds are a consistent and reliable environmental condition (Mohamed Hereher, 2014). In the fall, a bird will generally only experience high wind support and low crosswind conditions if it is travelling in the southwest direction. Thus, the wind can provide reliable compass-like orientation information. I included both tailwind and crosswind variables in geomagnetic models for both energetic and orientation purposes (Sergio et al., 2022). I encourage future integration of wind variables in orientation models because climate change and the resulting unpredictability in global atmospheric patterns may have both energetic and orientation consequences. These impacts are also not limited to the migration period as misdirection or delay of arrival at wintering or breeding grounds may carryover to other life stages as lower fitness (Cheng et al., 2019; Dossman et al., 2016; Strandberg et al., 2010).

3.4.2 Geomagnetic orientation in the eastern Sahara

The models suggest that across both seasons, all geomagnetic orientation models perform better than models that have just wind support and crosswind variables. I predicted that taxis based on inclination would be the best performing geomagnetic orientation cue out of all four possible strategies (Zein et al., 2021, 2022). For both individual and mixed effect models, constant heading – inclination had both the best performance (lowest AIC) and the best model fit (highest McFadden's Pseudo R^2). In the spring, the second-best model was taxis – inclination whereas in the fall, it was constant heading – total intensity. Overall, my results suggest that while wind conditions do vary between seasons and likely impact migratory behavior and trajectory, geomagnetic orientation has a significant impact on the movement decisions of white storks crossing the eastern Sahara.

Given that birds have the appropriate, functioning biological apparatus to sense and integrate geomagnetic field values, this invisible cue can generally provide reliable information in both space (predictable gradients) and time (minimal fluctuations) (Beggan, 2022; Finlay et al., 2020). Geomagnetic storms do occur, and values can fluctuate rapidly for a period of a few minutes to a couple hours. Some studies have recorded birds (Benitez-Paez et al., 2021; Bianco et al., 2019) and other animals (Granger et al., 2020) exhibiting disoriented behaviours during geomagnetic disturbances. Even though these storms are more frequent during the equinoxes when there is peak bird migration (Campbell, 2003), the individuals I studied were not likely to encounter to high geomagnetic activity levels during goal-directed flight, in part because these storms are more extreme at higher latitudes further away from the equator.

I did not fit models using geomagnetic declination. Goal-oriented migratory movement of birds in the eastern Sahara is largely along a North-South axis and the East-West gradation of declination values may not provide useful information as an orientation cue. Some virtual displacement studies suggest that birds can sense declination values to solve the 'longitude problem' (Chernetsov et al., 2017), which refers to the lack of reliable cues required for East-West orientation and positioning (Åkesson et al., 2005). Furthermore, unlike Zein et al. (2021, 2022), I did not create models with more than one geomagnetic component because inclination and intensity are highly correlated in the study area. While this may in fact be beneficial for migratory birds for redundant navigation information (Buehlmann et al., 2020), including both values in the statistical models might lead to over-fitting my data. Interestingly, theoretical models do suggest that birds could use a combination of total intensity and inclination to create a reliable bi-gradient map in certain areas of the world, including the Sahara (Boström et al., 2012). Though my focus was on compass-based orientation, it might be possible to test this geomagnetic bi-gradient map navigation using a similar step-selection model set up.

3.4.3 Scale

Basic mathematical calculations suggest that a bird would need to move 2 km to sense a change in total intensity or 112 km for a change in inclination (Campbell, 2003; Zein et al., 2022). However, lab-based results are unclear in demonstrating at what scale birds can sense these changes (Semm & Beason, 1990), if at all. Additionally, it is likely that different species have different capabilities which also vary depending on factors like internal states and external conditions like weather (Cheng et al., 2019; Curk et al., 2020; Davidson et al., 2019; Nathan et al., 2008). While I cannot directly address the question of a white stork's geomagnetic capabilities, I did partially circumvent the question of geomagnetic sensitivity ranges with the creation of a field of perception and the use of normalized scores. This modelling set-up allowed me to test for selection of relative patterns at the proposed scale of perception which is more aligned with the 'gradient' geomagnetic hypothesis, instead of using raw absolute values (Brothers & Lohmann, 2015; Komolkin et al., 2017; Wynn, Padget, et al., 2020).

While geomagnetic cues may be useful for white stork orientation when crossing the eastern Sahara, other cues might be more reliable for previous and subsequent legs of the migration or at different scales of navigation and orientation (Bellrose, 1972; Guilford & Taylor, 2014; Levin, 1992). Landscape features might be more important when birds are in the "narrowing-in" or "pinpointing-the-goal" phase of migration, which typically occurs at local and regional scales and not at the scale of continents (Mouritsen, 2018). Conversely, coarse geomagnetic gradients for total intensity and inclination may not provide useful information for smaller scale movement though there is some evidence that local movements for other taxonomic groups (reptiles and fish) may be informed by broad geomagnetic field patterns (Deutschlander et al., 1999; Nyqvist et al., 2020). There are also regions of the world where the geomagnetic field does not meet the reliability or predictability conditions necessary to function as a useful orientation cue. Some studies suggest that birds are disoriented as they approach the geomagnetic equator where inclination values are 0^{o} (Schwarze et al., 2016; W. Wiltschko & Wiltschko, 1972). Similar behaviour may also be observed for migratory birds near the North pole where the field fluctuates rapidly (Campbell, 2003). Alerstam (1987) and Schiffner et al.

