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An Avian-Centered Model for the Dispersal of *Ixodes scapularis* by Fall Songbird Migrants

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An Avian-Centered Model for the Dispersal of *Ixodes scapularis* by Fall Songbird Migrants

An Honors Thesis

Presented to

The Faculty of the Department of Biology

Bates College

In partial fulfillment of the requirements for the

Degree of Bachelor of Science

By

Benjamin Tonelli

Lewiston, Maine

March 28, 2018

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Table of Contents

Acknowledgements.....	ii
Table of Contents.....	iii
ABSTRACT.....	v
INTRODUCTION.....	6
<i>Host Species of I. scapularis and Range Expansion of the Lyme Vector</i>	8
<i>Reservoir Hosts</i>	9
<i>Avian Role in the Range Expansion of I. scapularis</i>	9
<i>Patterns of Tick Dispersal by Migratory Birds</i>	11
<i>Structure of Individual and Agent-Based Models</i>	12
<i>Outline of Research</i>	14
METHODS.....	18
<i>Preface</i>	18
<i>Initial Map Creation</i>	18
<i>Factors Relating to Spatial and Temporal I. scapularis Questing Behavior</i>	19
Spatial Distribution.....	19
Temporal Distribution & Phenology Differences.....	20
Tick Attachment Time.....	20
<i>Simulating Attachment on Avian Hosts</i>	21
Submodel: Determining Species' Propensity to Tick Attachment.....	21
Intensity Rate Underestimation.....	23
Location Factor and Relative Density Map.....	25
<i>Avian Factors</i>	26
Breeding Ranges.....	26
Initial Population Parameters – Juveniles and Adults.....	26
Orientation.....	27
Goal Headings.....	30
Flight over Water.....	31
Death Rates.....	32
Timing.....	34
Flight Speed.....	35
Stopover Behavior & Energy Conditions.....	37
VALIDATION.....	44

<i>Individual Migration Patterns</i>	44
<i>System-Level Migration Dynamics</i>	45
<i>Emergence – ‘Coastal Effect’ and ‘Edge Effect’</i>	47
RESULTS	64
<i>Relative Rates of Transport of I. scapularis by Wood Thrushes and Ovenbirds</i>	64
<i>Flight Distance</i>	65
<i>Tick Bearings from Origin and Spatial Patterns of Redistribution</i>	65
<i>Emergence – Coastal Migration and Tick Detachment</i>	67
<i>Synchronicity of Migration Timing and Tick Questing</i>	67
DISCUSSION	78
<i>Tick Dispersal, Range Expansion of I. scapularis, and Human Health Risks</i>	79
<i>Differences between Songbird Species</i>	81
Tick Attachment Rates – Difference between Species	81
Breeding and Migratory Densities	82
Timing of Migration	83
Emergence and Conclusion.....	83
<i>Impact of Climate Change</i>	85
Climate Change and Tick Phenology	85
Avian Behavior	86
Conclusion	87
<i>Implications for Gene Flow</i>	87
<i>Limitations of, and Improvement to, Current Model Parameters</i>	88
Intensity of Infestation	89
Spatial Tick Densities	90
<i>Further Applications and Expansion of the Model</i>	90
<i>Conclusions</i>	93
REFERENCES	96
Appendix A: Outline of Parameters and Sources	105

ABSTRACT

Lyme disease caused by *Borrelia burgdorferi* infection is the most common vector-borne illness in the United States, and has become increasingly reported since it was first described clinically. The tick species *Ixodes scapularis* is responsible for disease transmission between endothermic hosts. Consequently, the spatial patterns of human infection are positively correlated with population densities of the tick. Field observations have shown that migrating songbirds often carry ticks during the fall as they travel southward. However, no research currently predicts or demonstrates the magnitude of tick dispersal by fall migrants. The goal of this research was to develop an individual-based model of avian migration and bird-tick interactions to investigate species-specific patterns of *I. scapularis* dispersal within the continental United States by southward migrating songbirds. The model used in this research predicts the dispersal of over a million ticks outside of the current range of the species to most areas predicted to be climatically suitable for the tick, both presently and in the future. Out of areas without an established tick population, Eastern Minnesota, Iowa, Virginia and North Carolina experienced the highest level of tick detachment events, suggesting that birds may play a significant role in the range expansion of *I. scapularis* into these regions. This model suggests that the dispersal of *I. scapularis* by avian species is a critical factor in determining human infection risk to Lyme disease and other tick-borne pathogens in the United States. In the future, this model can be used as a virtual laboratory to analyze how local climate change patterns may impact the dispersal and range expansion of *I. scapularis* through changes to the phenological synchrony of ticks and songbirds.

INTRODUCTION

Lyme disease is the most commonly contracted tick-borne disease in the United States, with over 300,000 cases occurring yearly (Kuehn 2013). Although the Lyme-causing spirochete *B. burgdorferi* was present before European colonization, the rate of Lyme disease infection has never been greater than it is currently (Walter et al. 2017, Steere 2004). *B. burgdorferi* infects a variety of different species of endothermic hosts by means of a tick intermediary. The maintenance of the bacteria in animal populations leads to the eventual transmission of the disease to human hosts. Therefore, understanding host-vector relationships in nature is critical for assessing Lyme disease risk to human populations.

In the Eastern United States, the principal tick vector responsible for transmission of *B. burgdorferi* is *I. scapularis* (Steere 2004). Although most well known for being a carrier of Lyme disease, *I. scapularis* can transmit other pathogens, including *Anaplasma phagocytophilum* and *Babesia microti* (Varde et al. 2018). *I. scapularis* exist in three distinct life stages; larval, nymphal and adult. Each year, larvae attempt to attach to a host in order to consume a blood meal. If an individual successfully attaches and feeds, it will fall off the host and molt. After molting, the tick will attempt to feed again as a nymph. If successful, the nymph will molt into an adult and breed the same year. If feeding is unsuccessful at any life stage, ticks will attempt to survive until the next season (Steere 2004). As a result of the low success rate of feeding each year, the number of ticks that exist at each progressing life stage is less than the number existing in the last (Ostfield et al. 1996). During each feeding event a tick has the potential to ingest blood infected with *B. burgdorferi*. If this occurs, the tick then has the capability of transmitting the bacteria to hosts in future years during feeding (Couret et al. 2017, Piesman et al. 1987).

I. scapularis is responsible for transmission of the Lyme-causing spirochete between endothermic hosts, and subsequently the spatial and temporal patterns of human infection are highly correlated with population density and phenology of the vector (Brownstein et al. 2003, Diuk-Wasser et al. 2010, Pepin et al. 2012, Steere 2004). Currently, the highest rates of Lyme disease are reported in the Northeast and North Central regions of the United States (Fig. 1), where *I. scapularis* is endemic and population sizes are the largest (Steere 2004, Diuk-Wasser et al. 2010). The main drivers for the rise in reported human infections are the increase in size of existing *I. scapularis* populations, and the establishment of new populations in areas previously uninhabited (Eisen et al. 2016).

The range of *I. scapularis* is spreading to new areas from these historic centers at a rapid rate. The most expansive survey to date found that the number of U.S. counties reporting an established population of *I. scapularis* increased from 396 to 842 between 1998 and 2015 (Dennis et al. 1998, Eisen et al. 2016). In Canada, *I. scapularis* range is hypothesized to expand under current climate change expectations from the areas immediately surrounding the 39th parallel into the continental interior steadily over the next century (Ogden et al. 2008b). Likewise, in the United States, climate predictions for the next century suggest an increase of suitable habitat for reproducing *I. scapularis* populations (Brownstein et al. 2005). Concurrently, Walter et al. postulate that the range of *I. scapularis* was far greater when forests dominated much of the land area of the American East before European colonization (2017). After colonization, land cover changed as forested areas were converted for agricultural purposes. As much of this land has become reforested in recent years, *I. scapularis* is repopulating much of its pre-colonial range (Walter et al. 2017). Land cover change patterns have resulted in the increase of forest edge habitat, one habitat type that has been shown to be ideal for tick survival due to

favorable microclimate conditions (Bertrand et al. 1996). Range expansion and population growth of *I. scapularis* due to reforestation and changing climate conditions are likely driving the increase in Lyme infection rate in human populations (Dennis et al. 1998, Eisen et al. 2016, Walter et al. 2017, Steere 2004).

Host Species of *I. scapularis* and Range Expansion of the Lyme Vector

Range expansion of *I. scapularis* is dependent not only on the suitability of climate conditions, but also on movements of individual ticks. Areas without an existing population of *I. scapularis*, but where local habitat conditions are favorable for establishment, are likely to be colonized if ticks are introduced. However, ticks are unlikely to travel ecologically significant distances on their own accord (Falco and Fish 1991), so the spread of populations to new areas is overwhelmingly contingent on the dispersal of hosts after attachment (Leighton et al. 2012, Madhav et al. 2004). Depending on the movement patterns of host species, ticks can be displaced over varying ranges (Madhav et al. 2004, Ogden et al. 2008b, Scott et al. 2001). Importantly, hosts have the potential to transport *I. scapularis* into areas in which established populations do not currently exist.

In the United States, increase in white-tailed deer populations has been hypothesized to be responsible for the range expansion of *I. scapularis* (Walter et al. 2017). Deer are a common host of *I. scapularis* capable of carrying ticks of all stages across individual home ranges of around 10km² (Leighton et al. 2012, Grovenburg et al. 2009). Other mammals such as white-footed mice also have the capability of transporting *I. scapularis* during attachment over smaller home ranges of around 600m² (Anderson and Magnarelli 1984, Wolff 1985).

Reservoir Hosts

In addition to capacity to harbor *I. scapularis*, many species are competent reservoir hosts of the bacterial agent of Lyme disease. Reservoir host species are defined by their capability to harbor the spirochete and transmit the bacteria to an uninfected tick. The most commonly researched reservoir host of *B. burgdorferi* in the Eastern United States is the white-footed mouse, a species shown to harbor ticks at high rates during the summer and fall months (Anderson and Magnarelli 1984, Stafford et al. 1995, Anderson et al. 1987). Importantly, the white-tailed deer is not a reservoir host (Telford et al. 1988), and ticks transported by this species are not exposed to Lyme during feeding. Regardless of host incompetence, white-tailed deer are still relevant in the spread of ticks to new areas.

Avian Role in the Range Expansion of *I. scapularis*

In addition to white-tailed deer and white-footed mice, migratory songbirds have also been hypothesized to play a role in the range expansion of *I. scapularis* and *B. burgdorferi* due to their ability to harbor ticks, act as reservoir hosts of Lyme disease, and rapidly travel long distances (Brinkerhoff et al. 2009, Ogden et al. 2008a, Scott et al. 2001, Scott and Durden 2015). Due to the large number of songbirds resident in the United States during the breeding season, the impact of avian hosts on Lyme disease dynamics has likely not received due attention. The most expansive research effort to date (Brinkerhoff et al. 2009) found that 58.6% of North American songbird species surveyed serve as competent reservoir hosts for the bacteria, with many more parasitized by *I. scapularis* (see also Ogden et al. 2008a, Scott et al. 2001). Infections

of songbirds leading to transfer of the spirochete to non-infected ticks have been shown to last months (Richter 2000). Additionally, songbirds under migration conditions have been shown to exhibit a reactivation of latent Lyme infections as a result of decreased immune function, likely resulting in increased transmission of the bacteria during the spring and fall (Gylfe et al. 2000).

The relationship between migratory birds and the range expansion of *I. scapularis* has been explored both in the field and by using mathematical models (Elias et al. 2011, Leighton et al. 2012, Leo et al. 2017, Morshed et al. 2005, Ogden et al. 2005, Ogden et al. 2006(a-b), Ogden et al. 2008a, Ogden et al. 2008b, Scott et al. 2001). An estimate by Ogden et al. hypothesized, based on infestation rates of songbirds, that between 50 and 175 million *I. scapularis* ticks are brought into Canada every year by northward migrating birds, making these species a significant host responsible for the transport of ticks over long distances and geographical barriers (2008a). Scott et al. found *I. scapularis* and other tick species attached to migrating birds hundreds to thousands of kilometers from locations with established tick populations (2001). Although a considerable body of research exists regarding the possible northward range expansion of *I. scapularis* (see publications by Ogden), the same methodologies have not been applied to assessing the role of migratory birds during southbound fall migration. Understanding the potential for range expansion of *I. scapularis* due to southward migration is of paramount importance to understanding the risk to human populations within the United States.

Migratory bird species have been suggested to play a crucial role in the range expansion of *I. scapularis* in both the Midwest and Northeast United States that has been rapid over recent years (Bacon et al. 2008, Eisen et al. 2016). *I. scapularis* have been observed on songbirds migrating southward in Connecticut, New Hampshire, New York, Maine, Maryland, Minnesota and Wisconsin (Anderson et al. 1986, Battaly et al. 1987, Morris et al. 2007, Rand et al. 1998,

Scharf 2004, Weisbrod and Johnson 1989). This fieldwork is conclusive in demonstrating that ticks are transported southward along migration routes during the fall (Fig. 2). Rates of attachment to avian hosts during fall migration are similar to those observed by Ogden entering Canada in the spring, potentially indicating that dispersal of ticks during spring migration occurs on the same order of magnitude during the fall (2008a).

Patterns of Tick Dispersal by Migratory Birds

Understanding the relationship between migratory birds and human Lyme infection is contingent on the understanding of the relationship between avian hosts and *I. scapularis* ticks. As birds migrate southbound to their wintering grounds, they travel at high speeds, often over thousands of kilometers in total, stopping routinely to refuel (McKinnon et al. 2014, McKinnon et al. 2013, Stanley et al. 2015, Stanley et al. 2012, Stutchbury et al. 2009). As they undergo migration, birds travel through and from areas with established populations of *I. scapularis* ticks. If the tick attaches in one location to a migrating bird, it is possible that it is dropped off far from that origin point, and possibly to areas where no established population of the tick exists (Scott et al. 2001, Morris et al. 2007). Likewise, the avian host may pass blood containing *B. burgdorferi* to the feeding tick, or may become infected with the bacteria as a result of the tick feeding.

In all, the pattern of *I. scapularis* and *B. burgdorferi* redistribution during the fall migration season is the result of the interactions between many variables, among them aspects of migratory behavior, tick questing phenology, and tick attachment time. Thorough investigation of this phenomenon is impossible at a large scale in the field. It is prohibitively difficult to record the movements of individual ticks over space and time, while also measuring the status of

infection of these vectors. Adding to this difficulty is the necessity to gather data from a range of geographical locations in order to create a complete picture of dispersal.

As a result of these difficulties, investigating the patterns of *I. scapularis* dispersal during fall migration is most easily done using a model based on the factors contributing to these system-level patterns. The most readily available information in the literature does not describe the patterns of dispersal of ticks during migration, but rather the individual behaviors that lead to these patterns. To investigate of the impact of migrating birds on *I. scapularis* range expansion with the research available, it is most feasible to model the individual behaviors of the agents involved, and then measure the system-level dynamics that result.

Structure of Individual and Agent-Based Models

Individual-based models are one method for examining the effect of individual behavior between multiple agents on system-level patterns. An individual-based approach to modeling relies on a foundation of knowledge detailing the behaviors of agents, and the effect of the environment and other agents on these behaviors. In simulations, these behaviors are expected to contribute to system-level patterns in the same way the behaviors of individuals in the real world have observable effects on the environment in which they inhabit. In each example of models created using this methodology, a simulated environment is populated with agents that behave according to certain predetermined rules. Each agent has overarching goals and governing principles, which are highly variable between models, that impact the ways individuals act. These parameters are gathered from relevant experimental data gathered in field and laboratory settings, or based on mechanistic reasoning (see Railsback and Grimm 2011, Tang and Bennett

2010). Although individual-based models are not necessarily more thorough or accurate than their classical mathematical counterparts, the methodology is more relevant in situations where individual behaviors are better understood than system-level dynamics. From this ground-up method of modeling, system-level patterns emerge from regulating parameters of individual level behavior.

Individual-based models are one way of modeling complex systems, and have been used extensively to model a wide range of ecological processes, with the inclusion of both plants and animals as research subjects (see Grimm and Railsback 2005). Within the framework of ecological modeling, use of individual-based methodology has commonly been applied to research questions that are dependent in part on the individual movement of animals (Bonabeau 2002, Cohen et al. 2014, Mclane et al. 2011, Wenjun 2012). The patterns of tick dispersal during fall migration are largely dependent on patterns of movement of avian hosts, as well as the behavior and distribution of questing ticks. The components of these individual behaviors are numerous, and individual parameters relating to topics such as migration timing, orientation, stopover behavior, tick questing patterns, and tick population size each have a role in influencing the transport of *I. scapularis*. Luckily, all of these individual components have been researched to some degree in the field, making investigation based on individual level behaviors possible. In this way, understanding the impact of migrating birds on the movement of infected and non-infected *I. scapularis* through a model based on individual behavior is both appropriate and possible.

Outline of Research

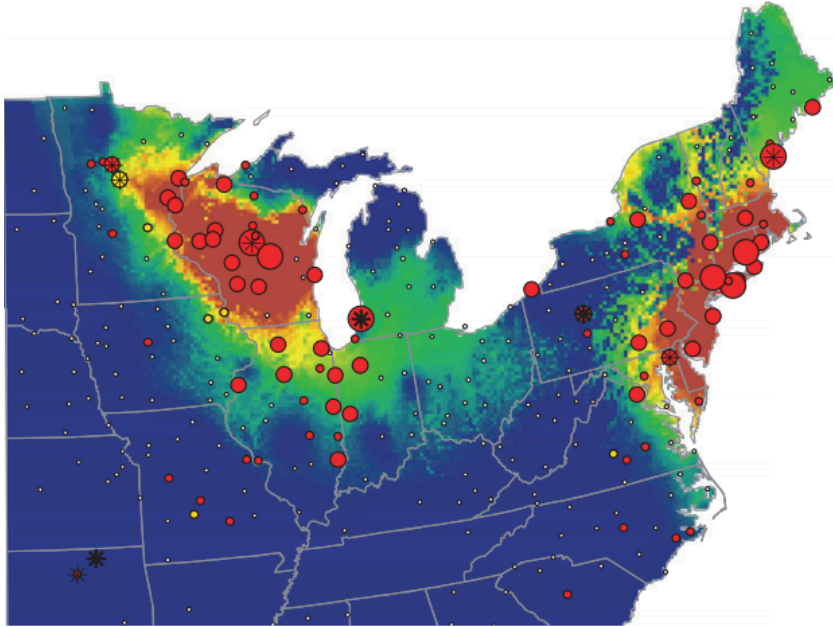
Computational models have demonstrated the potential of songbirds to contribute to the northern range expansion of *I. scapularis* into Canada (see publications by Ogden). Until now, a similar modeling-based approach has not been utilized to examine the potential for fall migrants to contribute to range expansion of *I. scapularis* within the United States. Previous research has demonstrated that *I. scapularis* attach to migrating avian hosts during the fall migration season. Because of the ability to transport ticks greater distances than other commonly researched mammalian hosts, avian species are a critical subject for assessing the potential range expansion of Lyme disease in North America.

