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TITLE:

LINKING PATTERN AND PROCESS: APPLYING AGENT-BASED MODELS AND SPATIAL BAYESIAN STATISTICS TO THE STUDY OF ANIMAL MIGRATION

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Doctor of Philosophy

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M.S., Biology, University of Cincinnati, 2020
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An abstract of
A dissertation submitted to the Faculty of the
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in partial fulfillment of the requirements for the degree of
Doctor of Philosophy
in the Graduate Division of Biological and Biomedical Science
in Population Biology, Ecology, and Evolution
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ABSTRACT

Animal migrations are the subject of widespread and interdisciplinary research. These movement events can vary significantly based on spatial and temporal scale (e.g., the cyclical migration of the sandhopper, *Talitrus saltator*, is measured in meters and hours as they follow transient tidal changes while the migratory movements of the Arctic tern, *Sterna paradisaea*, is measured in thousands of kilometers and months). Furthermore, the mechanisms and drivers activating and maintaining these behaviors can equally vary. To reach specific goals, whether that be habitats, mating opportunities, or influxes of resources that are utilized after a migration, animals have been found to use a variety of sensory and cognitive mechanisms to successfully migrate. The combination of these mechanisms determines an animal's navigation strategy, such as piloting, inertial, compass, vector, and true navigation. However, research inferring specific strategies from observed movement data is lacking in many systems and historically limited to model cases. This has hampered comparisons of navigation strategies across systems and behaviors and created confusing terminology in the literature. Terminology often depends on the scale of movement, rather than the actual biology of the system, resulting in unclear distinctions between different navigation strategies. In this dissertation, I provide two frameworks to effectively categorize animals' navigation strategies based on biology rather than geography. The first conceptual framework (1) unifies navigation terminology to be used regardless of movement scale; (2) summarizes unique characteristics of common navigation strategies to highlight differences in cognitive mechanisms between strategies; and (3) provides experimental and modeling approaches to define a strategy in an animal with special consideration on study design. The second, a statistical framework, utilizes simulations to predict geographic spread of migrants using varying navigation strategies to be comparable to observed patterns for the species. Applying this framework to the monarch butterfly as a case study, I found evidence that the butterfly's long-distance, thousands of kilometers, migration is consistent with vector navigation and thus true navigation is not necessary in the system (a long-standing research question in the system). Thus, these frameworks aids in classifying animal navigation strategies and unifying navigation research across movement scales and model organisms.

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TABLE OF CONTENTS

TITLE:

ABSTRACT

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

List of Figures

List of Tables

CHAPTER I - INTRODUCTION

The spatial movement of animals through their environment is vital for their survival and persistence. By moving through landscapes, animals transfer bodies and genes from one place to another, thereby affecting population structure and dynamics (Hanski, 1999; Morales et al., 2010). Moreover, animals provide resources for many other animals and decomposers; as such, animal movement is crucial for community and ecosystem functioning (Baguette et al., 2012; Baker, 1978; Swingland & Greenwood, 1983). Animal movement is the result of a diverse set of inter-related behaviors, each of which can vary temporally and spatially, and be affected by unique drivers. For example, whereas dispersal can be an innate propensity to move through landscapes with individuals differing in their directionality, migration is driven by seasonal changes in resources and climatic conditions with individuals on average moving in the same direction (Mueller & Fagan, 2008; Nathan et al., 2008). One of the longest movement behaviors is the migration by the Arctic tern, *Sterna paradisaea,* which travels about twice the circumference of the earth each year. This journey, measured with geolocators, covers an annual total migratory distance of 80,000 km, with birds utilizing distinct routes for autumn and spring flights, and stopover locations for refueling (Egevang et al., 2010). On a smaller scale, the sand hopper', *Talitrus saltator*, moves several meters between intertidal beach zones for foraging opportunities and predator avoidance on a daily basis (Ugolini, 2003). Despite their differences in scale, the successful completion of these movements is dependent on animals taking information from their environment to inform their goal-oriented movement in a process called *navigation*.

Navigation is most often associated with long-distance migratory behaviors. However, it can be used to refer to any movement that is directed. Here, I focus on migration and the consequences of different navigation strategies, but also incorporate navigation studies from other behaviors.

Animals can navigate in different ways, but despite the importance of movement, the precise navigation strategy used by particular animals remains poorly understood. This is partly due to confusing terminology in the literature and because direct observation of movement behaviors in nature is logistically challenging. Scientists often assign a particular navigation strategy to an animal based on the scale of their movement, even though similar navigation strategies can be used to move along centimeters or thousands of kilometers. Further, large-scale movements such as migration and nomadism (see Figure 1.1 for definitions) cannot be fully observed and thus require unique workarounds to determine a navigation strategy, such as behavioral assays, tracking studies, and quantitative analysis (DeAngelis & Diaz, 2019; Morales et al., 2004; Tang & Bennett, 2010). For example, a mixture of GPS tracking and

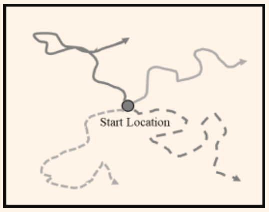
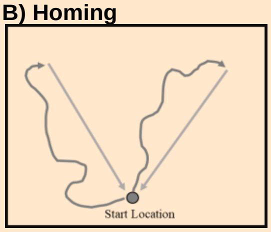
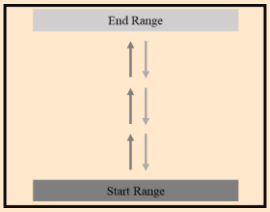
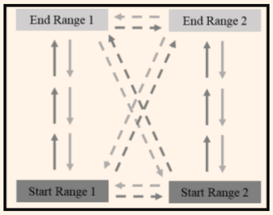
A) Dispersal  	• Dispersal can have numerous drivers, consequences, and scales. Additionally, it can describe the movement of genetic material and not the movement of an organism itself. These cases are not discussed here. • For animal movement purposes, dispersal tends to be relatively small-scale with direction and pathways differing between individuals.
B) Homing  	• The homing behavior is when an animal orients and moves to their original departure location. • Path accuracy for departure and return journeys do not need to follow those depicted here. For instance, contrary to the figure, departure can be highly targeted while homing can follow a wandering path.
C) Central point Foraging  	• Central point foraging is a type of foraging behavior where the animal returns to their start location after foraging. • The return journey can be thought of as homing given the animal orients and returns to a distant starting location.
D) Migration  	• Typically, migration is defined as a large cyclical movement behavior where animals move between habitats that are geographically isolated and suited for the life history of the animal. • Each cycle, the animal or population uses the same habitat ranges and movement corridors.
E) Nomadism  	• Nomadism has often conflicting definitions in the literature. • Here we define nomadism as a large-scale movement behavior between locations that is not cyclical and is instead a movement pattern that follows suitable habitat using a mixture of available routes. • Dashed lines represent alternative pathways.

Figure 1.1: Movement behaviors that require navigation. For each movement, the left panel shows movement routes using dark grey as the starting journey and light grey as the return journey. Ranges depicted are not to scale or in proportion to each other. Right pannels show summaries of the key defining features of the movement behavior.

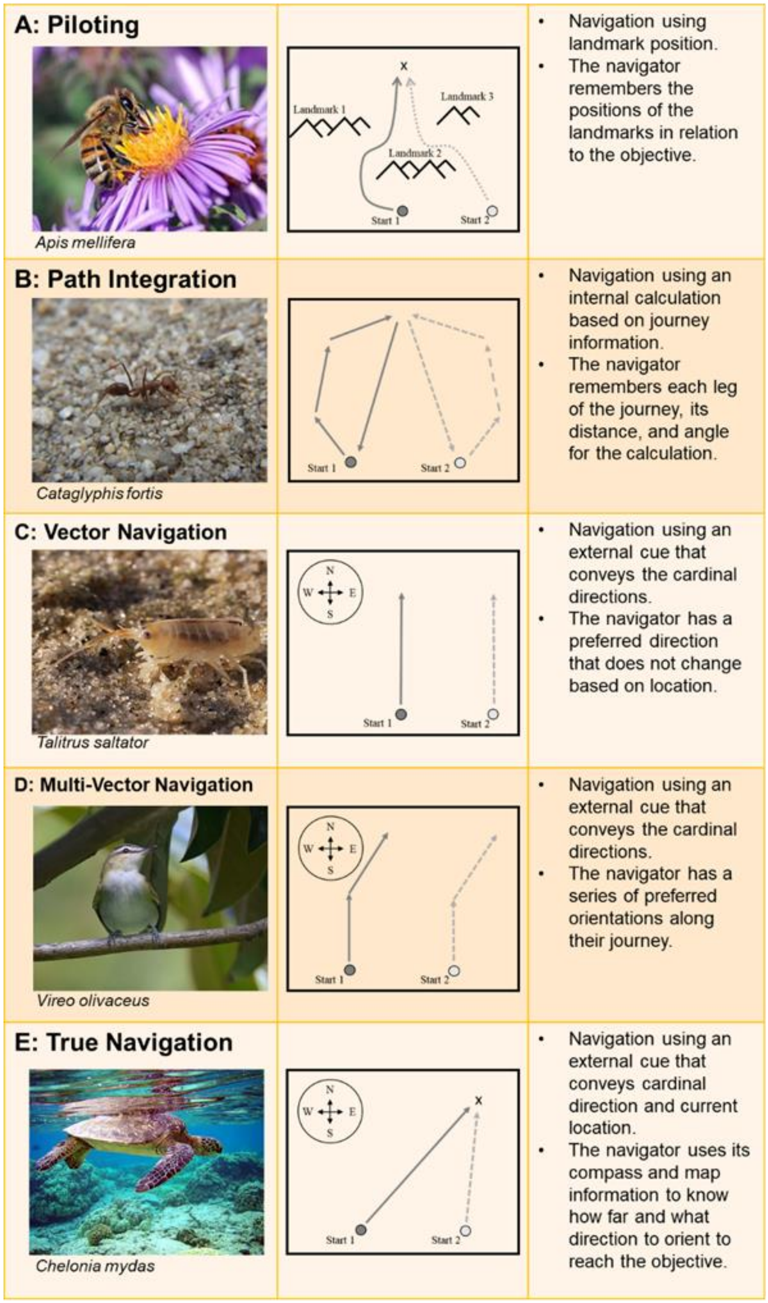
quantitative analysis was needed to study navigation used by migratory blue whales and nomadic ungulates (Abrahms et al., 2019; Teitelbaum & Mueller, 2019). However, not all animals can carry these GPS trackers, e.g., insects – with their relatively small body sizes and potentially long-distance movement behaviors – represent challenges in navigation research. For example, for the monarch butterfly, with its spectacular annual migration from the United States and Canada to Mexico, it remains controversial whether the insects use vector, multi-vector, or true navigation (Mouritsen et al., 2013; Oberhauser et al., 2013). Thus, inconsistent terminology, coupled with technical challenges when studying long-distance migration, has created gaps in navigation and migration research specific to taxa and behavior that has complicated comparisons between these taxa, navigation strategies, and movement behaviors.

My dissertation develops and applies modern spatial statistical approaches and simulation-based studies to provide a framework for studying animal movement, migration, and navigation, to address the gaps in migration and navigation research so that researchers can start to utilize the results from individual behavior-level experiments to predict population-level patterns—and to infer individual-level behaviors from population-level geographic observations. Below, I start by defining the common navigation strategies to clarify confusing terminology and highlight areas of research understudied. In Chapter II, I review an important factor in successful migration and animal movement, parasitism and its costs in migration success, where I propose increased research focus given 7 key mechanisms (Ch. II: Table 2.1). In Chapter III, I develop a novel approach to study animal migration using agent-based models and spatially explicit Bayesian statistics. This approach highlights the importance of focusing the study of migration and movement at a population level and highlights important considerations in experimental design. In Chapter IV, I use the framework developed in Chapter III to test which navigation strategy is likely used in the monarch butterfly, whose migration has been historically difficult to study given its size (Mouritsen et al., 2013; Oberhauser et al., 2013). This showcases the utility of the framework in testing specific hypothesis-driven research questions.

Overall, my dissertation showcases the importance of considering multiple factors, data sources, and research approaches when studying animal movement and migration to make holistic comparisons.

Navigation Strategies Conceptualized

To avoid confusion, I start by defining various aspects of movement behaviors. *Orientation* describes how organisms position their body given specific environmental cues. *Navigation* is the use of this information to inform "goal"-oriented and directed movements through the environment (while "goal" is often used in migration research, it is important to note the use of the word does not imply the animal are aware of the location, condition, or any other details of the locations they move to; instead, the goal is a location whereby the migrant would stop its movement behavior if it is reached). Navigation is often used when describing migrating species, given the clear goal they have, yet navigation can describe any oriented movement such as central point foraging or homing behaviors (Figure 1.2). I focus here on aspects of the movement behaviors in seasonal migration, dispersal, foraging, and nomadism (Figure 1.1) to express different navigation strategies. However, it is important to note that each navigation strategy can be used for any movement behavior and that the behaviors discussed here are not an exhaustive list. Further, there are other drivers that can explain the movement patterns of animals that are not strictly their navigation strategy and thus will not be discussed in this chapter (for further discussion of other factors see Chapter II). One such factor, the *resource wave tracking* or *green wave tracking* hypotheses postulates that animals can sync their movement behaviors with the movement or availability of suitable resource patches (Armstrong et al., 2016). Some species that use this strategy could be directly navigating toward suitable habitat, while other species may simply disperse randomly within suitable habitat but are also constrained geographically to remain within areas containing suitable habitat as these areas shift over the seasons. When suitable habitat moves temporally through space in a predictable manner, the non-oriented dispersing species would appear to move in a



A: Piloting

- Navigation using landmark position.
- The navigator remembers the positions of the landmarks in relation to the objective.

B: Path Integration

- Navigation using an internal calculation based on journey information.
- The navigator remembers each leg of the journey, its distance, and angle for the calculation.

C: Vector Navigation

- Navigation using an external cue that conveys the cardinal directions.
- The navigator has a preferred direction that does not change based on location.

D: Multi-Vector Navigation

- Navigation using an external cue that conveys the cardinal directions.
- The navigator has a series of preferred orientations along their journey.

E: True Navigation

- Navigation using an external cue that conveys cardinal direction and current location.
- The navigator uses its compass and map information to know how far and what direction to orient to reach the objective.

Figure 1.2: Navigation strategies and animals that use them. For each strategy, the left panel shows a navigator well studied within the navigation strategy provided, and the center panel visualizes the expected journey a navigator would take given two starting locations. These journey maps are not to be confused with the map sense of some of these navigators. The “x” in some panels represents a goal that the navigator is aware of and is orienting to during their journey. Right panels show summaries of each navigation strategy, as well as important sensory cues and how those are incorporated in the journey.

directed manner. Here, I specifically focus on navigation strategies that are involved in directed movements.

The available information for the orientation phase of movement ultimately determines the type of navigation an animal uses. For example, *homeward orientation*, i.e., *site fidelity*, is an orientation that can be based on different environmental cues and used for different movement behaviors. In honeybees and ants, homeward orientation and the resulting navigation toward that home rely heavily on orientation toward landmarks (Lehrer, 1996; Wehner & Srinivasan, 1981). In oceanic species, with sparse landmark information, elasmobranchs (Driggers III et al., 2014) and sea turtles (Avens et al., 2003) use geomagnetic fields for range exploration and migration respectively. I note each of these animals orients toward a similar goal, i.e., "home," yet their sensory mechanisms for orientation are vastly different as is their navigation strategy (each defined further on). Distance to the goal also influences navigation strategies, as long-distance orientations preclude the use of cues emanating from the destination available at smaller scales.

Piloting involves animals using learned landmarks and spatial attributes of these landmarks as orientation points (Figure 1.2A). Researchers speculate that a collection of landmarks creates a cognitive "map" for navigation (Gould, 1986; Kitchin, 1994; Tolman, 1948). Additionally, piloting individuals can utilize environmental cues to form a "compass" to measure angular relationships between their own and landmark positions. There has been some discussion and debate in the literature whether these landmarks form a type of mosaic map where spatial relationships between goals are represented as compass bearings (Guilford & Biro, 2014).

Piloting is useful for foragers leaving a nest or hive that must return to a specific location (central point foraging). For example, honeybees (Figure 1.2A) use a combination of landmarks and polarized light to find their hive and nectar sources (Collett, 1996; Gould, 1987; Lehrer, 1996). Honeybee journeys to a known nectar source begin with a compass, then rely on local landmarks to home in on their target (Cheng, 2000). The landmarks used and the angular measurements taken from light information suggest honeybees possess a cognitive map of their surroundings (Cheng, 2000; Gould, 1986; Menzel et al., 2005; Wehner & Menzel, 1990).

Learned landmarks may also be important for seasonal migration. In ungulates and other mammals, the use of memory in these migratory behaviors re-enforces the use of specific migratory pathways where the animals have learned key landmarks (Bracis & Mueller, 2017). Yet, the underlying navigation strategy of piloting is often not discussed in the literature relating to these migratory species. Instead, memory is the focus of many publications, even though memory's presence suggests the use of piloting as a strategy as described here. However, in navigating pigeons, research suggests that memorized visual landmarks can result in proper homing behavior even when in conflict with the pigeon's compass cues (Biro et al., 2007). When the piloting framework is used to discuss the pigeon's navigation, it is often discussed as a way for the species to realize true navigation (discussed further below) (Wiltschko, 2017). In contrast, the piloting strategy responsible for the small-scale movement of honeybees is not described as true navigation. Since some literature presents piloting and true navigation as synonyms and other literature avoids discussions of navigation strategies in a scale specific context, it is difficult to compare the use of piloting navigation concepts between local-scale foraging and large-scale movement behaviors.

Path integration is a navigation strategy where orientation toward a goal requires remembering the angle and length of each leg of a journey, then calculating the angle and distance required to find the starting location or final goal (Figure 1.2B). Though there is significant variation in the use of terms in the literature, I define path integration by *frame of* *reference* and *information source.* The frame of reference for the navigator's and goal's position can either be egocentric (relative to the navigator's perspective) or exocentric (relative to an external perspective) (Maurer & Séguinot, 1995). Regardless of the frame of reference, the source of positional information can be idiothetic (internal source; sometimes referred to as egocentric) or allothetic (external source; sometimes referred to as geocentric or exocentric) (see Layne et al., 2003). The desert ant, *Cataglyphis fortis* (Figure 1.2B), uses path integration to find its nest after foraging (Müller & Wehner, 1988; Wehner et al., 1996). This species measures the angle of each section of the journey via a celestial compass, an allothetic source, (Wehner & Lanfranconi, 1981) and measures distance by counting steps, an idiothetic source (Wittlinger et al., 2006). Though the positional information is allothetic and idiothetic, it is thought that desert ants integrate this information and perceive their position and goal's position using the egocentric framework (Bisch-Knaden & Wehner, 2001; Wehner, 2003). Thus, the source of the positional information does not imply the reference system.

The navigation literature includes other hypotheses for distance measurements that may apply to other organisms, e.g., the "energy hypothesis" for arthropods measuring distance via energy expenditure (Heran, 1952). In mammals, positional information is often determined to be idiothetic coming from inertial signals from acceleration in extravestibular gravity receptors (Delmon, 1998).

Regardless of the sensory sources or the frame of reference, path integration would be especially helpful for long-distance migration and nomadism if there were specific diversions from established movement pathways. Calculating the angle and distance of the divergence would allow navigators to re-orient and get back to where they started or calculate a new bearing to arrive at where they should be.

Typically, different navigation strategies are considered for longer distance movements or if the return location is less specific than in central point foraging. I first discuss the *clock and compass* navigation strategy (Figure 1.2C). As the names imply, animals orient to a “preferred” orientation using environmental cues as a compass. These cues often move temporally and thus animals use a measure of time to orient to them properly, though some celestial cues don’t need time compensation (Emlen, 1967; Perdeck, 1958). Historically, navigating using the clock and compass mechanism has also been called *vector navigation* in migrating species given these species often have multiple compasses that may not require a time compensation component (Berthold, 1990; Mouritsen, 1998). Vector navigators often maintain a preferred direction throughout their journey with deviations only due to topographic variation (e.g., elevation, barriers to travel, and resource heterogeneity) (Thomson, 1953) or to subtle variation in their ability to isolate the “correct” orientation (Mouritsen & Mouritsen, 2000). Both vertebrates (Gwinner & Wiltschko, 1978; Munro et al., 1993) and invertebrates (Wehner & Menzel, 1990) use this navigation strategy. Sand hoppers (Figure 1.2C), *Talitrus saltator*, use the solar azimuth to orient and move to wet bands of beach when displaced due to tide shifts (Pardi & Papi, 1953). Since the solar azimuth changes throughout the day, the sand hopper must compensate for this movement by using its circadian rhythm to orient appropriately to the cue (Figure 1.2C).

Some animals using the clock and compass navigation strategy use multiple directional vectors through their journey. This *multi-vector* strategy can lead to more complex population patterns than seen in the single-vector strategy. Instead of a single preferred orientation, multi-vector navigators use a series of vectors along their journey (Gwinner & Wiltschko, 1978; Munro et al., 1993). A classic example is the migratory red-eyed vireo, *Vireo olivaceus* (Figure 1.2D). Some populations start in western Canada, migrate south-east into the United States, south over the Gulf of Mexico, and finally, south-east again into the Amazon (Sandberg & Moore, 1996) in a “doglegged” pattern. Vectors change after a certain distance, sensed by the vireos through the depletion of fat stores; however, other “distance” measures or vector adjustments are possible (Sandberg & Moore, 1996). For example, in pied flycatchers, *Ficedula hypoleuca*, researchers suggest migrants alter direction when coming across local magnetic field values, called *signposts,* linked to locations associated with path changes (Beck & Wiltschko, 1988).

For both vector and compass strategies, movement is based on preferred direction alone. Preferred orientation does not change when individuals are moved off course and, as a result, their preferred orientation no longer points toward their destination (Figures 1.2C and D). This suggests that such navigators lack knowledge of their current location in relation to the end location. Instead, vector and compass navigators typically arrive at their destination because starting and end locations align with their preferred orientation. Geographic features help the navigators funnel through the landscape, and so does experience. It is thought that such navigators possess a compass but not a map. Consequently, subtle inaccuracies in compass orientation compound with distance, resulting in increased geographic spread of the population as it moves from its starting location (Mouritsen & Mouritsen, 2000). Further, in multi-vector navigation, subtle inaccuracies in “when” to change the vector could also contribute to geographic spread of the population. This is further complicated by the fact that some signals to switch vectors might create less variation than other signals. For example, the signpost mechanism is spatially explicit and might be more accurate than endogenous signals that can significantly vary from individual to individual. Modeling how these additional sources of variation contribute to navigating populations’ observed movement patterns requires additional investigation.

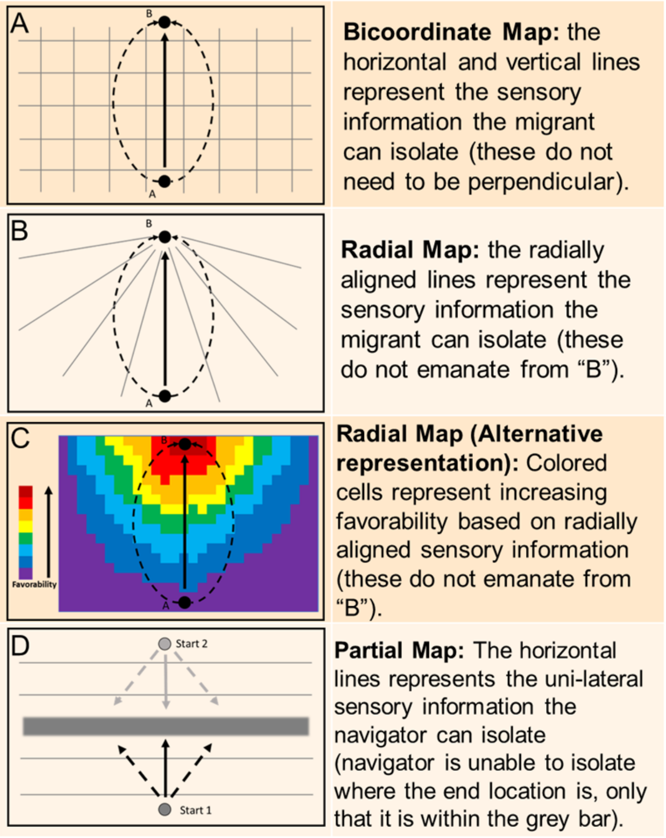
True navigation, unlike the clock and compass strategy, does not rely on a preferred orientation direction (Figure 1.2E). Rather, true navigators orient toward their destination relative to their current location without the use of emanating cues (Boles & Lohmann, 2003; Holland, 2014; Phillips et al., 1995). This ability is attributed to a *map sense* which is often defined by a perception the animal has of its present position and its goal's position. Knowing both allows the animal to orient toward the destination even when experimentally displaced (Chernetsov et al., 2008; Luschi et al., 1996). However, there has been debate on the utility of the concept of map senses since they are difficult to establish empirically and in some cases different navigation strategies do not require a map sense to reorient after displacement (Putman, 2021). For example, memory improves navigation and map formation for birds and some mammal species (Bracis & Mueller, 2017; Deutschlander et al., 2012; Perdeck, 1958), but seemingly memory is not required for migratory sea turtles (Avens et al., 2003). Juvenile loggerhead sea turtles are able to correctly orient when presented with simulated magnetic fields relating to their migratory goal prior to experiencing these fields (Lohmann et al., 2012). This ability to correctly orient passes the tests used for determining a map sense. However, researchers have been hesitant to attribute a map sense to juveniles, instead proposing that the turtles are responding to signposts of magnetic intensity and inclination angle that elicit the different orientations (Collett & Collett, 2011). Functionally, in both cases (map sense and signposts) animals can theoretically readjust after displacements with proper orientations, making it difficult to determine which strategy the juvenile sea turtles are using. There likely is a spectrum of the use of memory in this navigation strategy, ranging from completely genetic to memory dependent (Liedvogel et al., 2011). Regardless of these challenges, true navigation appears to be a more accurate navigation strategy than either vector or multi-vector navigation.

The scale of a movement behavior being investigated often biases the nomenclature used when describing navigation research. For some migrating taxa, research often ignores the potential use of piloting and path integration strategies; instead, research into these taxa often ascribes the navigation ability of migrants to true navigation without critical comparison to other strategies. Additionally, signposts can be used by migrants in either vector and true navigation. How many signposts are needed to be functionally distinguish between a vector vs. a true navigator is unknown.

Map Sense: Map-like Systems

There is no completely agreed upon definition as to what constitutes a map sense, and there is considerable debate in the literature. At its heart, many researchers agree that a map sense seems to include information about the location and attributes of the environment to inform navigators where they are in relation to their goal (Gould & Gould, 2012a; Kitchin, 1994; Putman, 2021). I have already discussed the theorized map used by piloting individuals (see above). Now I will focus on long-distance movements that can comprise distance and time scales that preclude the use of landmarks alone. Such maps typically are classified as *bicoordinate* or *radially* aligned map senses. As with path integration, map senses could theoretically be egocentric or exocentric and the source of information (idiothetic or allothetic) does not imply a reference system. Despite significant cognitive differences between reference systems and information sources, different map senses can conceptually be understood based on the spatial alignment reviewed here.

A *bicoordinate map sense* involves a combination of cues and their intersections (Figure 1.3A). Bicoordinate cues are often conceptualized to convey latitude and longitude (e.g., north-south and east-west). However, sensed coordinates do not have to align perfectly with latitudinal and longitudinal lines and likely do not require perpendicular coordinates. It is theorized that the geomagnetic field provides a sensory bicoordinate map for animals based on changes in magnetism (Boles & Lohmann, 2003; Keller et al., 2021; Kishkinev et al., 2021; Lohmann & Lohmann, 2006). Specifically, "latitude" may be sensed via the geomagnetic field inclination angle (the angle the field intersects the ground) and "longitude" sensed via either local field intensities or the declination angle (the angle the field deflects from true north) (Boles & Lohmann, 2003; Chernetsov et al., 2017; Lohmann & Lohmann, 2006). Given the spatial variation in the geomagnetic field, there are locations where these parameters are parallel or near parallel and therefore would not be usable for a bicoordinate map (Boström et al., 2012; Wynn et al., 2022). In such cases where a bicoordinate map sense is uninformative, animals may use other sensory information to continue navigating. For example,



Bicoordinate Map: the horizontal and vertical lines represent the sensory information the migrant can isolate (these do not need to be perpendicular).