(2011) also noted disoriented behaviour of migratory birds near a spatial geomagnetic anomaly in Sweden.

Migration in a relatively featureless landscape with minimal resources would have likely selected for development of redundant strategies to successfully cross a barrier (Åkesson et al., 2016; Sergio et al., 2022). Strategies after crossing such barriers however may have evolved due to different selection pressures that maximize other key migratory factors like resource refueling at stopovers (Beauchamp et al., 2020; Curk et al., 2020; Klinner et al., 2020), or protection from predators (Alerstam et al., 2003; Avgar et al., 2013; Houston, 1998; Lank et al., 2003). Coarse observations for my study individuals outside the arid regions suggest that after reaching Lake Chad in the fall, some individuals completely switch migration direction from southwest to east after slowing down in the Sahel (Figure 3-2 and Appendix 6). GPS tracks of some individuals even suggest that birds travel east along the Sahel border and then south along the edge of the continent until they reach South Africa. This fascinating behaviour suggests that while crossing the desert barrier, birds may trade-off direction of travel with energetic subsidies by flying with the north-easterly prevailing winds (Kemp et al., 2010; Shamoun-Baranes et al., 2003). They may compensate for this displacement at a track level by travelling a longer distance once outside of the desert to complete the remainder of their migration (Sergio et al., 2022).

Movement decisions may also vary greatly based on individual-level life history traits like age (Gupte et al., 2019; Sergio et al., 2022), sex (Morbey & Ydenberg, 2001), and timing of migration (Reed & Lovejoy, 1969). Comparing orientation strategies between juvenile and adult white storks may reveal tensions between innate and learned cues (Chernetsov et al., 2004; Harel et al., 2016; Rotics et al., 2016; Wynn, Collet, et al., 2020). It is also unclear to what extent flock demographics and dynamics influence migratory decisions. Long-term changes in the availability of resources and its impact on population-level movement decisions is also an emerging line of questioning which will require analysis of trade-offs at a larger scale (Flack et al., 2016). With individuals of the same species across Europe and Asia who are part of different flyways, comparing tracking data between white stork populations may help expand our understanding of how birds depend on physical and geophysical landscapes to complete successful migrations year after year and generation after generation.

3.5 Conclusion

The models, implemented in a step-selection analysis framework, suggest that white storks may be using geomagnetic orientation strategies to successfully migrate out of the eastern Sahara. Constant heading (menotaxis) based on geomagnetic inclination values is the most likely compass-based strategy for both spring and fall migration. However, given the high degree of correlation between inclination and total intensity values (in terms of the geomagnetic information they provide) in my study area, orientation based on total intensity could be a similarly reliable cue. In the spring, the birds are flying against the prevailing winds and experience less wind support and higher crosswind conditions leading to slower speeds and longer durations crossing the Sahara. The same winds in the fall likely subsidize flight and result in faster migrations and shorter durations. An increased energy expenditure in spring due to higher flight costs paired with a high motivation to reach breeding grounds in a timely manner may result in more dependence on reliable cues like the geomagnetic field for a successful migration. My work suggests that while movement of thermal soaring birds is largely dictated by wind conditions and thus varies by season, patterns in the geomagnetic field likely provide orientation information that could allow birds to successfully cross energetic and orientation barriers like the eastern Sahara.

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Chapter 4

4 Conclusion

In this thesis, I explore the development and application of tools to test how animals may use geomagnetic cues during long-distance migration. I work towards the overarching thesis objective by combining, testing, and applying different geospatial datasets and analyzing my results from a movement ecology perspective. Specifically, I highlight possible limitations and applications of a new open-source software called MagGeo that attaches high resolution geomagnetic data to animal tracking data.

4.1 High global accuracy when combining satellite geomagnetic data with animal tracking data

In Chapter 2, I achieve my first research objective by performing an error analysis for MagGeo. Specifically, I quantify how accurately MagGeo can model geomagnetic values and patterns as experienced by animals, especially during periods of high geomagnetic activity. To do this, I test MagGeo outputs against data from more than 100 terrestrial geomagnetic observatories across 7 years. I address research questions 1 and 2 respectively by comparing four interpolation methods and two different geomagnetic data sources within the MagGeo software.

I found that the overall absolute difference between MagGeo outputs and observatory values was less than 1% of the total possible range of values for geomagnetic components. Satellite data values closest in time to the point of interest (animal tracking fix) consistently had lowest error. This nearest neighbour in time interpolation can capture small continuous daily fluctuations as well as larger discrete events like geomagnetic storms. Combined model and satellite data also capture geomagnetic fluctuations better than model data alone across most geomagnetic activity levels. As expected, high geomagnetic activity usually predicts higher error though ultimately remaining within the 1% error range. Most of the remaining variation in error can be explained by location-specific effects originating largely from local crustal biases.

My results indicate that MagGeo provides open-source access to data and methods that accurately model how animals moving near the Earth’s surface may experience the geomagnetic field. MagGeo can thus help researchers explore how animals use the geomagnetic field to migrate long distances.