This research utilizes an individual-based modeling approach to explore the redistribution of *I. scapularis* during fall migration that emerges from individual behavior of two common migrating bird species, *Hylocichla mustelina* (wood thrush) and *Seiurus aurocapilla* (ovenbird). These species were chosen because of their capacity as a population to harbor large numbers of ticks (Stafford et al. 1995), their capacity to serve as reservoir hosts of *B. burgdorferi* (Giardina et al. 2000, Weisbord et al. 1989), and the existence of extensive research detailing migration behavior. Through analysis of the impact of these two avian species, this research hopes to qualitatively illuminate the impact of songbird species on the dispersal of *I. scapularis*.

The primary aim of this research is to assess the capability and likelihood of these two species to transport *I. scapularis* into areas without established populations that are predicted to be climatically suitable for the tick vector both currently and under near-future climate conditions. Understanding where *I. scapularis* ticks are likely to be dropped by migrating songbird hosts can inform predictions of the likelihood of population establishment in climatically suitable areas. In addition, this model will provide a foundation for investigating

how migration timing, tick phenology, population size, breeding distributions, and other factors may alter host-vector relationships in the future. Ultimately, this research will investigate how avian species may impact current and future tick-borne disease risk to human populations.

(A)



(B)

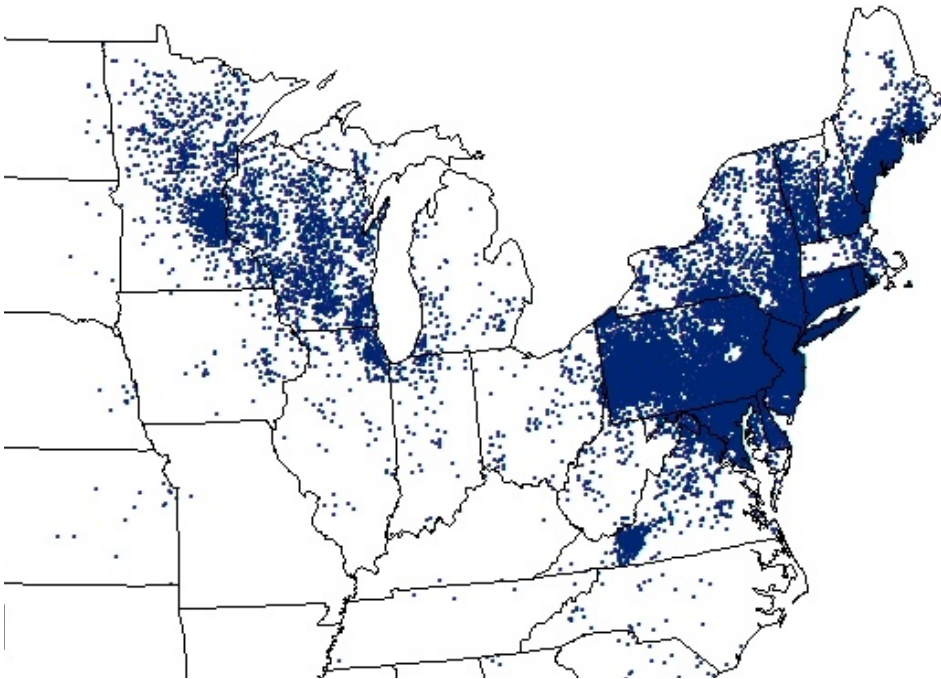


Figure 1. Modeled (indicated by shading) and empirically measured nymphal densities at study locations (indicated by size of circles) reprinted from Diuk-Wasser et al. 2010 (A). Individual Lyme disease occurrences reported to the Center for Disease Control in 2016, with each dot representing one confirmed case (B). Image accessible at cdc.gov/lyme/stats/maps.

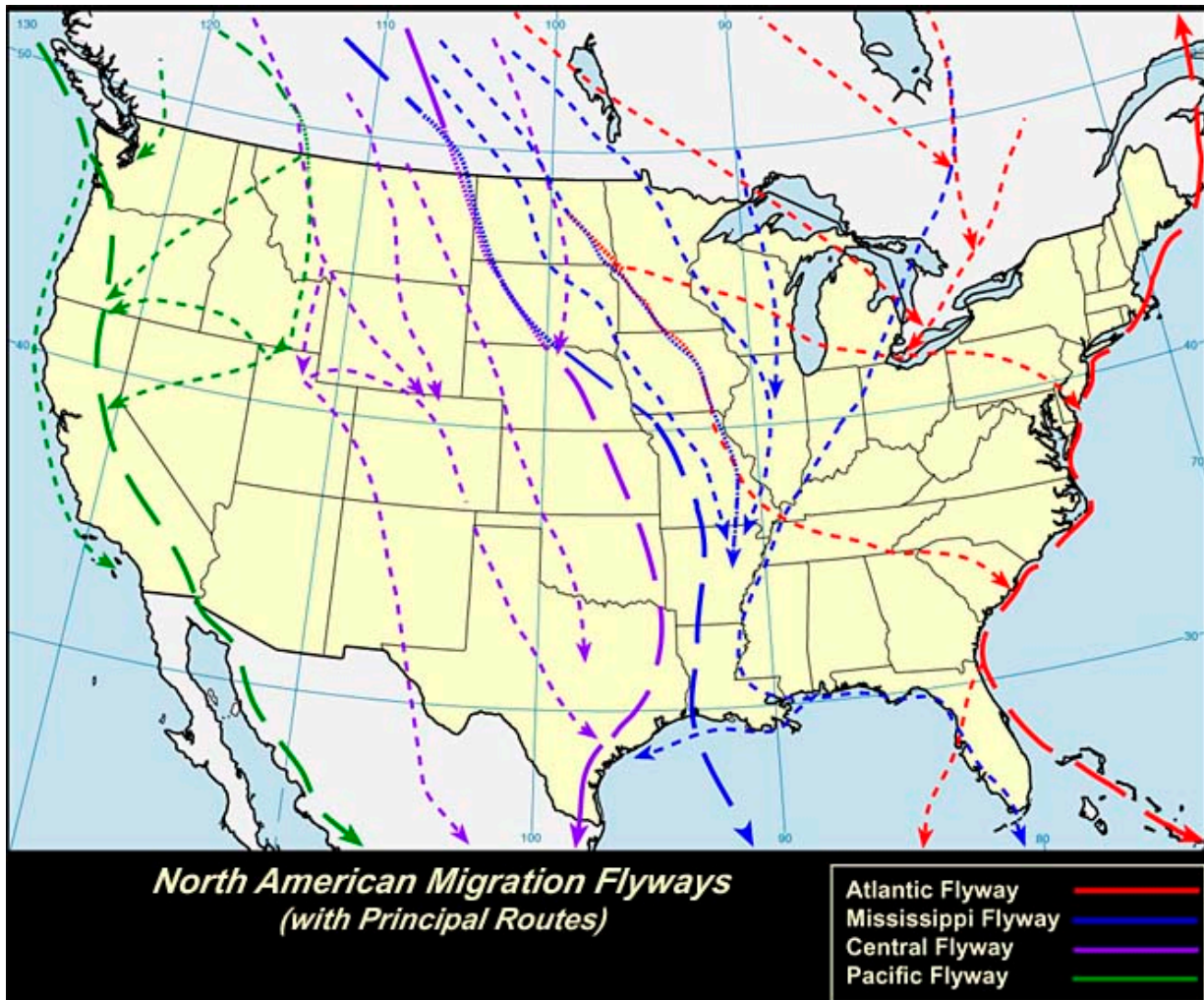


Figure 2. General flyways of southbound North American songbirds during fall migration. Image accessible via [nps.gov/pais/learn/nature/birds](https://www.nps.gov/pais/learn/nature/birds).

METHODS

Preface

This model is built on a vast foundation of fieldwork that, directly or indirectly, explains the nature of the interactions between *I. scapularis* and two avian host species. Without this extensive body of research, this model would be wholly impossible to create. The goal of this methods section is, first and foremost, to explain how parameters were attained from the literature and through mechanistic reasoning. Secondly, this section explains the limitations and inaccuracies inherent in each parameter. As much as this model relies on the results of various research projects to recreate avian-tick interactions, it is also sensitive to the inaccuracies and the shortcomings of these individual projects from which parameters are derived. This model is only as strong as its parameters, and with future fieldwork a more accurate model can be created. When appropriate, recommendations for future research that could help inform the improvement of model parameters are given. An outline of this section is provided in Appendix A, and a simplified version of model functions is provided in figure 3.

Initial Map Creation

The primary model and all sub-models were designed using MATLAB 2017a. The model utilizes a continuous space system for the movement of individuals, and a grid-based system with representations of 1-degree latitude by 1-degree longitude cells for certain parameters, including tick densities, questing behavior, and avian breeding locations. Grid-based data was primarily collected and imported into the model using Microsoft Excel.

The area represented by the model lies between the 22nd and 60th parallels N., and the 126th and 46th meridians W. Each cell is designed to have a constant width of 111km and height of 83km, ignoring distortion caused by the curvature of the earth. These standardized dimensions were calculated based on the distance between the 81st and 82nd meridian, and the 41st and 42nd parallel. This grid cell was chosen to serve as the standard in order to increase spatial accuracy of bird movements where the greatest number of bird-tick interaction events are expected, and due to its centrality in the simulated space. Longitudinal distortion caused by this map may prolong the migration times of individual ovenbirds breeding in Northwest Canada, but has little effect on birds primarily moving north to south. For a bird travelling due east from the 123rd to 92nd meridian, the distance covered by simulated birds is 1.35 times greater than that of birds in nature.

A map was created to describe whether the area within cells is parameterized to be water or land. All latitude-longitude cells that appeared to have a majority of area covered by water were considered to be 100% covered by water in the model, while those covered by less than 50% water were considered to be 100% land.

Factors Relating to Spatial and Temporal *I. scapularis* Questing Behavior

Spatial Distribution

The spatial distribution of *I. scapularis* populations was parameterized using reported data collected by the survey efforts of Diuk-Wasser et al. (2010). This survey describes densities of questing nymphs measured by flagging efforts across the United States. Density values gathered in the American South by Diuk-Wasser et al. were excluded in the current research due

to the propensity for reptilian host seeking behavior in *I. scapularis* populations at these latitudes (2010). Reported density values from individual study locations were grouped by latitude-longitude cell location, based on the grid system described above. The mean of values within each cell were calculated and used to create a map of relative tick densities across the model range.

Temporal Distribution & Phenology Differences

Timing of tick questing behavior differs between life stages and with respect to longitudinal position. Distributions of questing phenology roughly differentiate populations separated by the 80th meridian east (Gatewood et al. 2009). Best-fit unimodal normal functions were created to explain relative temporal questing frequency of nymphal and larval forms of *I. scapularis* in the Northeast and, separately, the Midwest using data recreated from Gatewood et al. (2009). The best-fit cubic functions calculated in the analysis by Gatewood et al. to fit these distributions were not used in this analysis, as these functions were unlikely to be an accurate representation of relative tick questing frequency during the fall months.

Tick Attachment Time

Tick attachment time was parameterized based on an experimental study measuring tick attachment behavior on laboratory-reared mice and hamster hosts (Hu et al. 1997). This study details the lengths of feeding times of both nymphs and larvae. This experiment is the most expansive single study that details this behavior, and is supported by the findings of others (see Bontemps-Gallo et al. 2016, Couret et al. 2017, des Vignes et al. 2001, Goddard et al. 2015,

Hodzic et al. 1998, Nakayama and Spielman 1989). Hu et al. were analyzing the relationship between feeding time and presence of *Babesia microti*, a bacteria responsible for a malaria type-disease. For use in this model, data was compiled from only the control groups consisting of non-infected hosts in order to avoid the presence of the possibly confounding variable of host infection by *B. microti*. All attachment times from non-infected hamsters and mice (n = 1,549) were grouped by life stage of tick and feeding time. The probability of detachment during each day following attachment was calculated for use in all models (Fig. 4).

It is unknown whether or not the time of attachment to rodents differs from attachment times for ticks attached to avian hosts. To the knowledge of the author, no research has yet investigated this question. For the purpose of this model, it is assumed that attachment time to avian species is the same as that to the rodents used in this experiment.

Simulating Attachment on Avian Hosts

Submodel: Determining Species' Propensity to Tick Attachment

Accurate simulation of avian-tick dynamics during fall migration is contingent on the ability to recreate infestation and intensity rates observed in the field. In order to accurately recreate these patterns, a submodel was built to determine how best to parameterize daily likelihood of tick attachment to a bird based on location and date. Tick attachment probabilities in a given cell are considered to be the product of spatially dependent questing tick numbers, reported by Diuk-Wasser et al. (2010), the temporal patterns of tick questing frequency, described by Gatewood et al. (2009), and the propensity of a given bird species to pick up ticks, an unknown constant to be determined. The goal of the sub-model was to combine these factors

to create a unique probability distribution representing the likelihood that any natural number of larvae and, independently, nymphs attach on each day in a given cell.

Stafford et al. describe temporal trends of *I. scapularis* attachment on both *Hylocichla mustelina* and *Seiurus aurocapilla* from 1989-1991 in the area around Lyme, Connecticut (1995). This empirical research provides the foundation for parameterizing the sub-model. The number of ticks attaching to a bird on each day was calculated by sampling a unique Poisson distribution dependent on date and local tick density. A Poisson distribution was chosen because of its usefulness in calculating the probability of a discrete number of independent events occurring during a given period. A Poisson distribution requires one scalar value, in this case number that encodes both the variance and mean tick attachment likelihood.

The submodel and model were built using the following equation to describe the probability of any number of ticks attaching to a given bird on each day in each cell:

$$P(x) = e^{-(\alpha \times \beta \times \delta)} \times (\alpha \times \beta \times \delta)^x / x!$$

Where:

α = relative population size of questing ticks.

β = intensity of tick questing, dependent on location phenology and life stage.

δ = species constant, determined for both life stages.

x = number of ticks attaching

The constant describing the relative rate at which members of each species (wood thrush and ovenbird) pick up larvae and nymphs, δ , was manipulated until the simulated infestation

rates adequately matched those reported by Stafford et al. (1995). The constants describing the propensity of each species to pick up ticks determined by this sub-model were then used in the final model.

Intensity Rate Underestimation

Stafford et al. report the mean intensity rate, defined as the average number of ticks attached to an infested bird, for each avian species and tick life stage. Mean number of larvae attached to infested individuals was 8.5 and 4.6 to ovenbirds and wood thrushes, respectively (1995). Nymphal intensity was lower, with a mean number of ticks on infested ovenbirds of 1, and 1.5 on wood thrushes. At the extreme, the maximum numbers of larvae attached to a single bird, reported by Stafford et al., were 35 and 40 to an ovenbird and a wood thrush, respectively (1995). Although the submodel was able to accurately reproduce infestation rates (Fig. 5), it was less successful at reproducing intensity rates. The submodel consistently underestimated intensity rates for both species and both life stages, with the exception of nymphs on ovenbirds (Table 1). Stafford et al. did not report temporal trends in intensity rates (1995), making it difficult to assess what relationship exists between intensity and infestation rates of the two study species. Results from this submodel suggest that while the final model accurately recreates experimental infestation rates, the mean number of ticks on simulated birds remains lower than that of birds in nature (Table 1).

There are many possible factors that may explain why the model ultimately underestimates the total number of ticks attached to infested birds. These possibilities both stem from errors in the methodology used to parameterize the model, as well as inaccuracies in the

data collected and reported by Stafford et al. The first source of error is the likely underreporting of tick attachments by Stafford et al. (1995). Ticks are difficult to spot as an observer, and researchers are much more likely to recognize a heavily infested bird in comparison to one infected with a single tick (see Ogden 2008a). With ticks on heavily infested birds recorded disproportionately, the mean number of ticks on each bird would be inflated, and the infestation rate underestimated. In addition, it is likely that heavily infested birds that may be diseased or disabled and unable to preen ticks skew the mean intensity rates. Another possibility for this discrepancy is that not all individual birds are equally likely to pick up ticks due to differing feeding behavior or experience avoiding parasites. The high mean intensity of attachment by larvae may be due to the existence of pockets of ticks with low movement capability and no prior displacement due to host attachment. This makes it more likely that a bird will pick up multiple larvae at a specific location at a given time, suggesting that instances of tick attachment are not independent. A lack of independence would indicate that the use of another probability distribution would be more appropriate than a Poisson distribution.

All of these factors may lead to the discrepancy between simulated and observed infestation rates, and each is a worthy investigation of future study. The ultimate impact of this discrepancy is that the model is likely to underestimate the total number of ticks attaching to birds. For instance, Morris et al. observed a mean intensity of 4 ticks per infested ovenbirds during the fall migration season, with a range between 1-16 ticks attached per bird (2007). In the model, these measures of intensity would be highly unlikely. In the final model, this underestimation of mean infestation intensity leads to fewer ticks being transported during migration than the observational data suggests. Despite this underestimation, the spatial pattern of tick dispersal is expected to remain the same.

Location Factor and Relative Density Map

The most extensive research detailing the temporal trends of attachment to avian hosts is from Lyme, Connecticut (Stafford et al, 1995). Location constants were calculated in the final model as a relative percentage of the tick density compared to the cell containing Lyme, Connecticut in order to represent how different *I. scapularis* spatial densities affect the rates at which the parasites attach to avian hosts. In this way, any cells with lower tick density values than that of Lyme, CT would experience lower rates of attachment, with larger density values having the opposite effect.

Comparing rates of attachment reported in the literature from across the country, a linear relationship between attachment rates to avian hosts and nymphal density seems to most appropriately describe the relationship between these two variables (Stafford et al. 1995, Scharf 2004, Battaly and Fish 1993, Smith et al. 1996). To simulate this observed pattern, larger nymphal densities lead to a greater chance of tick attachment to avian hosts in the model. For instance, simulated birds occupying a location with twice as many ticks as Lyme, CT experience double the rate of attachment. More spatially expansive research that explicitly measures tick density compared to attachment rates to songbirds could demonstrate a more nuanced relationship.

Although tick density was recorded in terms of nymphal questing behavior, there seems to be no evidence suggesting that relative spatial densities of larvae differ from densities of nymphs. In this model, it is assumed that nymphal density is a representation of the size of the larval population as well. In this way, a grid cell with a high density of nymphs is assumed to have an equally high relative density of larvae.

Avian Factors

Two bird species were utilized in this analysis, *Hylocichla mustelina* (wood thrush) and *Seiurus aurocapilla* (ovenbird). These species were chosen because of the availability of extensive research detailing migration behavior, breeding densities, and interaction with *I. scapularis* populations. Because of the differences in the primary literature describing wood thrushes and ovenbirds, it is important to note that the sources for parameterization differ between the two species.

Breeding Ranges

Relative density maps from the Breeding Bird Survey data were used to determine starting positions throughout the breeding ranges of ovenbird and wood thrush populations. The percentage of the total population expected to be breeding in each grid cell within the model range was calculated based on the relative density of wood thrush and ovenbird populations (Fig. 6). At the beginning of the model run, each bird is randomly assigned to one of these cells, with the probability of occupying each cell representative of the relative frequency described by BBS data (Sauer et al. 2003).