Radial Map: the radially aligned lines represent the sensory information the migrant can isolate (these do not emanate from "B").

Radial Map (Alternative representation): Colored cells represent increasing favorability based on radially aligned sensory information (these do not emanate from "B").

Partial Map: The horizontal lines represents the uni-lateral sensory information the navigator can isolate (navigator is unable to isolate where the end location is, only that it is within the grey bar).

Figure 1.3: Types of Map senses. For each map sense, the left panel shows a representation of the cognitive map that a navigator may possess, and the right panel provides context of the sensory information the navigator would have available with each map.

the waved albatross's navigation ability was not disrupted after removing their ability to sense the earth's magnetic field by attaching magnets to the birds' bodies (Bonadonna et al., 2005; Mouritsen et al., 2003). There is some debate on whether magnets are a proper assay for eliminating the map sense in birds (Packmor et al., 2021; Wang et al., 2006). However, because the albatross was still determined to be a true navigator (i.e. they reached their historical destination location), it is possible that the bird uses other cues for its map sense alongside or instead of the magnetic field values. Specifically, olfaction cues have been found important for true navigation and by extension the map sense in other bird taxa (Gagliardo, 2013).

The *radial map sense* is based on a cue or a combination of cues whose values change radially around the destination (Figure 1.3B) (Wallraff, 1981). Experiments reveal that homing pigeons use (at least in part) a radial map based on olfaction cues (Gould, 2015; Wallraff, 1981). Olfaction is the most well studied radial map cue and, to date, for long-distance movements has been primarily tested in bird species (Gagliardo, 2013). Radial cues do not emanate from the destination as in taxis responses, but instead the navigator needs to sense that preferred values converge at the destination (Figure 1.3C). Homing pigeons also have been suggested to use visual landmarks together with olfaction as the basis of this map (Wallraff, 2001); however, some populations of homing pigeons appear to not use olfaction at all (Wiltschko et al., 1987), further complicating the story. Though radial and olfaction cues are discussed as maps, these senses ultimately only convey direction to the goal and not distance. Typically, map senses have been talked about as conveying both. However, because the olfaction cues do not emanate from the source, functionally using olfaction aligns with true navigation. As such, the use of olfaction further brings into question the utility of equating true navigation with map senses.

As alluded to in the brief discussion of the role of memory above, some taxa's map sense seems to be *innate* while others' seem to be *learned*. An *innate map* is genetically preprogramed and does not require experience (Liedvogel et al., 2011; Lohmann et al., 2012). A *learned map,* in contrast, requires experience or cultural transmission of information to be fully expressed (Berdahl et al., 2018; Jesmer et al., 2018; Perdeck, 1958). Defining which map sense is used, innate or learned, requires careful control of the variables that define the different kinds of map senses (listed above), as well as comparisons of experienced and inexperienced individuals. If the map sense is learned, then only experienced migrants behave as true navigators. Some bird species, including starlings and chaffinches, require experience to develop their map sense, with juveniles behaving more as vector navigators with a preferred direction only (Chernetsov et al., 2008; Deutschlander et al., 2012; Perdeck, 1958). Experience can be culturally transmitted, as in some juvenile flock-living birds. For example, snow geese rely on experienced navigators guiding juveniles during early journeys (Åkesson et al., 2021). Further, ungulates follow experienced navigators until their individual map sense is formed (Jesmer et al., 2018). These experience/learned map senses can be thought of as a form of piloting since these navigators are remembering landmarks (visual or local environmental cues) that convey positional information as the bases of their map.

As discussed above, there is some debate regarding the utility of considering animals having a map sense, and, indeed, there is no set of features uniquely defining a single sort of "map sense". For example, the theorized cognitive alignments of the maps described above (radial and bicoordinate) are fundamentally different, could convey different information, and result in different types of "map sense" (i.e., radial olfaction maps often cannot convey distance while bicoordinate magnetic maps can). The aspect of "innate" map senses whose mechanisms are poorly understood and a taxa's functional ability (e.g., passing the displacement test) may well be explained by simpler mechanisms. Functionally, however, these map-like systems, though distinct mechanistically, allow navigators to reach distant locations with high degrees of accuracy, potentially more than other strategies (see Box 1).

Box 1: Road map to defining an animal's navigation strategy.

Often, defining the navigation strategy used by an animal requires a mixture of individual-level behavioral information along with population-level movement data. In some systems, individual-level information can be used alone to assign a navigation strategy, while other systems may require the use of modeling approaches to integrate both individual and population-level data. Here we describe a process – starting from the individual and moving into integrating individual with population-level data – to define navigation strategies, with a focus on long-distance movement behaviors.

1. Behavioral assays are ideal starting points when determining an animal's navigation strategy. These assays provide individual-level data on a navigator. The orientation assay is commonly used to isolate the environmental cues important for orientation, the animal's preferred orientation direction, and the accuracy/variation in the animal's orientation. Orientation assays can be coupled with displacement assays to determine if the animal possesses a map-sense.

2. Displacement experiments move individual navigators off their typical movement pathway and then test if that navigator can re-orient correctly toward their goal. This directly tests if a navigator has a map sense, which is the defining feature that separates the main navigation strategies (vector and true navigation) used in long-distance movement (see main text). The presence of memory can further define a map sense into those used in piloting. Additionally, some animal compasses convey latitudinal information and represent a potential partial map for the navigator, where latitudinal location is known but not longitudinal location. Often, orientation assays are used to measure re-orientations, but this method does not allow orientation under natural environmental context. Ideally, re-orientation is measured via GPS devices, which have high temporal resolution and allow for the animal to be exposed to natural context during their navigation. Displacement experiments should include both latitude and longitudinal displacements, as animals with a full map sense should be able to re-orient after both while animals with partial maps would only be able to re-orient after latitudinal displacement. Memory can be tested for by testing juvenile (inexperienced) and adult (experienced) navigators. If piloting was the prevailing strategy, then only adult navigators would be able to re-orient after displacements. Finally, in some navigating species cultural transmission of experience is possible so testing isolated juveniles and experienced individuals can determine if the transmission of information is necessary.

In a system that can carry GPS loggers, steps 1 and 2 would provide enough information to determine which navigation strategy is used. In species that are too small to carry a tracking device, however, mathematical models can be used instead. Models can be used to integrate the results from behavioral assays with alternative tracking studies such as tag/release and surveillance studies. These tracking studies can provide start/end location information for navigators, geographic spread of the moving population, and temporal shifts of the population but not high-resolution location information of an individual as provided by GPS loggers. Models can predict geographic spread of the population and arrival times of a moving population. Models for movement can categorize navigation mathematically or via simulation. Here we focus on a simulation approach.

3. Agent-based models are simulation models that are particularly useful for modeling a moving population. These models consist of a population of autonomous individuals, whose individual movement behavior can be broken down into two phases: first, the decision phase (to select an orientation), and second, the step phase (the agent moves in a given direction as selected during orientation). In real-world navigation, the decision phase has variation between individuals, with a shared mean orientation as the "preferred orientation." If there were no variations in this phase, each navigator would make the same decision with no deviation from the mean orientation (figure: left panels). If there is variation in the selected orientation between individuals, then migrants will deviate from the mean orientation causing increased geographic spread as the navigators continue to move. The increase in spread is a function of the distribution in selected orientations and the underlying navigation strategy (figure: center panels). The expected geographic distribution of a navigating population is expected to increase with distance from the start location for vector navigators (a parabolic function) and increase then decrease for true navigators (an ellipse function) (Mouritsen & Mouritsen, 2000). The results from an agent-based simulation for both true and vector navigation strategies follow these generalized parabolic and ellipse functions (figure: center panels). Comparisons of the observed geographic spread of a population with the model's predicted geographic spread has been used to determine navigation strategy in some bird species; however, the technique has failed to match results in other species of birds whose navigation strategy was already known (Thorup & Rabøl, 2001). One explanation is that neither model incorporates stochastic effects outside the individual navigator. Specifically, landscape heterogeneity could constrain moving populations and thus result in alterations to final geographic spread measures. Agent-based models can easily incorporate landscape variation into the orientation phase by taking GIS datasets for landscape values that are known to influence the animal's behavior. For example, for animals that preferentially move toward highly vegetative patches, agent-based models can incorporate this landscape heterogeneity by using vegetation measured at a pixel level on a raster GIS dataset. Agents are placed on the GIS grid, and the values directly surrounding the agent are the only values considered during movement. Behavioral adjustments incorporating this landscape heterogeneity significantly alter the overall variation in the realized movement paths taken by individual agents (figure: right panels). Note that center and right panel simulations in the figure use the same number of individuals, decision and step phases, and orientation accuracy. Observed differences in pattern are thus solely the result of individual navigation strategies (vector or true navigation) and landscape features. By simulating populations of individual navigators, we can produce distributions of synthetic data that can be used in Monte Carlo goodness of fit tests to compare with observed data (Waller et al., 2003). In this way, the lack of GPS tracking information can be compensated for by using alternative data sources and information from the behavioral assays already conducted on a study system.

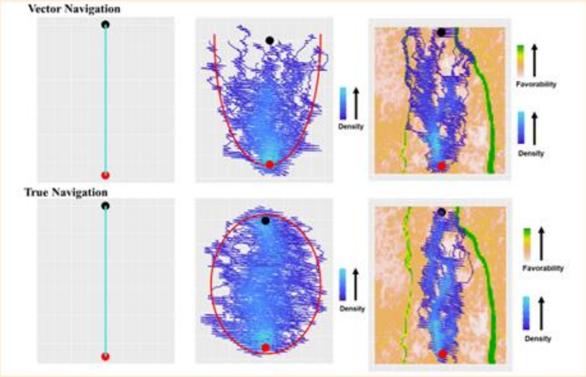


Figure: Agent-based model simulations of vector and true navigation strategy. For all panels, the red dot is the starting location, the black dot is the goal, and individual blue lines represent individual agents. Line coloration is the density of agents going through those same locations. Left panels show agent paths when there is no variation in orientations selected during movenent. Center panels add variation into orientation phase and additionally show mathematical model expectations in red. Right panels show the effects of a hypothetical landscape with two rivers (green) on either side of the starting and end locations.

References:

1. Mouritsen H., Mouritsen O. 2000 A mathematical expectation model for bird navigation based on the clock-and-compass strategy. *J Theor Biol* **207**, 283-291
2. Waller L.A., Smith D., Childs J.E., Real L.A. 2003 Monte Carlo assessments of goodness-of-fit for ecological simulation models. *Ecol Model* **164**, 49-63.

Defining Navigation: The Importance of Experimental Approaches

Given the subtle differences between the different navigation strategies, it comes as no surprise that empirical assessment of the navigation strategies used by a particular taxon can be a challenging task. In this section, I briefly review experimental approaches to determine navigation strategies.

Orientation assays determine orientation in lab- or field-based experiments. The organism can be affixed in the center of an apparatus with orientation measured by body direction (Perez et al., 1997); allowed free movement within an apparatus with preferred orientation measured based on time spent in various sections (Wiltschko & Wiltschko, 1972); or released with orientation determined as the animal disappears from view (Syposz et al., 2021). Orientation assays compare migratory vs. non-migratory populations, isolate the preferred orientation direction for vector navigators, and isolate environmental cues used for orientation (Perez et al., 1997; Wiltschko & Wiltschko, 1972). Of course, cues identified in these studies do not preclude the use of others during actual navigation. For example, orientation assays on lab-reared monarch butterflies (hypothesized to not display migratory phenotype) found no orientation preference, but expected migratory orientation was detected after release into the wild (tracked via radio towers) (Tenger-Trolander & Kronforst, 2020; Wilcox et al., 2021), suggesting navigation can involve factors not captured during orientation assays. These missing factors could cause orientation assays to be an unreliable method when specifying an underlying navigation strategy, given that the navigation strategy used is likely more complex than orientation to a single environmental cue.

Displacement experiments have been used to distinguish between vector and true navigators. These experiments move navigators off course, then utilize some measure of orientation (typically orientation assays) to test if the navigator compensates for this displacement. Displacement can either be *simulated* by exposing navigators to environmental cues found in different locations (Lohmann et al., 2012), or *physical* by taking navigators from one location to another (Avens et al., 2003). Physical displacement ensures all orientation cues (known or unknown), and other co-factors are available. However, navigators can compensate for physical displacement using path integration; to control for this, animals need to be transported without available orientation cues so they can no longer actively track the physical displacement. Given that orientation assays can be an unreliable way to measure the ability to compensate for a displacement, other measures of orientation can be used when available. In the previous monarch example, radio telemetry was used to track individual monarchs after release, providing orientations under natural contexts. Further, other studies have attached GPS trackers to displaced individuals to measure orientations throughout the navigator's journey (e.g., sea turtles, Luschi et al., 1996; blue whales, Abrahms et al. 2019; and elephant seals, Beltran et al., 2022). These alternative methods have the advantage of tracking navigators over time with important environmental cues and context intact. To fully test for a navigator with the displacement method, it is important to consider the method of orientation measurement and experiments need to document *longitude and latitude displacements, experienced vs. inexperienced migrants,* and *distance translocated* as detailed below.

Both *longitude and latitude displacements* are important to test for possession of a map sense (Boles & Lohmann, 2003; Holland, 2014; Putman et al., 2011). Reorientation after a single latitude or longitude displacement does not necessarily imply a map sense, since some compasses can isolate latitude (e.g., a magnetic inclination angle compass). True navigators should reorient to changes in both longitude and latitude. One can test learned vs. innate map sense by comparing experienced and inexperienced navigators via displacement experiments; innate maps are expressed in inexperienced navigators while learned maps require experience for full expression (Perdeck, 1958). For example, monarch butterflies have been shown to use the inclination angle to navigate on overcast days (in contrast, their primary compass is based on the position of the sun) (Etheredge et al., 1999; Guerra et al., 2014). Similarly, the bobolink, *Dolichonyx oryzivorus*, a vector navigator, also has been shown to orient using the inclination angle (Beason, 1989; Hamilton III, 1962). The inclination angle varies predicably with latitude and can theoretically be used to define part of the map senses discussed above. Animals such as the monarch and bobolink, who can only sense the inclination angle, could theoretically determine their latitude in relation to their goal's latitude (although, to date, such a hypothesis has not been directly tested in these systems). Determining latitude alone could be said to form a *partial map* and represent additional challenges when identifying navigation strategies (Figure 1.3D).

Some researchers hypothesize a true navigator's map sense could extend globally (Gould & Gould, 2012a). In some instances, true navigators with a learned map sense orient properly after physical displacement outside of their extended range, e.g., the Eurasian reed warbler (*Acrocephalus scirpaceus)* (Chernetsov et al., 2008). However, it is unknown if all true navigators have such a global map sense. The *distance translocated* in an experimental design should include such uncertainty and balance biologically relevant tests and statistical power. Very large displacements run the risk of falling outside the range of a navigator's map sense, resulting in orientations via other strategies, while very small displacements may lack statistical power to distinguish between a map sense and other types of navigation.

Modeling Navigation: Population Patterns

As previously discussed, the scale of a movement behavior can bias the choice of navigation nomenclature. Additionally, the scale also can bias the choice of preferred experimental approaches to study the movement behavior, since large-scale movement behaviors have only recently been observable due to the advent of small geolocation devices attachable to animals. The inability to directly observe the navigation behavior of migrant or nomadic species has caused researchers to employ alternative research approaches to study the underlying behaviors of those systems. Here, I outline how coupling the theoretical navigation strategies above with simulation modeling and the use of large data sets offers additional tools to study animal navigation.

Navigating populations can be thought of as a collection of entities, whose individual behaviors are quantifiable through observation or sensor technology, yet whose population-level properties can be hard to define empirically. Specifically, population properties such as movement success, final geographic distributions of the population, and preferred routes may escape observation for large-scale movement behaviors such as migration or nomadism. Experimental techniques, outlined above, provide the first steps in describing the processes and drivers behind individual-level behaviors regardless of the scale of the movement behavior. Modeling approaches also can be helpful in translating these individual-level processes to population properties. Furthermore, simulation models can collate experimental results in order to test hypotheses, frame the navigation hypothesis in ecological contexts, and predict future population level system states (Haefner, 2005; Marquet et al., 2014).

The highest resolution data for large movements come from GPS tracking loggers attached to individual animals. These loggers can take positional information and orientations of a tracked animal over their entire journey and usually has hourly tracking resolution. Tracking studies and straight-line path modeling found that ungulates with access to memory, experience, and social transmission migrated in straighter lines than those animals that did not have such access (Benhamou, 2004; Bracis & Mueller, 2017; Jesmer et al., 2018; Kauffman, Aikens, et al., 2021; Kauffman, Cagnacci, et al., 2021). Straight-line path modeling was also used to quantify the resolution of the map sense in hawksbill turtles, *Eretmochelys imbricata* (Hays et al., 2022). Classic linear correlations can be made with GPS tracking data. For example, it was found that water temperature, experience level, and nutrient availability were correlated with the speed of whale migration arrival times (Abrahms et al., 2019). Linear correlations also showed that elephant seals, *Mirounga angustirostis,* had a perception of time and space that resembles a map sense (Beltran et al., 2022).

Some animals, particularly insects, are too small to carry current GPS tracking technology, and thus cannot be observed as described above. To compensate for the inability to directly track the journey, researchers have employed large multi-year survey studies that track hundreds to thousands of navigators' start and end locations or their absence/presence in a particular area (e.g., *tag/release and citizen science observational data*). Tag/release data provide population level trends from start and end locations where navigators were captured, released, and re-captured (Horns et al., 2018; Neate-Clegg et al., 2020). Early work on monarch butterfly migration used citizen scientist tag/release data to identify elusive overwintering locations in central Mexico (Urquhart, 1976). Similar techniques revealed overwintering locations along the coast of California (James et al., 2018). Recent work tracking the common potoo, *Nyctibius griseus*, revealed some subpopulations migrate while others do not, a phenomenon missed until reviewing citizen science data (DeGroote et al., 2021). These tag/release data sets have historically been used to study the movement behavior of an animal and not their navigation strategy since the data do not provide high positional resolution. When these data have been used for navigation research, however, models fall into two categories, either *mathematical expectation* or *simulation* models.

Mathematical models of navigation from tag/release data typically build upon *random walks* (Wu et al., 2000) and *directed random walks* (Cheung et al., 2008; Morales et al., 2004). These describe navigation as random steps taken by each individual. The steps for individuals follow the same distribution with navigators moving on average toward their preferred orientation with individual variation around that average (directed random walk), compared to a null model with no directionality where steps in any direction are equally likely (random walk). Directed random walk equations for vector navigators (who orient toward a specific preferred direction) yield individual paths widening with migratory distance from a common departure point (Mouritsen & Mouritsen, 2000). Past research using directed random walks based on tag/release data for some bird species (Mouritsen & Mouritsen, 2000) and for monarch butterflies (Mouritsen et al., 2013) suggests that these animals' navigation is often more similar to vector navigation (directed random walks with shared mean direction) than true navigation (directed random walks with mean direction always at the end location). However, these modelling approaches remain controversial with monarchs (Oberhauser et al., 2013) and fail to provide satisfactory fit to observed distributions in some bird species (Thorup & Rabøl, 2001). One potential source of controversy arises from the fact that these models do not incorporate individual variation of animals who may have several vectors during their journey (described above as multi-vector navigation). Inter-individual variation in decision points in space and time regarding where and when to change vectors could theoretical increase the final geographic spread more than mathematical model with a fixed location and for vector changes would expect.

A readily available measure of movement success, regardless of the tracking study used, is the final geographic distribution of the navigating population. This distribution pattern can be the result of multiple navigation strategies responding to external cues, patterns, and heterogeneity of the landscape (Alerstam, 2006; Grimm et al., 2005). Given that landscapes can influence this measure, incorporating geographic information systems (GISs) and remotely sensed data into random and directed random walks models can further explain observed geographic patterns. A particularly useful modeling approach that can easily incorporate GIS and simulate directed random walks is that of *Agent-based/Individual-based models.* These models use computer simulations to generate individual behaviors that are summarized into population level observations. Agents are individual navigators set on a grid that represents the surface area of their journey. They are programed to follow a set of rules which dictates how to move and orient, i.e., these rules simulate an individual's navigation strategy. For example, vector navigators have a preferred mean orientation that does not change through their journey. True navigators, on the other hand, know their location in relation to their goal, with the mean of their orientation distribution always pointing toward their goal. Simulating a population of navigators using this method would generate the predicted emergent population geographic spread for each navigation strategy. If different strategies lead to distinctive patters of geographic spread, these geographics spreads can then be compared to the observed geographic spread measured using the tracking studies listed above.

Landscape GIS information can also be incorporated by populating the grid on which the agents navigate, with the values of landscape information important for travel. For example, altitude values for an area can be used with rules set to not allow agents to cross barriers that represent large geographic structures. Agent-based models have been used to model movements of birds (Wolff, 1994; Xu & Si, 2019), fish (Huse & Giske, 1998; Snyder et al., 2019), insects (Linard et al., 2009), and mammals (Bennett & Tang, 2006). As discussed above, mathematical expectation models for some migrating bird species, including the barred warbler, *Sylvia nisoria,* and marsh warbler, *Acrocephalus palustris*, have failed to adequately explain the final geographic distribution of the population, leading researchers to believe that landscape variation and funneling effects caused deviations from the expected distributions (Fransson et al., 2005; Thorup & Rabøl, 2001). Agent-based models coupled with GIS-based landscape data could test the hypothesis that landscape is causing the divergence in observed geographic distribution by creating several simulated populations of these birds, with each population using a different navigation strategy, and allowing their agents to navigate over detailed digital maps of the physical landscape that the bird species would encounter during their real journey.

The increased complexity required to model large-scale movement behaviors with coarse data has required creative workarounds to get at the underlying navigation strategy using empirical study designs described in the preceding sections. However, the simulation modeling methods and their results summarized in this section are relatively new and provide new tools for pushing the boundaries of quantitative analysis of animal navigation. The agent-based structure enables studies on power, effect size, and the required sample size of tracked individuals. Such studies will help us understand how best to design simulation studies in order to better understand how effective experimental, modeling, and hybrid approaches can be in identifying underlying navigation strategies. Further, current models of navigation and movement are linked to empirical data sets for a given species of interest and are not directly comparable to other species. Ideally, by moving toward common terminology and concepts, future navigation studies can move toward becoming comparable across species and movement scales to find if there are unique navigation components related to given species or scales.

Summary of Dissertation Chapters

In Chapter II, I investigate the complex relationship between migration and parasitism, using monarch butterflies and their protozoan parasite *Ophryocystis elektroscirrha* as a model system. Migration can both increase parasite exposure and reduce prevalence through mechanisms such as migratory culling, escape, and drop-out. Monarchs, particularly in North America, show reduced parasite loads due to these processes, but the rise of resident populations, driven by environmental changes and human intervention, is disrupting migration and amplifying parasite prevalence. I highlight the role of migratory behavior in controlling infection rates and the consequences of reduced migration for population dynamics. Additionally, I address how parasites might affect monarch cognition and migratory success, stressing the need for further research into the evolutionary pressures on parasites and the impact of human activities on monarch migration and disease dynamics.

In Chapter III, I develop a statistical and theoretical framework to study animal migration using agent-based models. This study highlights the utility of such approaches for creating predictive distributions of moving populations under different navigation strategies. These models force the critical evaluation of what information is available for a given species and how well that information can describe links between observed natural patterns and migration processes. With advances in computational efficiency, my proposed approach becomes easier to parameterize for a given system and serves as a viable and cost-effective way to bridge the results from empirical studies and statistical inference regarding driving processes and parameters. Comparing these simulated results with observations of real migrating populations provides a useful tool in determining the navigation strategies that migrants use to reach their destinations.

In Chapter IV, I focus on understanding the navigation strategies of the monarch butterfly in eastern North America, which travels thousands of kilometers to reach overwintering sites in Mexico. I model two navigation strategies—true navigation, where animals know their destination, and vector navigation, where they follow a consistent direction. Using agent-based models (ABMs), I simulate migration patterns based on these strategies and compare them with real-world data from iNaturalist. The results indicate that monarch migration is more likely explained by simpler vector navigation, where butterflies adjust their direction based on landscape features, rather than true navigation. My study emphasizes the importance of landscape and environmental factors in shaping migration routes and highlights how computational models can be used to investigate animal behavior at a large scale.

My dissertation showcases the importance of considering the complex relationships between migration and navigation when studying long-distance animal movement behaviors. Ultimately, the framework I provide helps researchers test assumptions related to migration so they can begin to have a more holistic understanding of the behavior.

CHAPTER II

INTERACTIONS BETWEEN PARASITISM AND MIGRATION IN MONARCH BUTTERFLIES

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Abstract

In many species, migration can increase parasite burdens or diversity as hosts move between diverse habitats with different parasite assemblages. On the other hand, migration can reduce parasite prevalence by letting animals escape infested habitats, or by exacerbating the costs of parasitism, leading to culling or drop-out. How the balance between these negative and positive interactions is maintained or how they will change under anthropogenic pressure remains poorly understood. Here, we summarize the relationship between migration and infectious disease in monarch butterflies, finding that migration can reduce parasite prevalence through a combination of migratory culling and drop-out. Because parasite prevalence has risen in recent decades, these processes are now resulting in the loss of tens of millions of monarchs. We highlight remaining questions, asking how migration influences population genetics and virulence, how the establishment of resident populations interferes with migration, and whether infection can interfere with migratory cognition.

Introduction

Seasonal migration is widespread among animals and often involves the mass-movement of individuals across large geographic distances (Dingle, 2014). Migration allows animals to avoid predators, parasites and deteriorating habitats, and to track seasonal resources across different regions (Alerstam et al., 2003; Altizer et al., 2011; Dingle, 2014; L. McKinnon et al., 2010). While migration benefits the survival and reproduction of populations, it can also be energetically costly, time consuming, and risky (Klaassen et al., 2014). Increasingly, scientists recognize that migration is essential for the functioning of ecosystems, with migrants serving as consumers, predators, food sources, nutrient transporters, pollinators, and seed dispersers (Bauer & Hoye, 2014; Holdo et al., 2011).

Animal migration has profound consequences for infectious diseases (Table 2.1). Migration can increase the spread of parasites, expose animals to more diverse parasite assemblages ("migratory exposure" hypothesis), or increase host susceptibility to infection due to physiological trade-offs between migration and immunity ("migratory susceptibility" hypothesis) (Poulin & de Angeli Dutra, 2021). For example, avian flu virus spreads through migratory waterfowl flyways and at shorebird stopover sites (Caliendo et al., 2022), and

Table 2.1: Glossary of migration-specific disease terminology

Term	Definition
Migratory exposure hypothesis	Long-distance migration increases exposure of migrating hosts to geographically diverse and potentially novel parasites.
Migratory susceptibility hypothesis	Potential trade-offs between migration and immunity lead to an increase in host susceptibility to infection.
Migratory escape	Animals migrate away from areas of high infection to areas of low infection.
Migratory culling	Animals fail to complete migration due to the negative effects of being parasitized.
Migratory recovery	The process of migration causes a reduction in total number of parasites infecting the migrant.
Migratory drop-out	Migrants stop their migration prior to full completion.
Migratory allopatry	Host migration causes spatial separation between adult and juvenile hosts and prevents parasite transmission from adult to juvenile hosts.

migratory bird species are known to harbor a greater diversity of haemosporidian parasites than their resident counterparts (de Angeli Dutra et al., 2021). Migration can also exacerbate the costs of infection: in some birds, infection from avian malaria causes a decrease in lipid reserves during migration and a reduction in body mass at arrival (Garvin et al., 2006; Merrill et al., 2018).