4.2 Long-distance thermal soaring migrants use geomagnetic orientation cues when crossing the eastern Sahara

In Chapter 3, I accomplish my second research objective by using the best performing MagGeo version to investigate how migratory birds use geomagnetic orientation to cross a relatively featureless landscape. Specifically, I build movement models using GPS tracking data from 68 white storks between 2014 and 2021 crossing the eastern Sahara during spring and fall migration. To address research question 3, I test two orientation strategies (taxis and constant heading) for two geomagnetic components (total intensity and inclination) to create a total of four geomagnetic orientation models. I address research question 4 by accounting for the seasonal effect of prevailing wind conditions on the movement decisions of these thermal-soaring migratory birds.

For both spring and fall migrations, I found that constant heading orientation models based on geomagnetic inclination values had the best performance. Additionally, all geomagnetic models were a significant improvement from models that included only wind conditions. Wind conditions did however influence white stork migratory route choice and behavior. In the fall, these birds selected for high wind support and low crosswind thus generally aligning with the northeasterly trade winds. These prevailing winds would provide important flight subsidies through the desert which is functionally an energetic barrier. Meanwhile in the spring, white storks adjusted their behavior to adverse wind conditions by travelling a shorter distance at slower speeds in the eastern Sahara.

These results suggest that while wind does have a strong influence on movement decisions, geomagnetic orientation cues may also be necessary for successful migration across featureless, energetic barriers. Future applications of my analysis framework can integrate multiple orientation cues for other geographical routes to illuminate how evolutionary pressures have shaped unique bird migration strategies.

4.3 Limitations and further considerations

4.3.1 Geomagnetism and animal migration

Sufficiently large animals can be fitted with magnetometers, in addition to GPS loggers, that record geomagnetic information at the location of the animal (Duriez et al., 2018; Kay et al., 2019). These devices would circumvent the necessity for data fusion as facilitated by MagGeo. Recent analyses however suggest that these magnetometer data might still be too noisy to accurately reflect the geomagnetic values at the location of the animal (Brum-Bastos et al., n.d., in preparation). Additionally, even if magnetometers did record perfect geomagnetic data, it is still unclear at what scale animals can sense and perceive geomagnetic values (Chernetsov et al., 2020; Kishkinev et al., 2021; Schwarze et al., 2016; Semm & Beason, 1990). It is very likely that there is a difference in sensitivity between human-made instruments and possibly equivalent anatomical structures and physiological pathways in animals (Johnsen et al., 2020). Lab-based experiments exploring these questions will illuminate biological limitations of the geomagnetic hypothesis which will subsequently provide a more relevant framework through which to analyze development and application of tools like MagGeo (Birnie-Gauvin et al., 2020).

Currently MagGeo outputs are limited by the inputted geomagnetic data sources which do not capture the local geomagnetic spatial nuances. These local anomalies have previously been noted to disorient migratory birds (Alerstam, 1987; Schiffner et al., 2011). Alternatively, these unique features in the geomagnetic landscape may also function as a non-visual signpost for animals with known trajectories across visually featureless landscapes (Wiltschko & Wiltschko, 2021; Wynn et al., 2022). Therefore, accessing open-source geomagnetic anomaly data within or alongside MagGeo would be necessary for a robust movement analysis (Lesur et al., 2016; Maus et al., 2009). Similarly, temporal anomalies like geomagnetic storms could also automatically be flagged within MagGeo to indicate to researchers where high geomagnetic activity may have influenced an animal’s movement process (Benitez-Paez et al., 2021; Bianco et al., 2019; Kikuchi, 2003; Krylov, 2017). These built-in process steps would help address the current limitations of MagGeo while also providing an automatic and accessible avenue to encourage researchers to consider the nuances of the complex geomagnetic landscape. Taking these extra steps would lead to a more realistic representation of how an animal might be experiencing the geomagnetic field.

4.3.2 Data availability to test orientation cues

Generally, robust movement analyses based on geospatial information are limited by the availability of remotely sensed data and global models. I used free and accessible platforms like Env-DATA (Dodge et al., 2013) and MagGeo (Benitez-Paez et al., 2021) to attach open-source wind and geomagnetic data to the white stork movement tracks from Movebank (Jetz et al., 2022; Kays et al., 2022). Due to the mismatch between the spatial and temporal resolution of the animal movement, wind, and geomagnetic data, I annotated tracking points using linear interpolation for wind values and nearest neighbour interpolation for geomagnetic values. As a result, I do not have truly contemporaneous values for the environmental conditions experienced by the bird at a specific location in space and time (Brum-Bastos et al., 2021; Davidson et al., 2019). I was also unable to test any other possible orientation cues due to lack of data collection and availability. For example, I could not test if gradients in volatile organic compounds could influence movement decisions through olfaction-based orientation cues (Bonadonna & Gagliardo, 2021; Gagliardo, 2013).