Initial Population Parameters – Juveniles and Adults

The MAPS program (Monitoring Avian Productivity and Survivorship) has collected extensive data from captures of both wood thrush and ovenbird populations across the United States (Michel et al. 2006). One reported factor is the proportion of unique hatch year birds captured by mist-netting efforts during the summer months. Although an imperfect way of

assessing the true number of hatch year birds in a population, to the knowledge of the author, this is the best estimate of entire population demographics available. Birds captured by mist-netting are mobile, and are likely to undergo migration. These hatch-year birds surviving until migration are those represented by the model. 77.5% of all unique wood thrush captures reported by MAPS sites across the country were adults. For the purpose of the model, hatch-year wood thrushes were considered to make up 22.5% of the population of the species. Likewise, ovenbird populations are considered to be composed of 67% adult individuals, and 33% hatch-year individuals.

Population size estimates provided by Rich et al. were used in calculations regarding the total impact of each species (2016). For calculations in this model, the population of wood thrushes was considered to total 12 million individuals. Ovenbird population size was considered to total 26 million (Rich et al. 2016).

Orientation

Factors relating to orientation during migration have been the subject of intense scholarship for at least the last century (see Alerstam and Christie 1993, Kerlinger and Archer 2008 for review). Despite this effort, the answers to many underlying questions related to orientation have yet to be decisively determined. In order to avoid the complexities of the ongoing debate about how birds orient and choose routes, this model instead focuses on defining the probabilistic outcome of these factors. In simplistic terms, each flight can be described as a vector, with a distance and direction. This vector comes to describe where a bird originates, and where the flight terminates.

The factors that contribute to the angle from departure location to arrival location during one night of flight are dependent on a variety of factors including innate and learned orientation cues, weather conditions, stopover choice, and breeding ground location. It is difficult to model each of these factors and behaviors individually, and is most efficient to instead model the outcome of these factors. In this case, little is known about what affects stopover choice, as well as the compensation of heading during drift due to wind. To complicate this issue further, evidence suggests that these factors are often species-specific (Alerstam and Christie 1993). For this reason, it is more efficient to utilize research that measures individual daily bird movements to determine the range of individual bird tracks. For the purpose of this model it was assumed the track of each bird during each flight night was determined by drawing from a normal distribution, with birds most often oriented towards their ‘goal.’

The most relevant information to inform the standard deviation of this distribution comes from radio tracking studies of individual birds during migration. Two studies examine this phenomenon extensively. Demong and Emlen investigate individual tracks of swainson’s thrush, gray-cheeked thrush and white-throated sparrows (1978). Cochran, in Birds of Two Worlds, describes the flight paths of swainson’s thrush during spring migratory flights (2005). For the purpose of this model, it is assumed that individual reported tracks in these studies describe the variability in the factors affecting individual orientation, such as climate and stopover choice. Because no discernible difference existed between the distributions among species, values from individuals of all species were grouped together. To that end, the distribution of headings was variable, with a standard deviation of 36.73 degrees around the mean heading for all birds in both studies (n=58). In the model, each bird is assumed to fly at a bearing chosen from a normal distribution with a mean as the ideal heading to a ‘goal’ point and a standard deviation of 36.73

degrees. This distribution of headings was determined from the above research by using the mean bearing of each species at each location as the assumed goal heading. There may be some level of inaccuracy in this designation, as birds were likely flying to differing sites, and so their true 'ideal heading' may have differed from the mean of all individuals recorded.

Emlen funnel experiments are the next best source in giving an estimate of the orientation differences present among migratory birds. Data reported by Moore of savannah sparrows kept in Emlen funnels during the migratory restlessness period exhibited angular deviations from the mean heading in a similar pattern found in the above experiments ($SD = 38^\circ$ for adult birds, 1984). In addition, this experiment and others demonstrate a much wider range of orientation bearings in hatch-year birds (see summary by Woodrey 2000). Although differences in orientation due to age may be species-specific, for the purpose of simplicity this model assumes hatch-year birds had a standard deviation in flight tracks that is 1.5 times that of adult birds based on data from Moore et al. (1984). The exact mechanism leading to this difference in observed flight tracks between juveniles and adults may be related to differences in wind compensation and lack of experience navigating through a foreign landscape.

This orientation parameter uses a random deviation from the ideal bearing for each individual bird regardless of location, although it is much more likely that all birds experiencing similar weather conditions may be pushed from their heading at a similar vector. There are consistent, although not constant, wind conditions that may affect birds flying in certain regions during the fall migration period. Integration of wind and weather data, along with a better foundation in understanding how juvenile and adult birds compensate for drift due to wind, would lead to a higher degree of precision in this model.

Goal Headings

All birds are assumed to have a goal heading that is determined each day according to the location of the bird in relation to their goal point. All birds are considered to know their position in relation to their goal point, an assumption supported by observations of displaced songbirds in nature (Thorup et al. 2007). Goal points are determined once at the start of the simulation for each individual wood thrush, and are uniformly distributed along the 23rd parallel between the 83rd and 86th meridian, in order to simulate variation in wintering sites along the Yucatan peninsula.

Ovenbirds exhibit a more complicated migration pattern than wood thrush, and have been shown to move within two distinct flyways during the fall migration period depending on breeding location. Eastern individuals pass through Florida during migration en route to winter in the Caribbean, while western birds pass over the Gulf of Mexico on their way to the Yucatan peninsula (Hallworth et al. 2015). This model separates populations by the 86th meridian, although in actual ovenbird populations this boundary is likely more nuanced. Goal points for ovenbirds depend on the region of the individual, and change throughout the migration period. Birds breeding in northwestern Canada are assumed to fly towards the Great Lakes, and then subsequently reorient towards the Gulf. Birds with breeding locations west of the 86th meridian, and south of the Great Lakes, are programmed to fly towards the Gulf. Ovenbirds with eastern breeding ranges are programmed to fly towards Florida, where they subsequently reorient as they depart overwater towards the Caribbean.

Flight over Water

During the course of migration, birds may encounter up to three significant water barriers: the Great Lakes, the Atlantic Ocean and the Gulf of Mexico. Evidence exists that overwater flight may be preferable to overland flight in terms of energetics (McKinnon et al. 2017), although the risks of drowning and disorientation remain. Water barriers can be potentially hazardous for migrating songbirds, especially juveniles during their first migration (see Ralph 1978, 1981). The exact mechanisms that affect orientation behavior over water barriers is unknown. Other models of bird migration assume that individuals may correct their course only if they can see land after flying for a full night (Reilly and Reilly 2009), although in nature this is an assumption complicated by visibility conditions. It does appear that overwater death occurs frequently in migrating songbirds, but that this death may be related to severe weather conditions rather than orientation mishaps (Diehl et al. 2014, Butler 2000, Ralph 1978). Because very little is known about this phenomenon, it is assumed by this model that each bird knows its own location with respect to the nearest land cell, and that re-orientation occurs accordingly. In each individual case where a bird within the model finds itself over water at the end of predetermined flight duration, it is assumed that the bird reorients itself to the nearest land cell, and flies until reaching land, or until its individual flight capacity reaches zero, and the bird perishes. Because bird movement is only relevant to the model before passage over the Gulf, water-specific parameters are only utilized when encountering the Great Lakes and Atlantic Ocean. Birds flying over the Gulf of Mexico are assumed to be making their flight to wintering grounds in either the Caribbean or the Yucatan peninsula, and at this point are considered to have completed the section of migration relevant to this model.

Overwater death due to all causes is underestimated in this model, as it does not account for death as a result of severe storms. Furthermore, the allowance of the model for landward reorientation assumes knowledge that birds may not have. Future research into the distribution and causes of mortality during migration seasons would allow for a more accurate model of differential rates of death during this period.

Death Rates

Parameterization of a daily chance of mortality is important, due to the high impact mortality could have on the movement of tick parasites. In nature, mortality occurs frequently from a variety of sources during migration, including tower collisions, hypothermia, predation, exhaustion, and drowning (Diehl et al. 2014, Longcore 2013, Sillet and Holmes 2002, Butler 2000, Ralph 1978.) Because of a lack of research quantifying the likelihood and distribution of death from these sources, this model assumes a daily chance of mortality due to all deaths, except by drowning. Drowning deaths are calculated from birds over water during migratory flights, and the way these deaths are calculated is explained above. For the purpose of this model it was assumed that mortality among all simulated songbirds was equivalent during the migration period, regardless of age. Much of mortality for juveniles seems to happen either in the nest, or shortly upon departure from the nest (Robinson et al. 1995). Only birds that survive up to the start of the migration are included in this model, and so mortality for juveniles and adults is considered to be the same during the migration period.

Death probability of both species was calculated based on Monitoring Avian Productivity and Survivorship data spanning two decades. Annual adult yearly survival over this period for

ovenbirds was .558, and .446 for wood thrush (Michel et al. 2006). MAPS data only explains survivorship from year to year, and does not describe mortality rates during migration.

According to Sillet and Holmes, 42.5% of mortality among another songbird, black-throated blue warblers, occurred during the fall migration season (2002). Assuming the same rate of mortality is true for wood thrush and ovenbird populations, 18.8% of adult ovenbirds, and 23.5% of wood thrush are expected to perish during fall migration. The probability of death was assumed to be constant throughout the migration period. The daily rate of mortality was calibrated in the model to lead to an overall reduction in the population by 18.8% for ovenbirds and 23.5% for wood thrush.

For the purpose of this model, death causes a ceasing of migratory movement, with no new ticks attaching to the deceased individual. All ticks attached before death are considered to have survived the death of the bird, except in cases of drowning, and drop from the bird in subsequent days.

The methodology of a constant daily rate of death oversimplifies a more complicated pattern of death in the natural world. Greater death rates during certain times and in certain locations, such as during extreme weather conditions and at sites of high-rise structures, concentrates incidences of deaths and may affect patterns of tick redistribution. Much of mortality appears to occur during trans-gulf flight due to storms and other weather variables (Diehl et al. 2014, Butler 2000, Ralph 1978). The model does not account for trans-gulf death, likely overestimating death prior to Gulf crossings. Unfortunately, monitoring avian mortality to such specificity and on such a broad geographical scale has not been accomplished in the field, so the model is most appropriately parameterized simplistically.

Timing

Geocator data collected by Stanley et al. describing the fall migration of wood thrushes from Pennsylvania to their wintering grounds was used in order to parameterize start dates for migration in the model (2012). A normal distribution of migration starting dates was calculated by recreating observations of start timing reported in Stanley et al. (2012). Six birds departed from their breeding grounds during a period when latitude estimates are not reliable, and so these birds were considered to have left uniformly throughout this interval. The calculated normal distribution estimated a mean departure date of Sep. 18th with a variance of 16.36 days, effectively determining 95% of birds leave their breeding grounds between August 16th and October 21st (n = 18). Timing of migration in this model was not considered to be dependent on breeding latitude or distance to wintering grounds.

Because of the lack of geocator data describing fall departure dates of ovenbirds, other sources were utilized to estimate the migration timing of the species. Luckily, data exists describing the arrival of ovenbird populations at their wintering grounds. In addition, data from banding efforts and tower kills describe migration timing along migratory flyways. Ovenbirds were recorded as having a mean arrival date between Sep. 16 and Sep. 27, with early arrival occurring around Aug. 11 at wintering grounds on the Yucatan Peninsula (Deppe and Rotenberry 2005). Thobelen et al. recorded peak migration from early September to early October in Ohio (1987). Taylor reported tower kills of ovenbirds from early September to late October in Florida, with the peak number of kills occurring in late September (1972). Acoustic monitoring and mist-net efforts along Lake Erie detected a peak in migration activity around early September (Sanders et al. 2014).

Although the information regarding the migration timing of this species is nebulous in form and source, this information provides an accurate framework for parameterizing the model. Taken as a whole, the literature suggests that departure timing stretches from early August through late September, with ovenbirds arriving at their breeding grounds from mid-August through October. Using the movement parameters of the ovenbird regarding flight speed and stopover duration, it is possible then to estimate a reasonable distribution of migration initiation dates. Simulation of ovenbird migration suggests that in order to achieve a mean passage date of September 27, the later estimate for breeding ground arrival for the species (Deppe and Rotenberry 2005), mean departure date from breeding grounds is August 18th. In order to recreate the early Yucatan arrival date of August 11th, the standard deviation of departure dates was considered to be 13 days. For the purpose of simplicity and for lack of species-specific information on the topic, migration initiation was not considered to be dependent on breeding latitude or distance from wintering grounds.

Knowledge of departure timing is critical in understanding how many ticks are transported during fall migration. Slight changes in the distribution of departure timings can lead to vastly different overlaps with tick questing behavior. Geolocator data, like that used in this analysis, is providing for more accurate assessments of migration timing. Future developments in this field will provide for a more accurate parameterization of this model.

Flight Speed

Flight speed for wood thrushes was calculated using geolocator data collected by Stutchbury et al. (2009). This tracking effort provides an average percentage of days during fall

migration spent in stopover (66%). McKinnon et al. reports that wood thrushes travel at an average rate of 167km per day during fall migration, including days spend in stopover (2013). Assuming this travel only occurs during the one third of total days spent migrating, wood thrushes travel at an average rate of 253km during nights of nocturnal flight. Research shows that nocturnal flight time of other thrush species during the spring ranges from 1-8 hours (Bowlin et al. 2005). Spring flight time is likely longer than flight time during the fall, as birds travel faster to acquire territories (see Nilsson 2013). For the purpose of this model it was assumed that wood thrush flight speed was 50.6km/h, and that flight time was 5 hours on average with a standard deviation of 1 hour. This parameter is similar to the theoretical estimates of flight speed, around 42km/h estimated by Alerstam et al. (2007). The discrepancy between these two values may be related to weather dependent flight decisions, and is similar to discrepancies between theoretical and measured flight speeds in other species (Alerstam and Christie 1993). In the context of the model, this means that the distance travelled by wood thrush during flight nights has a 95% chance of being between 152 and 354 kilometers.

The flight speed of ovenbirds was estimated using two theoretical speed equations detailed by Alerstam et al. (2007). The variables used in either equation are body mass and wing-loading. Body mass averages were gathered from tower kill data in Florida and parameterized as the mean for both adults and juveniles during migration (Taylor 1972). Belisle et al. report average wing loading of ovenbirds breeding in Canada (2007). Using these values and equations, hourly flight speed was calculated to be the average of the flight speeds estimated by these equations, or 39.76 kilometers per hour. Migratory length was assumed to have the same distribution as wood thrush, with a mean of 5 hours and standard deviation of 1 hour. This distribution is based on one thrush-specific example (Bowlin et al. 2005). This distribution gives

ovenbirds an average nightly flight distance of 199 kilometers, with 95% of night flights measuring between 119 and 278 kilometers.

Stopover Behavior & Energy Conditions

During migration, wood thrushes spend an average of two-thirds of days in stopover, time spent primarily to replenish fuel stores. For the purpose of this model, it is assumed that migrating birds depart their breeding grounds with full fuel stores, and replenish their fuel stores fully at each stopover. For the purpose of the model, simulated birds that consecutively fly multiple nights do not replenish their fuel stores during the day, but instead eat enough to maintain their energy levels. Yong and Moore estimate that wood thrushes have a maximum flight capacity of around 1200km, presumably with full energy reserves (1997). For the purpose of this model it is assumed that each bird starts migration with the capacity to fly 1200km over a series of night flights. Each day individuals consider their energy reserves, and make a ‘decision’ of whether or not to initiate stopover or to continue flying. Birds with a flight range greater than or equal to 1200km after a migratory flight will not initiate a stopover the following night. Likewise, a bird with a flight capability less than or equal to 354km has a 100% chance of initiating stopover. The effective maximum flight range of a single-night flight, as described above, determines this lower limit. The following functions describe likelihood of stopover initiation.

If flight capability \leq 354km, 100% likelihood of initiating stopover

If flight capability \geq 1200km, 0% likelihood of initiating stopover

If $354 < \text{flight capability} < 1200$

Percent likelihood of initiating stopover = $(1200 - \text{flight capability}) * .1548$

If a bird initiates a stopover, it will do so long enough to replenish its fuel stores fully, increasing flight range to at least 1200km. Each bird in stopover increases flight capacity by 126.5km per day, a parameter based on the same geolocator data used for flight speed calculations (McKinnon et al. 2013, Stutchbury et al. 2009). These stopover rules stay constant throughout the migratory period.

Stopover behavior and energy considerations for ovenbirds were determined using other sources. One extensive migratory survey of ovenbirds during flight nights demonstrated that individuals lost .20 grams of mass per hour during migratory flight (Hussell and Lambert 1980, see also Hussell 1969). Weight of ovenbirds during migration was shown to range anywhere from 18-26 grams (Taylor 1972). Assuming that the minimum weight in this range represents the lower limit for fat stores, and the upper range represents the maximum, birds with maximum fat loads have fuel stores to fly 1,590 kilometers. During stopover days, ovenbirds have been shown to regain .87 grams of mass per day (Moore and Kerlinger 1987). This mass gain represents an increase in flight capacity of approximately 172.96 miles per day. Based on tower kill data from Florida and the Midwest, ovenbirds tend not to lose weight during fall migration, and may actually gain weight as they travel southward (Caldwell et al. 1963, Taylor 1972). Ovenbirds were assumed to eat enough only to maintain energy levels during days between consecutive night flights. For the purpose of this model it was assumed that each individual ovenbird was cognizant of flight potential, with stopovers occurring more frequently as flight potential decreases. The following equation was used to determine chance of stopover:

If flight potential \leq 318km, 100% likelihood of initiating stopover

If flight capability \Rightarrow 1590km, 0% likelihood of initiating stopover

If $318 < \text{flight potential} < 1590$

Percent likelihood of initiating stopover = $(125 - \text{flight potential} * .0786)$

If a bird initiates a stopover, it will do so long enough to replenish its fuel stores fully, increasing flight range to at least 1394km. It is possible after this period for flight stores to exceed the starting potential.

Table 1. Average simulated and observed intensity rates in Lyme, CT reported by Stafford et al. from May to October (1995). N=1,000 simulated birds.

Bird species - tick life stage	Model predicted intensity rates (ticks per infested bird)	Observed mean intensity (ticks per infested bird)
Wood Thrush – Larvae	1.25	4.6
Ovenbird – Larvae	1.49	8.5
Wood Thrush – Nymphs	1.27	1.5
Ovenbird - Nymphs	1.05	1.0

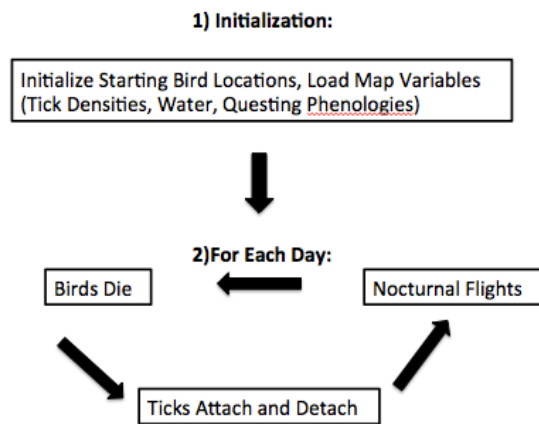


Figure 3. Simplified representation of model functions and sequence. Simulations run from May 1st to December 31st.