Migration can, on the other hand, reduce infection risk for many species (Hall et al., 2022). This occurs when animals periodically escape areas where parasites accumulate, known as “migratory escape”. Strenuous migration can also weed out and kill infected individuals, thereby reducing onward parasite transmission, called “migratory culling.” Migratory black-eyed juncos, for example, experience lower prevalence of haemosporidian parasites than non-migratory conspecifics, likely through migratory escape or culling (Slowinski et al., 2018). “Migratory recovery” occurs when parasites are lost during migration, reducing transmission or parasitic load. For example, spiny common toads lose fungal infections during post-breeding migrations (Daversa et al., 2018). “Migratory allopatry”, exemplified by Pacific salmon and sea lice, occurs when juveniles develop in freshwater habitats inhospitable to lice, and are protected from adult-origin sea louse infestation until later in life (Krkošek et al., 2007). Finally, parasite infection could make individuals less likely to migrate, known as migratory “drop-out”. While this reduces parasite prevalence amongst migrants, it can increase parasite prevalence among resident populations. Thus, migration can have costs and benefits for individuals and populations: migratory exposure and susceptibility increase individual parasite risk; migratory escape and recovery reduce individual parasite risk; and migratory culling and drop-out reduce infection risk at the population level.

Anthropogenic impacts, including habitat destruction, light pollution, and climate change, are affecting migratory animals, to the extent that many scientists now consider migration an endangered phenomenon. Some migratory animals now travel shorter distances, arrive sooner, or depart later from seasonal breeding grounds, or are being replaced by resident populations (Kubelka et al., 2022). With animal species losing their migrations, it is important to better understand the interaction between migration and infectious disease. Monarch butterflies and their protozoan parasites provide a flagship system to study the impacts of loss of migration. Here, we summarize current understanding of the interactions between parasites and migration in monarchs, discuss implications for conservation and habitat management, and provide recommendations for future research.

Monarch migration and parasite infection patterns

Eastern North American monarchs have one of the most spectacular migrations of the animal kingdom (Gustafsson et al., 2015; S. M. Reppert & J.C. de Roode, 2018), with millions of butterflies migrating up to 4,500 km from breeding grounds as far north as Canada to overwintering sites in central Mexico (Figure 2.1A) (Lincoln P Brower, 1995; Flockhart et al., 2017; F. A. Urquhart & N. R. Urquhart, 1978). Monarchs in western North America migrate shorter distances to overwinter along the California coast (Lyons et al., 2012). Monarch caterpillars are specialized on milkweed host plants, the vast majority of which die back seasonally in North America, which prevents year-round breeding. Late-summer and autumn-hatched caterpillars enter reproductive diapause and a migratory phenotype, facilitating the long migration and survival throughout the winter months. Overwintering monarchs remain in a non-reproductive state until late winter and early spring, at which point they mate and fly north to recolonize their breeding range over 2-4 successive generations (Flockhart et al., 2013).

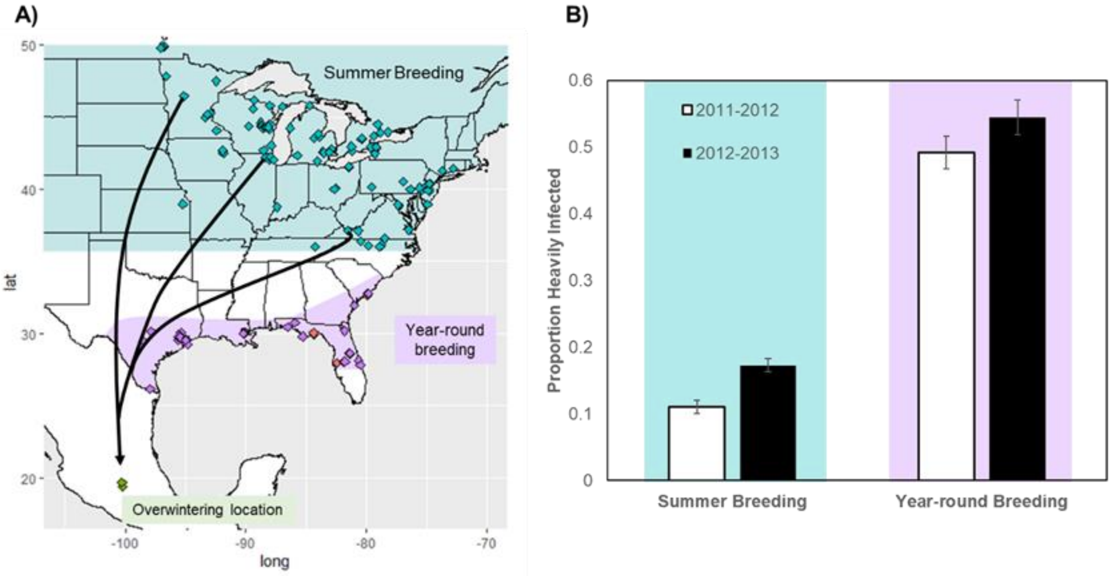

Figure 2.1: Map of the eastern North American monarch's migratory ranges A) summer breeding, in blue and year-round breeding in purple. Red dots show location of non-breeding U.S. winter monarchs. B) Proportion of heavily infected migratory monarchs (blue) and year-round resident monarchs (purple). Panels A and B are adapted from (Satterfield et al., 2015).

Monarchs are commonly infected with a debilitating protozoan parasite, *Ophryocystis elektroscirrha* (Altizer & de Roode, 2015; McLaughlin & Myers, 1970). Infection occurs when monarch caterpillars ingest dormant parasite oocysts (often referred to as spores) scattered by adults onto the surface of egg choria and foliar tissues (Altizer & Oberhauser, 1999). Oocysts lyse within the larval gut, and sporozoites enter the larval hypoderm (McLaughlin & Myers, 1970). The parasite then replicates in the monarch's tissues to ultimately produce hundreds of thousands to millions of oocysts on the outside of adult butterflies (de Roode et al., 2007). Virulence manifests as reduced pre-adult survival, and reduced adult lifespan, fecundity, and flight ability (Altizer & Oberhauser, 1999; C. A. Bradley & S. M. Altizer, 2005; de Roode et al., 2008). Parasite transmission occurs both vertically, when mothers transfer oocysts to their own offspring via eggs or milkweed foliage, or horizontally, when deposited oocysts on milkweeds are ingested by unrelated caterpillars. Males can also transfer oocysts to females during mating, which subsequently make it to milkweed where they can be ingested by caterpillars. The combination of these three transmission modes can sustain virulent *O. elektroscirrha* parasites, result in high prevalence, and reduce monarch population abundance by up to fifty percent (Majewska et al., 2019).

While monarchs are known for their migration in North America, they also occur in resident populations around the world. Genomic analyses and historical records indicate that monarchs from North America colonized locations across the Pacific, Caribbean/Neotropics, and Atlantic through three independent dispersal events (Pierce et al., 2014; Zhan et al., 2014). As they established these new tropical and sub-tropical resident populations, monarchs experienced greater parasite prevalence than their ancestral North American population, with prevalence reaching 90-100% in some locations (Altizer & de Roode, 2015). Experimental, field, and modeling studies suggest that this high prevalence results from the absence of migratory escape and culling; parasites accumulate and transmit from adults to caterpillars without interruption when milkweed and adult butterflies are continually present (Figure 2.1B) (Majewska et al., 2019).

Parasitism reduces monarch migration success

A recent study estimated that tens of millions of infected eastern North American monarchs fail to reach their overwintering locations each year (Majewska et al., 2022) (Figure 2.2). Migratory culling plays a large role in this reduced migration success. Flight mill tests have shown that infection with *O. elektroscirrha* reduces monarch flight speed, duration, and distance (C. A. Bradley & S. Altizer, 2005). Moreover, parasite prevalence decreases as monarchs fly south toward their overwintering sites (Figure 2.2D) (R.A. Bartel et al., 2011), and stable isotope analysis has shown that infected monarchs at the overwintering sites in Mexico tend to originate from more southern latitudes (Altizer et al., 2015). Further, infected monarchs have lower flight efficiency (the distance flown using the same available lipid reserves) (C. A. Bradley & S. Altizer, 2005). These results suggest that reduced migratory success results from a reduction in lipid use efficiency instead of an overall reduction in lipid reserves. Infection can also impact phenotypic and life history traits important for migration; wings of infected monarchs are smaller and have significantly weaker tensile strength and are thus more likely to break (Davis & de Roode, 2018), potentially increasing migratory failure (Dockx, 2007). Infected monarchs also shorter lifespans, decreasing their ability to survive long enough to complete their migration and breed in the following spring season (de Roode et al., 2009).

In natural populations, there are strong signs of migratory culling in the eastern monarch sub-population (Figure 2.2B), with more limited migratory culling in western North America. Thus, in eastern North America, where monarchs travel thousands of kilometers to reach overwintering sites in Mexico, overwintering monarchs experience significantly lower parasite prevalence than late summer breeding or fall migrating monarchs. In western North America, where monarchs travel shorter distances to reach overwintering sites on the California coast, overwintering monarchs experience lower prevalence than summer-breeding monarchs, but not migrating monarchs (Majewska et al., 2022). It is possible that monarchs sampled later in the migratory journey have comparable infection rates to the overwintering monarchs, or that shorter migratory distances reduce the pressure of migratory culling. Importantly, releasing infected monarchs to study migration routes and success (James et al., 2018; James & Kappen, 2021) could inadvertently increase parasite prevalence by allowing infected monarchs to reach overwintering locations and increase natural population infection loads. (Note that we are strongly opposed to any releases of infected monarchs, as this can increase parasite risk regardless of population). One study that released thousands of captive-reared monarchs in western North America (both healthy and infected) concluded that parasites may not cause migratory culling (James & Kappen, 2021). However, infected monarchs in this study appeared to have lower parasite loads, which are known to have minimal to no negative fitness consequences (de Roode et al., 2009). Moreover, the sample sizes in this study were exceedingly small (6 recovered infected monarchs, 0.41% of 1473, compared to 2 uninfected, 0.44% of 450 released, for the same given area), thus preventing statistical analysis. More broadly, the vast majority of evidence strongly supports migratory culling as a mechanism for reducing parasite prevalence in monarchs.

Reduced migration in monarchs could also arise from migratory drop-out, particularly when migratory monarchs stop their migration and become reproductive when encountering resident populations (Figure 2.2F) (Satterfield et al., 2018). This is in part due to the availability of viable mates and exposure to actively growing host plants, especially *Asclepias curassavica* (Majewska & Altizer, 2019). Importantly, the rate to which migratory monarchs stop depends on infection status (Figure 2.2E). A study that used stable isotopes and cardenolide fingerprints found that monarchs sampled from Texas stopover sites with nectar plants only (and no visible milkweed) were exclusively migrants (from northerly latitudes), non-reproductive, and had very low infection prevalence (< 4%). In contrast, monarchs sampled at Texas sites with resident breeding monarchs and *Asclepias curassavica* were a mix of residents and migrants (the latter again from northerly latitudes), with the migrants showing higher (20%) infection prevalence and reproductive activity (Majewska et al., 2022; Satterfield et al., 2015). This pattern is likely due to infected monarchs joining resident monarchs and becoming reproductive at higher rates than their uninfected counterparts (Figure 2.2E), consistent with the migratory drop-out hypothesis.

Migration reduces parasite prevalence and transmission

Although parasite infection lowers individual monarch migration success, migration also reduces parasite transmission and infection prevalence at the population level. As monarchs breed throughout the summer and increase in population density, they spread parasite oocysts to milkweeds. As a result, long-lived (weeks to months (Sánchez et al., 2021)) oocysts build up on milkweed steadily over time, increasing infection risk (Figure 2.2C) (Majewska et al., 2019). With the onset of autumn conditions, milkweeds die back, thereby removing this environmental reservoir of oocysts. Migration thus reduces parasite transmission by allowing monarchs to escape high-risk breeding grounds in the fall, and recolonize largely parasite-free habitats in the spring (R.A. Bartel et al., 2011).

Because fewer infected monarchs reach the overwintering sites owing to migratory culling and drop-out, migration puts a second annual brake on parasite spread (Figure 2.2A and B) (Majewska et al., 2022). With respect to migratory drop-out, it is unclear what the net effect is on parasite prevalence. If infected monarchs are more likely to cease migration and take up a residential lifestyle, fewer infected monarchs will reach the overwintering sites. However, these infected monarchs could contribute to the growing parasite prevalence in sedentary populations across the southern coastal U.S. Since sedentary and migratory monarchs can interact (Satterfield et al., 2018), especially during fall and spring migration, such increases could amplify parasite exposure in the migratory population as well.

Whether migratory recovery contributes to reductions in parasite prevalence in monarchs remains unknown. It is also important to note that “recovery” for monarchs means reduced parasite loads, but not the clearance of infection. While we know that monarchs lose oocysts over their adult life (de Roode et al., 2009), it remains unknown whether oocyst losses during autumn migration and overwintering reduce parasite levels enough to result in reduced transmission during spring breeding.

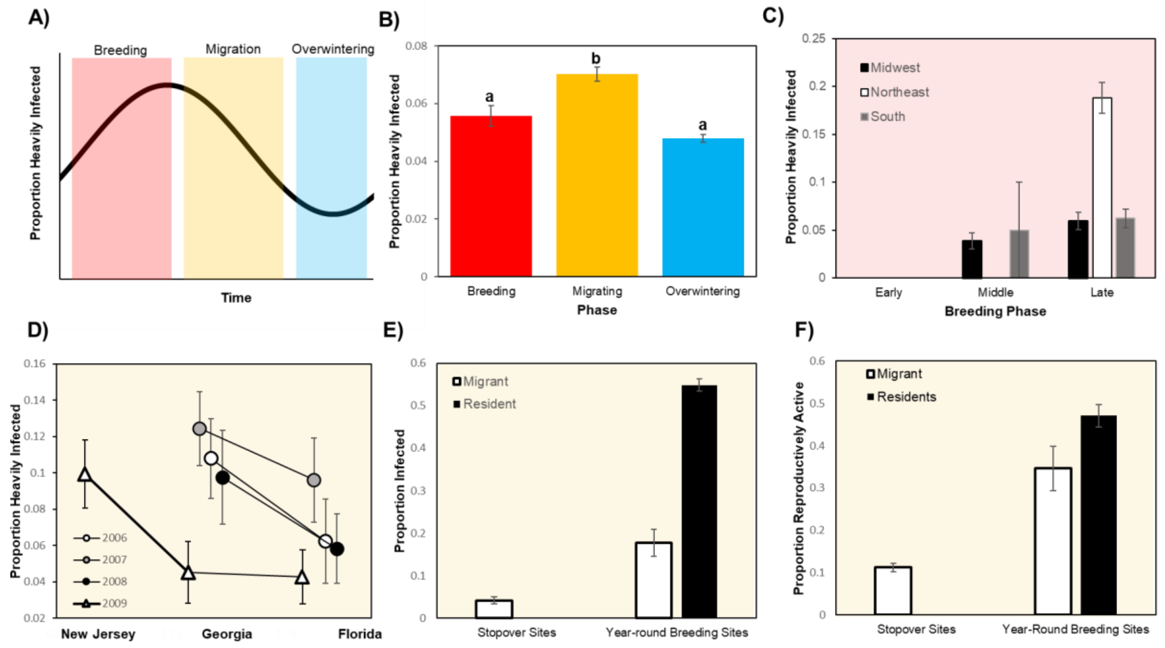

Figure 2.2: Monarch-protozoan interactions throughout the annual migration cycle. A) Hypothetical changes in parasite transmission and prevalence (solid line) in relation to the monarch's annual cycle: breeding, migration, and overwintering. B) The average proportion of heavily infected eastern North American monarchs from 1968 – 2019 by migration phase, showing that infection prevalence is lowest among overwintering (post-migration) monarchs. Letters above bars indicate significant differences (α = 0.05). Adapted from (Majewska et al., 2022). C) Proportion of heavily infected monarchs measured in the 2009 breeding season in three geographic regions. The observed increase throughout the season was also found in the three previous years (not shown). Note that south in this figure excludes the region of year-round breeding. Adapted from (Rebecca A Bartel et al., 2011). D) Decrease in the proportion of heavily infected monarchs along their eastern migratory journey from 2006-2009 with New Jersey being the closest location to the migration start and Florida being the furthest. These results suggest that heavily infected monarchs fail to advance (or drop out) during the fall migration. Adapted from (Rebecca A Bartel et al., 2011). E) Proportion of infected monarchs between migratory stopover sites and year-round breeding sites, sampled during the fall migration in Texas. The year-round breeding sites have significantly higher infection rates for both migrants (open bars) and resident monarchs (closed bars), as determined from wing chemistry assays. F) Proportion of monarchs that are reproductively active between migratory stopover sites and year-round breeding sites. Migratory monarchs (open bars) that encounter residents (closed bars) in tropical milkweed patches have higher rates of reproductive activity and thus are more likely to drop out of the migratory population. Both E and F are adapted from (Satterfield et al., 2018).

Parasites and monarch migration in a changing world

The North American monarch migratory phenomenon is quickly changing. Over the last two decades, some monarchs have stopped migrating and have taken up residential lifestyles along the Atlantic Coast, the Gulf of Mexico and the California coast (Figure 2.1A) (Howard et al., 2010). This is a result of increased temperature and milder winters, as well as year-round milkweed availability. As milkweed habitat declines, nature enthusiasts are eager to provide habitat in their yards by planting nectar and host plants. A popular milkweed used is the non-native tropical milkweed (*A. curassavica*), which is attractive, easy to grow, and commonly sold by nurseries. Unlike most native milkweeds that enter dormancy in the fall, tropical milkweed persists, even growing year-round in mild climates. Further, now some native species (*A. fascicularis)* are starting to become persistent during warming winter seasons.

Monarch winter breeding prevents migratory escape, and resident populations in the southern coastal U.S. are characterized by sky-rocketing parasite prevalence, upwards of 80-90% (Satterfield et al., 2015; Satterfield et al., 2016). While tropical populations of monarchs can apparently sustain high infection prevalence (de Roode et al., 2019), high prevalence in North America can negatively impact migration: as discussed here, infected breeding populations can spread their parasites to migratory monarchs, and thereby reduce overall migration success. To mitigate these negative effects, monarch researchers are increasingly calling for the planting of native milkweeds, the vast majority of which naturally die back in the autumn, or for cutting down tropical milkweeds in fall and winter to reduce the likelihood of pulling monarchs out of their migratory phenotype.

We underscore the need to consider the effects of parasite infection when formulating monarch conservation strategies, and to discourage practices that are known to amplify transmission. Protozoan infections have increased, on average, three-fold since 2002 (Majewska et al., 2022). Activities that have become popular with the general public, such as captive rearing of caterpillars in efforts to ‘raise the migration’, can increase parasite transmission from adults to caterpillars when monarchs are raised in close quarters and containers are not sanitized carefully between generations. The potential crowding of monarchs into smaller breeding habitats in urban areas, and diminished migratory behaviors associated with mild winters and year-round breeding habitats, could also increase future parasite transmission. Because higher infection levels can feed back negatively on monarch migration, greater attention is needed to monitor parasite infection and mitigate the unintentional spread of parasites.

Outstanding questions and areas for future work

While it is clear that infection results in migratory culling and drop-out in eastern North American monarchs – and to a lesser extent in western monarchs – the role of migratory physiology and cognitive processes in these phenomena remains unknown. In some animals, infection can cause cognitive changes, ranging from perception, processing, and motivation to act on environmental information (Townsend et al., 2022). Negative cognitive effects might affect perception (how well monarchs can navigate), migratory motivation (willingness to conduct the journey) or environmental perception (detecting the cues that activate migration). To better understand this, researchers could study the effects of parasite infection on diapause induction, lipid accumulation and utilization, hormonal changes and circadian clock regulation related to migration phenotypes (Iiams et al., 2019; Zhu et al., 2009). Additionally, researchers could compare the orientation behavior of infected and uninfected monarchs on flight simulators, in outdoor flight cages, or using long-distance tracking technologies (Parlin et al., 2021; Wilcox et al., 2021).

Researchers have uncovered several ways that parasites affect monarch migration, but a need remains to quantify selective pressures on parasites arising from migration (Box 1). Past work showed clear evidence for genetic variation in virulence among *O. elektroscirrha* strains, and found that parasites from eastern migratory monarchs were significantly less virulent than those from populations in California and Hawaii (Rebecca A Bartel et al., 2011; de Roode & Altizer, 2010). This is consistent with the expectation that migration selects for strains of lower virulence, which makes sense given the importance of monarch survival during migration and overwintering for parasite persistence. Importantly, an open question remains as to whether virulence increases have occurred in parasites from newly established resident monarchs, and whether relaxed selection is strong enough to overcome presumably high gene flow between parasite isolates from migratory and resident populations.

Finally, a need remains to explore how coupled migrant-resident interactions influence, and are affected by, monarch-parasite interactions. For example, during spring recolonization, migratory monarchs fly through areas with resident breeding monarchs in the southern US, laying eggs in resident patches with high levels of parasite contamination. Careful monitoring of monarch abundance, distribution and infection levels can help determine the extent to which spring migrant progeny become infected with parasites sourced from resident monarchs. Furthermore, modeling approaches are needed to explore how coupled migrant-resident interactions affect parasite transmission dynamics and the longer-term persistence of monarch migration and resident behavior. These models can account for competition and parasite transmission across a network of resident and seasonal breeding habitats, and include processes such as migratory drop-out, migratory culling, and the potential for parasite evolution. Such approaches could explore scenarios under which climate warming and urbanization expand the extent of resident breeding habitat, and how management strategies and public outreach efforts that decrease resident breeding habitats will influence monarch abundance and infection prevalence in future decades.

Box 1: Reciprocal effects of parasitism and migration

Research on the interaction between parasitism and migration has heavily focused on the effects on monarchs. However, parasites also experience selective pressures from monarchs and their migration. For example, one prediction is that parasites in migratory monarch populations may evolve lower virulence levels, which would reduce the intensity of migratory culling and thereby ensure parasite overwintering survival and transmission. Consistent with that prediction, previous work showed that parasites from migratory populations and monarch populations that migrate larger distances display lower levels of virulence than those from resident populations or from migratory populations that migrate shorter distances (de Roode & Altizer, 2010; Sternberg et al., 2013). However, with the planting of non-native milkweeds and climate change providing more year-round breeding habitat, more resident populations have formed, reducing the selection pressure against high virulence and migratory culling. How this will affect virulence evolution is an important question that should be addressed with future studies.

Another prediction is that parasites in migratory populations have evolved greater durability and environmental persistence than those in non-migratory populations. When studying the persistence of parasites under different conditions in the laboratory, it was found that lower temperatures, as experienced by parasites on overwintering monarchs, results in higher longevity of parasite oocysts (Sánchez et al., 2021). However, the same study did not reveal clear differences in the longevity of parasites from monarch populations that vary in their migratory behavior.

Other outstanding questions relate to the population genetics of parasites. While it is known that monarchs can passively exchange parasite oocysts when huddled together at their overwintering sites, we do not yet know the effects of this passive transfer on the genetic mixing of parasites. Moreover, because many infected monarchs do not make it to the overwintering sites, parasites in migratory monarchs experience a bottleneck on an annual basis, with potentially important consequences for their adaptability and evolution. Exploring these questions will be aided by the recent availability of the *O. elektroscirrha* genome (Mongue et al., 2023).

CHAPTER III

Inferring the relative importance of navigation and landscape effects for migratory populations using agent-based models

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Submitted

Abstract

Seasonal migration is a vital behavior for numerous animal species, and provides ecological services such as seed dispersal, pollination, and resource influxes. Moving populations represent unique challenges for descriptive and predictive population dynamic models given the importance of both time and space. This study focuses on modeling two navigation strategies—true navigation and vector navigation—to describe the hypothesized migratory success and distribution structures of migrating populations. True navigators are hypothesized to use a combination of location and directional information to reach specific destinations, while vector navigators follow consistent directions throughout their journey, without altering these directions with respect to their destination. Although these navigation strategies have received much attention from migration biologists, we lack a framework to describe the spatial and temporal patterns of animals using these strategies, impeding our ability to distinguish between them. Here, we use a combination of agent-based models (ABMs) and species-distribution models (SDMs) to simulate the spatio-temporal distribution of migrating animals and compare simulated and observed data to compare migration strategies directly and under various environmental conditions. Our simulations demonstrate that there are distinct distribution patterns for each navigation strategy based on the types of landscape migrants travel

through, highlighting the importance of including such landscape information in modeling approaches. In a case study on monarch butterflies, our ABM simulations aligned closely with opportunistic, publicly sourced observed migration patterns, validating vector navigation as a plausible strategy in this species. However, our results also reveal potential limitations and biases in our data sets, namely how preferential sampling needs to be accounted for in these predictive models, emphasizing the need for further research into sampling methodologies. Ultimately, this study showcases the utility of combining SDMs and ABMs to predict migratory distributions.

Introduction

Billions of animals undertake long-distance seasonal migrations (Dingle, 2014). The energetic demands of migrating these large distances are immense and require physiological changes from the navigator. Hypothetically, such investments are offset by more favorable climates, predator avoidance, lower disease risk, and increased reproduction (Altizer et al., 2011; Kendzel et al., 2023; L McKinnon et al., 2010). Moreover, migrating species provide ecosystem services such as seed dispersal, crop pollination, and resource influxes for other animals and decomposers; as such, these movements are crucial for community and ecosystem functioning (Horns & Şekercioğlu, 2018; Kremen & Ostfeld, 2005). Despite their value, many migrating species are threatened and difficult to conserve given their large geographic range, multiple habitat requirements, and their ability to migrate across political boundaries.

The factors responsible for a successful migration are important for understanding and conserving these species and these can vary considerably based on distance, sensory capabilities, habitat requirements, and the overall navigation strategy used to complete the journey (Abrahms et al., 2019; Hays et al., 2022; Helm & Muheim, 2021; Kauffman, Aikens, et al., 2021). Here, we do not try to explain the diversity of these factors but instead focus on two historically discussed and extensively studied navigation hypotheses: true navigation and vector navigation. True navigators appear capable of orienting toward their migratory destination regardless of their current location and even in unfamiliar territories (Able, 2001). Often, this strategy is conceptualized as animals with a perception of direction (compass) and location (map sense). Vector navigators only have a perception of direction, and thus, maintain a consistent average direction throughout their entire migration (Berthold, 1991; Mouritsen, 1998). This preferred migratory vector is isolated via environmental cues that convey directionality (Kramer, 1950; Mouritsen & Larsen, 2001; Schmidt-Koenig, 1990; Ugolini et al., 2003); differential success in the accuracy of selecting this orientation results in errors and variation between individuals, thereby increasing the average spread of the population over longer migratory distances. The mechanisms for true navigation remain unresolved, and there is debate on the validity of the hypothesis (Putman, 2021); however, it is clear that some species seem capable of extreme precision (reaching small, specific destinations from thousands of kilometers away) that the use of vectors alone cannot explain (Avens et al., 2003; Lohmann et al., 2004; Lohmann et al., 2012). Possible mechanisms for the strategy are a magnetic map sense (Gould, 2015; Hays et al., 2022; Keller et al., 2021; Naisbett-Jones et al., 2017), learning and memory (Guilford & Biro, 2014; Menzel et al., 2005), olfaction (Pollonara et al., 2015; Reynolds et al., 2015), or some combination of context-dependent environmental information. Typically, true navigation is hypothesized to be the more accurate of the two strategies, with individuals using this strategy predicted to have a smaller spatial spread that is more localized on specific habitats or “destinations” than what would be predicted with vector navigators (Figure 3.1).