Additionally, I assumed that the physical landscape of eastern Sahara is uniform and therefore unlikely to provide useful visual cues especially at the flight altitudes for white storks in this region. High-resolution satellite imagery data may identify key semi-permanent landscape features (Mohamed Hereher, 2014) that could challenge my assumption and demand further analysis of the bird’s perception and interaction with what I assumed to be a featureless physical landscape (Buechley et al., 2018; Van Loon et al., 2011). For example, the Red Sea mountains are east of the Nile and may represent an important linear visual border (Clouet & Joachim, 2013; Soultan et al., 2020). In addition to serving as a reliable north-south orientation cue, wind patterns around this montane region may also provide further energetic subsidies. Orographic uplift occurs when wind is deflected off ridges and hills and provides additional energetic subsidies by reducing the necessity of flapping flight for bulky birds like white storks (Bishop et al., 2015; Jobson et al., 2021; Nourani et al., 2021). As my results show, this might be specifically important during spring migration when birds are travelling against the prevailing northeasterly winds to reach their breeding grounds (Mohamed Hereher, 2014). However, as with patterns in trade winds and the Nile as a linear feature, it is unclear if the birds would be using these landscape and geophysical features for energetic or orientation purposes. It is also unclear to what extent this distinction would be useful for future studies.

4.3.3 Collaboration opportunities

A two-pronged approach is required to address at least some of these limitations (Birnie-Gauvin et al., 2020). Development of new on-board sensors for both satellites and in-situ tags will expand the diversity of variables that can be used to better represent the environmental conditions experienced by the bird during migration (Bonadonna & Gagliardo, 2021; Brum-Bastos et al., 2021; Demšar, 2019; Jetz et al., 2022). This information will allow us to build more nuanced models that test the leading theory of multi-sensory navigation and orientation (Guilford et al., 2011; Holyoak et al., 2008; Nathan et al., 2008). Simultaneously, further research centered on the anatomy, physiology, and behaviour of the migratory birds is required, especially for candidates of model migratory species like white storks. Together these findings will aide in the development of more accurate and biologically founded movement models (Avgar et al., 2016; Bellrose, 1972; Birnie-Gauvin et al., 2020; Fieberg et al., 2021). These models can then be rigorously applied to predict how animals will respond to their changing environment (Holland, 2014). Eventually, a greater understanding of the animal’s relationship to its external conditions will hopefully help us engage in effective conservation practises.

4.4 Final remarks

Avian migration across geographical barriers likely requires a multi-sensory and redundant set of orientation and navigation strategies. I highlight how access to novel remotely sensed datasets has unlocked the capacity to revisit many of these fundamental hypotheses about animal migration from a geospatial perspective. I have also provided a deeper exploration of animal movement across previously inaccessible but ecologically unique regions such as deserts. Combining and applying geospatial datasets to answer complex research questions however presents the expected challenges of data interpolation and scale mismatch. These obstacles are further exaggerated when working with animals whose behavior could be influenced by a myriad of internal states and external conditions. Adequately addressing these questions requires an interdisciplinary approach where experts from all relevant fields assess the feasibility of the data fusion and critically evaluate the validity and scope of the results. Encouraging these collaborations will be necessary for maximizing all available tools to understand how migratory animals are dependent on their landscape, especially as they navigate thousands of kilometers across vast barriers to reach their final destinations.