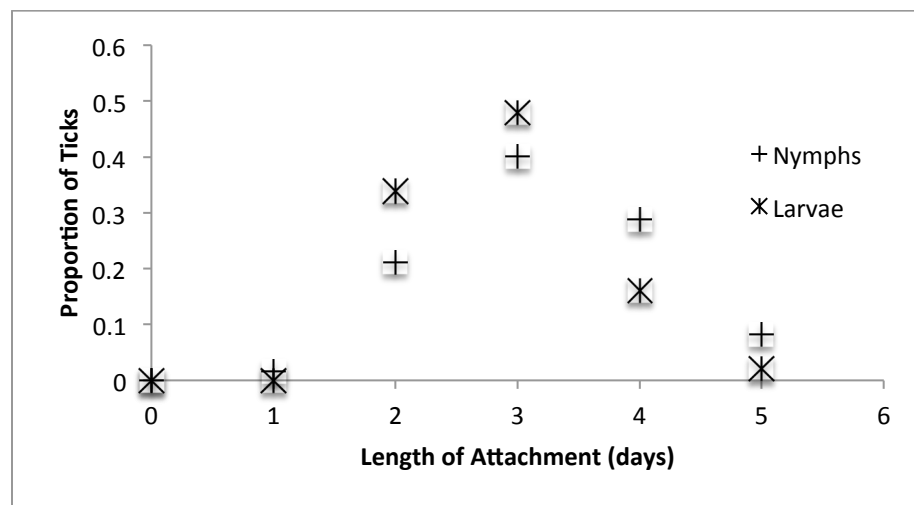
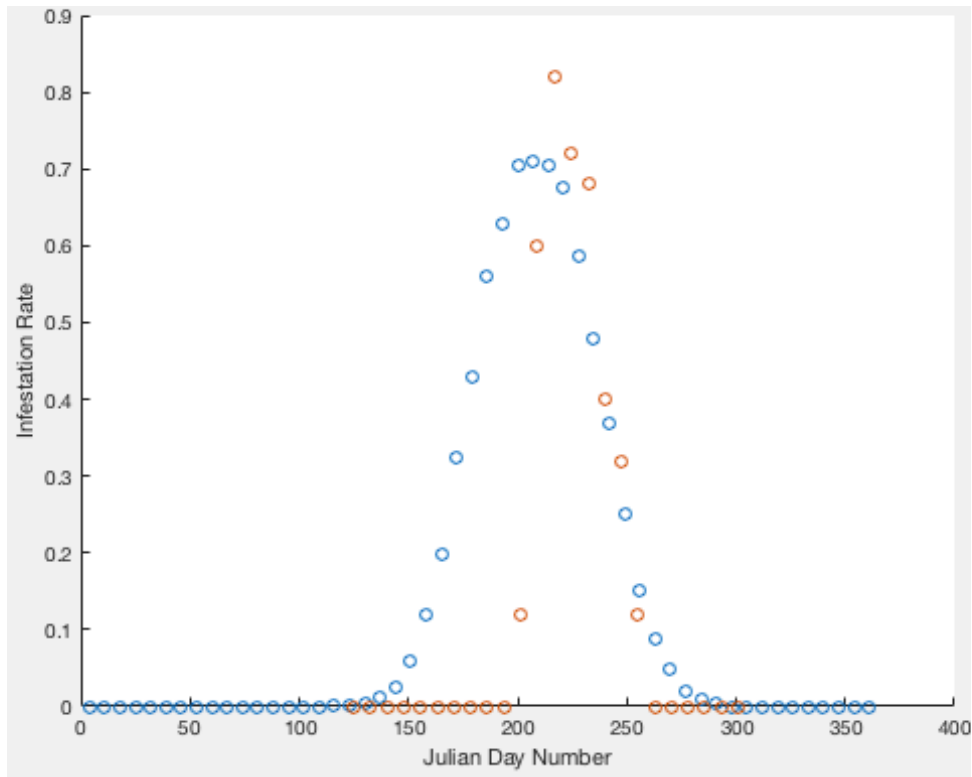
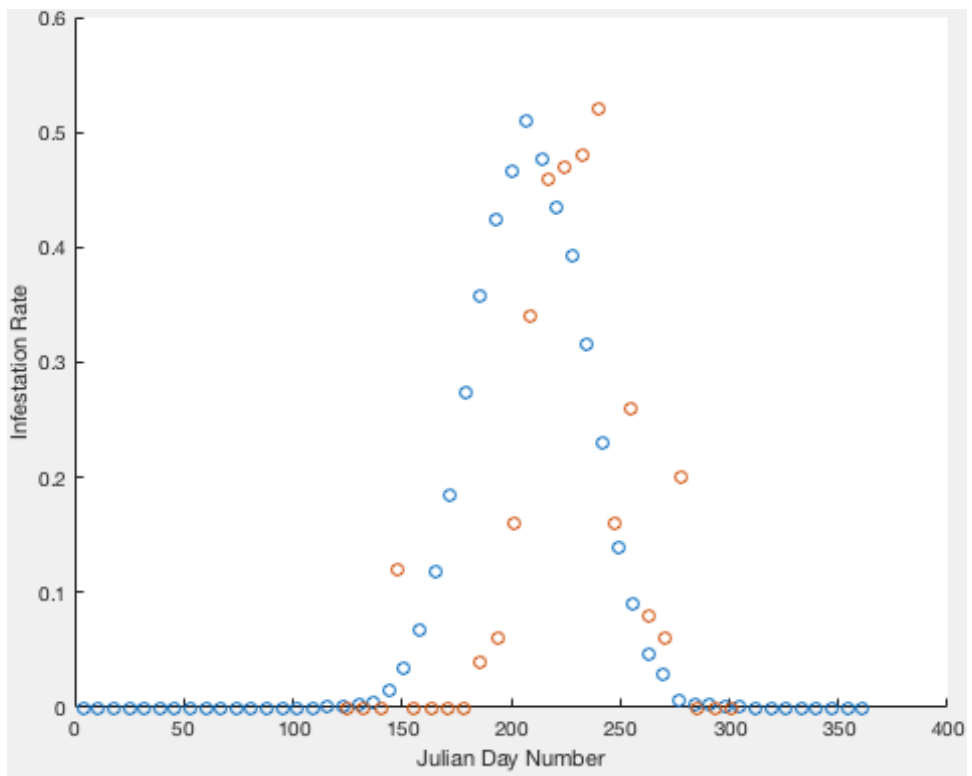


Figure 4. Length of attachment for larvae and nymphal *I. scapularis*. Recreated from Hu et al. (2007)

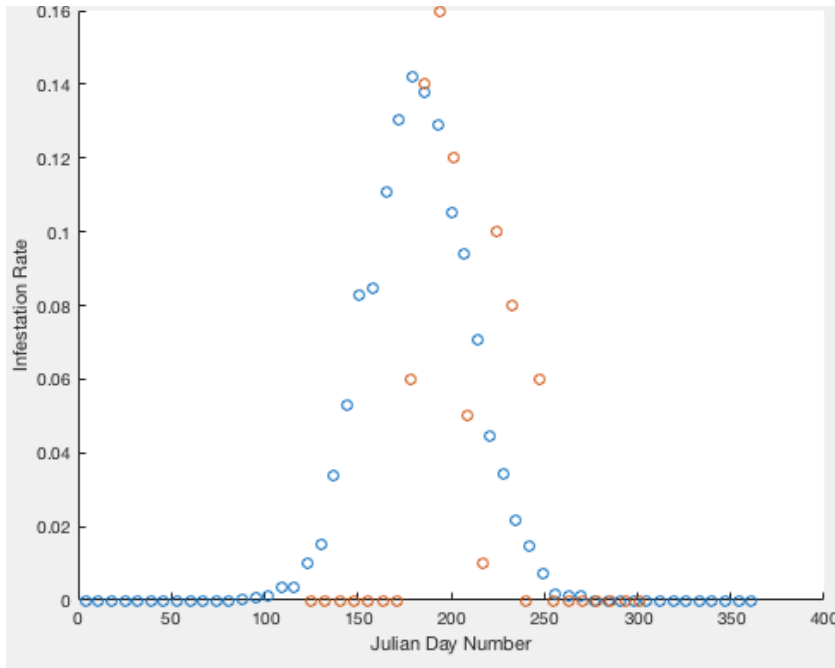
A)



B)



C)



D)

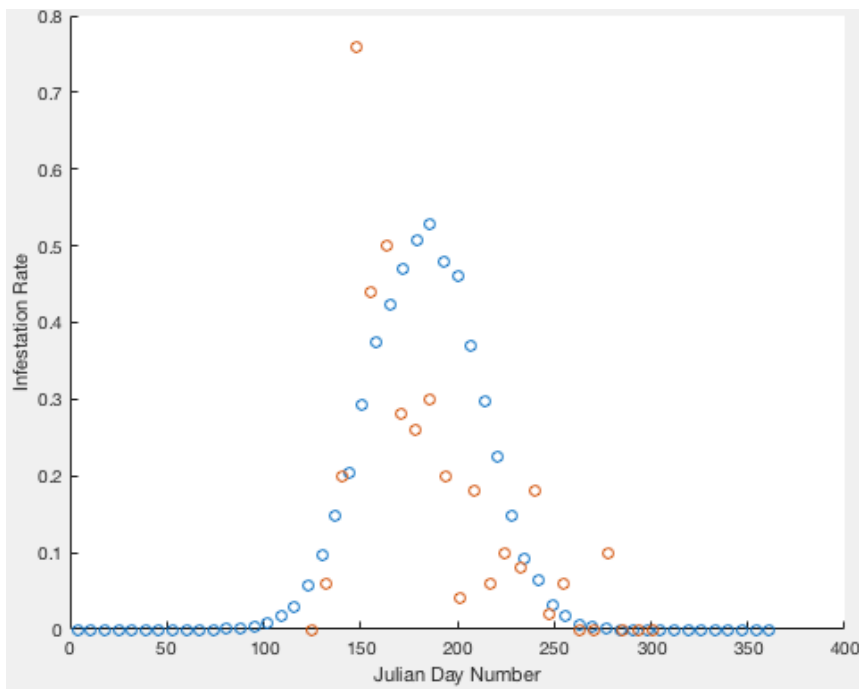
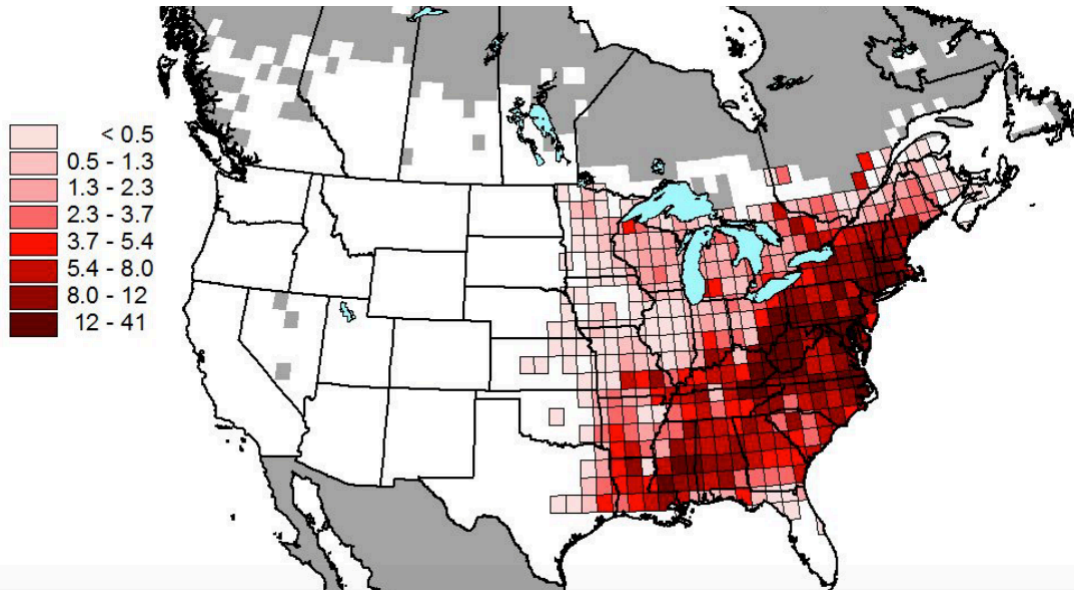


Figure 5. Weekly infestation rates (i.e. the proportion of birds parasitized by at least one tick) of wood thrushes (B,D) and ovenbirds (A,C) for larvae (A,B) and nymphs (C,D) as predicted by the sub-model (blue) and observed (orange) in Lyme, CT by Stafford et al. (2005).

A)



B)

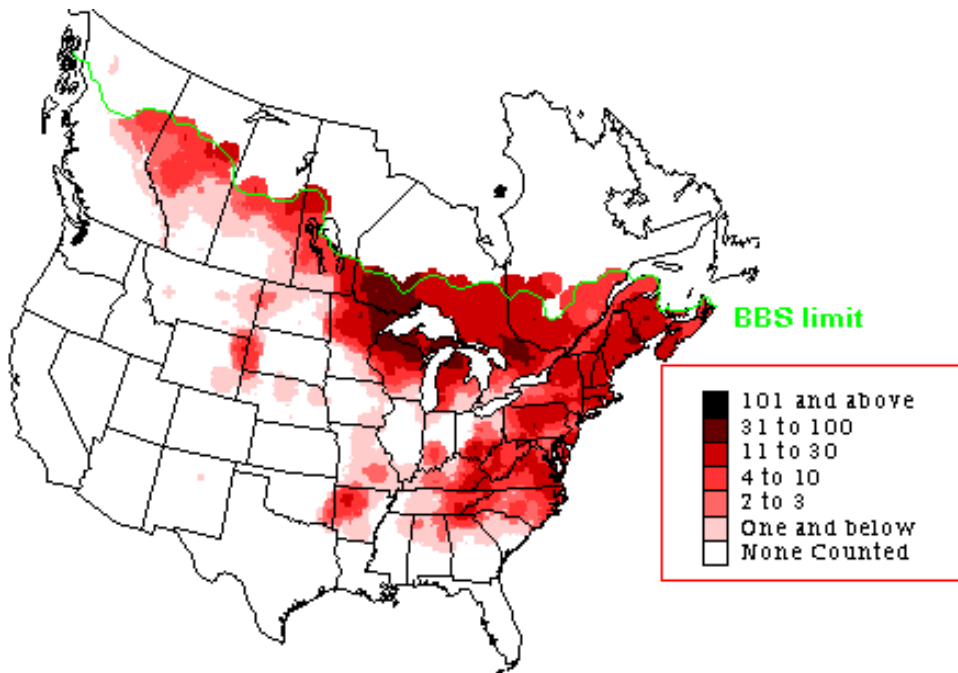


Figure 6. Breeding densities of wood thrush (A) and ovenbird (B) populations as reported by the Breeding Bird Survey (Sauer et al. 2003). Scale indicates the average number of individual birds counted by an observer along a predetermined route.

VALIDATION

This model relies on field data detailing tick behavior, bird migration, and the convergence of these vectors and hosts for parameterization. Due to the nature of this model, and the purpose of this research, the validation of simulated patterns of bird movement is critical. Comparisons of individual and population-level measures of simulated and real movement are necessary for validation. As detailed below, the model appeared to recreate population-level and individual patterns of migration seen in nature for both species.

Individual Migration Patterns

Migratory routes from geolocator data were shown to vary between individuals originating at similar breeding locations, and among individuals year-to-year. In both observed and simulated routes, some degree of longitudinal deviation from an ‘ideal path’ was the norm (Fig. 7, Fig. 8). In the model, wood thrushes took both inland and coastal routes observed empirically by geolocator data. In all, these comparisons suggest that, on an individual level, wood thrushes within the model are migrating similarly to their counterparts in the real world.

Most likely because of the weight of geolocators relative to the mass of smaller songbirds, little geolocator data exists detailing the migratory movements of ovenbirds during fall migration. For studies in which geolocators have been used, the early migratory timing of the species in relation to the fall equinox makes accurate location derivation during the fall migration period nearly impossible. As a result, there is a lack of data by which to validate the individual level migratory movements of simulated ovenbirds with the methodology utilized above. However, because of the consistency of orientation parameters within the model between the two species, if ovenbirds show similar longitudinal deviations from their routes compared to wood

thrushes during migration in the real world, the model is likely to accurately recreate their behavior. Importantly, many of the longitudinal deviations observed in nightly flights may be related to wind conditions. Displacement due to wind would likely affect ovenbirds and wood thrushes similarly. However, in order to confirm this assumption, and to validate individual movement patterns of ovenbirds, comparison with future ovenbird tracking studies will be needed.

System-Level Migration Dynamics

To validate the system-level patterns created by the model, sighting data and established estimates of ranges for either species are the most valuable resources. Range maps are one general tool used by birders and scientists alike. These maps detail the areas in which a given species are observable during breeding, migration and nonbreeding seasons. Range maps consist of general estimates that lack accuracy at smaller spatial levels. Furthermore, they do not represent densities of populations during migration or breeding. Regardless of these inaccuracies and shortcomings, range maps outline areas in which members of a given species are expected during migration at a continental scale. To this end, comparing these migratory routes to those observed within simulations is one source for validation of the model. For both ovenbird and wood thrush populations, the model recreated migration routes consistent with general migration range maps (Fig. 9). An expected discrepancy exists between simulated migratory routes and range maps for both species. In range maps for ovenbirds and wood thrushes, a migratory route around the Gulf is present, a pattern not present in the simulated flyway record. This discrepancy is expected, as this migratory path is only utilized during spring migration for both species, and so is not encoded or expected to occur in this model.

In addition to recreating individual migration movement patterns, the model produces system level migration patterns that are validated by temporal sighting data. The Cornell Lab of Ornithology and eBird have created continental-scale maps based on observation reports by citizen-scientists that reproduce average monthly densities of ovenbirds and wood thrushes (accessible via ebird.org/birdvis). These density maps are vulnerable to a myriad of inaccuracies, and are in no way perfect estimates of bird locations during migration. For instance, underreporting results in underestimation of densities of populations in certain geographic areas. Important to this model, wood thrushes are conspicuous and drab fall migrants, making them hard to observe during migratory periods, leading to underreporting of positions by citizen-scientists.

Despite these inaccuracies and shortcomings BirdVis, the platform used to observe temporal population densities, is the most expansive estimate of continental-level migration songbird movements. For that reason, the locations of simulated birds were compared to BirdVis data from July-November, at the specificity of the monthly time-step, the smallest time interval reported within the BirdVis platform. Despite some odd patterns created by the BirdVis data, likely the result of underreporting and the conspicuous nature of migratory wood thrushes, the simulated locations of both ovenbirds and wood thrushes during migration season consistently match sighting data (Fig. 10).