As two different processes, vector navigation and true navigation should result in different observed population-level patterns of location. A fundamental goal in ecology and conservation studies is to describe this pattern and seek to infer the process responsible for generating it (Vellend, 2010). As such, it should theoretically be possible to infer strategy from the observed patterns of migrating animals. Mathematically, the pattern for vector navigators over a homogeneous landscape has been modeled as a parabolic function, where the expected spatial spread increases with migratory distance (Figure 3.1). Specifically, if we assume that migrants' orientations are approximately normally distributed around their preferred migratory direction, 68% (1 standard deviation) of the population should be within this parabolic function for a given distance (Mouritsen & Mouritsen, 2000). This model has been used to describe the spatial spread of several vector navigating bird species (Mouritsen & Mouritsen, 2000). Unfortunately, there is no expectation model for the geographic distribution for true navigators and there is very little spatial nuance captured with the parabolic function (i.e., it does not predict locations of high or low density or capture the spatial pattern except for spatial spread). Furthermore, the expectation model for vector navigation has no way to incorporate stochastic environmental changes which may limit or shift viable migration pathways through time and thus change the expected geographic spread of the migration. As such, migration

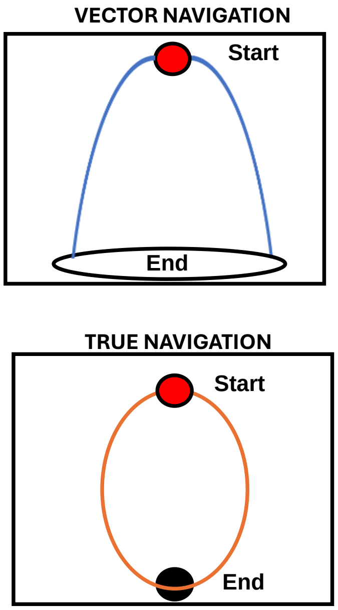


Figure 3.1: Hypothetical population level accuracy for the different navigation strategies. Blue and orange lines represent the population's spatial spread as the it moves away from the start location. The end locations can be species specific habitats or environmental conditions.

researchers currently have no way to use known biological responses to predict migrator migration patterns, ranges, or pathways.

Shifting from the existing parabolic functions over simplified landscapes, we pose that species distribution models (SDMs) describe the spatial patterns of migrants more effectively (Peterson et al., 2015). SDMs are increasingly popular for their predictive capabilities to project geographic range shifts under climate change (Wiens & Zelinka, 2024) and prioritize conservation efforts (Rathore & Sharma, 2023). These models are often used to answer two related questions simultaneously with differential success: one, how are the observed data distributed spatially (pattern description: highly effective), and two, what is the process responsible for that distribution (process description: less effective and typically based on correlative inference)? Despite limitations of this modeling approach as a result of data quality issues, positional uncertainty, and generalizability (Cayuela et al., 2009; Naimi et al., 2014; Vaughan & Ormerod, 2005), SDMs can be developed to include environmental factors and landscape effects to allow some inference of the underlying processes that produce observed data. For example, the distribution of migrating populations is certainly correlated with environmental factors such as viable movement corridors or access to resources. Using known physiological constraints (say, a need to access freshwater sources while moving) and the environmental factors as covariates (location of rivers, ponds, and lakes), SDMs can help predict presences in locations where there are otherwise no observations. However, an SDM is ultimately a pattern description based on where the species was seen and seeks to infer the process responsible for the generated observed distributions based on the spatial distribution and intensity of the covariates used. Thus, the SDM approach provides more spatial nuance when describing populations but still has limitation for detailed description of the underlying migration process, especially when the underlying processes vary over space (for further discussion on this limitation in correlative spatial models and discussion on scale see (Fotheringham & Sachdeva, 2022)).

To address the process description gap and the gap in our inability to predict migratory locations from known biological responses and landscape features, we propose using agent-based models to simulate migratory patterns from the hypothesized processes of navigation and compare these to observed location data. By fitting SDMs to observations of a given species, we can calculate how well that model performs when presented with results of simulations using varying navigation strategies and environmental responses. To highlight the utility of such an approach, we performed two experiments, one completely in a simulated landscape and the second using the migration of the monarch butterfly (*Danaus plexippus)* as a case study. North American monarch butterflies undergo one of the most popular migrations of the animal kingdom (Gustafsson et al., 2015; S. M. Reppert & J.C. de Roode, 2018), with up to hundreds of millions of butterflies migrating up to 4,500 km to reach their overwintering sites in central Mexico (L. P. Brower, 1995; Flockhart et al., 2017; F. A. Urquhart & N. R. Urquhart, 1978). While monarchs are best known for this eastern migration, monarchs that inhabit breeding grounds west of the Rocky Mountains migrate shorter distances to overwintering sites along the California Pacific Coast. Many western monarchs reach the California Coast by flying less than 500km, although some may fly over 1,400km (Yang et al., 2016). This smaller distance migration will be the focus of this study given its relatively lower computational burden. The specific locations for overwintering of the west-coast monarchs were provided by the Xerces society and can be found in the supplement.

Thus, the framework proposed can provide new, spatially explicit, insights into migrating populations that otherwise could not be explored with previous modeling approaches or behavioral assays. Our proposed approach leverages the strengths of both model strategies: using SDMs to describe patterns and ABMs to create predicted results under varying processes. This allows us to create hypothetical, context-dependent expectations of predicted geographic locations based on various navigation strategies and landscape effects.

2. Methods

The ABM model description follows the ODD (Overview, Design concepts, and Details) protocol for describing agent-based models (Grimm et al., 2020). The model was implemented in R version 4.3.3 and the code to simulate both the simulation experiments and the monarch case study are stored on GitHub. For a full list of packages required, and the covariate sources see supplemental table S3.1.

2.1 Purpose and Pattern

2.1.1 Purpose

The proximate purpose of the model was to predict the spatial spread of migrating animals at the end of their migration under varying navigation strategies and landscapes. The ultimate purpose of the model, which is presented as follow-up work, was to predict this pattern through time, during the entire migration, and with changing landscape features.

2.1.2 Pattern

We evaluated our model by its ability to reproduce the spatial range pattern of animals after they completed their migration. We made the decision to focus on the end because the largest predicted difference between the navigation strategies was at the end of the migration (Figure 3.1). Furthermore, for many species, particularly small migratory insects who cannot be tracked over time, the only information available was opportunistic observations, which only provides time and location. Thus, for these types of datasets, the spatial range provided was a snapshot in time and not a tracked pathway.

2.2 Entities, state variables, and scale

2.2.1 Spatial scale

For all simulations, the area of study was defined as a spatially explicit grid with a side length of 1 km, A. The migratory destination, D, and start location, L_0, were within the study region, $D \in A$ and $L_0 \in A$. Both the start and end locations could be single points, multiple points, or complex spatial vectors that could match geographic features or habitat conditions. In our simulation experiments, the landscapes were small, 153x153 (23,409 km²) cells with an impassable barrier on each of the four sides. Cells had values that indicated their relative favorability for agents to move toward them (stored as probabilities). Six landscapes were used: an even landscape with all values the same, a randomly generated landscape, a channel with preferred values aligned in the middle, a divergent landscape with poor values aligned down the center of the landscape, and a complex, real-world area in the North Cascades National Park, Washington, USA (Figure 3.4). The small size was chosen to develop and test the strength of the landscape effect by seeing how much the migrating populations were shifted while using the different navigation strategies. Lastly, in our real-world case study, using the monarch butterfly migration, the landscape was the large western migratory range for the monarch and was 2119x1882 (3,987,958 km^2) to assess how well the model replicated a well-known migration while simulating true and vector navigation.

2.2.2 Entities

The following entities were included in the model: agents representing migrating individuals and grid cells representing the landscape with elevation information.

2.2.3 State variables

The state variables for the agents and the cells were listed in Table 3.1. Because there were so many cells, static cell values were treated as state variables. Furthermore, since the start location could vary between agents, it too was considered a state variable.

2.3 Process overview and scheduling

2.3.1 Processes

The model was developed to be generalizable and cover the totality of a migration for a given species. It comprised three processes: one related to cells (landscape effects), and two regarding the migrants themselves (orientation and cell selection).

Table 3.1: Agent and cell state variables.

Entity	Variable Name	Variable type and units	Meaning
Agent	nd	time (days), dynamic	The current number of days simulated. Updated after all movement steps for a single day.
	start	X,Y coordinates, static	Cell where the migrant starts their journey.
	location	X,Y coordinates, dynamic	The cell the agent starts their current movement step at. Updates at the end of each movement step.
	is_within?	True/False, dynamic	Checks if current location is at or within the end range at the begin and end of each step.
	ns	time (movement per time), dynamic	The current number of movement steps made per unit time. Updates at the end of each movement step.
cells	landscape	probability, static	The values of the landscape, converted to movement probabilities. These probabilities are used to modify the agent's movement choices toward that cell. The conversion is described in section 2.5.1 and the use of these values is described in section 2.7.2

2.3.2 Schedule

For each time step (1 day), the process of migration followed the given order (Figure 3.2). Model entities (agents and cells) were processed independently of one another, and changes in the state variables were updated immediately. The submodels implementing these processes were described in detail in section 2.7. Note, we denoted two phases that grouped related model actions in line with previous mathematical models for migration: first, the orientation phase, and second, the movement phase (Mouritsen and Mouritsen, 2000). The order of these phases assumed that the general migratory orientation was the default orientation when the landscape itself had no influence. The result of both phases was a single step. For simplicity, we assumed each step was independent and time was discrete. The total summarized results of all steps for all agents represented a migrating population and followed the following order:

1. Each agent determines their current time and location
2. True navigation: orientation phase. Generates a circular probability distribution with the mean angle toward the destination.
3. Vector navigation: orientation phase. Generates a circular probability distribution with the mean as a constant angle.
4. Modify probability distribution with the values of the landscape surrounding the current location if available.
5. Select an orientation from modified distribution.
6. Move to the cell corresponding to the orientation selected.
7. Determine how many steps are left in a single day. If there are more, cycle through 2-6. Once the number of steps is exhausted, continue to the next day.
8. Agents cycle through 1-7 until the number of days is exhausted or they reach the end location.
9. Plot final locations for all agents.

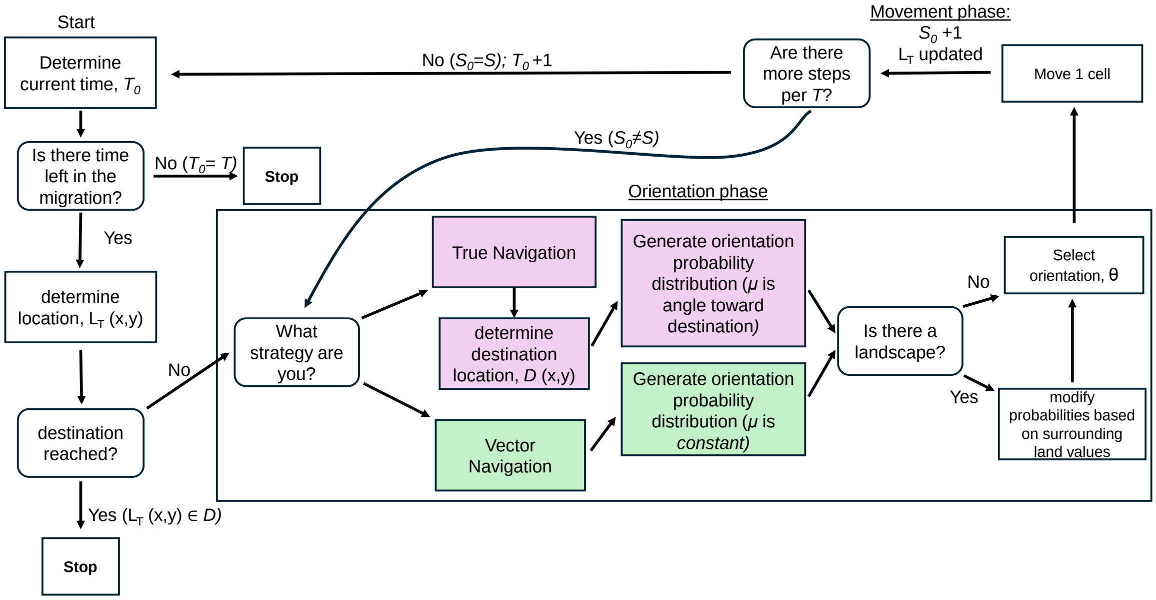


Figure 3.2: Agent-based model flow chart for Vector (green) and True Navigators (purple). In these simulations, the only difference between the two navigation strategies is that true navigators' mean orientation, μ, is dynamic and is updated based on the location of where the agent is compared to its destination. For a complete parameter see Table 1.

2.4 Design Concepts

2.4.1 Basic principles

This model was designed to generate the predicted spatial distributions of migrating animals using different navigation strategies, and to compare these distributions to empirical observations. Without such a model, it was impossible to infer navigation strategy from observed data. For example, a prevailing assumption in migration and navigation research was that migrants reaching specific locations in high numbers was evidence for true navigation (Gould and Gould, 2012). However, such a conclusion made implicit assumptions about migration success that may or may not have been realistic. Having our model based on the basic principles of navigation and landscape choices and parameterizing it to a migratory animal provided real-world, context-based predictions for geographic ranges under the varying navigation hypotheses, so that it became possible to test the long-standing assumptions of navigation research using a wide range of taxa.

2.4.2 Emergence

The primary outcome for the model was the population level geographic distribution pattern for a migrating population after the completion of their journey. This included the final spatial spread and success rates of reaching known migratory destinations. These were then compared to the observed spatial spread for the animal of interest.

2.4.3 Adaptation

The model migrants had one adaptive behavior that was shared regardless of navigation strategy: whether to move to a location based on the landscape values surrounding their current location. The decision to move was modeled via a min-max conversion because this conversion maintained the original relationship of the landscape values, altitude in meters, and preserved the range of the values. Furthermore, true navigators adapted their orientation throughout the entire journey, always orienting toward their primary destination.

2.4.4 Stochasticity

Stochasticity was incorporated into the process of orientation as the circular probability distribution. Selecting from this distribution, on average, resulted in orientations toward the mean direction with variation parameterizable to a given species.

2.4.5 Observation

Population level observations were made at the end of the migration as a measure of spatial spread. The predicted densities were modeled as described in section 2.8 “analysis” and graphed over the entire spatial study region.

2.5 Initialization

2.5.1 Landscape initialization

The initial state of the landscape was converted to movement probabilities. Here, we used a global min-max normalization that changed the altitude to have a range from 2 to 0.016 with lower altitudes closer to the 2 and high altitudes approaching 0.016 (equation 1).

$$normalized = 0.016 + \frac{(altitude_i - \max altitude) * (2 - 0.016)}{\max altitude - \min altitude}; \text{equation 1}$$

This normalization method converted each cell value at, i, location. It was chosen because it preserves the relationships between the original data points in terms of their relative order and spacing but changes their scale to one that can be used as probability modifiers as described in the section 2.7.2.

2.5.2 Agent initialization

All parameters and their values are summarized in Table 3.2.

For the simulation experiment, agents started their migration at a set location at x,y-coordinates of (77, 100). The end location, or destination, was set at (77, 5), or 95 cells directly south of the start location. For vector navigating simulations, the mean migratory direction was "south," or 180 degrees from true north. True navigators had dynamic orientation that updated throughout the simulation instead of being set at the start. For both simulation types, agents had a k-value, the accuracy in selecting their migratory direction, equal to 1.225. This k was chosen from the value calculated for vector navigating juvenile birds (pied flycatchers) and served as a reasonable accuracy parameter for our simulations (Mouritsen, 1998). For a description of generating the distribution of orientations, see section 2.7.1. Each agent was set to take 1 step per day, and their migration was 150 days long. This allowed each agent to travel a total of 150 cells in any direction. These values were set but can vary between agents if both were modeled as random variables. The 150 number was selected because it resulted in an average y-movement away from the start location of 100, meaning that, on average, the agents would have enough movements to reach the destination. A total of 100 agents were simulated per navigation strategy on the 6 different landscapes for a total of 1200 simulated agents in this experiment.

For the monarch case study, each simulation consisted of a population of 1000 agents that were randomly assigned a start location within the states of Oregon, Idaho, Washington, Nevada, and Utah, which represented western monarch summer breeding ranges that primarily migrated to western overwintering locations (Yang et al., 2016). Arizona was not included because monarchs there contributed to both eastern and western populations. The end location, or destination was defined as the areas 10 km around the overwintering locations (10 cells), the primary one being Pismo Beach. Vector navigating monarchs had a mean orientation of 225° aligned with a previously estimated monarch orientation, measured in the eastern North American monarch populations (Mouritsen and Frost, 2002). These monarch populations were genetically identical (Talla et al., 2020), and thus we had no reason to assume that this orientation would be different in the western monarch. We simulated a total of 5 populations: 1) vector navigators with a k =1.225, 2) true navigators with a k = 1.225, 3) vector navigators that were half as accurate as 1) with a k = 0.61, 4) true navigators with a k = 0.61, and 5) true navigators that were 1/8th as accurate as 2) with k = 0.15. The first k =1.225 was used based on another flying vector navigator, the pied flycatcher, as described above. We then altered the parameter, lowering agent accuracy, to test how sensitive the simulations were to this value. After seeing that true navigators fit better to the observed monarch distribution, we further lowered their k-value significantly to k = 0.15. Each agent had their average steps split between 60 days, calculated as described in section 2.7.3, so that each would travel on average 1400 km from their start location (the maximum range of the western monarch migration). To keep the simulation computationally simple, we used a single landscape feature to modify the agent's behavior. Here, we used altitude because mountain ranges were generally believed to form migration barriers for monarchs (Freedman et al., 2021).

Table 3.2: Simulation Parameters

Parameter	description	Simulation case study	Monarch case study	Monarch Source
θ	Orientation Selected	Updated at each step	Updated at each step	-
T	Total time	150	60	Yang et al., 2016
N_S	total number of steps available for migration	Equation 3	Equation 3	Mouritsen and Mouritsen, 2000
S	number of steps per time unit	1	T/ N_S	N_s/T
A	Study area	153 x 153	based on observation data	iNaturalist
D	Destination location	77, 100 (x,y)	based on publicly available overwintering locations	Xerces Society
L_0	Start location	77, 5 (x,y)	based on summer breeding range	Yang et al. 2016
k	circular distribution concentration	1.225	0.15, 0.66, and 1.225	Mouritsen and Mouritsen, 2000
u	mean direction	180	225	Mouritsen and Frost, 2002

2.6 Input data

For both the simulation experiments and the monarch case study, the input data were the landscape values, loaded into the environment prior to the simulation being run. For the simulation experiments, these were the six landscapes as described in section 2.2.1. For the monarch case study, this was the western monarch landscape range, also described in 2.2.1 and edited as described in section 2.5.1. Furthermore, the overwintering locations for the monarch western migration, the areas considered to have completed a migration, were loaded into the environment as a complex spatial vector corresponding to its locations and shape. The files for these can be found in the GitHub repository.

2.7 Submodels

2.7.1 Orientation phase

At the start of this phase, each agent generated a circular von Mises probability distribution for all possible 360° orientations, and selected a single orientation, θ, from this distribution (equation 2).

$$f(\theta \mid \mu, k) = \frac{exp(k\ cos(\theta - \mu))}{2\pi I_o(k)};\ \text{equation 2}$$

where $I_o(k)$ was a modified Bessel function of the first kind of order 0, μ was the expected angle of the function and in our case the mean migratory direction, and *k* was a measure of concentration and was analogous to the reciprocal of variance in a normal distribution. Randomly sampling from this distribution at each step created independent migratory orientations for each agent in line with previous models of the behavior (Mouritsen, 1998; Mouritsen & Mouritsen, 2000).

Vector navigation was simulated by setting μ as a constant angle that, for real-world examples, was matched to species-specific mean orientation. For simulations, it was set to be the direction toward the destination from the original start location. True navigation had a dynamic μ, with the mean always changing at the start of the orientation phase to point toward the destination regardless of the agent's position. Thus, for true navigation, μ was updated at each step and a new probability distribution was generated. All circular distributions were generated with the R package “circular” (Agostinelli & Lund, 2023).

2.7.2 Landscape effects

Since migrants take cues from their environment to inform their movements along with their overall migratory direction, μ, we can use covariate information to alter the behavior of agents. In the orientation phase, we generated a probability distribution of the set of possible orientation angles. In gridded data, if we assume an agent is in the center of a grid value, then the direction toward the center of each of the surrounding cells represents our set of possible movement directions. By having the agent consider the values of these eight cells, it can weigh their relative quality with respect to movement. Converting these qualities to probabilities, we then multiplied the orientation distribution by the probabilities to move to specific grid cells. Here, grid cell values > 1 increased the probability and values < 1 decreased the probability of movement toward that cell (Figure 3.3).

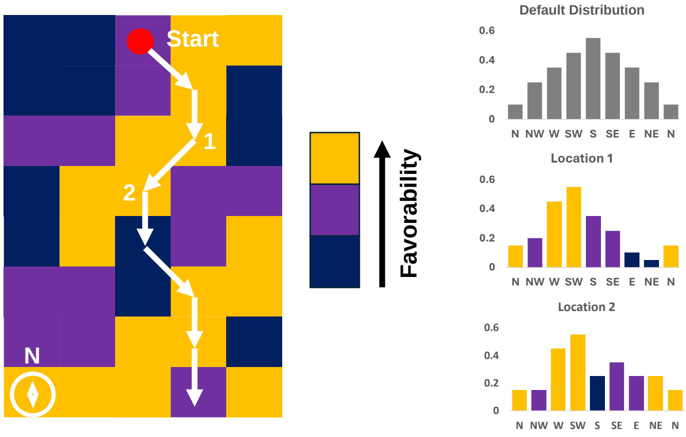


Figure 3.3: Conceptual diagram of landscape effects incorporated into a simulation. White arrows indicate the choice direction and movement of an agent. At each step, the values of the 8 cells surrounding the agent are used to modify their default distribution (grey distribution). North is included twice because the circular distribution is cut and transformed into a linear distribution for illustrative purposes. At location 1, the agent chose to move to the southwest cell. At location 2, the agent chose to move south, even though it was an unfavorable cell. This was shown to highlight that though it was more likely to move south-west, movements to unfavorable locations are possible, just less probable.

2.7.3 Movement phase

After an orientation was selected, agents moved in the selected direction by modifying their X and Y coordinates, representing a single step. Here, we had agents move to the center of the chosen adjacent cell. However, continuous movement is possible but additional rules would need to be used when considering landscape effects. The total number of available steps was calculated based on equations 7 and 15 from Mouritsen and Mouritsen, 2000, which described the average number of steps needed to reach an average displacement distance. Modifying these equations to include the maximum range of a migration, we get equation 3.

$$N_s = \frac{Max\ Range}{e^{\left(-\frac{1}{k}\right)}};\ equation\ 3$$

2.8 Analysis

Our SDMs were not directly integrated into the ABMs. Instead, they were used to describe the pattern that our ABMs generated, which made it possible to compare simulations or simulations to observations. To describe these spatial patterns, we used a point-process model to define the spatial density associated with locations of either reported observations of individual monarchs or locations of agents. Specifically, we used a log-Gaussian Cox process (LGCP) model (Møller et al., 1998) with the approach developed by Simpson et al. (2016) and Simpson et al. (2017) and by extension earlier work by Illian et al. (2012). In these models, the locations of observations derive from an underlying spatial point process, with first-order (mean) patterns modeled via an intensity surface (i.e., the expected rate of an observation at each location within the study region). Models were fitted via a hierarchical Bayesian model using integrated nested Laplace approximations to estimate the full spatial posterior predictive distribution of observation locations.

For the monarch case study, we first fitted the LGCP to observations of the monarch during overwintering months. We used opportunistic data from iNaturalist for its broad range coverage. This data set consisted of 3846 “research grade” monarch observations during the overwintering months between November and February through years 2018-2022, west of longitude -115.05° W and within the study region (iNaturalist contributors, 2023). Research grade in this context refers to observations accompanied by photographic evidence with the species identified by more than one user. We allowed the estimated intensity to depend on local landscape covariate information for altitude, human population density, and habitat type in a completely factorial paradigm. The data sources for each of these covariates were listed in Table S3.1. To select which of these models fit best to the observations for monarchs, we used the deviance information criterion calculated for each (DIC) (Spiegelhalter et al., 2002), which balances model fit with model complexity. Using the model with the lowest DIC value associated with habitat conditions (Table S3.2), we tested its performance when presented with the new simulated data for each of our navigation strategies under varying *k-values.* The performance of this model when presented this new data was measured globally with a relative mean square error (RMSE). To compare the local fit and the observed spatial distributions between simulations and observed monarch densities, we took a relative risk ratio (RRR), which compares the deviation of the predicted densities between the simulation and observation at each location (Bithell, 1990). Finally, we provided general data exploration and summarization of quantities of interest such as percentage of individuals that reached migration destinations and percentage of agents too far from these locations to be presumed dead. All models were fitted with the R-packages “INLA” and “Inlabru” (Bachl et al., 2019; Rue et al., 2009).

3. Results

3.1 Simulation experiments

For all simulations and landscapes used, true navigators were more likely to reach the destination than vector navigators, as one might expect. The percentage of individuals ending a single cell away or directly on the end location were presumed to have reached the destination and are summarized in Table 3.2. Of those agents who did not reach the end location, vector navigators were more evenly distributed around the end compared to true navigators who were more likely to be north of this destination (i.e., true navigators who did not reach the end ran out of time; Figure 3.4: predicted distributions). Overall, the distribution pattern for each type of navigation strategy was similar for all landscapes except for the divergent channel which pushed navigators away from the center of study region. The relative risk ratio of observations between

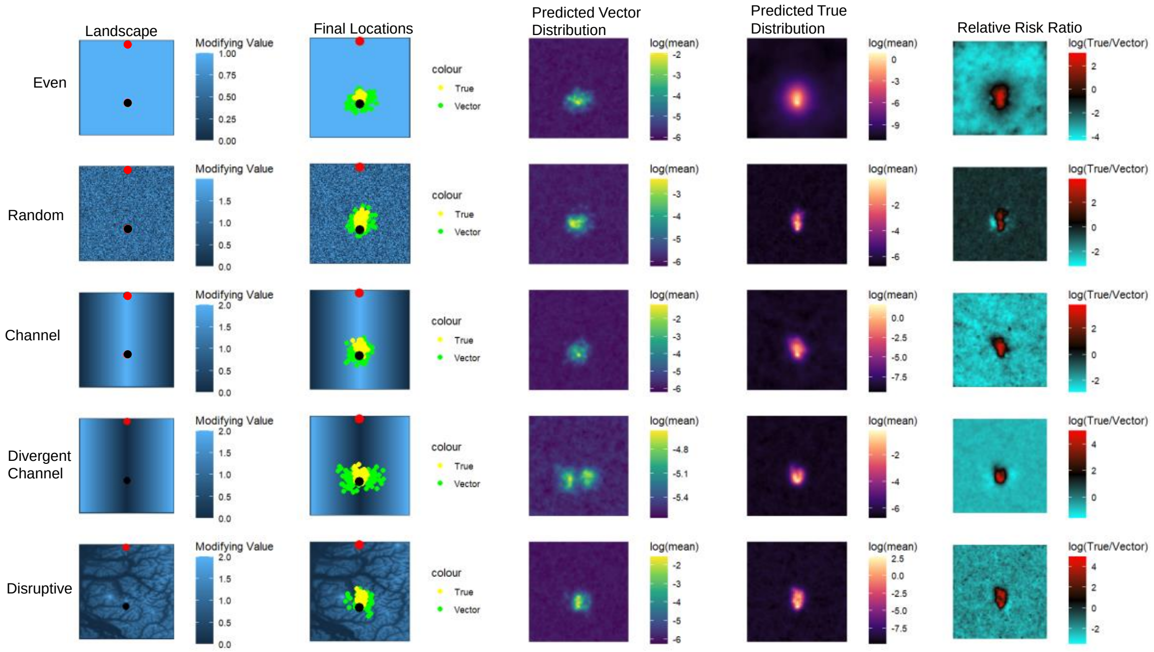


Figure 3.4: Simulated Navigation Strategy Results. For all panels, the agents start on the red dot "north" of the target and end location, the black dot. Vector navigators had a consistent mean orientation of 180° "south" while true navigators had a dynamic mean orientation that was always toward the end. Predictive surfaces for both vector and true navigators did not incorporate the landscape information and thus represent only the density of observations. The relative risk ratio takes the results from the predicted vector and true navigation distribution and compares each at each cell.

true vs. vector navigators highlighted that for each landscape true navigators were more likely to be found near or north of the end location (red) while vector navigators were more likely to be found elsewhere in the study region (cyan).