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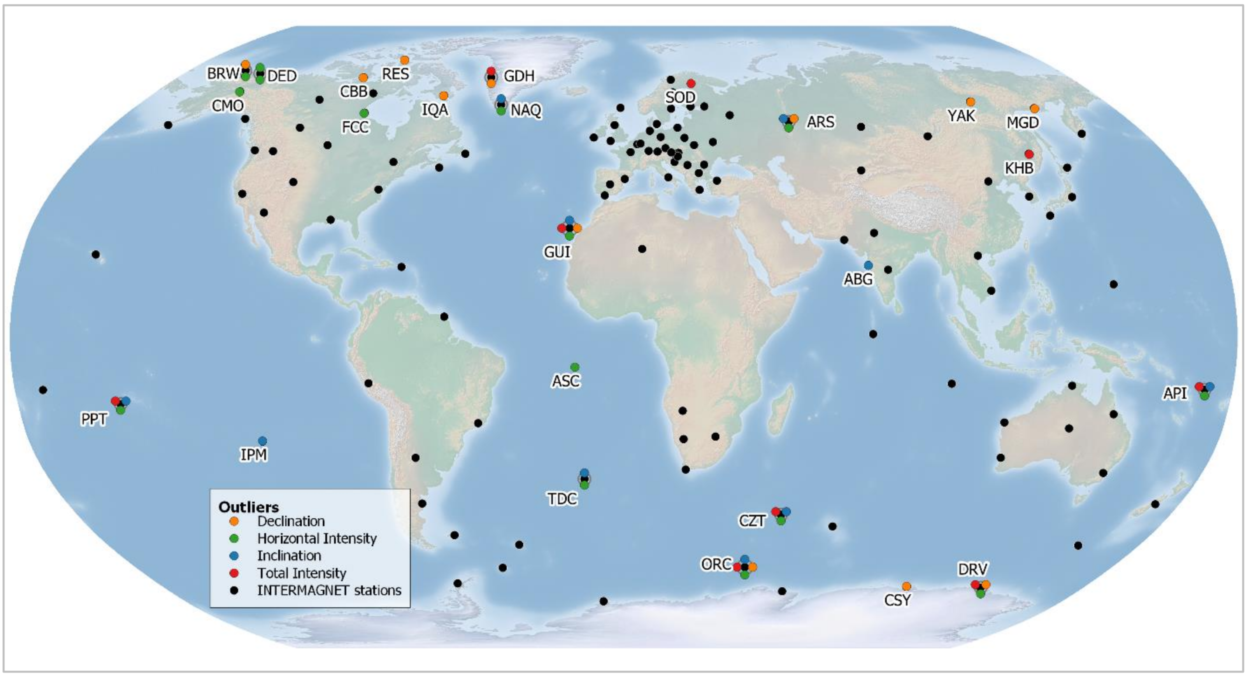
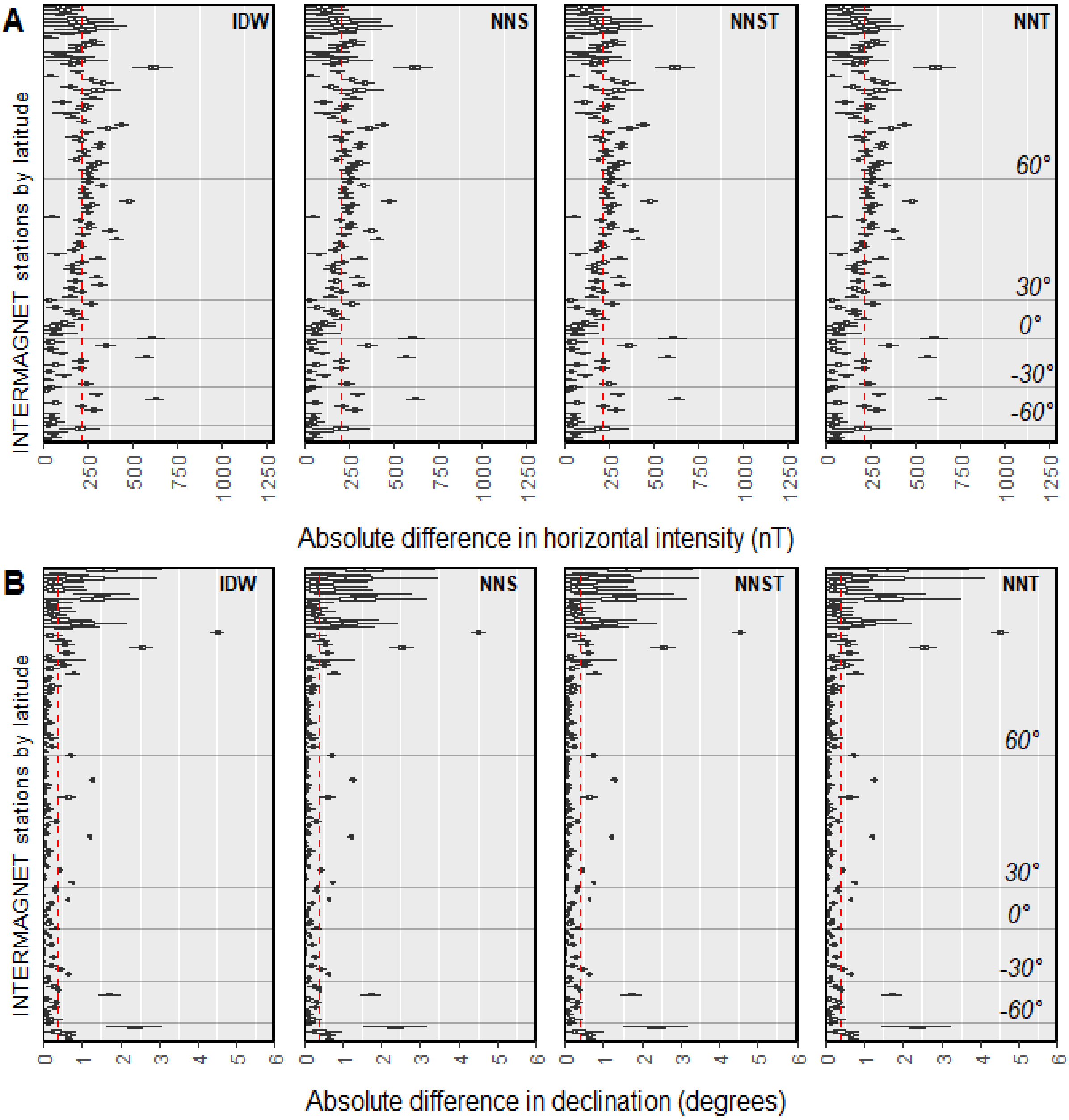
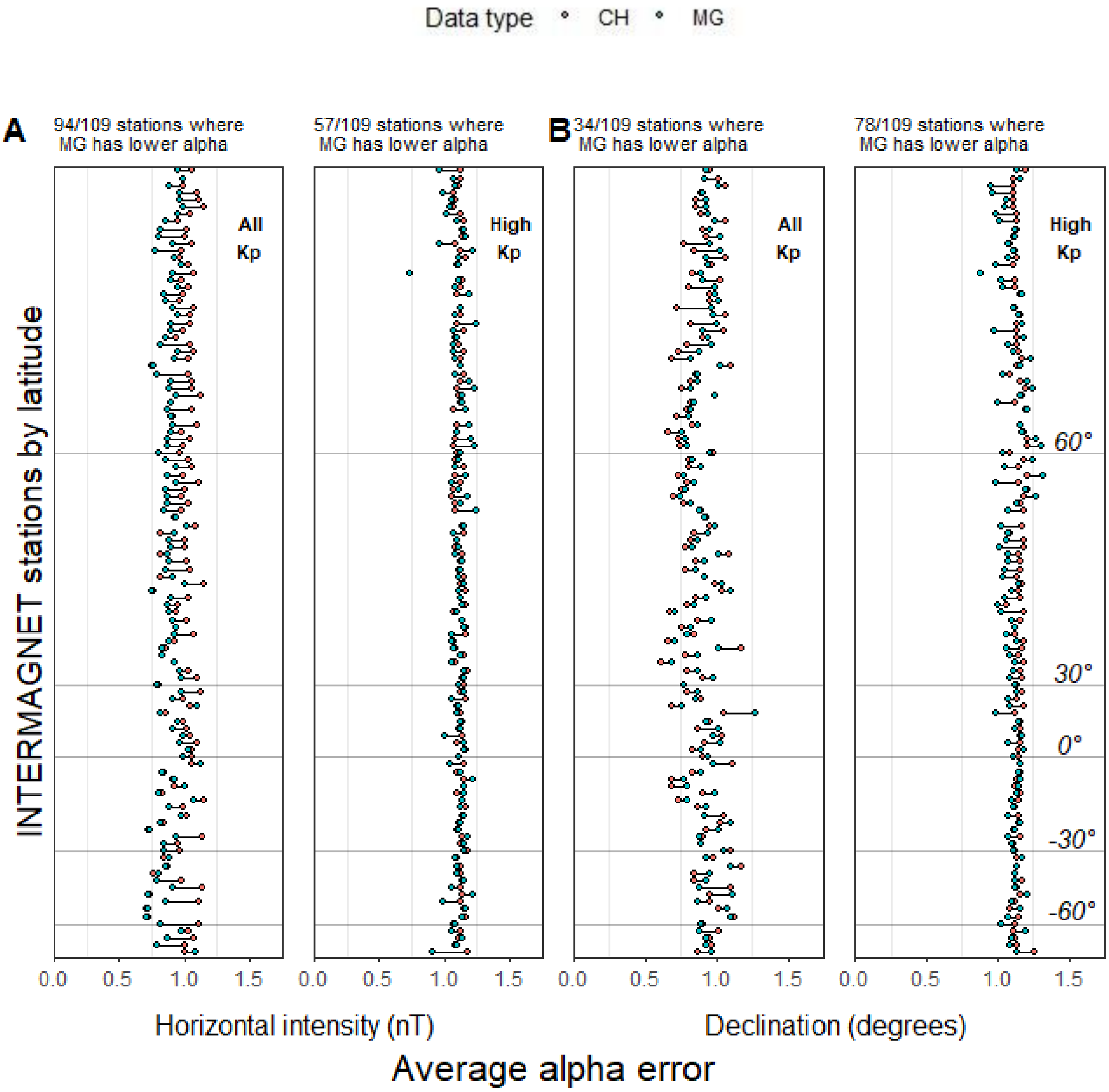
Appendices