Wood thrush density reported by BirdVis decreases rapidly in the U.S. during the late summer months, and migratory birds are not reported along the Gulf Coast and in Florida throughout the entire migratory period. BirdVis density data likely represents the positions of birds still present at their breeding ground, with few observations of birds conspicuously migrating. Ovenbird density reported by BirdVis represents migratory locations of the entire

population much more completely than that of wood thrush. However, densities are still underreported within the Gulf Coast States, which appears as gap in the migratory flyway of the species. The density maps also appear to underrepresent rural ovenbird locations during the month of October, with significant densities only being reported around urban areas. Regardless of the inaccuracies in BirdVis data for either species, this temporal data provides a geographically expansive source for validation of the model.

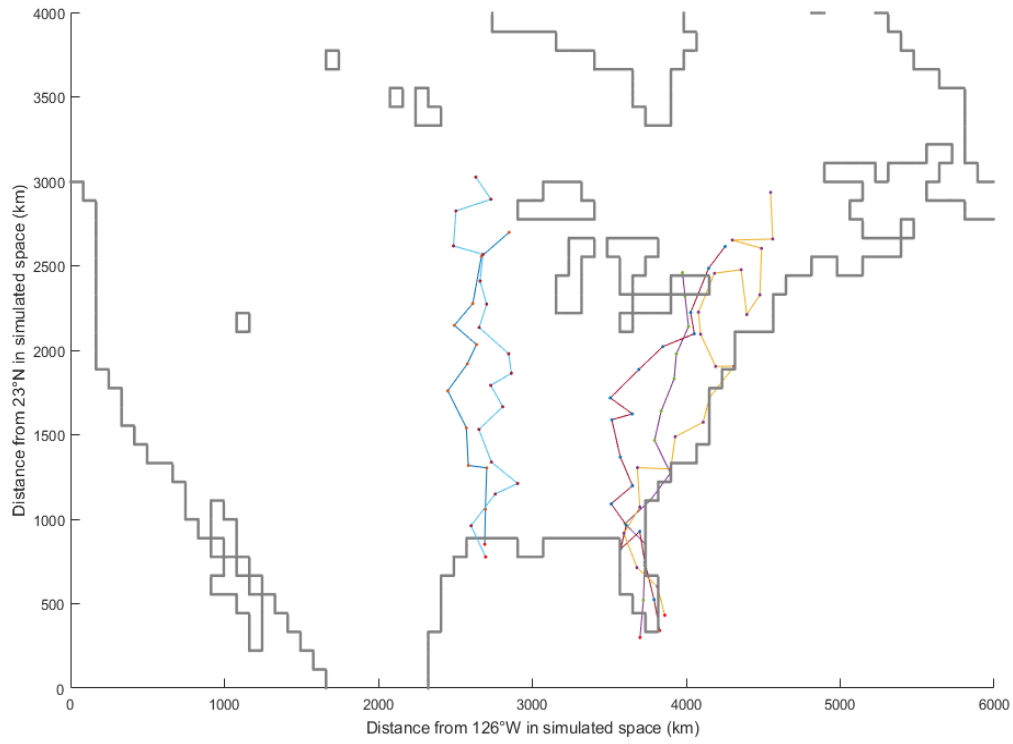
Emergence – ‘Coastal Effect’ and ‘Edge Effect’

Simulated migratory movement recreated the differences in spatial densities of juvenile and adult birds observed by capture surveys during migration (Fig. 11). Juvenile birds have been shown to be overrepresented at the edges of species-level migratory flyways, specifically the Atlantic coast (Ralph 1981, reviewed by Able and Bingman 1987). In the model, both the ‘edge effect’ and ‘coastal effect’ was observed for both species, with juveniles overrepresented both along the Atlantic Coast and along the extremes of inland flyways. Augmenting this phenomenon was the elongation of the migration period observed for juveniles compared to adults. Time from start of migration to initiation of trans-Gulf flight averaged roughly 30% longer for juvenile ovenbirds and wood thrush compared to adults. Because simulated juveniles spent a longer time migrating, hatch-year birds were overrepresented throughout the flyway. Thus, juveniles are predicted to make up a greater proportion of captures during the migration period by banding surveys than the true proportion of juveniles in the population, and specifically in areas along the edge of whole-species flyways.

In all, the model demonstrates realistic individual and system-level dynamics of migration movements, and recreates the ‘coastal effect’ and ‘edge effect’. The emergence of this

phenomenon is significant in that it is not directly encoded into the model, and instead results from simple navigation rules that aim to capture differences between the orientation of juveniles and adults. Emergence of the 'coastal effect' and 'edge effects' lends credence to the strength of the orientation parameters used in the model.

A)



B)

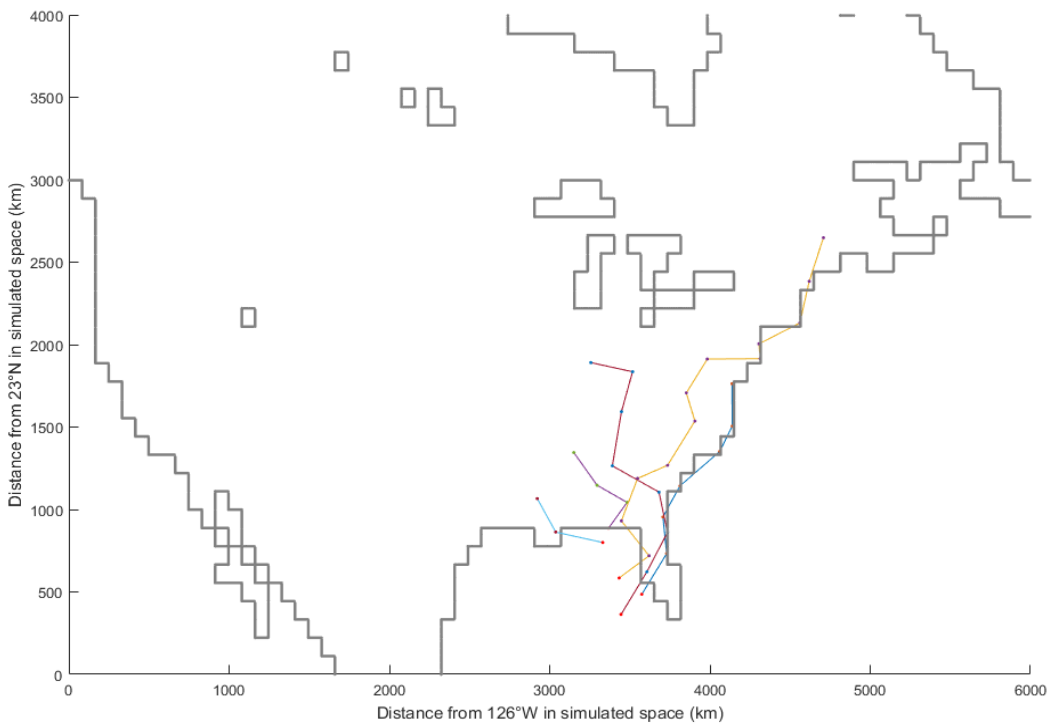


Figure 7. Migratory paths from breeding grounds of five simulated ovenbirds (A) and wood thrushes (B).

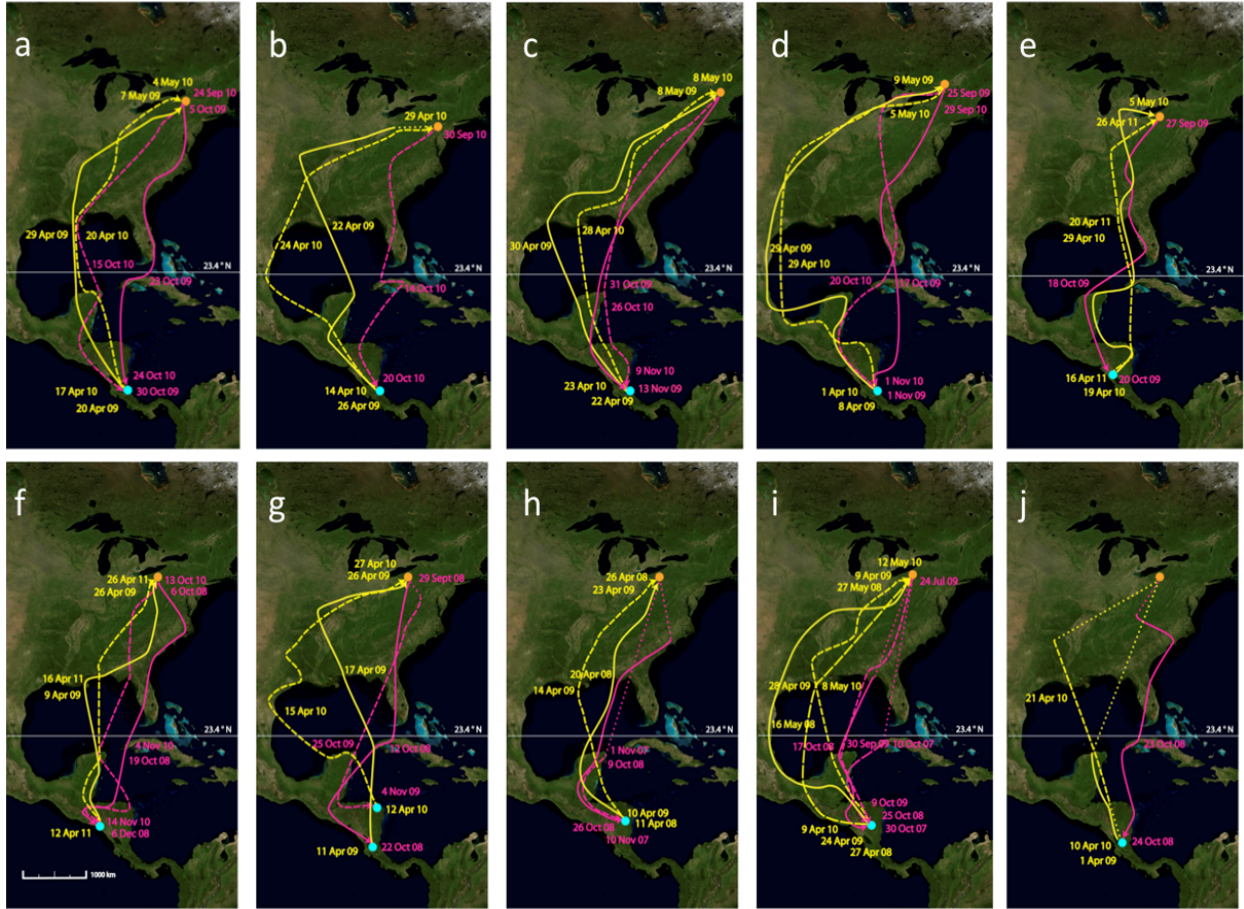
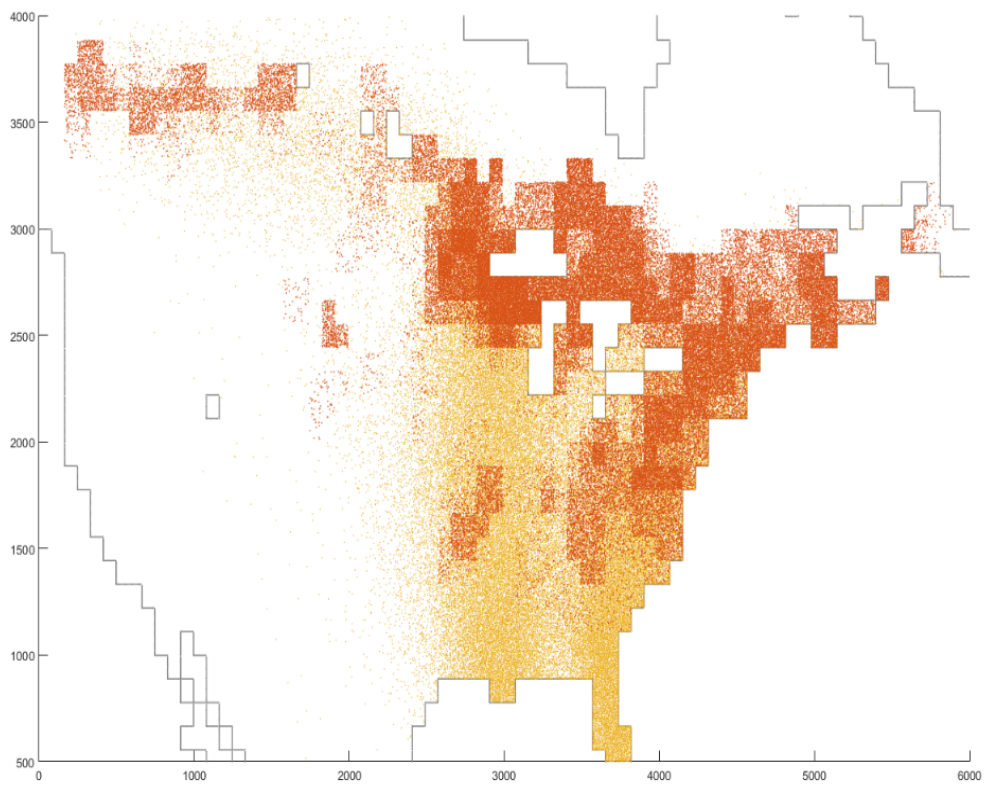


Figure 8. Fall (pink) and spring (yellow) migration routes of individual wood thrush tracked by geolocators. Reprinted from Stanley et al. 2012.

A)

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B)

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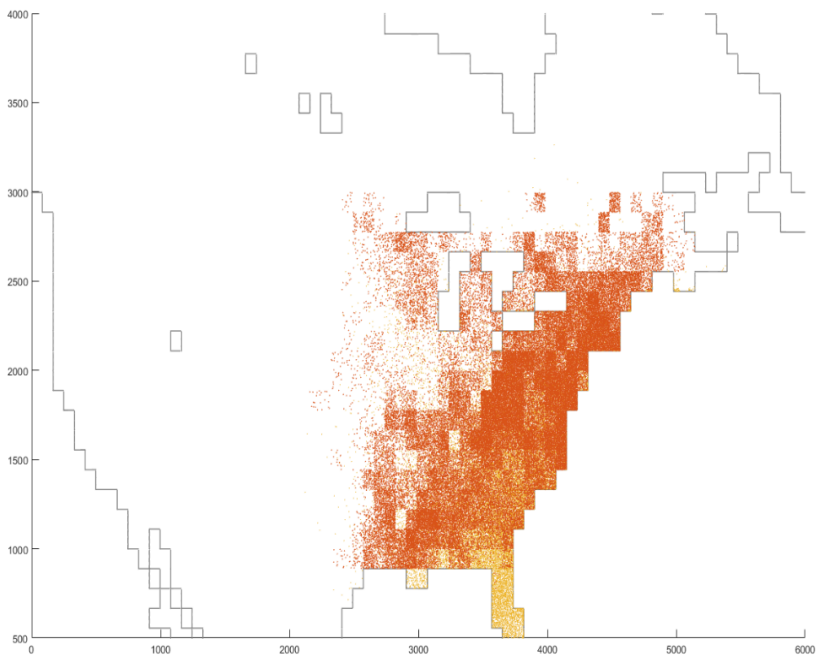
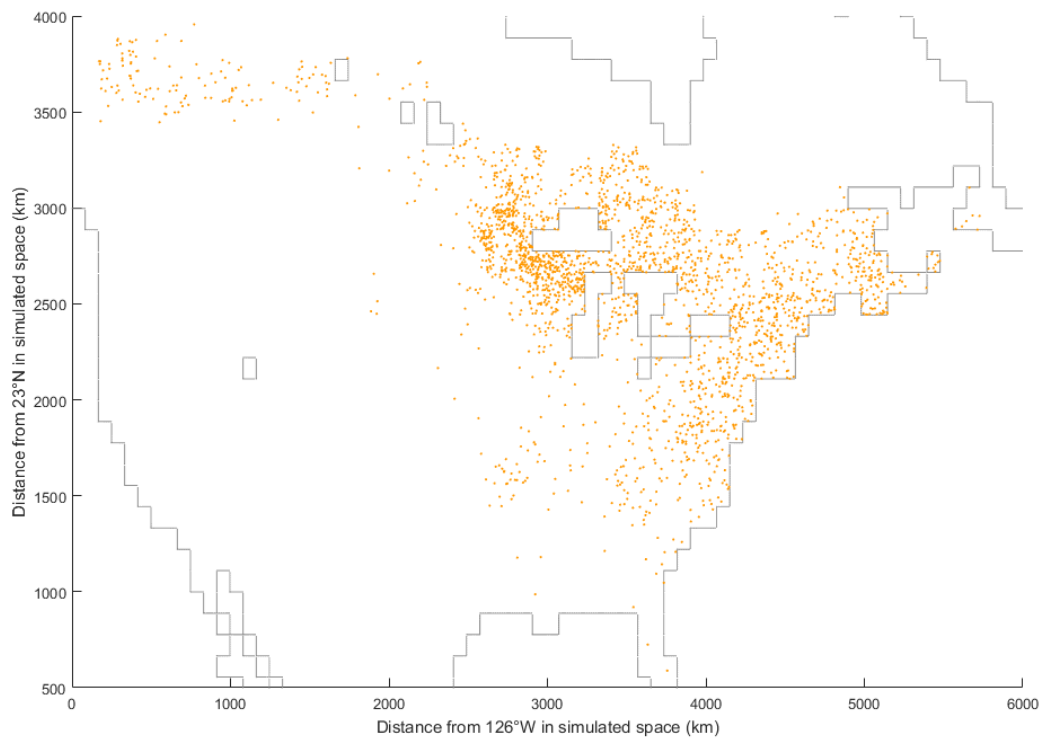