3.2 Monarch Case study

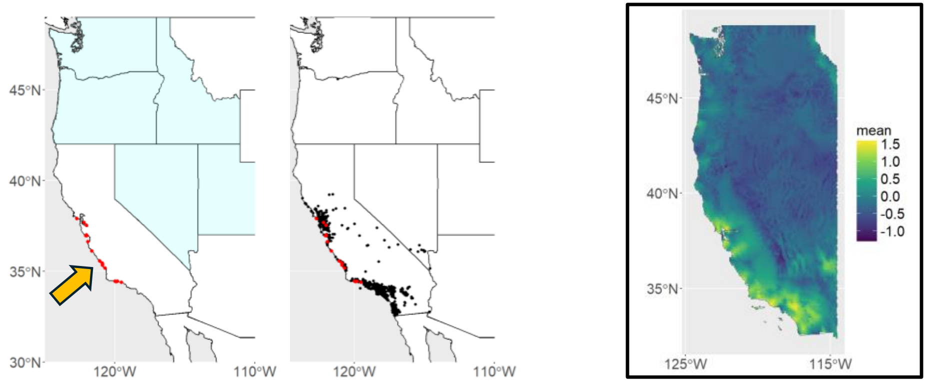
The observed monarch distribution was concentrated along the coast of California in line with expectations (Figure 3.5A and B). The best fitting model, while balancing model complexity, included human population density and elevation as covariates (Table S3.2). Considering this model was comparable to the model with elevation alone and elevation is the only well-fitting environmental covariate, we chose to make our simulations comparisons to the elevation alone model for monarch observations.

Agents who ended their journey by flying out into the Pacific Ocean were presumed dead and thus not considered when comparing to the observed monarch locations. True navigators were less likely to fly into the ocean and were more likely to reach the primary overwintering location, Pismo Beach (Table 3.4). However, the true navigators had the lowest global fit to the observed monarch distribution, even when varying the *k* value (Table 3.4). Initially, lowering the *k* value increased global model fit for true navigators; however, once *k* was lowered significantly, the model's performance decreased (Figure S3.2). Vector navigators, on the other hand, had comparable predicted distributions to the observed monarch distribution (Figure 3.5C). Just as the observed distribution, vector navigators had high densities along the coast of California regardless of *k* value. Vector navigators fit locally more than true navigators (Figure 3.5D). Here, values approaching zero, where observed and simulated predictions are the same, are in gray;

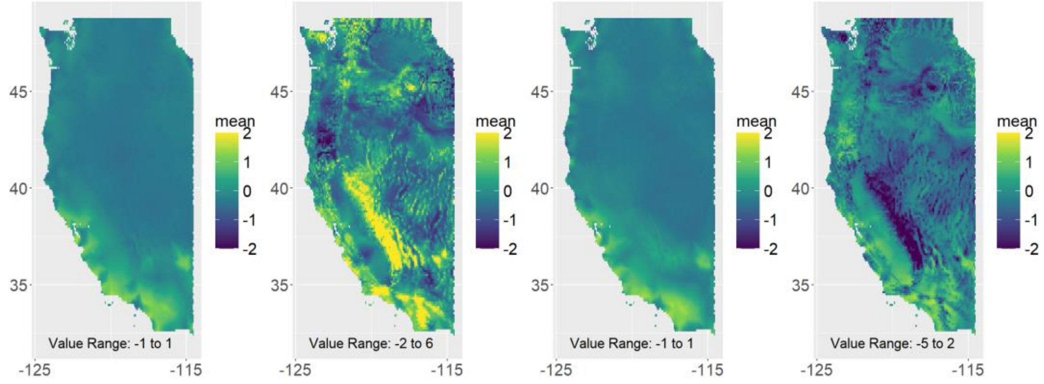
positive values, where simulation predictions are greater than observed, are in red; and negative values, where observed is greater than simulation prediction, are in blue. Thus, for our simulated predictions, vector navigation with $k = 1.225$ provided the best global fit and local fit to our observed monarch distribution. For all end location points, see Figure S3.1.

A) Study Region and Monarch Observations

B) Monarch Observed Distribution



C) ABM Fitted to Monarch Distribution


Vector Navigation k= 1.225

True Navigation k= 1.225

Vector Navigation k= 0.61

True Navigation k= 0.61

D) Relative Ratio between Monarch and ABM distributions

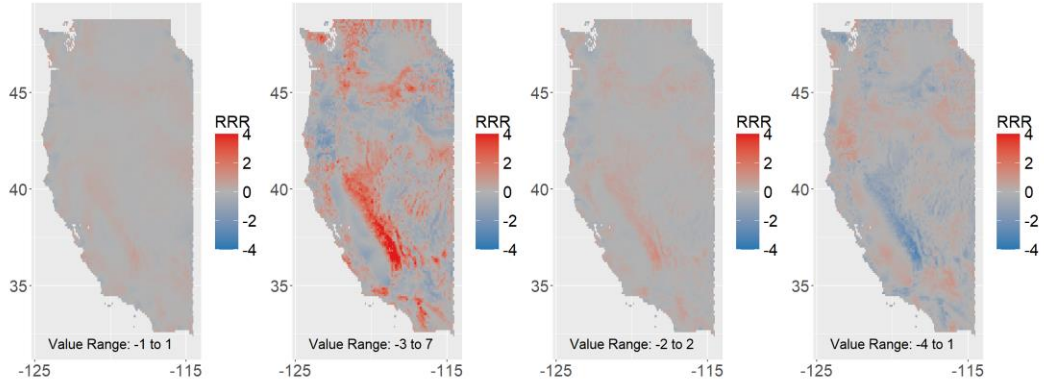


Figure 3.5: Monarch case study results. For all panels, the study region is outlined and based on where simulated agents and monarch observations were located during overwintering months. For panel A, the highlighted cyan region is the monarch summer breeding range as well as the start location that agents are randomly assigned within. The red dots are the overwintering locations, and the arrow indicates the location of the largest overwintering region, Pismo Beach. The black dots are the locations of the observed monarchs during overwintering months. B) the results of the fitted LGCP model for monarch observations. This outlined distribution and the model underlying it is what the simulation results are compared to. C) the predicted distributions based on navigation strategy and *k-value*. Each represents a population of 1000 agents with their end locations fitted to the model shown in panel B) the predicted monarch location model. D) the relative risk ratio, comparing local model performance at each cell, between the monarch distribution and the results of the simulation directly above. Values approaching 0, where the models have the same predicted value, are in gray. Where the simulation is predicted in higher numbers is in red, and where the monarch model predicts higher numbers is in blue.

Discussion

In our simulated case study, we show how different navigation strategies results in different patterns (Figure 3.4: even landscape row). Further, when landscape processes are included, the patterns for both navigation strategies become dependent on the landscape traveled through, and thus both processes (landscape and navigation strategy) should be considered when modeling migrating populations. For example, on the homogeneous landscape, 31% of true navigators reached the destination and were distributed on or just north of the end location compared to only 5% of vector navigators, who were more evenly distributed around the study region. Therefore, in this simplified case, the probability of reaching the destination and the distribution of individuals can be used to estimate the likelihood that a migrant uses a specific navigation strategy. However, on other landscapes, even though our landscape process had a relatively small influence on agent behavior (Figure 3.4), the percentage of agents reaching the end significantly varied; on the divergent channel, where agents were less likely to move toward the center of the landscape, only 10% of true navigators reached the area, which is similar to the approximately 10% of vector navigators who reached the end while on the channel landscape (Table 3.2). If the landscape was not considered in this comparison and we were trying to determine navigation strategy from observed pattern alone, we could thus erroneously assign what is a true navigator as a vector navigator simply based on the low probability of reaching a specific end location and the assumption that if the individual knew where to go, they would reach it. Our results indicate this is not a safe assumption and that one

Table 3.3: Percent of agents reaching the destination on simulated landscapes

	Navigation Strategy	
	Vector	True
Landscape	% reached destination	
Even	5	31
Random	1	14
Channel	10	31
Divergent	1	10
Disruptive	7	27

cannot use the likelihood of reaching a location (i.e., the observed pattern) alone as evidence of a specific strategy without considering the landscape between the start and end locations. This is where the utility of the agent-based model comes into play since it can consider and adjust to context-dependent locations and landscape features to make predictions (i.e., how likely an individual is to take its next movements in a given direction based on the surrounding landscape) that previously could not be incorporated. It is also important to note that while we use the "destination" as the end location, this example could easily apply to specific areas throughout a migration, such as specific refueling and stopover locations often associated with these animals (Guo et al., 2024; Hagelin et al., 2021)

Monarch case study

The results for our simulated predicted distribution for vector navigation aligned with the observed monarch distribution (Figure 3.5C and D). In fact, halving the accuracy of the agents (k/2) did not alter the fit significantly nor did it increase the error beyond what was measured for true navigators (Table 3.4), suggesting that the value used for *k* had little affect on migratory success for vector navigators. While true navigation did successfully reach Pismo Beach in high numbers, only about one percentage reached the other overwintering locations. Furthermore, the strategy's predictions did not capture the total overwintering range for the monarch and thus had low global and local fit (Figure 3.5C and D). Specifically, the predictions from true navigation failed to fit with monarch observations through the Siera Nevada mountain range (Figure 3.5D). Given these results vector navigation emerges as a valid hypothesis to explain the observed migration of monarchs on the west coast. However, below we acknowledge a few limitations that should be researched further to improve model performance.

Table 3.4: Exploratory measures of simulation performance based on navigation strategy

Measure	Navigation Strategy			
	Vector; k = 1.225	Vector; k = 0.61	True; k = 1.225	True; k = 0.61
% Died	5.8	1.8	0	0
% Reached any overwinter	51.7	38.2	48.9	29.5
% Reached Pismo Beach	1.1	0.3	47.8	28.1
Global model fit (RMSE)	0.17	0.24	0.98	0.52

Our simulated vector navigators end their migration north of the 40° N latitude line then is observed through iNaturalist data (Figure S3.1). This involves areas in which monarchs would likely not survive the winter. A possible explanation for this finding is that we made the assumption that monarch vector navigators use a single vector only. However, if monarchs are indeed vector navigators, they may have multiple vectors that shift throughout their migration rather than the single vector of 225° as simulated here. In fact, many vector-navigating animals have multiple preferred orientations based on the stage of their migration (Gwinner & Wiltschko, 1978; Munro et al., 1993). For example, some migratory red-eyed vireo, *Vireo olivaceus,* start their migration in Canada with a preferred orientation of southeast, but once they reach Mexico, their preferred orientation shifts to the south (Sandberg & Moore, 1996). Previous orientation research on the monarch has not focused on these possible changes. Instead, studies worked to isolate the environmental information used to orient which required the removal of other external cues and journey stage context via controlled flight simulator trials (Mouritsen & Frost, 2002). An orientation study that does not remove this landmark information or can track natural monarch migration over large distances could help illuminate how monarchs respond to coastlines, heterogeneous habitats, or geographic barriers. This could then be used to help parameterize future simulated studies. Such studies could also help estimate monarch orientation accuracy as done in the pied flycatcher, whose accuracy was used in this study as a placeholder. Further, we highlighted that our predictive surfaces appear to be biased based on human population size. Our two best-fitting models considered human population density along with elevation (Table S3.2) in adjusting the local estimates of probability of observation (proportional to the estimated intensity in the fitted point process model). Thus, more complete predictive monarch distributions via more detailed SDMs could correct for this bias, via adjusting the LGCP to more closely model an underlying spatial probability of observations made by iNaturalist users.

Going further, the preferential sampling correction literature is extensive and has powerful approaches for correcting such bias (Conn et al., 2017; Diggle et al., 2010; Gelfand et al., 2012). This literature focuses on situations where the probability of sampling is related to the probability of presence. In the monarch example, this could happen if iNaturalist observations are more likely in areas where monarchs are more likely to be found (a reasonable assumption). For moving and migrating populations, whose data are sampled via opportunistic efforts from the public in crowdsourced citizen science data frameworks like iNaturalist, future extensions of our approach could explore incorporating preferential sampling adjustments to correct for this bias. One way to assess this is by simulating a set of migrations via the agent-based model and then sample simulated results with observational bias matching that of the real data sets (e.g., proportional to population density). Using preferential sampling approaches on such simulated data sets with preferential sampling would allow us to see how well such analytic adjustments correct for said bias. Furthermore, since we can overlay sampling paradigms onto the agent-based simulation results, we could propose specific real-world sampling efforts to further compensate for the biases observed.

Conclusion

This study highlights the utility of agent-based simulations for creating predictive distributions of moving populations under different migration strategies and the ability of such models to critically evaluate what information we have for a given species and how well that information can describe links between observed natural patterns and migration processes. With the advances in computational efficiency, these approaches have become easier to parameterize for a given system and serve as a viable and cost-effective way to bridge the results from empirical studies and statistical inference regarding driving processes and parameters. Comparing these simulated results with observations of real migrating populations provides a useful tool in determining the navigation strategies that migrants use to reach their destinations.

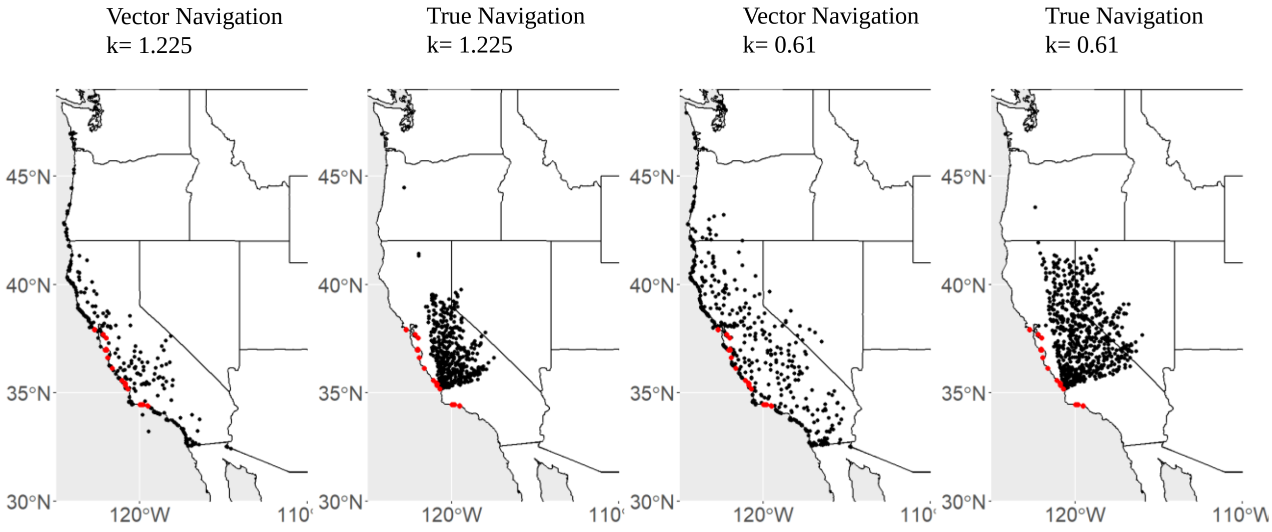
Supplemental Information

Table S3.1: Data sources and R packages used for ABMs and SDMs

RESOURCE	**SOURCE**	**IDENTIFIER**
Deposited Data		
Data on monarch observations	iNaturalist (iNaturalist contributors, 2023)	https://doi.org/10.15468/dl.6yj5bq
Data on simulation locations	This study	GitHub: https://doi.org/10.5281/zenodo.13741315
Data on overwintering locations	Xerxes Society	https://westernmonarchcount.org
Data on elevation	USGS	https://doi.org/10.5066/F7DF6PQS
Data on land cover	Buchhorn et al.	https://doi.org/10.5281/zenodo.3939050
Data on human population density	CIESIN	https://doi.org/10.7927/H45Q4T5F
Software		
R version 4.3.3	R development team	N/A
Code for simulations	This study	GitHub: https://doi.org/10.5281/zenodo.13741315
INLA	Rue et al. (Rue et al., 2009)	https://inla.r-inla-download.org/R/stable
Inlabru	Bachl et al. (Bachl et al., 2019)	https://github.com/inlabru-org/inlabru
circular	Agostinelli and Lund (Agostinelli & Lund, 2023)	https://doi.org/10.32614/CRAN.package.circular
CircStats	Agostinelli and Lund (Lund & Agostinelli, 2018)	https://doi.org/10.32614/CRAN.package.CircStats
raster	Hijmans et al. (Hijmans & van Etten, 2020)	https://doi.org/10.32614/CRAN.package.raster
BBmisc	Bischl et al. (Bischl et al., 2017)	https://doi.org/10.32614/CRAN.package.BBmisc
sf	Edzer (Pebesma et al., 2021)	https://doi.org/10.32614/CRAN.package.sf
terra	Hijmans (Hijmans, 2022)	https://doi.org/10.32614/CRAN.package.terra

Table S3.2: DIC comparisons between varying covariate information in the monarch observation models.

Model	DIC	Change in DIC
Elevation and Human Population Density	-53953	0
Human Population Density	-53943	10
Elevation	-51712	2241
Habitat	-37007	16946
Habitat and Elevation	-36553	17400
Habitat and Human Population Density	-36523	17430
No covariates	-5095	48858
All covariates	44622	98575



Vector Navigation
k= 1.225

True Navigation
k= 1.225

Vector Navigation
k= 0.61

True Navigation
k= 0.61

Figure S3.1: Raw end location data for each simulation.

A) ABM predicted distribution

B) Relative risk ratio between monarch and ABM

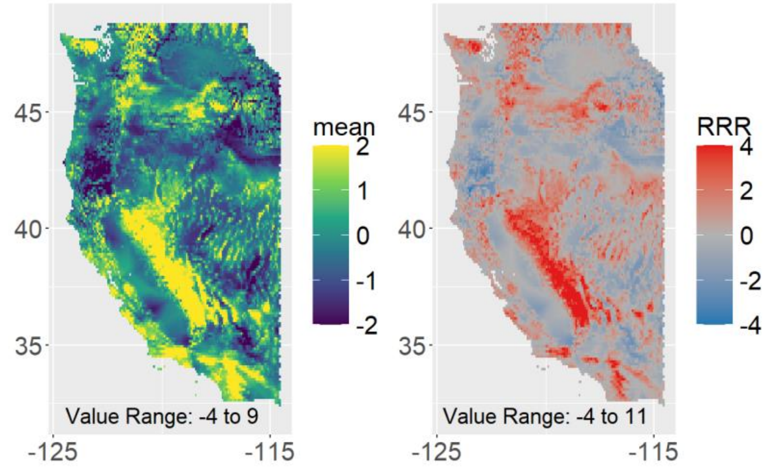


Figure S3.2: Results for true navigation simulations with *k* =0.15. A) the predicted distribution's global fit to the monarch distribution (RMSE) is equal to 1.42. B) the value range in our relative risk ratio exceeds by far the other simulations with a maximum difference between simulation and observations of 11.

CHAPTER IV

Simple behavioral rules can explain the complex migration patterns of monarch butterflies

Mitchell J. Kendzel, Lance A. Waller, Jacobus C. de Roode

Submitted

Summary:

Many animals undertake seasonal migrations, traversing up to thousands of kilometers through ever-changing landscapes. Yet, even with significant advancements in migration research, critical knowledge gaps persist regarding the mechanisms by which these animals navigate toward their destination (Flack et al., 2022). As a case in point, North American monarch butterflies (*Danaus plexippus*) travel upwards of 4,500 km to specific overwintering sites in central Mexico (Steven M Reppert & Jacobus C de Roode, 2018; Urquhart, 1976). The mechanisms enabling this spectacular journey have fascinated researchers for decades (Mouritsen et al., 2013; Oberhauser et al., 2013). Leading hypotheses pose that monarchs either possess an innate ability to navigate to these sites (true navigation) or are guided by landscape features, migrating southwest for most of their journey and fine-tuning their direction as they near their destination (vector navigation) (Reppert et al., 2010). Here, we employed an agent-based model (ABM), parameterized to mimic monarch behavior, to investigate how different navigation strategies and landscape features influence predicted population patterns. We then compared the predicted distributions from these simulations to observed data from iNaturalist. Surprisingly, we found that simpler navigation strategies, where agents either migrated southwest throughout (vector navigation) or adjusted their direction southward mid-journey (multi-vector

navigation), aligned more closely with observed patterns versus those with agents that knew where to go (true navigation). Simulated agents with vector navigation matched with sightings in Texas, Florida, and along the Gulf Coast (iNaturalist contributors, 2023), highlighted known migratory corridors east of the Sierra Madre Oriental (Lincoln P Brower, 1995), and had arrivals at specific overwintering sites. Our results suggest that true navigation is not needed to explain monarch migration and that the use of landscape funnels and a general southward movement can allow them to reach their overwintering sites.

Results and Discussion:

Within migration research, there has been fierce debate on the sensory and cognitive bases for navigation (Gould & Gould, 2012b; Wehner et al., 1999). Two general navigation models are *true navigation* and *vector navigation*. True navigation is supported in an animal if they can orient toward their goal following a displacement into unfamiliar territory. If the individual cannot orient correctly, instead maintaining their original direction, they are thought to be vector navigators (Gould & Gould, 2012b). Thus, true navigators are thought to possess a sense of direction (often referred to as a compass sense) and a sense of location (often referred to as a map sense) allowing the individual to have multiple orientations based on where they are, while vector navigators only possess a sense of direction and thus always orient in the same direction (Bennett, 1996; Gould, 2015; Gould & Gould, 2012a). Although displacement experiments are seen as the gold standard in determining an animal's navigation ability, they have limitations, precluding their use in some species, particularly small insects that cannot carry heavy trackers. We therefore used an alternative approach that is applicable to any species to distinguish between these two navigation strategies, focusing on monarch butterflies as a model system.

Monarchs are well known for their spectacular migration, which involves the movement of up to hundreds of millions of monarchs from a 4.5 million km^2 North American breeding range east of the Rocky Mountains to a small number of overwintering sites in Central Mexico, each encompassing only a few square kilometers (Figure 4.1) (Flockhart et al., 2013). How monarchs navigate to their overwintering sites remains a topic of debate (Oberhauser et al., 2013). To date, the navigation sensory mechanisms isolated in monarchs, with robust repeatability, are compass strategies: a time-compensated sun compass (Froy et al., 2003) and, to a lesser extent, a magnetic compass (Guerra et al., 2014). These mechanisms provide directional (compass) information that does not point toward the goal (map sense). Furthermore, given historic changes to the local magnetic field in Mexico, it is unlikely that the magnetic compass could be used as a magnetic map, as suggested to exist in other systems (Gould, 2015; Guerra et al., 2022; Keller et al., 2021). Therefore, these mechanisms cannot be used to orient toward the overwintering locations as required for true navigation. Fundamentally, true navigation as a hypothesis in monarchs persists solely based on the observation that they reach a specific location in high numbers, coupled with the assumption that this accuracy cannot be achieved with simpler strategies (Gould and Gould, 2012b). Our goal was therefore to employ a novel modeling approach to leverage large-scale observation data sets to determine whether the population patterns of migrating monarchs are better explained assuming true or vector navigation. This approach consisted of simulating the movement of thousands of migrating monarchs based on alternative navigation strategies and comparing resulting distribution patterns with empirical data.

For our simulations, we built an Agent-Based Model (ABM) where agents migrated across the North American landscape and were either true navigators (mean orientation is toward the destination regardless of geographic position), vector navigators (consistent single mean orientations throughout their entire journey), or multi-vector (mean orientation changes throughout their journey based on distance traveled). For all simulations, 1000 agents were randomly assigned a start location within the summer breeding range (Figure 4.1), and all had the same orientation accuracy calibrated to what has been calculated for monarchs based on orientation studies in flight simulators (i.e., they all had the same probability of selecting their mean orientation regardless of navigation strategy) (Mouritsen et al., 2013; Mouritsen & Mouritsen, 2000). This accuracy parameter is based on a circular probability distribution for all possible directions of movement at each step of the journey, which results in orientation variation between agents and within each individual agent's path over time. Because of this variation, each agent was given a maximum travel distance of 6,700 km, which was calculated to ensure that each would have an average straight-line displacement from their start location of 4,500 km (the maximum migration distance of the

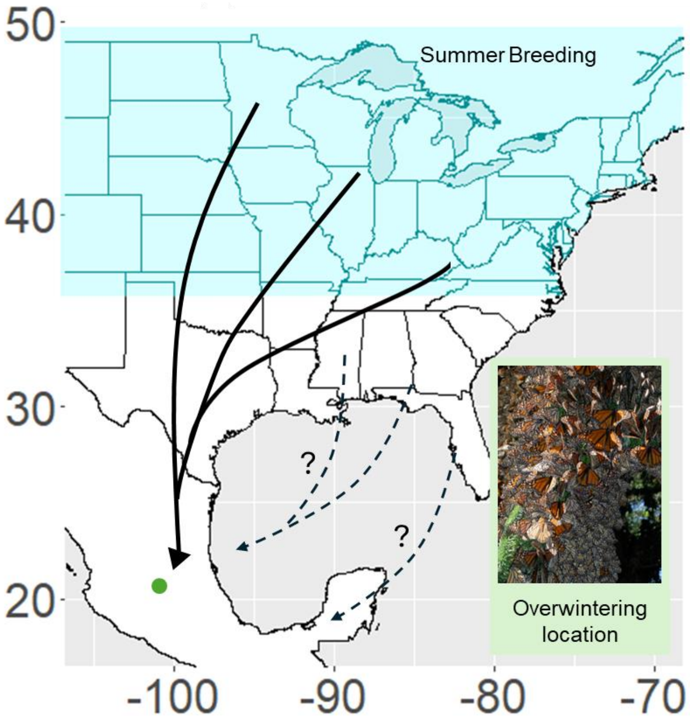


Figure 4.1: Map of eastern North American monarch migration and summer breeding ranges. Adapted from Kendzel et al. 2023 (Kendzel et al., 2023). Summer breeding range (cyan area) based on Urquhart and Urquhart 1978 (Satterfield et al., 2015). Migratory routes (black lines) based on maps from Brower 1995 (Lincoln P Brower, 1995) and review from Reppert et al. 2010 (Reppert et al., 2010). Dashed lines indicated unknown but hypothesized migratory routes from Brower 1996 (Brower, 1996) and Dockx et al. 2023 (Dockx et al., 2023). The green dot indicates the location of the overwintering sites, with the insert showing a typical view of dense clusters of overwintering monarchs (photo by J.C. de Roode).

eastern North American monarchs) to insure that each agent had enough steps to reach the overwintering location (Mouritsen et al., 2013; Steven M Reppert & Jacobus C de Roode, 2018). We modeled three alternative navigation strategies: (1) true navigation, where the mean orientation of agents was adjusted at each step based on their current location relative to the location of the overwintering sites; (2) vector navigation, where the mean orientation was held constant throughout the journey (225° from true north); and (3) multi-vector navigation, where agents were programmed to travel on average southwest (225° from true north) for the first half of their available steps and south (180 ° from true north) for the second half of their available steps. The choice of 225° was based on the observed directionality of migrating monarchs in a flight simulator, while the additional choice of 180° was based on previous hypothesized orientation shifts monarchs might perform through Mexico (Brower, 1996).