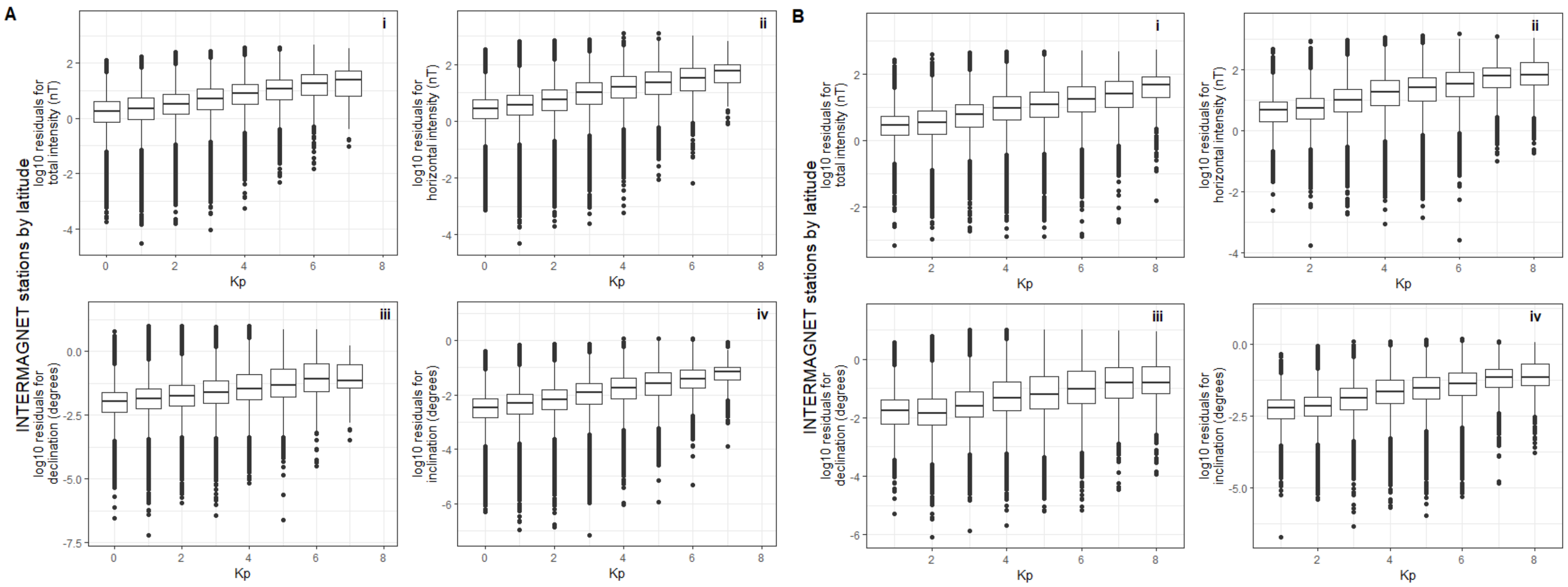
Appendix 1. A total of 126 INTERMAGNET stations where the labelled 27 stations have outliers. For labelled stations, each color represents an individual geomagnetic component that has been flagged as having consistent outliers: total intensity (red), inclination (blue), horizontal component of intensity (green) and declination (orange). Only stations with erroneous data for 3+ geomagnetic components were removed from further analysis.