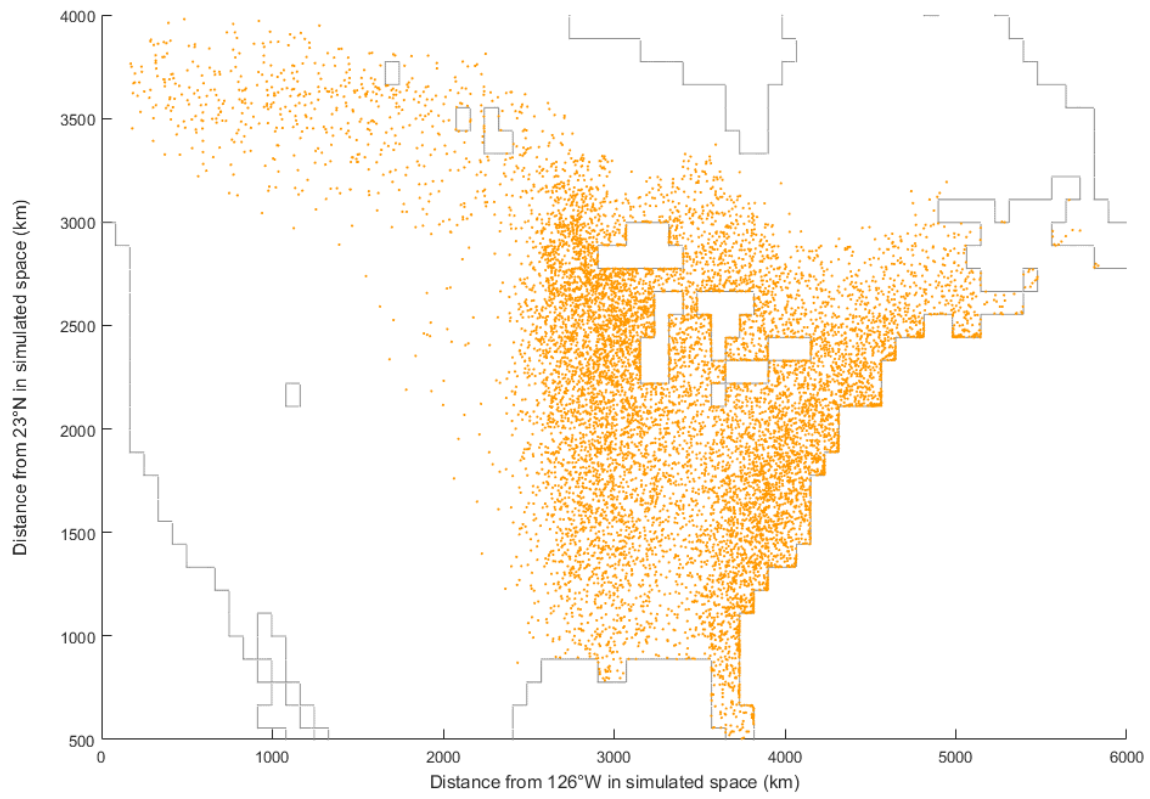
Figure 9. Range maps reprinted from the Cornell Lab of Ornithology and simulated ranges of ovenbird (A) and wood thrush (B) populations. For simulation figures, dots represent individual breeding locations (orange), and daily migration positions (gold). N = 5,000 birds for each species for simulation maps. Range maps accessible at birdsna.org.

i)

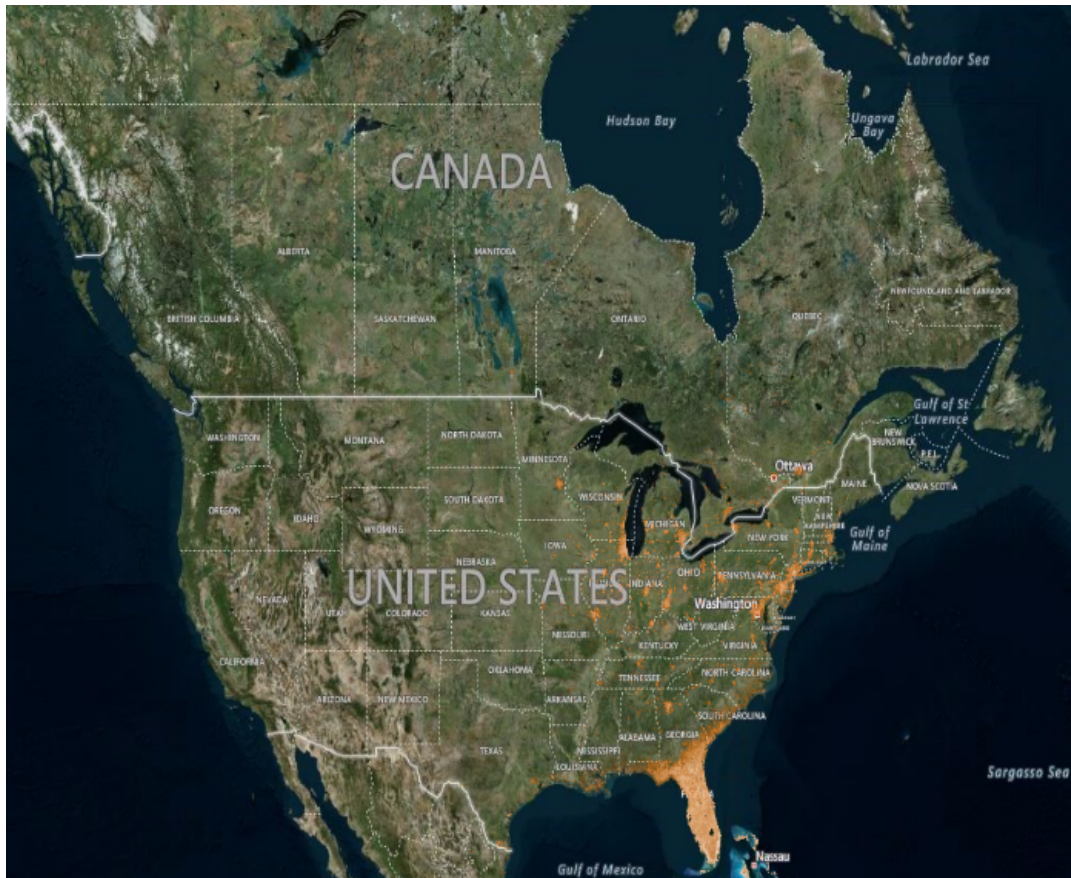
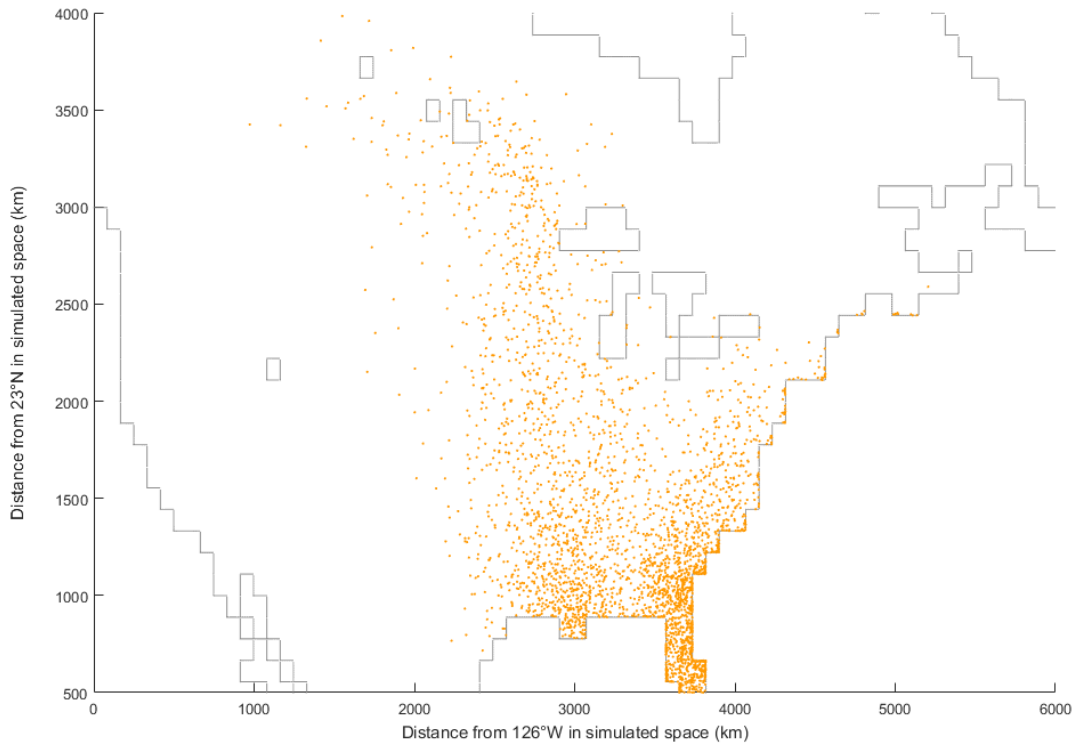
A)



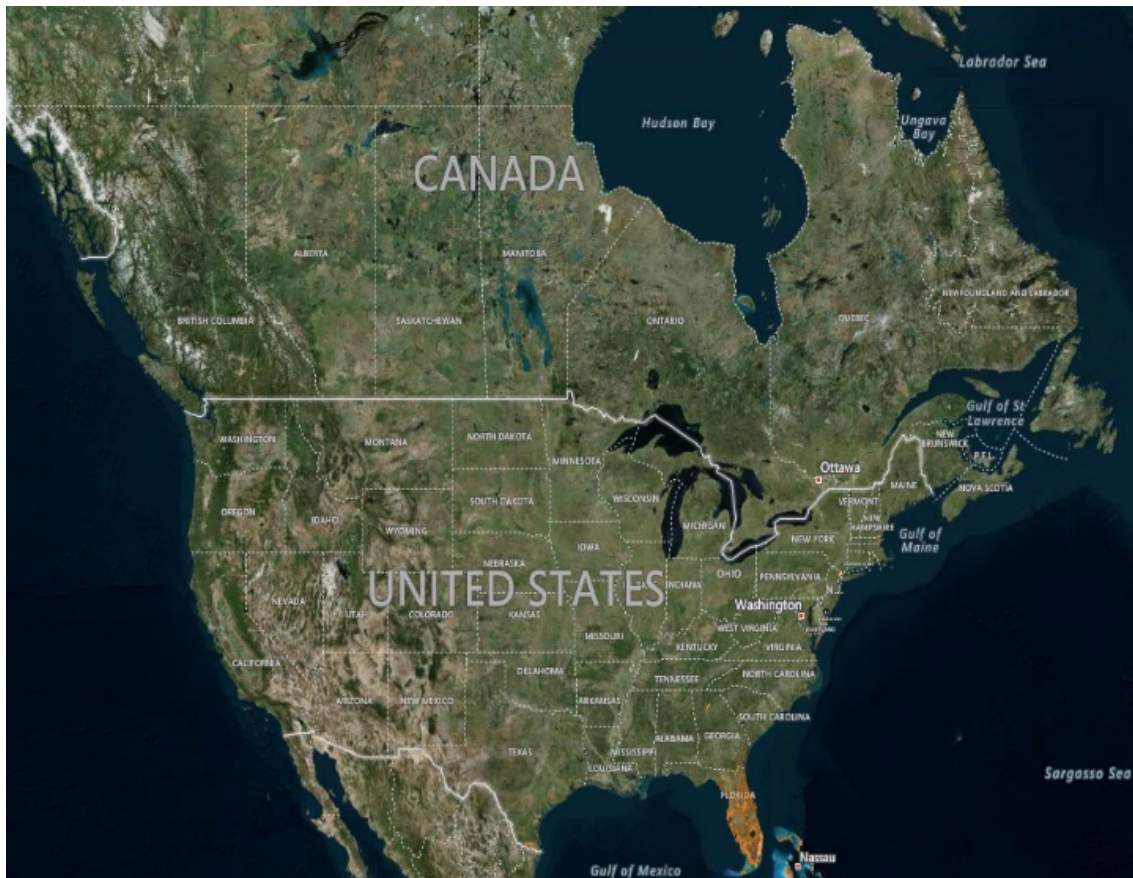
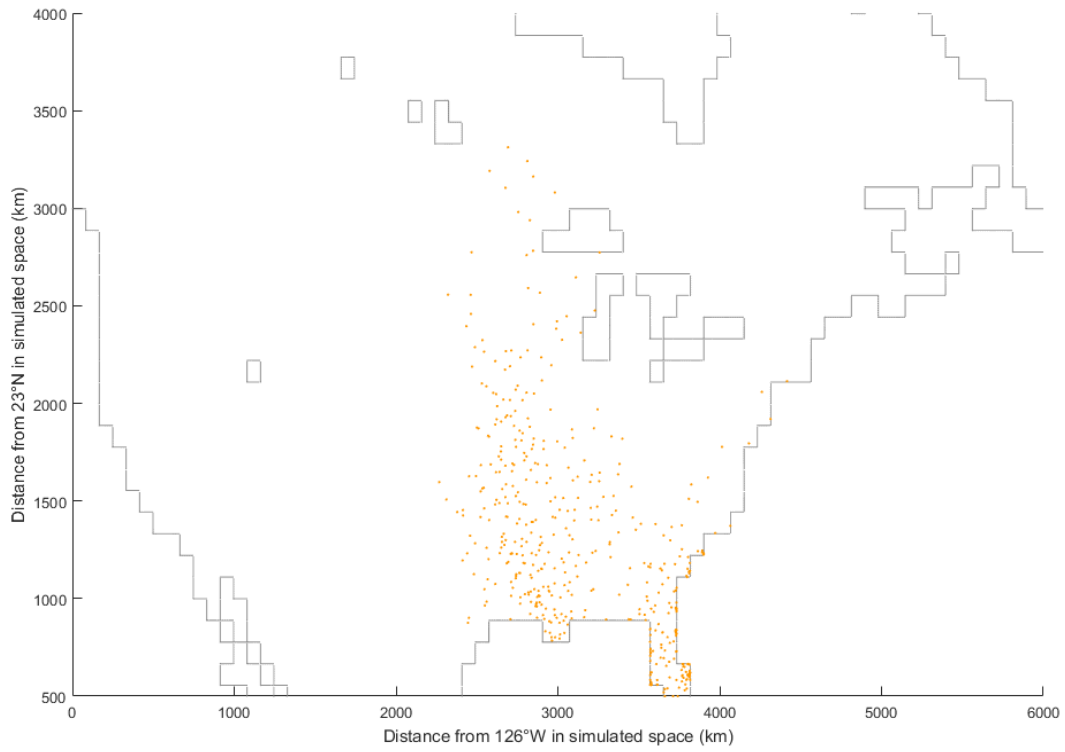
B)



D)

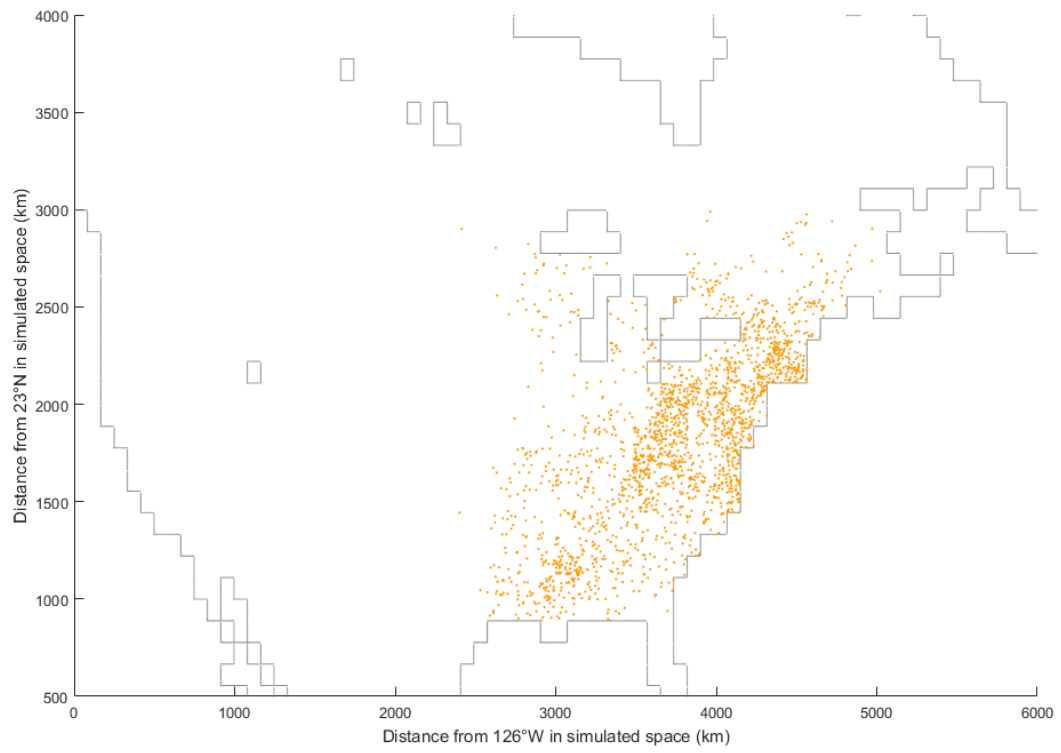


E)

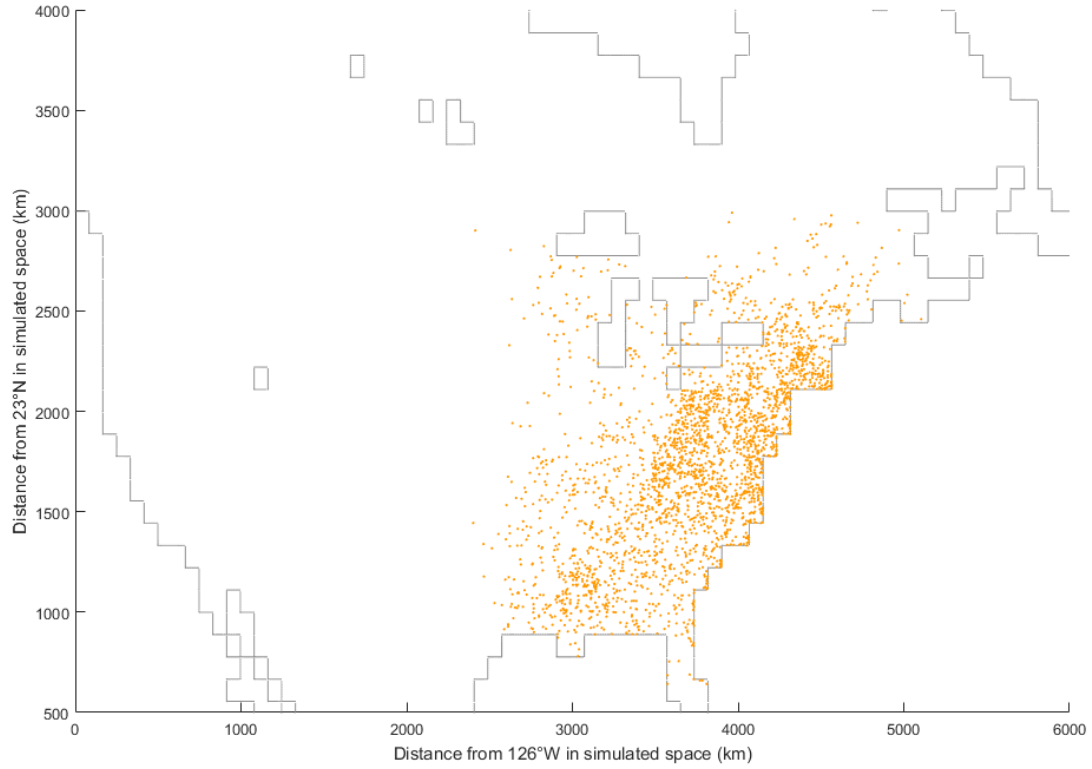


ii)