We further modified agent behavior by incorporating altitude and water body values to modify the probability of agents moving in the direction of these geographic features. Specifically, the Rocky Mountains, Appalachian Mountains, Sierra Madre Oriental Mountains, and the Gulf of Mexico are all prominent geographic barriers for the monarch's migration, so we made agents less likely to travel toward and through these features. Although we would intuitively expect these landscape features to be major barriers, their effects were not always enough to override movements toward the preferred migratory direction for all butterflies within our simulations. This is best highlighted in the paths for some individual vector navigators who continued to fly southwesterly into the southern Rockies and the Gulf of Mexico (Figure 4.2: top row). However, the geographic features were enough to keep most agents from these areas.

We then quantified the simulated monarch distributions by fitting a log-Gaussian Cox process model (LGCP) (Møller et al., 1998; Simpson et al., 2016; Simpson et al., 2017). This approach provides an intensity surface with the average expected number of observations modeled as a function of location across the study region, allowing us to compare the simulated data to empirical spatial data for the monarch obtained during the winter months, after their migration, as a proxy for real-world final locations(Møller et al., 1998; Simpson et al., 2016; Simpson et al., 2017). We derived the empirical data from opportunistic observations from the participatory science program iNaturalist (iNaturalist contributors, 2023). We included landcover type as a covariate in the LGCP, as this provided the best fit to the empirical data while balancing model complexity (Table S4.1) (Spiegelhalter et al., 2002). The estimated surface and the observations themselves highlight the specific overwintering area in Mexico and the band of area around it often associated with viable habitat (Figure 4.2: bottom row) (F. Urquhart & N. Urquhart, 1978; Urquhart, 1976). They also highlight areas of Florida, along the Gulf Coast, and US states further north, which are typically not included in monarch migratory conversations because these individuals likely will never reach the overwintering areas. However, these southern areas provide suitable habitat for breeding and surviving the winter, and winter breeding is increasingly recognized as an important factor in monarch biology (Satterfield et al., 2015). Thus, we used this full geographic surface to make holistic comparisons between simulated and observed data that both include locations of migrants that do not reach their overwintering destination or end up breeding in southern habitats during the winter.

Overall, all three navigation strategies reproduced empirical data to some extent, but the multi-vector navigators matched the observed data best; these agents followed the expected migratory pathways through southern Texas and into areas east of the Sierra Madre Oriental, matched the total observed geographic distribution for monarchs during the winter months and after the migration (including those not reaching the overwintering sites) and reached the specific overwintering location (Figures 4.2 and 4.3). Using a global measure for fit, relative mean squared error (RMSE), we found that data simulated with multi-vector and vector navigation fit globally better to the observed monarch distribution than data generated with true navigation (Table S4.2). Furthermore, multi-vector agents also ended their migration along the gulf coast and in areas of Florida (Figure 4.2: density estimate panels). True navigation, on the other hand, while having more agents reach the specific overwintering location (Table 4.1), created a simulated geographic distribution that is heavily concentrated and matched worse to the observed monarch distribution (Figure 4.2: relative ratio panels). Finally, although single-vector navigation simulations did have comparable total geographic ranges compared to monarch observations, single-vector agents failed to move southwardly into Mexico at rates comparable to that observed in the empirical data. Our simulations thus demonstrate that the broad geographic range of monarchs and their reaching of specific overwintering locations can be better explained by the more parsimonious strategies of vector navigation and multi-vector navigation than by the less parsimonious true navigation. It is important to emphasize that this conclusion is based on the total distribution of monarchs after their migration as proxy for final location (we only used iNaturalist data for the months November-February). While it may seem surprising that relatively few of our simulated monarchs successfully reached the overwintering sites, this is in fact consistent with estimates based on tagging studies, which have reported recovery rates as low as 0.01% of the millions of monarchs tagged and released through 1998 – 2015 (Taylor Jr et al., 2020).

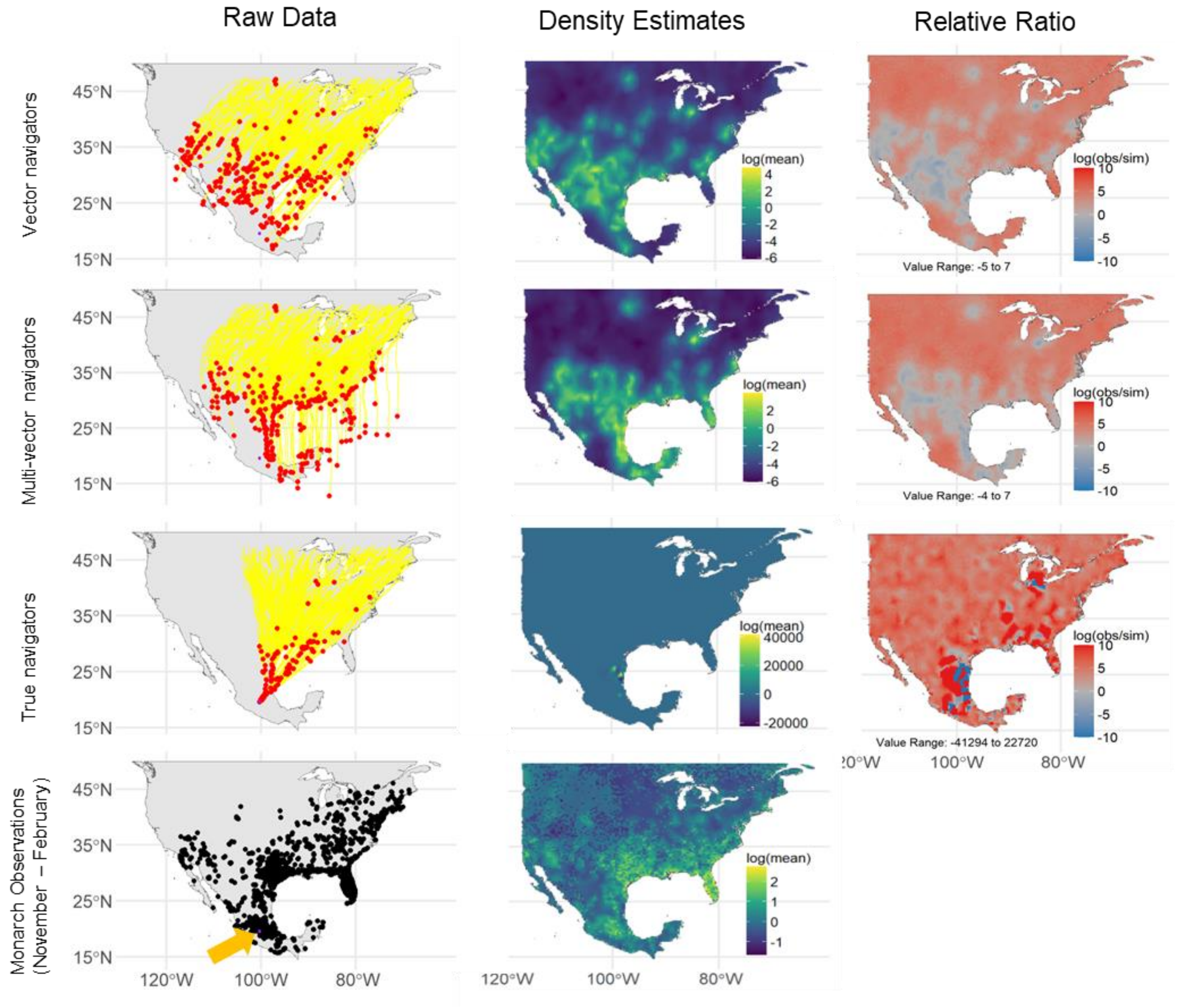


Figure 4.2: Agent based model results compared to monarch location observations. For the left columns, the purple dot is the overwintering location. Due to its small size, it is further highlighted in the bottom left panel with an orange arrow. For each simulation shown, 1000 agents started their journey in the northeast and took on average the same number of steps. The maps in the "Raw Data" column illustrate the final locations of all simulated (red dots) and reported butterflies (black dots). The yellow lines indicate the full path journey of each agent. The maps in the "Density Estimates" column illustrate the spatial intensity (average number of agents per unit area) of the final locations. The maps in the "Relative Ratios" column show the ratio of the intensity of each model's final location to the intensity of the observed iNaturalist observations, with red indicating that simulations underestimated densities, blue indicating that simulations overestimated densities, and grey indicating a close match between simulated and observed data. Agents who flew out into the ocean or ended their journey in the ocean were not included in the density analysis.

Our findings align with several previous studies, including an investigation that used a mathematical expectation model and geographic displacement coupled with orientation assays to conclude that monarchs are not true navigators (Mouritsen et al., 2013). Additionally, our results align with existing hypotheses that the bulk of the migration is in a southwesterly direction, that it shifts more southwardly through Mexico, and that there may be some effect nearer the overwintering location that further directs the population to that area (Reppert et al., 2010). This effect is referred to as "beacon," or a zone that once a migrant is within, they can further home into the end location. When we simulated both vector and multi-vector navigators with varying beacon sizes (where once the agent was within the given range, they could home in on the final location as a true navigator would), agents under both strategies managed to find the overwintering location with beacons larger than 120 km (Figure 4.3), but multi-vector navigators had a higher success rate than single-vector navigators (Table 4.1). The specific cue or combination of cues for this beacon (whether based on forest traits, monarch pheromones, or magnetism) have not been isolated, but our simulations lend credence to the idea that such a beacon could exist.

Table 4.1: Percentage of simulated agents reaching the specific overwintering location in Mexico.

Navigation Strategy (beacon size)	Percentage reaching overwintering location	Percentage within 240 km range
vector (none)	0.0%	
vector (60 km)	0.0%	
vector (120 km)	1.1%	
vector (240 km)	1.3%	2.6%
multi- vector (none)	0.0%	
multi- vector (60 km)	0.0%	
multi- vector (120 km)	0.1%	
multi- vector (240 km)	3.0%	5.3%
True (full range)	11.0%	32.0%

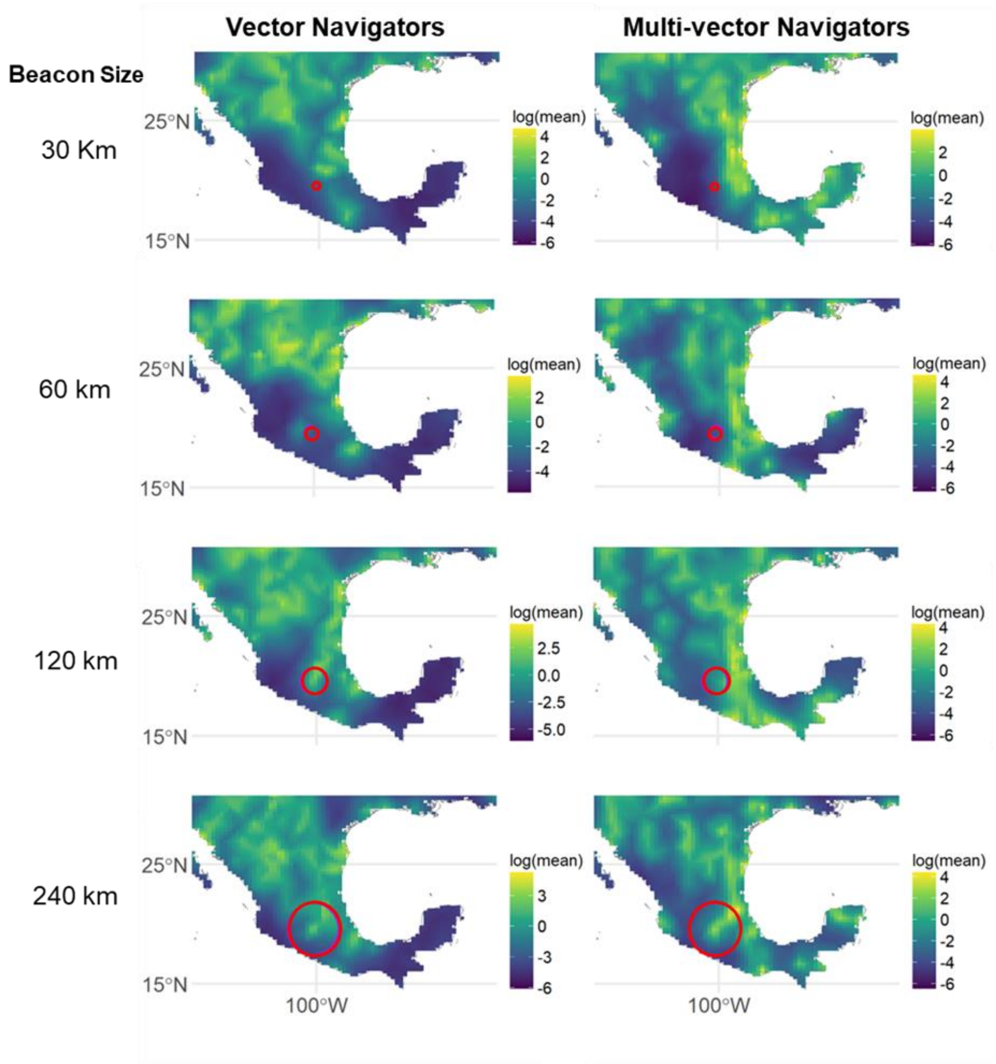


Figure 4.3: The effect of beacon range size on vector navigators reaching overwintering locations. For all panels, 1000 simulated agents were released, and their resulting end locations were modeled using a LGCPs model. The red circle represents the scale of the beacon range used for each simulation. For all simulations, there was a predicted monarch presence at the overwintering location. However, as the beacon range increased in size to 120 km in diameter, far more agents reached the location, corresponding to an increased predicted density in this region.

One potential reason for the finding that simulated vector navigators showed a better fit with empirical data than true navigators is that we chose an orientation accuracy parameter (*k*) that is too high. Counter-intuitively, high accuracy may reduce the success rate of true navigators reaching the overwintering sites because they can get “stuck” in the landscape, rather than finding ways around geographic barriers (analogous to deterministic optimizers getting stuck in local, but not global, maxima). For example, using a k-value of 1.225, as measured in the orientation studies (Mouritsen et al., 2013), true navigation simulations created a highly dense estimation northeast of the primary overwintering location (Figure 4.4: True navigation). To test the extent to which lowering this value (decreasing the agent accuracy) could result in better model fit, we halved the k-value and re-ran our simulations. Although this did increase the true navigation model fit globally when compared to the observed monarch distribution (true navigation, k =0.61: RMSE = 4.51; true navigation, k=1.225l: RMSE = 948), the density fit in Mexico decreased, and only a single agent reached the overwintering location (Figure S4.1). We found similar reductions in local fit for the single-vector and multi-vector though we found globally these models continued to fit better than the true navigation strategy (Table S4.2).

Our study used a simple model that only incorporated orientation choices and landscape features, but ignored many other factors, such as wind direction, habitat type, and temperature changes, which are often thought to be important in monarch migration (Reppert et al., 2010). Future addition of these covariates may help prevent agents from flying into mountainous regions and further funnel them toward overwintering locations as observed in the monarch population. Furthermore, monarchs are known to roost and cluster together during their fall migration and these roosts have been used to track the migration (Steven M Reppert & Jacobus C de Roode, 2018; Tracy et al., 2019). This social behavior was not simulated here due to its increased computational load; however, it could further explain the funneling effect as observed in the monarch distribution. Despite these limitations, our simple models did capture the essence of monarch migration based primarily on navigation strategy. It is important to note that our results are not meant to suggest a definitive model for monarch migration. While our simulations demonstrate that a simple model of multi-vector navigation *can* explain monarch migration, it does not preclude the possibility that monarchs have undiscovered abilities that allow true navigation.

To further determine the role of vector navigation, we recommend additional research along the following line. To date, all published orientation research on monarchs has been done in Canada and the United States. Most has focused on the northern or central United States which may not translate to how monarchs behave during the second half of their journey. Since our models suggest that monarchs that would switch orientation from 225° to 180° from due north aligns better with observational data than monarchs that do not switch direction, it will be important to quantify the mean orientation of monarchs in more southern states, such as Texas, to verify if monarchs indeed switch their mean orientation. Our simulations highlighted the area east of the overwintering location as a likely funnel point for a major group of monarchs (Figures 4.2 and 4.3). How monarchs orient at this location could illuminate how they reach the overwintering location. One hypothesis is the beacon effect as simulated here. Another hypothesis is that monarchs can sense latitude and orientate based on their current latitude by using their inclination angle magnetic compass (Beason, 1989; Guerra et al., 2014). However, neither hypothesis has been tested nor is it known if the monarch's mean orientation shifts throughout Mexico.

Broadly, true navigation as a strategy is challenging to test in any given species, and the necessary sensory mechanisms have been equally difficult to ascertain. Displacement experiments certainly have their place in navigation research, particularly in isolating proposed sensory mechanisms. However, there are still several fundamental questions that remain unanswered: does the map sense need to extend globally; how many displacements are needed to fully test for true navigation; what are the implications of this ability for cognitive spatial processing in the animal; and how do the varying hypotheses translate to population level patterns that can be measured (Putman, 2021)? Our study highlights how agent-based models can be a powerful and helpful tool to address aspects of these difficult questions. These simulations are highly configurable and can be parameterized to any model species to test if the hypothesized mechanism, when applied across a sample of individual agents, results in the patterns observed in that species. In this way, agent-based models open new possibilities for exploring the multiple models of sensory and behavioral mechanisms underlying animal migration.

Star Methods:

Key Resource Table

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Data on monarch observations	(iNaturalist contributors, 2023)	https://doi.org/10.15468/dl.6yj5bq
Data on simulation locations	This study	GitHub: https://doi.org/10.5281/zenodo.13741315
Data on elevation	USGS	https://doi.org/10.5066/F7DF6PQS
Data on land cover	Buchhorn et al.	https://doi.org/10.5281/zenodo.3939050
Data on human population density	CIESIN	https://doi.org/10.7927/H45Q4T5F
Software and algorithms		
R version 4.3.3	R development team	N/A
Code for simulations	This study	GitHub: https://doi.org/10.5281/zenodo.13741315
INLA	(Rue et al., 2009)	https://inla.r-inla-download.org/R/stable
Inlabru	(Bachl et al., 2019)	https://github.com/inlabru-org/inlabru
Circular	(Agostinelli & Lund, 2023)	https://doi.org/10.32614/CRAN.package.circular
CircStats	(Lund & Agostinelli, 2018)	https://doi.org/10.32614/CRAN.package.CircStats
Raster	(Hijmans & van Etten, 2020)	https://doi.org/10.32614/CRAN.package.raster
BBmisc	(Bischl et al., 2017)	https://doi.org/10.32614/CRAN.package.BBmisc
Sf	(Pebesma et al., 2021)	https://doi.org/10.32614/CRAN.package.sf
Terra	(Hijmans, 2022)	https://doi.org/10.32614/CRAN.package.terra

Resource availability

Lead contact

Further information and requests for resources and code should be directed to and will be fulfilled by the lead contact, Mitchell Kendzel (mkendzel@gmail.com).

Materials availability

This research did not generate new reagents.

Data and code availability

The raw research-grade occurrence dataset for the monarchs is stored on GBIF.org (https://doi.org/10.15468/dl.6yj5bq). The covariates used in the analysis and simulations were sourced as follows: Altitude stored on usgs.gov (https://doi.org/10.5066/F7DF6PQS), Land cover type, stored on zenodo.org (https://doi.org/10.5281/zenodo.3939050), and human population density, stored on sedac.ciesin.columbia.edu (https://doi.org/10.7927/H45Q4T5F). The raw agent results, as well as the R scripts to fully simulate, process covariates, and replicate the analysis, are available at the Github repository (https://doi.org/10.5281/zenodo.13741315)

Experimental model and subject details

The analysis and comparisons were carried out on the volunteer-based, opportunistic dataset from iNaturalist users who observed monarch butterfly (*Danaus plexippus)* location information during the winter months of November, December, January, and February of years 2018, 2019, 2020, 2021, 2022, and 2023.

Method details

Monarch data

We used data on adult monarch butterfly locations from the opportunistic sighting dataset curated by iNaturalist (iNaturalist contributors, 2023). Opportunistic, in this sense, refers to the unstructured sampling by users of the iNaturalist application. We used only the research grade and confirmed sightings. These were filtered to the eastern North American monarch ranges east of the Rocky Mountains during the winter months November through February during years 2018-2023.

Agent-based model

The agent-based model was built using R version 4.3.3 (see listed GitHub for code). A full list of the packages can be found above, and the parameters required can be found in the supplement (Table S4.3). The model simulated a moving population through an environment containing values for elevation and open water bodies. This landscape was large, about 23 million cells aligned in a grid, which limited the number of agents that could be simulated at a single time. We found that 1000 agents provided enough samples while limiting the length of simulations to several hours. For a full ODD protocol of the ABM see Chapter III.

Navigation strategies

All agents had two phases: first, the *orientation* phase, and second, the *movement* phase. The results of both phases, a timestep, were independent from each other (although this could be updated to account for memory). The only difference in the three navigation strategies, (1) true navigation, (2) vector navigation, and (3) multi-vector navigation, is in the orientation phase. At the start of the phase, each agent generated a circular, von Mises probability distribution with the mean of this distribution as either a constant angle (vector and multi-vector navigation strategies) or dynamic and always pointing toward the goal (true navigation). The concentration of this distribution around the mean (the reciprocal of variance in a normal distribution), *k,* was the same for each agent, set at 1.225 regardless of navigation strategy, based on monarch orientation accuracy (Mouritsen et al., 2013). Agents would select a direction from this distribution during their orientation phase. After the selection, agents moved in that direction. Given the resulting orientations selected were a product of these distributions, there is variation in the direction chosen. The trace of all steps taken represents the migration of an individual agent.

Landscape effects

The landscape in which the agents moved through was gridded at 1 km^2. Each step resulted in a displacement of 1 of these grided cells. The grid was populated with values representing elevation in meters or water body presence. At each orientation phase, agents considered the values of the 8 cells directly surrounding them, then converted their values into probabilities using a min-max normalization with the max value approaching 2 and the minimum value approaching 0.016.

$$normalized = 0.016 + \frac{(altitude_i - \max altitude) * (2 - 0.016)}{\max altitude - \min altitude}; \text{ equation 1}$$

Cells of lower altitude were given values above 1 (more likely to move toward) while those with higher altitudes or water bodies took on values below 1 (less likely to move toward). The original von Mises distribution was then modified by taking these normalized values, multiplying the probability at each angle corresponding to the cell’s location, and then re-generating a new distribution with the modified probabilities. In this way, agents consider their original mean migratory direction, the probability to go in that direction, and the surrounding landscape when making a movement decision at each step of their migration.

Eastern North American monarch simulations

All agents were assigned a start location randomly selected within the summer breeding range for eastern North American monarchs. The shape of this area was based off a previous study that looked at migratory monarchs in summer and year-round breeding sites (Satterfield et al., 2015) and the shape file can be found in the GitHub repository linked above. Each agent was followed for 6,700 steps, which was calculated to ensure that each would have an average straight-line displacement from their start location of 4,500 km (the maximum range of the eastern North American monarchs) (Mouritsen et al., 2013; Steven M Reppert & Jacobus C de Roode, 2018).

$$max\,steps = 4500/e^{-0.5k}; \text{ equation 2}$$

Equation 2 considers the accuracy of the agents, k, and ensures that each has enough steps to reach the overwintering location.

The overwintering location was at latitude:19.5905 and longitude:-100.3087. A buffer of varying sizes was drawn around this location. If agents were in this buffer, then their mean orientation was always pointing toward the overwintering location, while if they were outside of it, they had a constant orientation. For true navigation, the buffer was large enough to encompass the entire study region, and thus, they always oriented toward the overwintering location. For vector and multi-vector strategies, the buffer varied in size with a radius of 30 km to 240 km.

Once agents were within 10 km of the overwintering location, they were considered to have reached the overwintering site and we stopped tracking additional steps in their migration.

Quantification and statistical analysis

In order to statistically compare the resulting spatial point pattern of simulated locations to point locations of observations within iNaturalist, we used a point-process model to characterize the spatial density associated with either reported monarch sightings or the locations of agents. Specifically, we used a log-Gaussian Cox process (LGCP) model (Møller et al., 1998) with the approach developed by Simpson et al. (2016, 2017) and Illian et al. (2012). In these models, observation locations are derived from an underlying spatial point process, with first-order (mean) patterns modeled via an intensity surface, which provides the expected rate of an observation at each location within the study region. We estimated these intensities allowing dependence on local landscape covariate information for altitude, human population density, and habitat type. We fit a hierarchical Bayesian model using integrated nested Laplace approximations to estimate the full spatial posterior predictive distribution of locations. For model selection, we used the deviance information criterion (DIC) (Spiegelhalter et al., 2002) and found that habitat type alone had the most predictive capabilities while balancing model complexity (Table S4.1). To compare between our simulation and observation distributions we calculated a relative risk ratio surface (i.e., the ratio of intensity function values, i.e., the local expected numbers of observations at a given location, between each of two different models). The relative risk surface showcases local differences between observed and each of the model-based expected spatial intensity functions (Bithell, 1990). Finally, we provided general data exploration and summarization of quantities of interest such as percentage of individuals reaching migration goal. All models were fitted with the R-packages “INLA” and “Inlabru” (Bachl et al., 2019; Rue et al., 2009).

Supplemental Information

Table S4.1: DIC values for each model

Model	DIC
Habitat	-106581.80
Habitat and Elevation	-105925.11
Habitat and Human Density	-105925.10
SPDE only	-43753.50
Elevation	-43595.13
Human Density	-42928.19
Elevation and Human Density	82648.30
All covariates	130689.92

Table S4.2: Relative mean squared error between simulations and monarch observed distribution

Model	Relative Mean Squared Error (RMSE)
Vector Navigation, *k* = 1.225	3.73
Vector Navigation, *k* = 0.61	3.24
Multi-vector Navigation, k= 1.225	4.12
Multi-vector Navigation, k= 0.61	4.17
True Navigation, k= 1.225	948
True Navigation, k= 0.61	4.5

Table S4.3: Model Parameters

Parameter	description	Monarch case study	Monarch Source
θ	Orientation Selected	Updated at each step	-
T	Total time	60	Yang et al., 2016
N_S	total number of steps available for migration	Equation 2	Mouritsen and Mouritsen, 2000
S	number of steps per time unit	T/ N_S	N_s/T
A	Study area	based on observation data	iNaturalist
D	Destination location	based on publicly available overwintering locations	Xerces Society
L_0	Start location	based on summer breeding range	Yang et al. 2016
k	circular distribution concentration	0.66, and 1.225	Mouritsen and Mouritsen, 2000
u	mean direction	225	Mouritsen and Frost, 2002

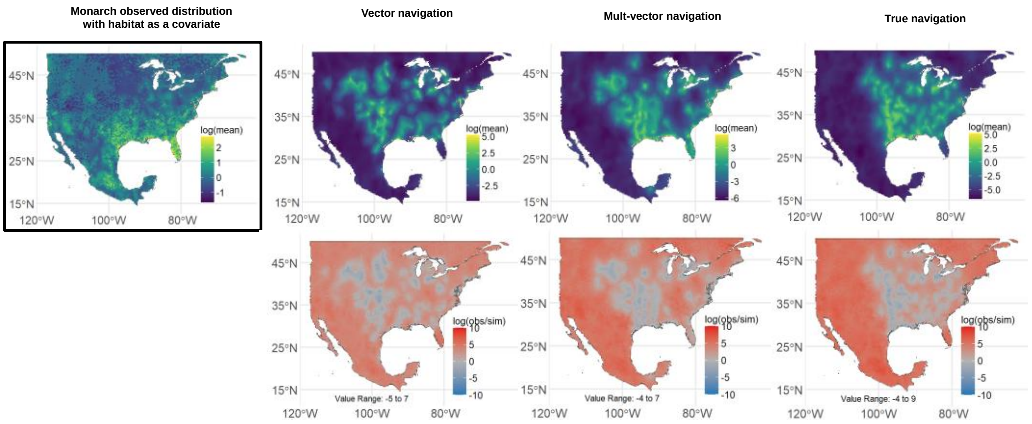


Figure S4.1: Results of simulations using *k* = 0.61. Outlined panel is the observed monarch distribution whose fit is compared to all simulations. Simulations failed to reach the overwintering location in high numbers and failed to reach Mexico in expected numbers.