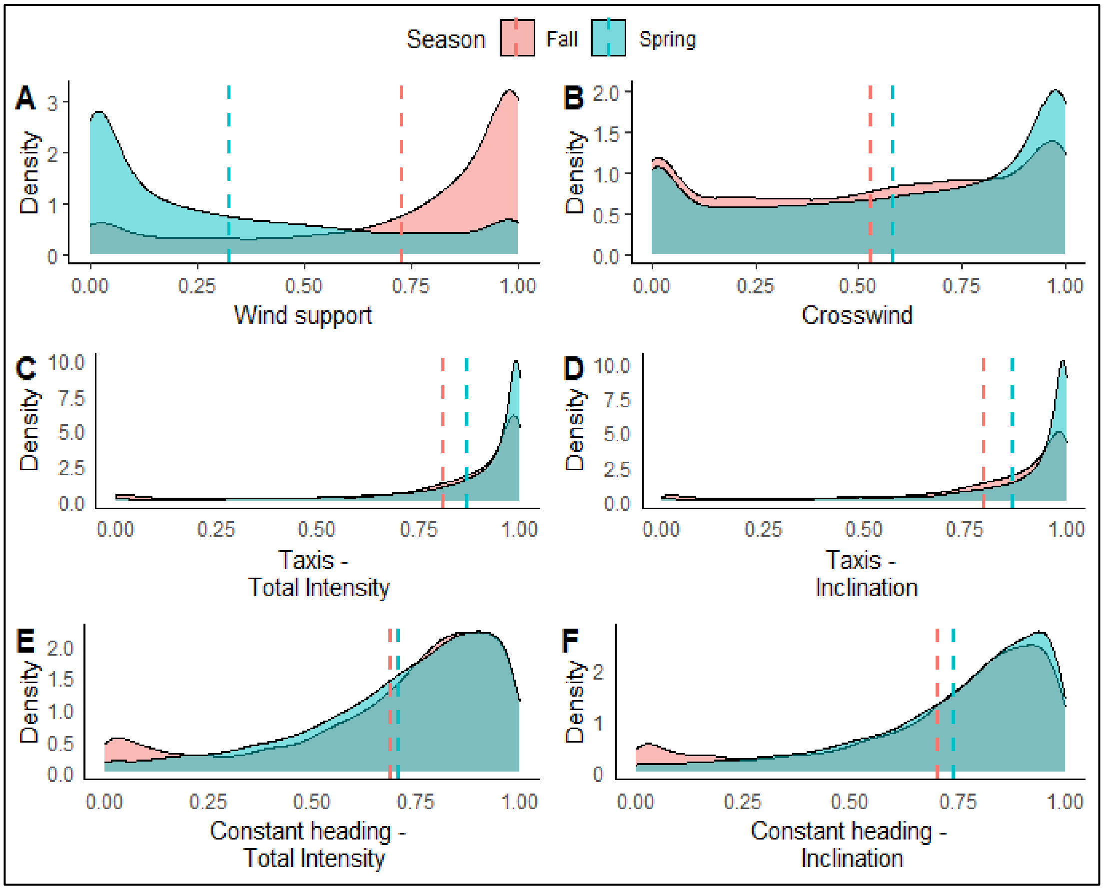
Appendix 2. Absolute difference metric (d) for each individual INTERMAGNET station arranged by latitude from northernmost (top) to southernmost (bottom). Each panel represents one of the four possible MagGeo spatiotemporal interpolation methods: inverse-distance weighting (IDW), nearest neighbour in space (NNS), spacetime (NNST) and time (NNT). Dotted red line represent overall average error for absolute difference. Figures are arranged by geomagnetic component: horizontal component of intensity (**A**) and declination (**B**). For similar figures for total intensity and inclination, see Figure 2-4.