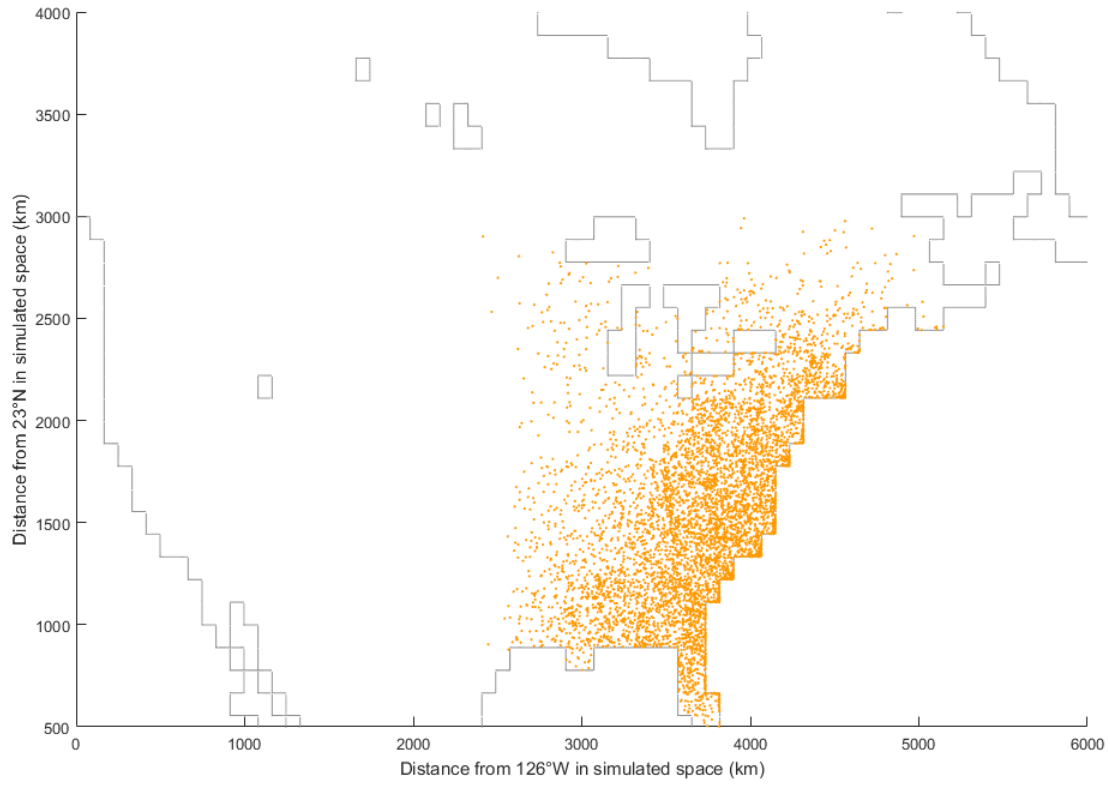
A)



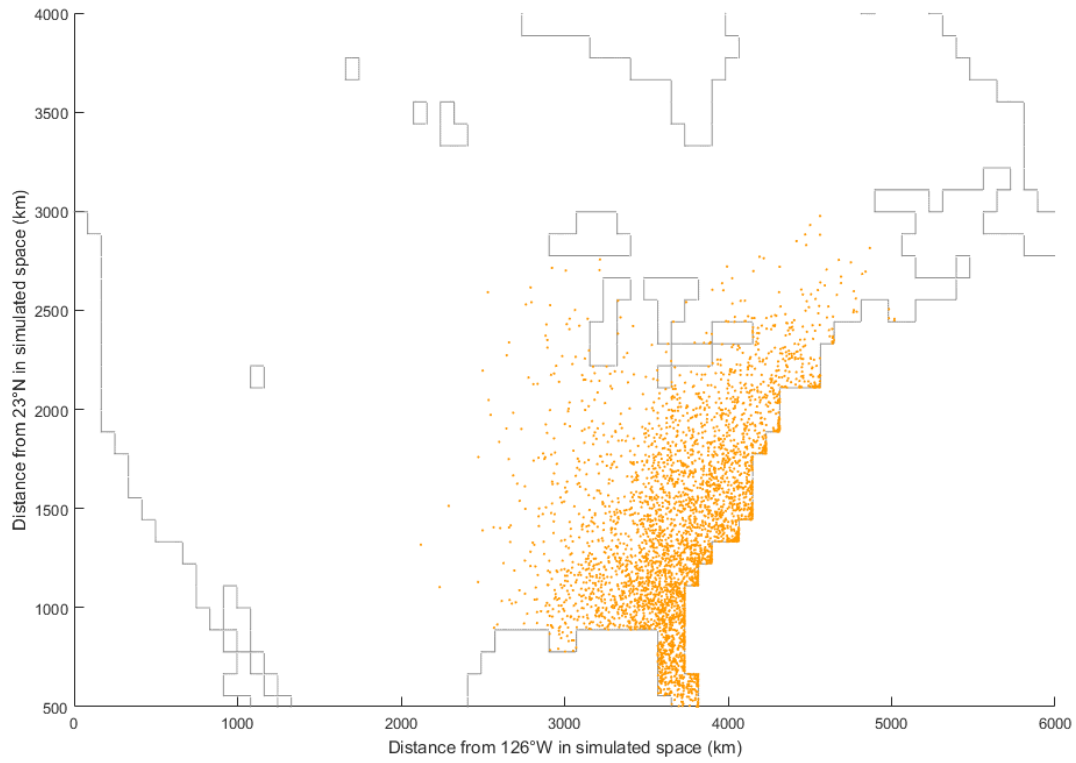
B)



C)



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E)

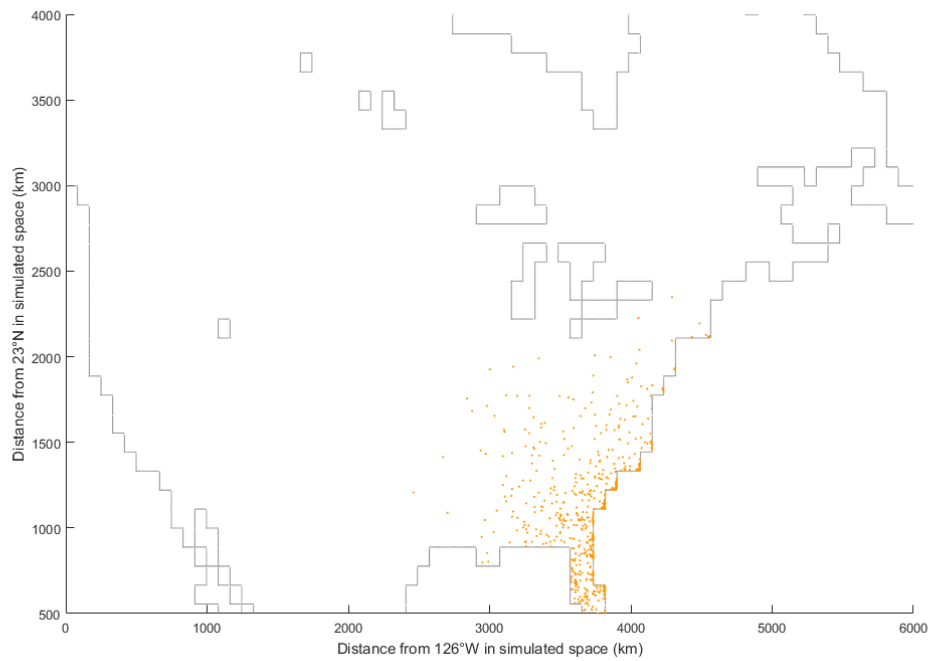
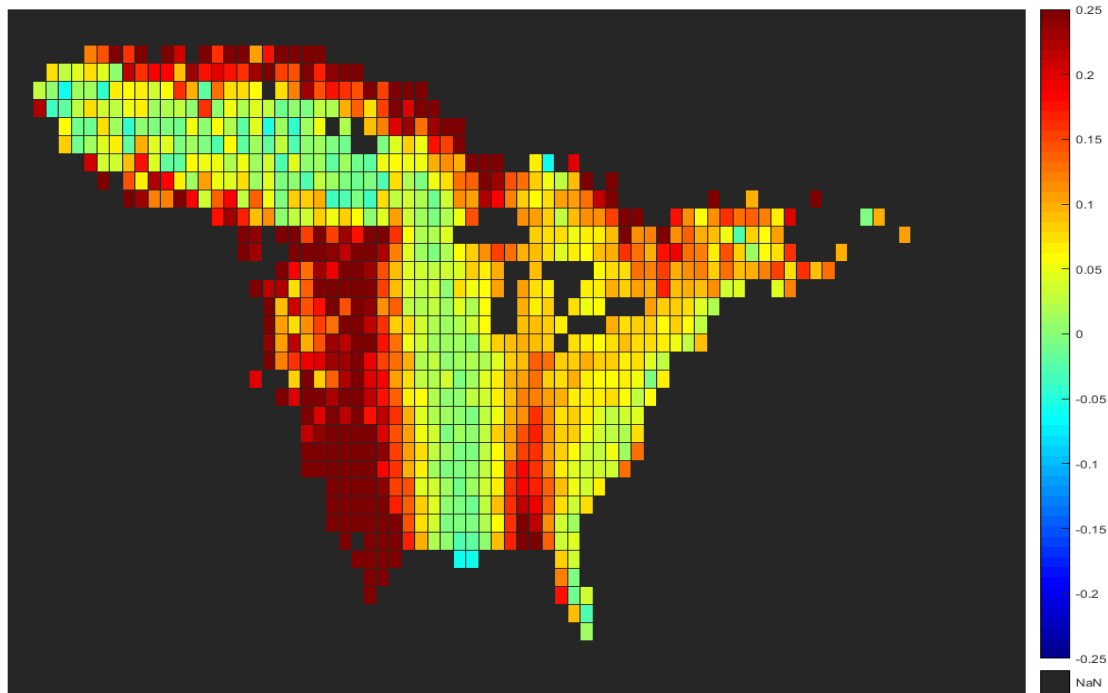


Figure 10. Simulated and observed locations of ovenbirds (i) and wood thrushes (ii) during July (A), August (B), September (C), October (D), and November (E). Observed locations reported by citizen-scientists and compiled in the eBird database. Density estimates are accessible at ebird.org/birdvis. Dots in simulation figures each represent a single daily migration or breeding location. N = 1,000 birds for each species.

A)



B)

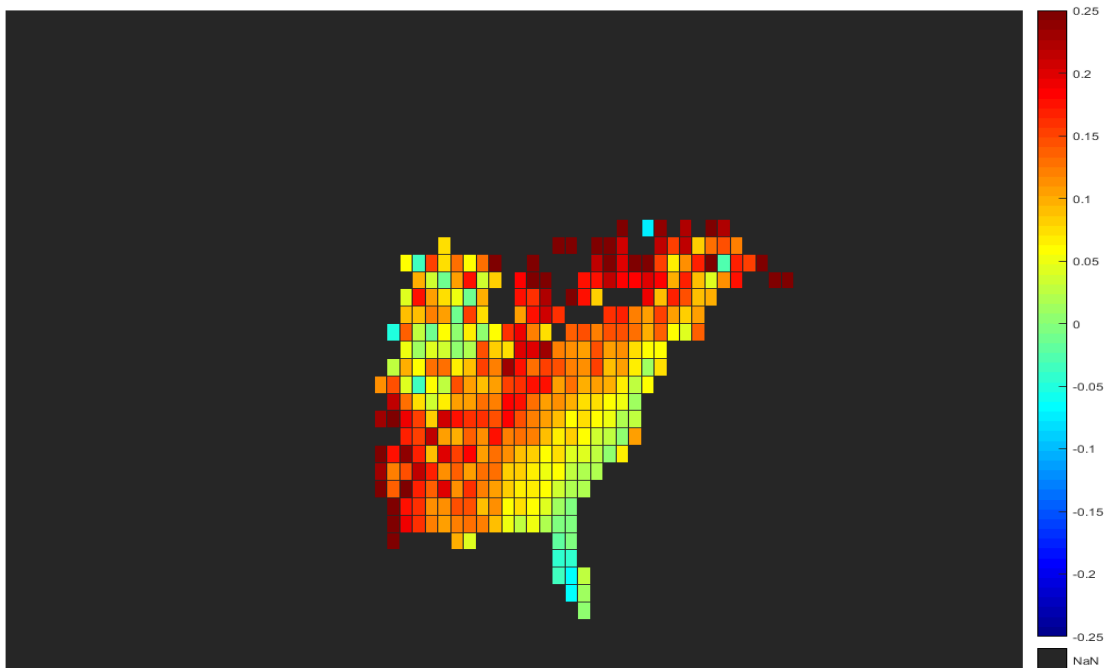


Fig 11. Proportion of migrating juvenile ovenbirds (A) and wood thrushes (B) in each lat-long cell relative to the proportion in the whole population averaged throughout the migration period. Black cells indicate areas where no birds spent days. $N = 5,000$.

RESULTS

Ten trials with 10,000 birds each were run consecutively to simulate 100,000 birds in total for both wood thrushes and ovenbirds. The entirety of these simulations represents approximately 0.83% of the total population size for wood thrushes and 0.38% of that of ovenbirds. After review of the output of the model to confirm functionality, the records from these trials were exclusively used to investigate the research questions detailed below. This simulation size was chosen to balance ease of analysis with an output that reflects the true dispersal rate of *I. scapularis*. A larger sample size would likely reduce some of the stochasticity inherent in the model, although the qualitative patterns described below remain unchanged between simulations. It is important to understand that the exact measured values may change if the simulation was run again, due to the dependence of the model on drawing from probability distributions for many parameters (Fig. 12).

Relative Rates of Transport of *I. scapularis* by Wood Thrushes and Ovenbirds

The number of *I. scapularis* dispersed by ovenbirds was greater than that of wood thrushes. Ovenbirds transported more nymphs and larvae, with respect to both rate of transport, and when considering the effect of the total population (Table 2). The model suggests that ovenbirds transport over twenty times the amount of ticks as a population compared to wood thrushes. Notably, transport of ticks by ovenbirds occurred on average earlier than those transported by wood thrushes (Fig. 13).

Flight Distance

Ticks transported by wood thrushes were, on average, displaced roughly 70km farther from position of attachment than those transported by ovenbirds (Table 3, Fig. 14). The maximum simulated displacement distance was 926km for all ticks transported by wood thrush and 912km for all those attached to ovenbirds. The tick transported the farthest on a wood thrush traveled from the area surrounding New York City to South Carolina. The tick traveling the farthest on an ovenbird originated in Southeast Minnesota and detached in Tennessee. Nymphs were carried farther than larvae on average. The average dispersal distance of nymphs was 4.3% greater than larvae for those carried by ovenbirds and 5.7% for those carried by wood thrushes (Table 3). This difference is likely due to the tendency for nymphs to make up a larger percentage of all ticks being carried by simulated birds during the first few, rapid, migratory flights after departure from breeding grounds.

Tick Bearings from Origin and Spatial Patterns of Redistribution

Ticks that attached along the Eastern seaboard were generally displaced southwest of their origin. Those attaching in the Midwest were generally transported southward (Fig. 15). Notably, 6.2% and 4.3% of ticks attached to ovenbirds and wood thrushes were dispersed north of their origin, respectively. In all, the directional dispersal of ticks reflected the variability in area-dependent migration movements of simulated birds.

Latitude-longitude cells were assigned a status based on tick population establishment probability both in the present and by the 2080s. Cells fit into one of four categories: tick population currently established, tick population establishment unlikely at present and in the

future, tick population establishment likely in the future but not at present, tick establishment likely at present and in the future.

72.3% of all dispersed ticks detached within the established range of the species (Table 4). 21.4% detached in areas where climatic conditions are either currently suitable, or are predicted to be suitable by the 2080s (Table 4). The distribution of ticks was highly variable but widespread. Considering those displaced by both species, ticks were redistributed into 43 of 47 (91.5%) latitude-by-longitude cells currently climatically suitable for the establishment of the species in the U.S., and into 57 of 96 (59.4%) of cells predicted to be newly suitable by the 2080s (Fig. 16). It is important to note that a larger sample size would likely result in a low density of ticks being dispersed to other cells. The simulation of a greater number of birds would result in the spread of low levels of ticks to more grids due to the inherent stochasticity of the model, but low levels of dispersal are unlikely to correspond with a significant risk to human health.

Out of areas at risk for population establishment currently and by the 2080s, the model predicts two distinct foci of tick deposition by ovenbirds. Areas that experienced the greatest rates of tick detachment events were those directly west of the current Midwestern range of the tick, including most of Iowa and Southwestern Michigan, and the coastal Southeast, an area including Southern Virginia and North Carolina. Ticks transported by wood thrushes showed a distinctively different pattern of redistribution, with few ticks attaching and detaching in the Midwest. Similar to the pattern of ticks being transported by ovenbirds in the Atlantic flyway, ticks transported by wood thrushes outside of the currently established range were most commonly spread to areas in the coastal Southeast. The large area southwest of the current Midwestern range of the tick that is predicted to be climatically suitable by the 2080s, a range

including parts of South Dakota, Nebraska and Kansas, did not experience tick dispersal by songbirds of either species.

Emergence – Coastal Migration and Tick Detachment

The model predicts a high rate of tick detachment in areas near the coast (Fig. 17). This pattern is a result of migration orientation parameterization that redirects simulated birds overwater after the normal night flight period to coastal areas. As a result, higher densities of simulated birds are found along the coast in comparison to directly inland sites. In cells bordering the Atlantic Ocean, density of tick detachment events was observed to be clustered along the coastal edge.

Synchronicity of Migration Timing and Tick Questing

In order to understand how the number of ticks transported by ovenbirds and wood thrushes may be affected by changes in tick and songbird phenology, simulations were run that either delayed or advanced mean migration departure for each species. This adjustment was performed in order to alter the synchronicity of tick questing and bird migration timing. Results from this experiment are relevant in understanding how temporal changes in either tick questing or migration may lead to differing rates of tick displacement.

For both species, synchronicity of tick questing and mean migration departure timing was positively correlated with the number of ticks predicted to be displaced (Fig. 18). Results from this experiment suggest that the number of ticks displaced by songbirds will increase with either delayed tick questing phenology, or earlier migration timing.

Table 2. Rate of *I. scapularis* transport by simulated ovenbirds and wood thrushes. N = 100,000 individuals per species.

Species	Tick life stage	Number of ticks transported per 10,000 birds	Number of ticks transported, whole population*
<u>Ovenbird</u>	Larvae	1,556.8	4,259,060
	Nymphs	81.3	211,380
Total		1,638.1	4,470,440
<u>Wood thrush</u>	Larvae	136.3	163,560
	Nymphs	35.1	42,120
Total		171.4	205,680

*Calculated with ovenbird and wood thrush population sizes of 26 and 12 million, respectively (Rich et al. 2006)

Table 3. Measures of simulated *I. scapularis* dispersal distance. N = 100,000 individuals per species.