CHAPTER V - CONCLUSIONS

Proper navigation is important for animals to successfully move through their environment. Determining the mechanism responsible for successful movement requires an extensive understanding of how animals navigate and the factors that contribute to the success of that movement. This dissertation provides two frameworks helpful in the study of migration and navigation: 1) a list of cohesive terminology (Chapters I and II) and 2) a statistical methodology (Chapters III and IV).

The provided cohesive navigation terminology has the goal to simplify definitions of each navigation strategy regardless of taxa or scale the behavior is used in. First, I define the multiple different strategies appearing in varying literatures and then I review the unique properties of each that are important to consider and be controlled for when designing experiments. In this way, I provide a "road map" of considerations, experimental designs, and data needed to determine a used navigation strategy, with an emphasis on limitations and broad applicability (Chapter 1: Box 1). Additionally, I review and highlight commonly ignored factors in successful migration: parasitism and landscapes that can shift migratory populations. To date, Chapter II's paper serves as the only single publication that defines and utilizes each of the seven relationships between a migrating species and their parasite, and Chapters III and IV are the only examples of models that can incorporate landscape into the prediction of migratory populations under varying navigation strategies. As such, both frameworks highlight the importance of incorporating these relationships in future studies of migration, specifically studies on migration successes, migratory drivers, and maintenance of the migration behavior.

Finally, using the monarch butterfly as a case study, I use the proposed navigation nomenclature and the statistical framework to test which navigation strategy the migratory butterfly most likely uses during its four-thousand-kilometer journey. By simulating populations under the varying navigation hypotheses, I find that the observed spatial distribution of monarchs after their migration more closely aligns with models for vector and multi-vector navigation, a result that further supports previous research and contradicts long-standing assumptions in the field (Mouritsen et al., 2013; Oberhauser et al., 2013).

Future directions

The validation of the new statistical framework and the statistical power to detect differences in the data simulated for migratory populations is currently unexplored and thus ripe for quantitative study. Specifically, there are two sources of uncertainty in the proposed statistical framework: 1) it is currently difficult to ascertain the appropriate sample sizes needed to model navigation strategy from the tracking studies discussed and 2) the predicted surfaces for both the observed and simulated patterns are estimates and thus have associated error around those estimates. However, the proposed framework provides a methodology to both estimate the power for the data we already have and incorporate inference based on the intensity estimates. For example, I can simulate and quantify the patterns of migration under the varying navigation strategies, which provides populations of migrants whose total paths, locations, and resulting end location is known. Subsampling these data sets based on location, timing, or in such a way to imitate real-world sampling efforts could highlight when, where, and how many samples of a given species are needed to detect signals of the different strategies. Furthermore, given the intensity surfaces used to quantify the observed and simulated patterns were generated using a

Bayesian framework, the posterior distributions for each point estimate can be used to calculate the spatial contour of where these distributions are significantly different when calculating the relative risk ratio. Specifically, Monte Carlo randomization tests are commonly used to compare two posterior distribution estimates by subsampling both distribution and calculating the probability that the observed difference occurred by chance. These model performance studies can attract cross-disciplinary collaboration and encourage researchers without movement behavior backgrounds to study the causes, drivers, and methods that animals use to move and navigate. Additionally, studies can begin to systematically identify navigation strategies in systems that previously provided contradicting results.

Furthermore, throughout the case studies, consistent issues were found regarding data quality that can be corrected for in future designed experiments. Specifically, opportunistic data, the highest resolution data available for most species, is particularly biased given it is sampled by volunteers and there is no sampling structure to it. The species distribution models used, particularly Log-Gaussian Cox Process models, can be allowed to integrate sampling effort into their predicted surfaces. In this way, the models provided in Chapters III and IV can be further refined to account for the preferential sampling inherent in the data.

Finally, incorporating parasitic relationships and the costs of parasitism on movement could further strengthen the results between observed and simulated migration patterns. Agent-based models are incredibly customizable and can integrate varying considerations such as energy budgets (Liao et al., 2021), fitness (Hayes & Grüter, 2023), and disease dynamics (Shoukat & Moghadas, 2020). An important consideration introduced in Chapter II is “migratory culling” whereby individual migrants fail to migrate due to the imposed cost of parasitism. Often this is theorized by lower energy availability (see Chapter II), which can be simulated by altering energy budget parameters so that infected agents either are less efficient with their available energy or have less overall for movement. Another mechanism hypothesized to explain the culling is that parasitism has cognitive costs for migrants and that they are less accurate when navigating compared to healthy migrants. ABMs could incorporate this by simulating individuals who are less accurate as done in Chapters III and IV. In fact, both chapters found that lowering accuracy of the agents resulted in less reaching important habitat associated with the migration. In these ways, ABMs can be parameterized to a wide range of species interaction simultaneously that otherwise would be difficult to express mathematically.

Overall, I hope that this dissertation and the frameworks it provides will help researchers integrate individual-level behavioral assays with real-world and simulated population-level data. The integration of these studies can begin to fill gaps in navigation research imposed by the scale of the behavior, the taxa, and the movement behavior of interest. It is my hope that comparisons between all three will help further our understanding of animal navigation, migration, and raises the bar in assigning true navigation beyond assuming that animals must be it if they reach small specific areas from far away.

REFERENCES

Able, K. P. (2001). The concepts and terminology of bird navigation. *Journal of Avian Biology*, *32*(2), 174-183.

Abrahms, B., Hazen, E. L., Aikens, E. O., Savoca, M. S., Goldbogen, J. A., Bograd, S. J., Jacox, M. G., Irvine, L. M., Palacios, D. M., & Mate, B. R. (2019). Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences*, *116*(12), 5582-5587. https://doi.org/10.1073/pnas.1819031116

Agostinelli, C., & Lund, U. (2023). R package 'circular': Circular Statistics. In: 0.5-0.

Åkesson, S., Bakam, H., Martinez Hernandez, E., Ilieva, M., & Bianco, G. (2021). Migratory orientation in inexperienced and experienced avian migrants. *Ethology Ecology & Evolution*, *33*(3), 206-229. https://doi.org/10.1080/03949370.2021.1905076

Alerstam, T. (2006). Conflicting evidence about long-distance animal navigation. *science*, *313*(5788), 791-794. https://doi.org/10.1126/science.1129048

Alerstam, T., Hedenstrom, A., & Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, *103*(2), 247-260. <Go to ISI>://000186985700002

Altizer, S., Bartel, R., & Han, B. A. (2011). Animal migration and infectious disease risk. *Science*, *331*(6015), 296-302. https://doi.org/10.1126/science.1194694

Altizer, S., & de Roode, J. C. (2015). Monarchs and their debilitating parasites: immunity, migration, and medicinal plant use. In K. O. Oberhauser, S. Altizer, & K. Nail (Eds.), *Monarchs in a Changing World: Biology and Conservation of an Iconic Insect* (pp. 83-93). Cornell University Press.

Altizer, S., Hobson, K., Davis, A., de Roode, J., & Wassenaar, L. (2015). Do healthy monarchs migrate farther? Tracking natal origins of parasitized vs. uninfected monarch butterflies overwintering in Mexico. *PLoS One*, *10*(11), e0141371.

Altizer, S. M., & Oberhauser, K. S. (1999). Effects of the protozoan parasite *Ophryocystis elektroscirrha* on the fitness of monarch butterflies (*Danaus plexippus*). *Journal of Invertebrate Pathology*, *74*, 76-88. https://doi.org/10.1006/JIPA.1999.4853

Armstrong, J. B., Takimoto, G., Schindler, D. E., Hayes, M. M., & Kauffman, M. J. (2016). Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. *Ecology*, *97*(5), 1099-1112. https://doi.org/10.1890/15-0554.1

Avens, L., Braun-McNeill, J., Epperly, S., & Lohmann, K. J. (2003). Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*). *Marine Biology*, *143*(2), 211-220. https://doi.org/10.1007/s00227-003-1085-9

Bachl, F. E., Lindgren, F., Borchers, D. L., & Illian, J. B. (2019). inlabru: an R package for Bayesian spatial modelling from ecological survey data. *Methods in Ecology and Evolution*, *10*(6), 760-766.

Baguette, M., Benton, T. G., & Bullock, J. M. (2012). *Dispersal ecology and evolution*. Oxford University Press.

Baker, R. (1978). *Evolutionary ecology of animal migration*. Holmes & Meier Publishers.

Bartel, R. A., Oberhauser, K. S., de Roode, J. C., & Altizer, S. (2011). Monarch butterfly migration and parasite transmission in eastern North America. *Ecology*, *92*, 342-351.

Bartel, R. A., Oberhauser, K. S., De Roode, J. C., & Altizer, S. M. (2011). Monarch butterfly migration and parasite transmission in eastern North America. *Ecology*, *92*(2), 342-351.

Bauer, S., & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *science*, *344*(6179), 1242552.

Beason, R. C. (1989). Use of an inclination compass during migratory orientation by the bobolink (*Dolichonyx oryzivorus*). *Ethology*, *81*(4), 291-299. https://doi.org/10.1111/j.1439-0310.1989.tb00775.x

Beck, W., & Wiltschko, W. (1988). *Magnetic factors control the migratory direction of pied flycatchers (Ficedula hypoleuca Pallas)*

Beltran, R. S., Yuen, A. L., Condit, R., Robinson, P. W., Czapanskiy, M. F., Crocker, D. E., & Costa, D. P. (2022). Elephant seals time their long-distance migrations using a map sense. *Current Biology*, *32*(4), R156-R157. https://doi.org/10.1016/j.cub.2022.01.031

Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, *229*(2), 209-220. https://doi.org/10.1016/j.jtbi.2004.03.016

Bennett, A. T. (1996). Do animals have cognitive maps? *The Journal of Experimental Biology*, *199*(1), 219-224.

Bennett, D. A., & Tang, W. (2006). Modelling adaptive, spatially aware, and mobile agents: elk migration in Yellowstone. *International Journal of Geographical Information Science*, *20*(9), 1039-1066. https://doi.org/10.1080/13658810600830806

Berdahl, A. M., Kao, A. B., Flack, A., Westley, P. A., Codling, E. A., Couzin, I. D., Dell, A. I., & Biro, D. (2018). Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170009. https://doi.org/10.1098/rstb.2017.0009

Berthold, P. (1990). Spatiotemporal programs and genetics of orientation. *Experientia*, *46*(4), 363-371.

Berthold, P. (1991). Spatiotemporal programmes and genetics of orientation. *Orientation in birds*, 86-105.

Biro, D., Freeman, R., Meade, J., Roberts, S., & Guilford, T. (2007). Pigeons combine compass and landmark guidance in familiar route navigation. *Proceedings of the National Academy of Sciences*, *104*(18), 7471-7476.

Bisch-Knaden, S., & Wehner, R. d. (2001). Egocentric information helps desert ants to navigate around familiar obstacles. *Journal of Experimental Biology*, *204*(24), 4177-4184.

Bischl, B., Lang, M., Bossek, J., Horn, D., Richter, J., & Surmann, D. (2017). BBmisc: Miscellaneous helper functions for B. In (Vol. 1.13, pp. 2017).

Bithell, J. F. (1990). An application of density estimation to geographical epidemiology. *Statistics in Medicine*, *9*(6), 691-701. https://doi.org/https://doi.org/10.1002/sim.4780090616

Boles, L. C., & Lohmann, K. J. (2003). True navigation and magnetic maps in spiny lobsters. *Nature*, *421*(6918), 60-63. https://doi.org/10.1038/nature01226

Bonadonna, F., Bajzak, C., Benhamou, S., Igloi, K., Jouventin, P., Lipp, H., & Dell'Omo, G. (2005). Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1562), 489-495. https://doi.org/10.1098/rspb.2004.2984

Boström, J. E., Åkesson, S., & Alerstam, T. (2012). Where on earth can animals use a geomagnetic bi-coordinate map for navigation? *Ecography*, *35*(11), 1039-1047. https://doi.org/10.1111/j.1600-0587.2012.07507.x

Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1855), 20170449. https://doi.org/10.1098/rspb.2017.0449

Bradley, C. A., & Altizer, S. (2005). Parasites hinder monarch butterfly flight: implications for disease spread in migratory hosts. *Ecology Letters*, *8*(3), 290-300. https://doi.org/10.1111/j.1461-0248.2005.00722.x

Bradley, C. A., & Altizer, S. M. (2005). Parasites hinder monarch butterfly flight: implications for disease spread in migratory hosts. *Ecology Letters*, *8,* 290-300. https://doi.org/10.1111/j.1461-0248.2005.00722.x

Brower, L. (1996). Monarch butterfly orientation: missing pieces of a magnificent puzzle. *The Journal of Experimental Biology*, *199*(1), 93-103.

Brower, L. P. (1995). Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857-1995. *Journal of the Lepidopterists' Society*, *49*(4), 304-385.

Brower, L. P. (1995). Understanding and misunderstanding the migration of the monarch butterfly(Nymphalidae) in North America: 1857-1995. *Journal of the Lepidopterists Society*, *49*(4), 304-385.

Caliendo, V., Lewis, N. S., Pohlmann, A., Baillie, S. R., Banyard, A. C., Beer, M., Brown, I. H., Fouchier, R. A. M., Hansen, R. D. E., Lameris, T. K., Lang, A. S., Laurendeau, S., Lung, O., Robertson, G., van der Jeugd, H., Alkie, T. N., Thorup, K., van Toor, M. L., Waldenström, J., . . . Berhane, Y. (2022). Transatlantic spread of highly pathogenic avian influenza H5N1 by wild birds from Europe to North America in 2021. *Scientific reports*, *12*(1), 11729. https://doi.org/10.1038/s41598-022-13447-z

Cayuela, L., Golicher, D., Newton, A., Kolb, M., De Alburquerque, F., Arets, E., Alkemade, J., & Pérez, A. (2009). Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. *Tropical Conservation Science*, *2*(3), 319-352.

Cheng, K. (2000). How honeybees find a place: lessons from a simple mind. *Animal Learning & Behavior*, *28*(1), 1-15. https://doi.org/10.3758/BF03199768

Chernetsov, N., Kishkinev, D., & Mouritsen, H. (2008). A long-distance avian migrant compensates for longitudinal displacement during spring migration. *Current Biology*, *18*(3), 188-190. https://doi.org/10.1016/j.cub.2008.01.018

Chernetsov, N., Pakhomov, A., Kobylkov, D., Kishkinev, D., Holland, R. A., & Mouritsen, H. (2017). Migratory Eurasian reed warblers can use magnetic declination to solve the longitude problem. *Current Biology*, *27*(17), 2647-2651. https://doi.org/10.1016/j.cub.2017.07.024

Cheung, A., Zhang, S., Stricker, C., & Srinivasan, M. V. (2008). Animal navigation: general properties of directed walks. *Biological Cybernetics*, *99*(3), 197-217. https://doi.org/10.1007/s00422-008-0251-z

Collett, T. (1996). Insect navigation en route to the goal: multiple strategies for the use of landmarks. *The Journal of Experimental Biology, 199*(1), 227-235. https://doi.org/10.1242/jeb.199.1.227

Collett, T. S., & Collett, M. (2011). Animal navigation: following signposts in the sea. *Current Biology*, *21*(20), R843-R846.

Conn, P. B., Thorson, J. T., & Johnson, D. S. (2017). Confronting preferential sampling when analysing population distributions: diagnosis and model-based triage. *Methods in Ecology and Evolution*, *8*(11), 1535-1546.

Daversa, D., Monsalve-Carcaño, C., Carrascal, L., & Bosch, J. (2018). Seasonal migrations, body temperature fluctuations, and infection dynamics in adult amphibians. *PeerJ*, *6*, e4698.

Davis, A. K., & de Roode, J. C. (2018). Effects of the parasite, *Ophryocystis elektroscirrha*, on wing characteristics important for migration in the monarch butterfly. *Animal Migration*, *5*(1), 84-93.

de Angeli Dutra, D., Fecchio, A., Braga, É. M., & Poulin, R. (2021). Migratory birds have higher prevalence and richness of avian haemosporidian parasites than residents. *Internation Journal for Parasitology*, *51*(10), 877-882.

de Roode, J. C., & Altizer, S. (2010). Host-parasite genetic interactions and virulence-transmission relationships in natural populations of monarch butterflies. *Evolution*, *64*, 502-514.

de Roode, J. C., Altizer, S., & Hunter, M. D. (2019). Multi-trophic interactions and migration behaviour determine the ecology and evolution of parasite infection in monarch butterflies. *Wildlife Disease Ecology: Linking Theory to Data and Application*, 480-510.

de Roode, J. C., Chi, J., Rarick, R. M., & Altizer, S. (2009). Strength in numbers: high parasite burdens increase transmission of a protozoan parasite of monarch butterflies (*Danaus plexippus*). *Oecologia*, *161*(1), 67-75.

de Roode, J. C., Gold, L. R., & Altizer, S. M. (2007). Virulence determinants in a natural butterfly-parasite system. *Parasitology, 134*, 657. https://doi.org/10.1017/S0031182006002009

de Roode, J. C., Yates, A. J., & Altizer, S. M. (2008). Virulence-transmission trade-offs and population divergence in virulence in a naturally occurring butterfly parasite. *PNAS*, *105*, 7489-7494. https://doi.org/10.1073/pnas.0710909105

DeAngelis, D. L., & Diaz, S. G. (2019). Decision-making in agent-based modeling: A current review and future prospectus. *Frontiers in Ecology and Evolution*, *6*, 237. https://doi.org/10.3389/fevo.2018.00237

DeGroote, L. W., Hingst-Zaher, E., Moreira-Lima, L., Whitacre, J. V., Slyder, J. B., & Wenzel, J. W. (2021). Citizen science data reveals the cryptic migration of the common potoo *Nyctibius griseus* in Brazil. *Ibis*, *163*(2), 380-389. https://doi.org/10.1111/ibi.12904

Delmon, I. (1998). Dissociation between distance and direction during locomotor navigation. *Wayfinding behavior: cognitive mapping and other spatial processes. Johns Hopkins University PressBoyadjian A, Marin L, Danion F (1999) Veering in human locomotion: the role of the effectors. Neurosci Lett*, *265*, 2124.

Deutschlander, M. E., Phillips, J. B., & Munro, U. (2012). Age-dependent orientation to magnetically-simulated geographic displacements in migratory Australian silvereyes (*Zosterops l. lateralis*). *The Wilson Journal of Ornithology*, *124*(3), 467-477. https://doi.org/10.1676/11-043.1

Diggle, P. J., Menezes, R., & Su, T.-l. (2010). Geostatistical inference under preferential sampling. *Journal of the Royal Statistical Society Series C: Applied Statistics*, *59*(2), 191-232.

Dingle, H. (2014). *Migration: the biology of life on the move*. Oxford University Press, USA.

Dockx, C. (2007). Directional and stabilizing selection on wing size and shape in migrant and resident monarch butterflies, *Danaus plexippus* (L.), in Cuba. *Biological Journal of the Linnean Society*, *92*(4), 605-616.

Dockx, C., Hobson, K. A., Kronforst, M., Kardynal, K. J., Pozo, C., Schuster, J., Green, D. A., Dix, M., Nallu, S., & Lynch, S. (2023). Migration of Eastern North American monarch butterflies via the South-east and the Atlantic: evidence from stable isotopes, thin layer chromatography, DNA and phenotype. *Biological Journal of the Linnean Society*, *139*(3), 294-325.

Driggers III, W. B., Frazier, B. S., Adams, D. H., Ulrich, G. F., Jones, C. M., Hoffmayer, E. R., & Campbell, M. D. (2014). Site fidelity of migratory bonnethead sharks *Sphyrna tiburo* (L. 1758) to specific estuaries in South Carolina, USA. *Journal of Experimental Marine Biology and Ecology*, *459*, 61-69. https://doi.org/10.1016/j.jembe.2014.05.006

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., & Silk, J. R. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences*, *107*(5), 2078-2081. https://doi.org/10.1073/pnas.0909493107

Emlen, S. T. (1967). Migratory orientation in the indigo bunting, passerina cyanea: part i: evidence for use of celestial cues. *The Auk*, *84*(3), 309-342.

Etheredge, J. A., Perez, S. M., Taylor, O. R., & Jander, R. (1999). Monarch butterflies (*Danaus plexippus L.*) use a magnetic compass for navigation. *Proceedings of the National Academy of Sciences*, *96*(24), 13845-13846. https://doi.org/10.1073/pnas.96.24.13845

Flack, A., Aikens, E. O., Kölzsch, A., Nourani, E., Snell, K. R., Fiedler, W., Linek, N., Bauer, H.-G., Thorup, K., & Partecke, J. (2022). New frontiers in bird migration research. *Current Biology*, *32*(20), R1187-R1199.

Flockhart, D. T. T., Fitz-gerald, B., Brower, L. P., Derbyshire, R., Altizer, S., Hobson, K. A., Wassenaar, L. I., & Norris, D. R. (2017). Migration distance as a selective episode for wing morphology in a migratory insect [Article]. *Movement Ecology*, *5*, 7, Article 7. https://doi.org/10.1186/s40462-017-0098-9

Flockhart, D. T. T., Wassenaar, L. I., Martin, T. G., Hobson, K. A., Wunder, M. B., & Norris, D. R. (2013). Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America [Article]. *Proceedings of the Royal Society B-Biological Sciences*, *280*(1768), 20131087, Article 20131087. https://doi.org/10.1098/rspb.2013.1087

Fotheringham, A. S., & Sachdeva, M. (2022). Scale and local modeling: new perspectives on the modifiable areal unit problem and Simpson's paradox. *Journal of Geographical Systems*, *24*(3), 475-499.

Fransson, T., Jakobsson, S., & Kullberg, C. (2005). Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas. *Journal of Avian Biology*, *36*(1), 6-11. https://doi.org/10.1111/j.0908-8857.2005.03471.x

Froy, O., Gotter, A. L., Casselman, A. L., & Reppert, S. M. (2003). Illuminating the circadian clock in monarch butterfly migration. *science*, *300*(5623), 1303-1305.

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *Journal of Experimental Biology*, *216*(12), 2165-2171.

Garvin, M. C., Szell, C. C., & Moore, F. R. (2006). Blood parasites of nearctic–neotropical migrant passerine birds during spring trans-gulf migration: impact on host body condition. *Journal of Parasitology*, *92*(5), 990-996.

Gelfand, A. E., Sahu, S. K., & Holland, D. M. (2012). On the effect of preferential sampling in spatial prediction. *Environmetrics*, *23*(7), 565-578.

Gould, J. L. (1986). The locale map of honey bees: do insects have cognitive maps? *science*, *232*(4752), 861-863. https://doi.org/10.1126/science.232.4752.861

Gould, J. L. (1987). Landmark learning by honey bees. *Animal Behaviour*, *35*(1), 26-34. https://doi.org/10.1016/S0003-3472(87)80207-5

Gould, J. L. (2015). Animal navigation: birds have magnetic maps. *Current Biology*, *25*(19), R836-R838. https://doi.org/10.1016/j.cub.2015.08.041

Gould, J. L., & Gould, C. G. (2012a). The map sense. In *Nature's Compass* (pp. 185-226). Princeton University Press.

Gould, J. L., & Gould, C. G. (2012b). *Nature's compass: the mystery of animal navigation*. Princeton University Press.

Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., DeAngelis, D. L., Edmonds, B., Ge, J., Giske, J., & Groeneveld, J. (2020). The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. *Journal of Artificial Societies and Social Simulation*, *23*(2).

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegand, T., & DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *science*, *310*(5750), 987-991. https://doi.org/10.1126/science.1116681

Guerra, P. A., Gegear, R. J., & Reppert, S. M. (2014). A magnetic compass aids monarch butterfly migration. *Nature Communications*, *5*, 4164, Article 4164. https://doi.org/10.1038/ncomms5164

Guerra, P. A., Parlin, A. F., & Matter, S. F. (2022). Lack of evidence for a fine-scale magnetic map sense for fall migratory Eastern North American monarch butterflies (Danaus plexippus). *Ecology and evolution*, *12*(11), e9498. https://doi.org/https://doi.org/10.1002/ece3.9498

Guilford, T., & Biro, D. (2014). Route following and the pigeon's familiar area map. *Journal of Experimental Biology*, *217*(2), 169-179.

Guo, F., Buler, J. J., Smolinsky, J. A., & Wilcove, D. S. (2024). Seasonal patterns and protection status of stopover hotspots for migratory landbirds in the eastern United States. *Current Biology*, *34*(2), 235-244. e233.

Gustafsson, K. M., Agrawal, A. A., Lewenstein, B. V., & Wolf, S. A. (2015). The monarch butterfly through time and space: the social construction of an icon. *Bioscience*, *65*(6), 612-622.

Gwinner, E., & Wiltschko, W. (1978). Endogenously controlled changes in migratory direction of the garden warbler, *Sylvia borin*. *Journal of Comparative Physiology, A*, *125*(3), 267-273. https://doi.org/10.1007/BF00656605

Haefner, J. W. (2005). *Modeling biological systems: principles and applications,* . Springer.

Hagelin, J. C., Hallworth, M. T., Barger, C. P., Johnson, J. A., DuBour, K. A., Pendelton, G. W., DeCicco, L. H., McDuffie, L. A., Matsuoka, S. M., & Snively, M. A. (2021). Revealing migratory path, important stopovers and non-breeding areas of a boreal songbird in steep decline. *Animal Migration*, *8*(1), 168-191.

Hall, R. J., Altizer, S., Peacock, S. J., & Shaw, A. K. (2022). Animal migration and infection dynamics: recent advances and future frontiers. In *Animal Behavior and Parasitism* (pp. 111). Oxford University Press.

Hamilton III, W. J. (1962). Does the bobolink navigate? *The Wilson Bulletin*, *74*(4), 357-366.

Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press.

Hayes, L., & Grüter, C. (2023). When should bees be flower constant? An agent-based model highlights the importance of social information and foraging conditions. *Journal of Animal Ecology*, *92*(3), 580-593.

Hays, G. C., Atchison-Balmond, N., Cerritelli, G., Laloë, J.-O., Luschi, P., Mortimer, J. A., Rattray, A., & Esteban, N. (2022). Travel routes to remote ocean targets reveal the map sense resolution for a marine migrant. *Journal of the Royal Society Interface*, *19*(190), 20210859.

Helm, B., & Muheim, R. (2021). Bird migration: clock and compass facilitate hemisphere switching. *Current Biology*, *31*(17), R1058-R1061.

Heran, H. (1952). Untersuchungen über den temperatursinn der honigbiene (*Apis mellifica*) unter besonderer berücksichtigung der wahrnehmung strahlender wärme. *Zeitschrift für vergleichende Physiologie*, *34*(2), 179-206.

Hijmans, R. J. (2022). terra: Spatial Data Analysis. R package version 1.5-21. In.

Hijmans, R. J., & van Etten, J. (2020). Raster: geographic data analysis and modeling. R package. In: 3.6-23.

Holdo, R. M., Holt, R. D., Sinclair, A. R., Godley, B. J., & Thirgood, S. (2011). Migration impacts on communities and ecosystems: empirical evidence and theoretical insights. In E. J. Milner-Gulland, J. M. Fryxell, & A. R. E. Sinclair (Eds.), *Animal Migration: A Synthesis* (pp. 131-143). Oxford University Press.

Holland, R. (2014). True navigation in birds: from quantum physics to global migration. *Journal of Zoology*, *293*(1), 1-15. https://doi.org/10.1111/jzo.12107

Horns, J. J., Adler, F. R., & Şekercioğlu, Ç. H. (2018). Using opportunistic citizen science data to estimate avian population trends. *Biological Conservation*, *221*, 151-159. https://doi.org/10.1016/j.biocon.2018.02.027

Horns, J. J., & Şekercioğlu, Ç. H. (2018). Conservation of migratory species. *Current Biology*, *28*(17), R980-R983. https://doi.org/10.1016/j.cub.2018.06.032

Howard, E., Aschen, H., & Davis, A. K. (2010). Citizen science observations of monarch butterfly overwintering in the southern United States. *Psyche: A Journal of Entomology*, *2010*, 689301.