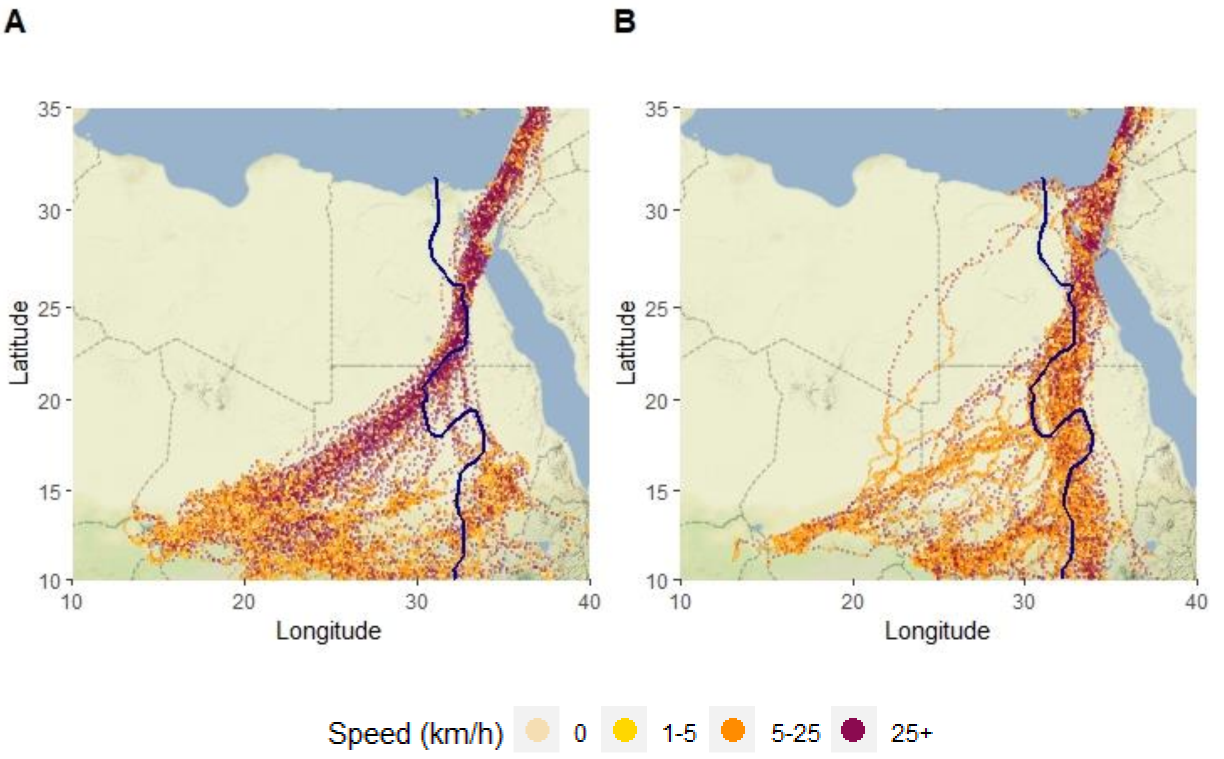
Appendix 3. Comparison of average alpha measure (α) between CH (red dots) and MG (blue dots) for each individual INTERMAGNET station arranged by latitude from northernmost (top) to southernmost (bottom). "All Kp" includes data from all Kp levels whereas "High Kp" includes only data where Kp>6 which is when there is high geomagnetic activity. Individual plot titles indicate count of stations where MG had lower alpha error. Figures are arranged by geomagnetic component: horizontal intensity (**A**) and declination (**B**). For similar figures for total intensity and inclination, see Figure 2-5.



Appendix 4. Log-linear relationship between satellite residuals for each Kp value. Results are from data with periods of variable geomagnetic activity (“All Kp”; A) and periods of high geomagnetic activity (“High Kp”; B). Individual plots for each figure represent all four geomagnetic components: total intensity (i), horizontal component of intensity (ii), declination (iii) and inclination (iv).



Appendix 5. Wind and geomagnetic normalized scores for all observed steps during spring (blue) and fall (orange) migration. All values are unitless and between 0-1. Dotted lines represent the average per season. For wind support (**A**), values closer to 1 indicate that the subsequent step had high wind support (tailwind). For crosswind (**B**), values closer to 1 indicate that the bird experienced stronger wind conditions perpendicular to direction of travel. For both geomagnetic taxis (**C** and **D**) and constant heading (**E** and **F**) for both total intensity (**C** and **E**) and inclination (**D** and **F**), values closer to 1 indicate higher probability of geomagnetic orientation-based movement. Based on distribution curves and mean dotted lines, birds experienced higher wind support, lower crosswind, and slightly lower probability of geomagnetic orientation in fall compared to spring.



Appendix 6. Hourly step speed (km/h) for white storks during fall (A) and spring (B) migration with a specific focus on the eastern Sahara. Speeds are categorized into 4 levels: 0 (pale brown), 1-5 (yellow), 5-25 (orange), and 25+ (red). Within the study region, birds travel faster in the fall (more red steps) compared to the spring (more orange).

Curriculum Vitae

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Iyer, A. (2021, April 28). *How migratory birds know exactly which route to take*. CBC. https://www.cbc.ca/life/hellospring/how-migratory-birds-know-exactly-which-route-to-take-1.6004106#:~:text=The%20Earth's%20magnetic%20field%20is,and%20where%20they%20should%20go.