Huse, G., & Giske, J. (1998). Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour. *Fisheries Research*, *37*(1-3), 163-178. https://doi.org/10.1016/S0165-7836(98)00134-9Get

Iiams, S. E., Lugena, A. B., Zhang, Y., Hayden, A. N., & Merlin, C. (2019). Photoperiodic and clock regulation of the vitamin A pathway in the brain mediates seasonal responsiveness in the monarch butterfly. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(50), 25214-25221.

Illian, J. B., Sørbye, S. H., & Rue, H. (2012). A toolbox for fitting complex spatial point process models using integrated nested Laplace approximation (INLA). *The Annals of Applied Statistics*, *6*(4), 1499-1530, 1432. https://doi.org/10.1214/11-AOAS530

iNaturalist contributors. (2023). *iNaturalist Research-grade Observations* accessed via GBIF.org on 2023-01-17. https://doi.org/https://doi.org/10.15468/ab3s5x

James, D. G., James, T. S., Seymour, L., Kappen, L., Russell, T., Harryman, B., & Bly, C. (2018). Citizen scientist tagging reveals destinations of migrating monarch butterflies, Danaus plexippus (L.) from the Pacific Northwest. *The Journal of the Lepidopterists' Society*, *72*(2), 127-144. https://doi.org/10.18473/lepi.v72i2.a5

James, D. G., & Kappen, L. (2021). Further insights on the migration biology of monarch butterflies, Danaus plexippus (Lepidoptera: Nymphalidae) from the Pacific Northwest. *Insects*, *12*(2), 161.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., & Monteith, K. L. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *science*, *361*(6406), 1023-1025.

Kauffman, M. J., Aikens, E. O., Esmaeili, S., Kaczensky, P., Middleton, A., Monteith, K. L., Morrison, T. A., Mueller, T., Sawyer, H., & Goheen, J. R. (2021). Causes, consequences, and conservation of ungulate migration. *Annual Review of Ecology and Systematics*, *52*, 453-478.

Kauffman, M. J., Cagnacci, F., Chamaillé-Jammes, S., Hebblewhite, M., Hopcraft, J. G. C., Merkle, J. A., Mueller, T., Mysterud, A., Peters, W., & Roettger, C. (2021). Mapping out a future for ungulate migrations. *science*, *372*(6542), 566-569.

Keller, B. A., Putman, N. F., Grubbs, R. D., Portnoy, D. S., & Murphy, T. P. (2021). Map-like use of Earth's magnetic field in sharks. *Current Biology*, *31*(13), 2881-2886. https://doi.org/10.1016/j.cub.2021.03.103

Kendzel, M. J., Altizer, S. M., & de Roode, J. C. (2023). Interactions between parasitism and migration in monarch butterflies. *Current Opinion in Insect Science*, *59*, 101089.

Kishkinev, D., Packmor, F., Zechmeister, T., Winkler, H.-C., Chernetsov, N., Mouritsen, H., & Holland, R. A. (2021). Navigation by extrapolation of geomagnetic cues in a migratory songbird. *Current Biology*, *31*(7), 1563-1569. https://doi.org/10.1016/j.cub.2021.01.051

Kitchin, R. M. (1994). Cognitive maps: what are they and why study them? *Journal of Environmental Psychology*, *14*(1), 1-19. https://doi.org/10.1016/S0272-4944(05)80194-X

Klaassen, R. H., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K. M., Bairlein, F., & Alerstam, T. (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, *83*(1), 176-184.

Kramer, G. (1950). Orientierte Zugaktivität gekäfigter Singvögel. *Naturwissenschaften*, *37*(8), 188-188.

Kremen, C., & Ostfeld, R. S. (2005). A call to ecologists: measuring, analyzing, and managing ecosystem services. *Frontiers in Ecology and the Environment*, *3*(10), 540-548. https://doi.org/10.2307/3868610

Krkošek, M., Gottesfeld, A., Proctor, B., Rolston, D., Carr-Harris, C., & Lewis, M. A. (2007). Effects of host migration, diversity and aquaculture on sea lice threats to Pacific salmon populations. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1629), 3141-3149.

Kubelka, V., Sandercock, B. K., Székely, T., & Freckleton, R. P. (2022). Animal migration to northern latitudes: environmental changes and increasing threats. *Trends in Ecology & Evolution*, *37*(1), 30-41.

Layne, J. E., Barnes, W. J. P., & Duncan, L. M. (2003). Mechanisms of homing in the fiddler crab Uca rapax 2. Information sources and frame of reference for a path integration system. *Journal of Experimental Biology*, *206*(24), 4425-4442.

Lehrer, M. (1996). Small-scale navigation in the honeybee: active acquisition of visual information about the goal. *Journal of Experimental Biology*, *199*(1), 253-261. https://doi.org/10.1242/jeb.199.1.253

Liao, B., Shan, X., & Chen, Y. (2021). Preliminary Assessment of a Coupled Dynamic-Energy Budget and Agent-based Model (DEB-ABM) for Predicting Individual and Population-Level Dynamics: A Case Study on Anchovy, Engraulis japonicus. *Pakistan Journal of Zoology*, *53*(3).

Liedvogel, M., Åkesson, S., & Bensch, S. (2011). The genetics of migration on the move. *Trends in Ecology & Evolution*, *26*(11), 561-569.

Linard, C., Ponçon, N., Fontenille, D., & Lambin, E. F. (2009). A multi-agent simulation to assess the risk of malaria re-emergence in southern France. *Ecological Modelling*, *220*(2), 160-174. https://doi.org/10.1016/j.ecolmodel.2008.09.001

Lohmann, K. J., & Lohmann, C. M. (2006). Sea turtles, lobsters, and oceanic magnetic maps. *Marine and Freshwater Behaviour and Physiology*, *39*(1), 49-64. https://doi.org/10.1080/10236240600563230

Lohmann, K. J., Lohmann, C. M., Ehrhart, L. M., Bagley, D. A., & Swing, T. (2004). Geomagnetic map used in sea-turtle navigation. *Nature*, *428*(6986), 909-910.

Lohmann, K. J., Putman, N. F., & Lohmann, C. M. (2012). The magnetic map of hatchling loggerhead sea turtles. *Current Opinion in Neurobiology*, *22*(2), 336-342. https://doi.org/10.1016/j.conb.2011.11.005

Lund, U., & Agostinelli, C. (2018). Circular Statistics, from "Topics in Circular Statistics" (2001). In: 0.5-0.

Luschi, P., Papi, F., Liew, H., Chan, E., & Bonadonna, F. (1996). Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. *Journal of Comparative Physiology, A*, *178*(4), 447-452. https://doi.org/10.1007/BF00190175

Lyons, J. I., Pierce, A. A., Barribeau, S. M., Sternberg, E. D., Mongue, A. J., & De Roode, J. C. (2012). Lack of genetic differentiation between monarch butterflies with divergent migration destinations. *Molecular Ecology*, *21*(14), 3433-3444.

Majewska, A. A., & Altizer, S. (2019). Exposure to non-native tropical milkweed promotes reproductive development in migratory monarch butterflies. *Insects*, *10*(8), 253.

Majewska, A. A., Davis, A. K., Altizer, S., & de Roode, J. C. (2022). Parasite dynamics in North American monarchs predicted by host density and seasonal migratory culling. *Journal of Animal Ecology*, *91*(4), 780-793.

Majewska, A. A., Sims, S., Schneider, A., Altizer, S., & Hall, R. J. (2019). Multiple transmission routes sustain high prevalence of a virulent parasite in a butterfly host. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1910), 20191630.

Marquet, P. A., Allen, A. P., Brown, J. H., Dunne, J. A., Enquist, B. J., Gillooly, J. F., Gowaty, P. A., Green, J. L., Harte, J., & Hubbell, S. P. (2014). On theory in ecology. *Bioscience*, *64*(8), 701-710. https://doi.org/10.1093/biosci/biu098

Maurer, R., & Séguinot, V. (1995). What is modelling for? a critical review of the models of path integration. *Journal of Theoretical Biology*, *175*(4), 457-475.

McKinnon, L., Smith, P., Nol, E., Martin, J., Doyle, F., Abraham, K., Gilchrist, H., Morrison, R., & Bêty, J. (2010). Lower predation risk for migratory birds at high latitudes. *science*, *327*(5963), 326-327. https://doi.org/10.1126/science.1183010

McKinnon, L., Smith, P. A., Nol, E., Martin, J. L., Doyle, F. I., Abraham, K. F., Gilchrist, H. G., Morrison, R. I. G., & Bêty, J. (2010). Lower predation risk for migratory birds at high latitudes. *science*, *327*(5963), 326-327. https://doi.org/10.1126/science.1183010

McLaughlin, R., & Myers, J. (1970). *Ophryocystis elektroscirrha* sp. n., a Neogregarine Pathogen of the Monarch Butterfly *Danaus plexippus* (L.) and the Florida Queen Butterfly *D. gilippus* berenice Cramer 1. *The Journal of Protozoology*, *17*(2), 300-305.

Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., Bundrock, G., Hülse, S., Plümpe, T., & Schaupp, F. (2005). Honey bees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences, USA*, *102*(8), 3040-3045. https://doi.org/10.1073/pnas.0408550102

Merrill, L., Levengood, J., England, J. C., Osborn, J., & Hagy, H. M. (2018). Blood parasite infection linked to condition of spring-migrating Lesser Scaup (*Aythya affinis*). *Canadian Journal of Zoology*, *96*(10), 1145-1152.

Møller, J., Syversveen, A. R., & Waagepetersen, R. P. (1998). Log gaussian cox processes. *Scandinavian journal of statistics*, *25*(3), 451-482.

Mongue, A. J., Martin, S. H., Manweiler, R. E., Scullion, H., Koehn, J. L., de Roode, J. C., & Walters, J. R. (2023). Genome sequence of Ophryocystis elektroscirrha, an apicomplexan parasite of monarch butterflies: cryptic diversity and response to host-sequestered plant chemicals. *bioRxiv*, doi: 10.1101/2019.1112.1111.123456.

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., & Fryxell, J. M. (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, *85*(9), 2436-2445.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H., & Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2289-2301.

Mouritsen, H. (1998). Modelling migration: the clock-and-compass model can explain the distribution of ringing recoveries. *Animal Behaviour*, *56*(4), 899-907.

Mouritsen, H., Derbyshire, R., Stalleicken, J., Mouritsen, O. Ø., Frost, B. J., & Norris, D. R. (2013). An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators. *Proceedings of the National Academy of Sciences*, *110*(18), 7348-7353. https://doi.org/10.1073/pnas.1221701110

Mouritsen, H., & Frost, B. J. (2002). Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(15), 10162-10166.

Mouritsen, H., Huyvaert, K. P., Frost, B. J., & Anderson, D. J. (2003). Waved albatrosses can navigate with strong magnets attached to their head. *Journal of Experimental Biology*, *206*(22), 4155-4166. https://doi.org/10.1242/jeb.00650

Mouritsen, H., & Larsen, O. N. (2001). Migrating songbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass. *Journal of Experimental Biology*, *204*(22), 3855-3865. https://doi.org/10.1242/jeb.204.22.3855

Mouritsen, H., & Mouritsen, O. (2000). A mathematical expectation model for bird navigation based on the clock-and-compass strategy. *Journal of Theoretical Biology*, *207*(2), 283-291. https://doi.org/10.1006/jtbi.2000.2171

Mueller, T., & Fagan, W. F. (2008). Search and navigation in dynamic environments–from individual behaviors to population distributions. *Oikos*, *117*(5), 654-664.

Müller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences, USA*, *85*(14), 5287-5290. https://doi.org/10.1073/pnas.85.14.5287

Munro, U., Wiltschko, W., & Ford, H. A. (1993). Changes in the migratory direction of yellow-faced honeyeaters *Lichenostomus chrysops* (Meliphagidae) during autumn migration. *Emu*, *93*(1), 59-62. https://doi.org/10.1071/MU9930059

Naimi, B., Hamm, N. A., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, *37*(2), 191-203.

Naisbett-Jones, L. C., Putman, N. F., Stephenson, J. F., Ladak, S., & Young, K. A. (2017). A magnetic map leads juvenile European eels to the Gulf Stream [Article]. *Current Biology*, *27*(8), 1236-1240. https://doi.org/10.1016/j.cub.2017.03.015

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059.

Neate-Clegg, M. H., Horns, J. J., Adler, F. R., Aytekin, M. Ç. K., & Şekercioğlu, Ç. H. (2020). Monitoring the world's bird populations with community science data. *Biological Conservation*, *248*, 108653, Article 108653. https://doi.org/10.1016/j.biocon.2020.108653

Oberhauser, K. S., Taylor, O. R., Reppert, S. M., Dingle, H., Nail, K. R., Pyle, R. M., & Stenoien, C. (2013). Are monarch butterflies true navigators? The jury is still out. *Proceedings of the National Academy of Sciences*, *110*(39), E3680. https://doi.org/10.1073/pnas.1308369110

Packmor, F., Kishkinev, D., Bittermann, F., Kofler, B., Machowetz, C., Zechmeister, T., Zawadzki, L. C., Guilford, T., & Holland, R. A. (2021). A magnet attached to the forehead disrupts magnetic compass orientation in a migratory songbird. *Journal of Experimental Biology*, *224*(22), jeb243337.

Pardi, L., & Papi, F. (1953). Ricerche sull'orientamento di *Talitrus saltator* (Montagu)(Crustacea—Amphipoda). *Zeitschrift für vergleichende Physiologie*, *35*(6), 459-489.

Parlin, A. F., Stratton, S. M., Guerra, P. A., & Evolution. (2021). Assaying lepidopteran flight directionality with non-invasive methods that permit repeated use and release after testing. *Methods in Ecology*, *12*(9), 1699-1704.

Pebesma, E., Bivand, R., Racine, E., Sumner, M., Cook, I., Keitt, T., Lovelace, R., Wickham, H., Ooms, J., & Müller, K. (2021). sf: Simple Features for R. *R package version*, *1*.

Perdeck, A. (1958). Two types of orientation in migrating starlings, *Sturnus vulgaris L.*, and chaffinches, *Fringilla coelebs L.*, as revealed by displacement experiments. *Ardea*, *55*(1), 1-37.

Perez, S. M., Taylor, O. R., & Jander, R. (1997). A sun compass in monarch butterflies. *Nature*, *387*, 29. https://doi.org/10.1038/387029a0

Peterson, A. T., Papeş, M., & Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, *1*, 28-38.

Phillips, J., Adler, K., & Borland, S. (1995). True navigation by an amphibian. *Animal Behaviour*, *50*(3), 855-858.

Pierce, A. A., Zalucki, M. P., Bangura, M., Udawatta, M., Kronforst, M. R., Altizer, S., Fernández Haeger, J., & de Roode, J. C. (2014). Serial founder effects and genetic differentiation during worldwide range expansion of monarch butterflies [Article]. *Proceedings of the Royal Society B-Biological Sciences*, *281*(1797), 20142230, Article 20142230. https://doi.org/10.1098/rspb.2014.2230

Pollonara, E., Luschi, P., Guilford, T., Wikelski, M., Bonadonna, F., & Gagliardo, A. (2015). Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea. *Scientific reports*, *5*(1), 16486.

Poulin, R., & de Angeli Dutra, D. (2021). Animal migrations and parasitism: reciprocal effects within a unified framework. *Biological Reviews*, *96*(4), 1331-1348.

Putman, N. F. (2021). Animal navigation: what is truth? *Current Biology*, *31*(7), R330-R332.

Putman, N. F., Endres, C. S., Lohmann, C. M., & Lohmann, K. J. (2011). Longitude perception and bicoordinate magnetic maps in sea turtles. *Current Biology*, *21*(6), 463-466. https://doi.org/10.1016/j.cub.2011.01.057

Rathore, M. K., & Sharma, L. K. (2023). Efficacy of species distribution models (SDMs) for ecological realms to ascertain biological conservation and practices. *Biodiversity and Conservation*, *32*(10), 3053-3087.

Reppert, S. M., & de Roode, J. C. (2018). Demystifying monarch butterfly migration. *Current Biology*, *28*, R1009–R1022.

Reppert, S. M., & de Roode, J. C. (2018). Demystifying monarch butterfly migration. *Current Biology*, *28*(17), R1009-R1022.

Reppert, S. M., Gegear, R. J., & Merlin, C. (2010). Navigational mechanisms of migrating monarch butterflies. *Trends in Neurosciences*, *33*(9), 399-406.

Reynolds, A. M., Cecere, J. G., Paiva, V. H., Ramos, J. A., & Focardi, S. (2015). Pelagic seabird flight patterns are consistent with a reliance on olfactory maps for oceanic navigation. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1811), 20150468.

Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, *71*(2), 319-392.

Sánchez, C. A., Ragonese, I. G., de Roode, J. C., & Altizer, S. (2021). Thermal tolerance and environmental persistence of a protozoan parasite in monarch butterflies. *Journal of Invertebrate Pathology*, *183*, 107544.

Sandberg, R., & Moore, F. R. (1996). Migratory orientation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. *Behavioral Ecology and Sociobiology*, *39*(1), 1-10. https://doi.org/10.1007/s002650050261

Satterfield, D. A., Maerz, J. C., & Altizer, S. (2015). Loss of migratory behaviour increases infection risk for a butterfly host. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1801), 20141734.

Satterfield, D. A., Maerz, J. C., Hunter, M. D., Flockhart, D. T., Hobson, K. A., Norris, D. R., Streit, H., de Roode, J. C., & Altizer, S. (2018). Migratory monarchs that encounter resident monarchs show life-history differences and higher rates of parasite infection. *Ecology Letters*, *21*(11), 1670-1680.

Satterfield, D. A., Villablanca, F. X., Maerz, J. C., & Altizer, S. (2016). Migratory monarchs wintering in California experience low infection risk compared to monarchs breeding year-round on non-native milkweed. *Integrative and Comparative Biology*, icw030.

Schmidt-Koenig, K. (1990). The sun compass. *Experientia*, *46*(4), 336-342.

Shoukat, A., & Moghadas, S. M. (2020). Agent-based modelling: An overview with application to disease dynamics. *arXiv preprint arXiv:2007.04192*.

Simpson, D., Illian, J. B., Lindgren, F., Sørbye, S. H., & Rue, H. (2016). Going off grid: Computationally efficient inference for log-Gaussian Cox processes. *Biometrika*, *103*(1), 49-70.

Simpson, D., Rue, H., Riebler, A., Martins, T. G., & Sørbye, S. H. (2017). Penalising Model Component Complexity: A Principled, Practical Approach to Constructing Priors. *Statistical Science*, *32*(1), 1-28, 28. https://doi.org/10.1214/16-STS576

Slowinski, S. P., Fudickar, A. M., Hughes, A. M., Mettler, R. D., Gorbatenko, O. V., Spellman, G. M., Ketterson, E. D., & Atwell, J. W. (2018). Sedentary songbirds maintain higher prevalence of haemosporidian parasite infections than migratory conspecifics during seasonal sympatry. *PLoS One*, *13*(8), e0201563.

Snyder, M. N., Schumaker, N. H., Ebersole, J. L., Dunham, J. B., Comeleo, R. L., Keefer, M. L., Leinenbach, P., Brookes, A., Cope, B., & Wu, J. (2019). Individual based modeling of fish migration in a 2-D river system: model description and case study. *Landscape Ecology*, *34*(4), 737-754.

Society, X. (2024). *Xerces Society western monarch overwintering location*.

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *64*(4), 583-639.

Sternberg, E. D., Li, H., Wang, R., Gowler, C., & de Roode, J. C. (2013). Patterns of host-parasite adaptation in three populations of monarch butterflies infected with a naturally occurring protozoan disease: virulence, resistance, and tolerance [Article]. *American Naturalist*, *182*(6), E235-E248. https://doi.org/10.1086/673442

Swingland, I. R., & Greenwood, P. J. (1983). *The ecology of animal movement*. Clarendon Press Oxford.

Syposz, M., Padget, O., Wynn, J., Gillies, N., Fayet, A. L., & Guilford, T. (2021). An assay to investigate factors influencing initial orientation in nocturnally fledging seabirds. *Journal of Avian Biology*, *52*(1), e02613. https://doi.org/10.1111/jav.02613

Tang, W., & Bennett, D. A. (2010). Agent-based modeling of animal movement: a review. *Geography Compass*, *4*(7), 682-700.

Taylor Jr, O. R., Pleasants, J. M., Grundel, R., Pecoraro, S. D., Lovett, J. P., & Ryan, A. (2020). Evaluating the migration mortality hypothesis using monarch tagging data. *Frontiers in Ecology and Evolution*, 264.

Teitelbaum, C. S., & Mueller, T. (2019). Beyond migration: causes and consequences of nomadic animal movements. *Trends in Ecology & Evolution*, *34*(6), 569-581.

Tenger-Trolander, A., & Kronforst, M. R. (2020). Migration behaviour of commercial monarchs reared outdoors and wild-derived monarchs reared indoors. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1932), 20201326. https://doi.org/10.1098/rspb.2020.1326

Thomson, S. A. L. B. (1953). The study of the visible migration of birds: an introductory review. *Ibis*, *95*(2), 165-180. https://doi.org/10.1111/j.1474-919X.1953.tb00684.x

Thorup, K., & Rabøl, J. (2001). The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. *Journal of Avian Biology*, *32*(2), 111-119. https://doi.org/10.1034/j.1600-048X.2001.320203.x

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*(4), 189-208. https://doi.org/doi.org/10.1037/h0061626

Townsend, A. K., Sewall, K. B., Leonard, A. S., & Hawley, D. M. (2022). Infectious disease and cognition in wild populations. *Trends in Ecology & Evolution*.

Tracy, J. L., Kantola, T., Baum, K. A., & Coulson, R. N. (2019). Modeling fall migration pathways and spatially identifying potential migratory hazards for the eastern monarch butterfly. *Landscape Ecology*, *34*, 443-458.

Ugolini, A. (2003). Activity rhythms and orientation in sandhoppers (Crustacea, Amphipoda). *Frontiers in Bioscience*, *8*, 722-732. https://doi.org/10.2741/1041

Ugolini, A., Fantini, T., & Innocenti, R. (2003). Orientation at night: an innate moon compass in sandhoppers (Amphipoda: Talitridae). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1512), 279-281. https://doi.org/10.1098/rspb.2002.2221

Urquhart, F., & Urquhart, N. (1978). Autumnal migration routes of the eastern population of the monarch butterfly (Danaus p. plexippus L.; Danaidae; Lepidoptera) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. *Canadian Journal of Zoology*, *56*(8), 1759-1764.

Urquhart, F. A. (1976). Found at last: the monarch's winter home. *National Geographic*, *150*(2), 161-173.

Urquhart, F. A., & Urquhart, N. R. (1978). Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus p. plexippus* L.; Danaidae; Lepidoptera) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. *Canadian Journal of Zoology*, *56*(8), 1759-1764. <Go to ISI>://A1978FN22600015

Vaughan, I. P., & Ormerod, S. J. (2005). The continuing challenges of testing species distribution models. *Journal of Applied Ecology*, *42*(4), 720-730.

Vellend, M. (2010). Conceptual synthesis in community ecology. *Quarterly Review of Biology*, *85*(2), 183-206.

Wallraff, H. G. (1981). The olfactory component of pigeon navigation: steps of analysis. *Journal of Comparative Physiology, A*, *143*(4), 411-422. https://doi.org/10.1007/BF00609907

Wallraff, H. G. (2001). Navigation by homing pigeons: updated perspective. *Ethology Ecology & Evolution*, *13*(1), 1-48.

Wang, K., Mattern, E., & Ritz, T. (2006). On the use of magnets to disrupt the physiological compass of birds. *Physical Biology*, *3*(3), 220.

Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *Journal of comparative physiology A*, *189*(8), 579-588.

Wehner, R., & Lanfranconi, B. (1981). What do the ants know about the rotation of the sky? *Nature*, *293*(5835), 731-733. https://doi.org/10.1038/293731a0

Wehner, R., Lehrer, M., & Harvey, W. (Eds.). (1999). *Navigation [special issue]* (199 (1) ed., Vol. 199). The Journal of Experimental Biology.

Wehner, R., & Menzel, R. (1990). Do insects have cognitive maps? *Annual Review of Neuroscience*, *13*(1), 403-414. https://doi.org/10.1146/annurev.ne.13.030190.002155

Wehner, R., Michel, B., & Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *The Journal of Experimental Biology*, *199*(1), 129-140. https://doi.org/10.1242/jeb.199.1.129

Wehner, R., & Srinivasan, M. V. (1981). Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of Comparative Physiology, A*, *142*(3), 315-338. https://doi.org/10.1007/BF00605445

Wiens, J. J., & Zelinka, J. (2024). How many species will earth lose to climate change? *Global Change Biology*, *30*(1), e17125.

Wilcox, A. A., Newman, A. E., Raine, N. E., Mitchell, G. W., & Norris, D. R. (2021). Captive-reared migratory monarch butterflies show natural orientation when released in the wild. *Conservation Physiology*, *9*(1). https://doi.org/10.1093/conphys/coab032

Wiltschko, R. (2017). Navigation. *Journal of comparative physiology A*, *203*(6), 455-463.

Wiltschko, W., & Wiltschko, R. (1972). Magnetic compass of European robins. *science*, *176*(4030), 62-64. https://doi.org/10.1126/science.176.4030.62

Wiltschko, W., Wiltschko, R., & Walcott, C. (1987). Pigeon homing: different effects of olfactory deprivation in different countries. *Behavioral Ecology and Sociobiology*, *21*(5), 333-342. https://doi.org/10.1007/BF00299971

Wittlinger, M., Wehner, R., & Wolf, H. (2006). The ant odometer: stepping on stilts and stumps. *science*, *312*(5782), 1965-1967. https://doi.org/10.1126/science.1126912

Wolff, W. (1994). An individual-oriented model of a wading bird nesting colony. *Ecological Modelling*, *72*(1-2), 75-114. https://doi.org/10.1016/0304-3800(94)90146-5

Wu, H.-i., Li, B.-L., Springer, T. A., & Neill, W. H. (2000). Modelling animal movement as a persistent random walk in two dimensions: expected magnitude of net displacement. *Ecological Modelling*, *132*(1-2), 115-124. https://doi.org/10.1016/S0304-3800(00)00309-4

Wynn, J., Padget, O., Morford, J., Jaggers, P., Davies, K., Borsier, E., & Guilford, T. (2022). How might magnetic secular variation impact avian philopatry? *Journal of Comparative Physiology, A*, *208*(1), 145-154.

Xu, F., & Si, Y. (2019). The frost wave hypothesis: How the environment drives autumn departure of migratory waterfowl. *Ecological Indicators*, *101*, 1018-1025.

Yang, L. H., Ostrovsky, D., Rogers, M. C., & Welker, J. M. (2016). Intra-population variation in the natal origins and wing morphology of overwintering western monarch butterflies *Danaus plexippus*. *Ecography*, *39*(10), 998-1007. https://doi.org/10.1111/ecog.01994

Zhan, S., Zhang, W., Niitepõld, K., Hsu, J., Haeger, J. F., Zalucki, M. P., Altizer, S., de Roode, J. C., Reppert, S. M., & Kronforst, M. R. (2014). The genetics of monarch butterfly migration and warning colouration [Article]. *Nature*, *514*(7522), 317-321. https://doi.org/10.1038/nature13812

Zhu, H. S., Gegear, R. J., Casselman, A., Kanginakudru, S., & Reppert, S. M. (2009). Defining behavioral and molecular differences between summer and migratory monarch butterflies. *BMC Biology*, *7*, 14. https://doi.org/10.1186/1741-7007-7-14