Species	Tick life stage	Max flight (km)	Mean distance (km)	Median distance (km)
<u>Ovenbird</u>	Larvae	892.06	276.33	238.91
	Nymphs	911.77	288.40	244.49
<u>Wood thrush</u>	Larvae	926.43	340.62	305.40
	Nymphs	897.15	359.98	308.75

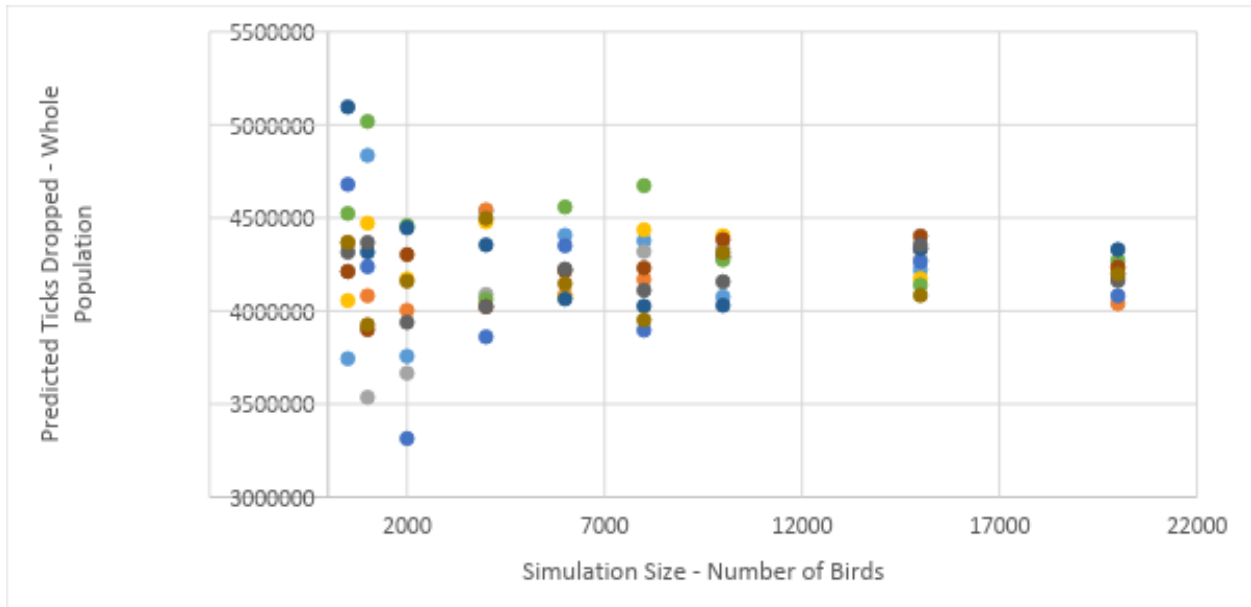
Table 4. *I. scapularis* detachments classified by current and future suitability of climate conditions for population establishment of the vector. Reported here as proportions of all detachments. N = 100,000 per species.

Species	Endemic	Suitable presently & by 2080s	Suitable by 2080s, not presently	Not suitable presently, or by 2080s	Total ticks transported
<u>Ovenbird</u>	.747	.156	.057	.041	16,381
<u>Wood thrush</u>	.745	.217	.019	.019	1,714

Table 5. Percentage of *I. scapularis* detachments classified by the attachment site. N = 100,000 per species.

Species	Attachment region	Detached within Eastern range (%)	Detached within Midwest range (%)	Detached within Southern range (%)	Detached in non-endemic range (%)
<u>Ovenbird</u>	East	56.13	0	1.71	12.32
	Midwest	0.01	16.81	0.07	12.96
<u>Wood thrush</u>	East	64.53	0	8.75	24.21
	Midwest	0	1.05	0.12	1.34

A)



B)

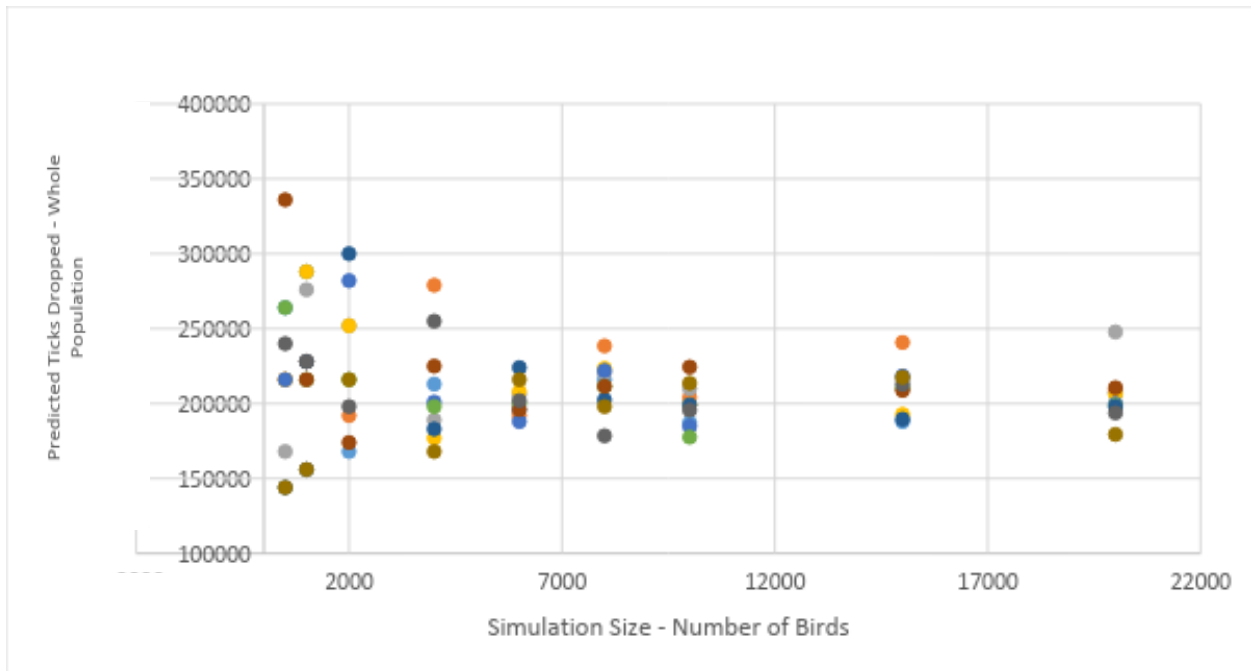
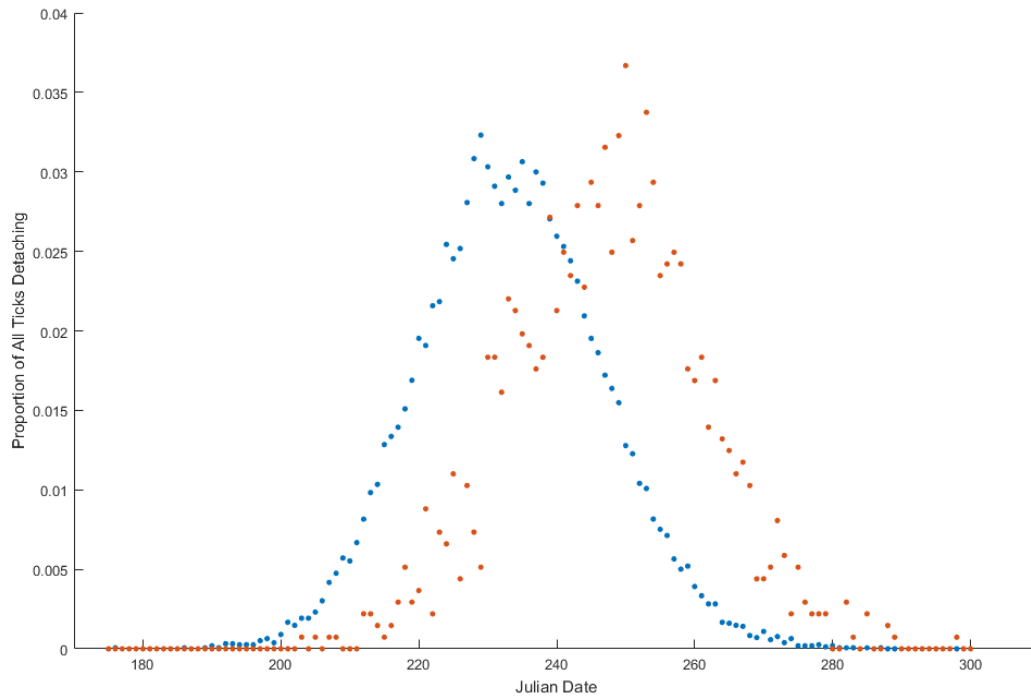


Figure 12. Predicted number of ticks transported by entire species from simulations of varying sizes of ovenbirds (A) and wood thrushes (b). 10 simulations were run for each trial size.

A)



B)

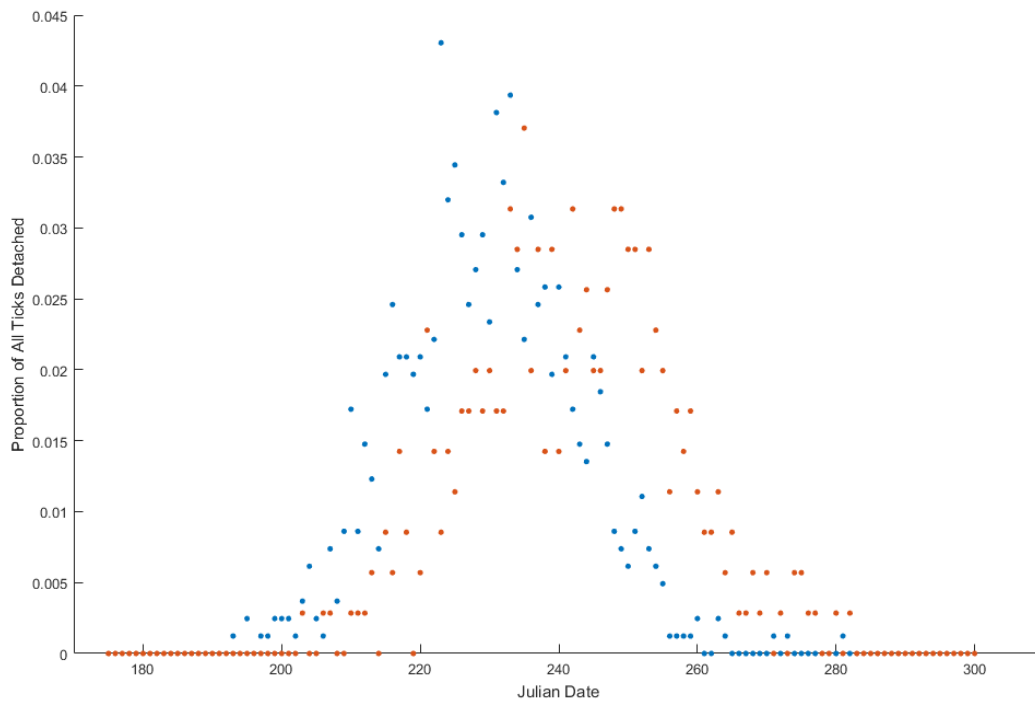
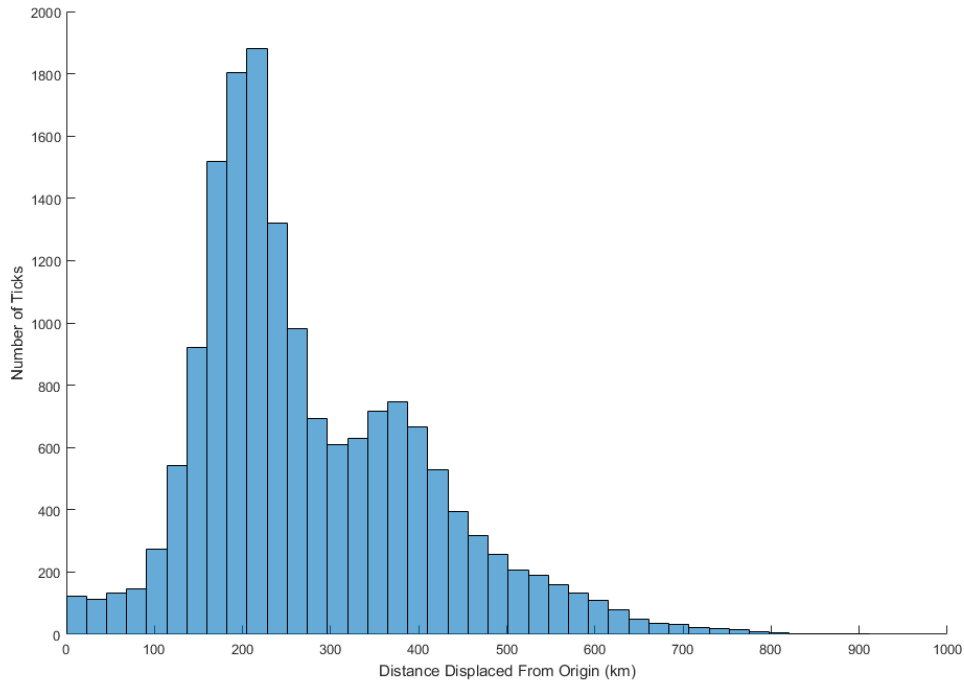


Figure 13. Proportion of all dispersed larvae (A) and nymphs (B) detaching from wood thrushes (orange) and ovenbirds (blue) by Julian date. N = 100,000.

A)



B)

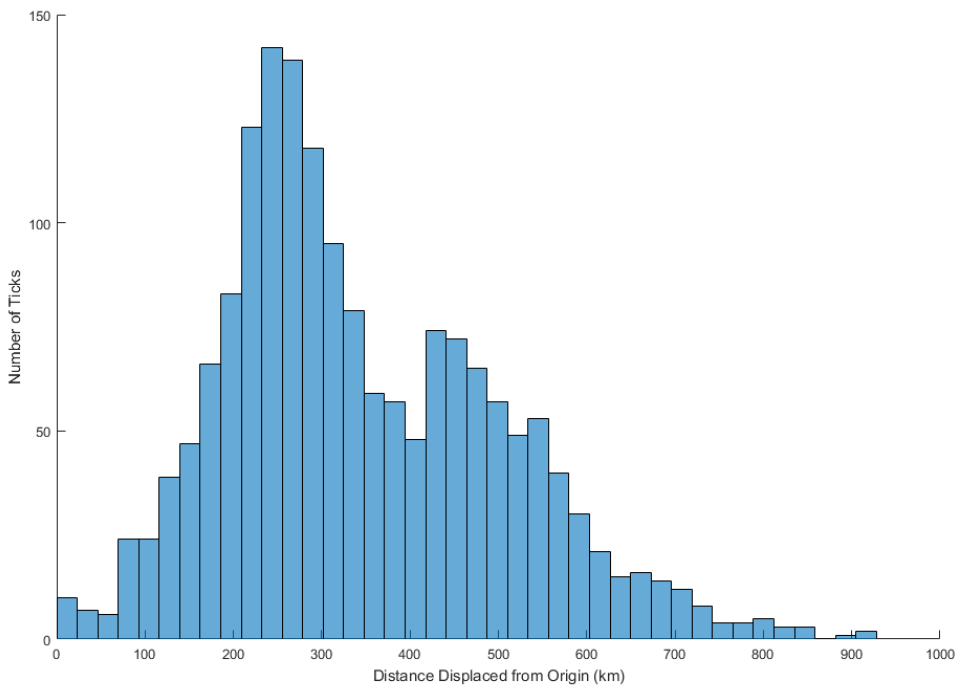
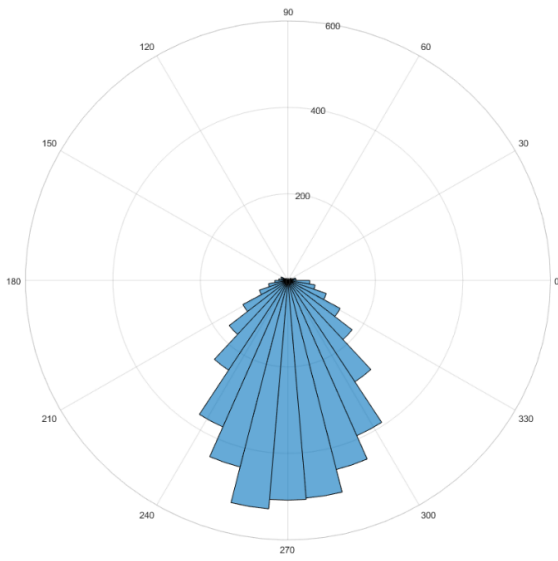
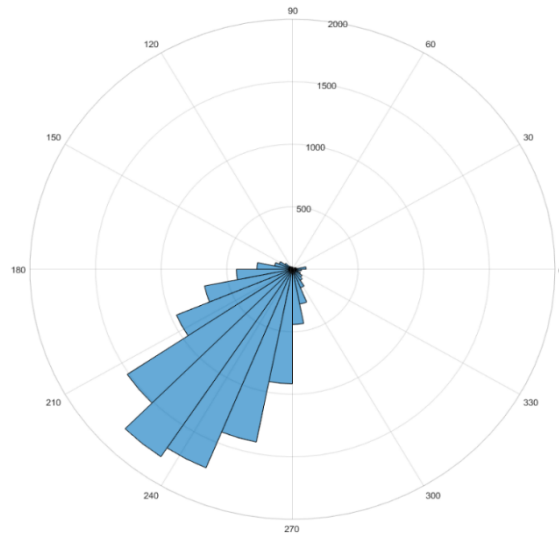


Figure 14. Frequency of dispersal distance of ticks transported on ovenbirds (A) and wood thrushes (B).

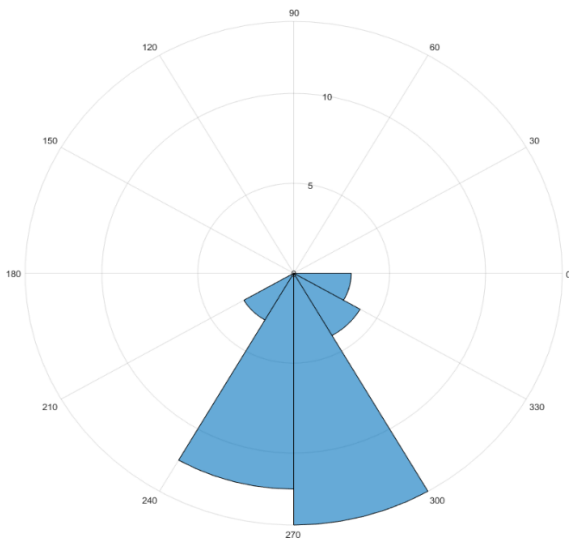
A)



B)



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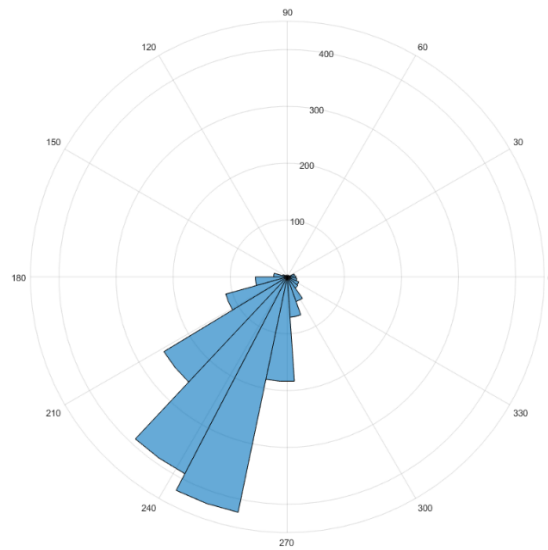
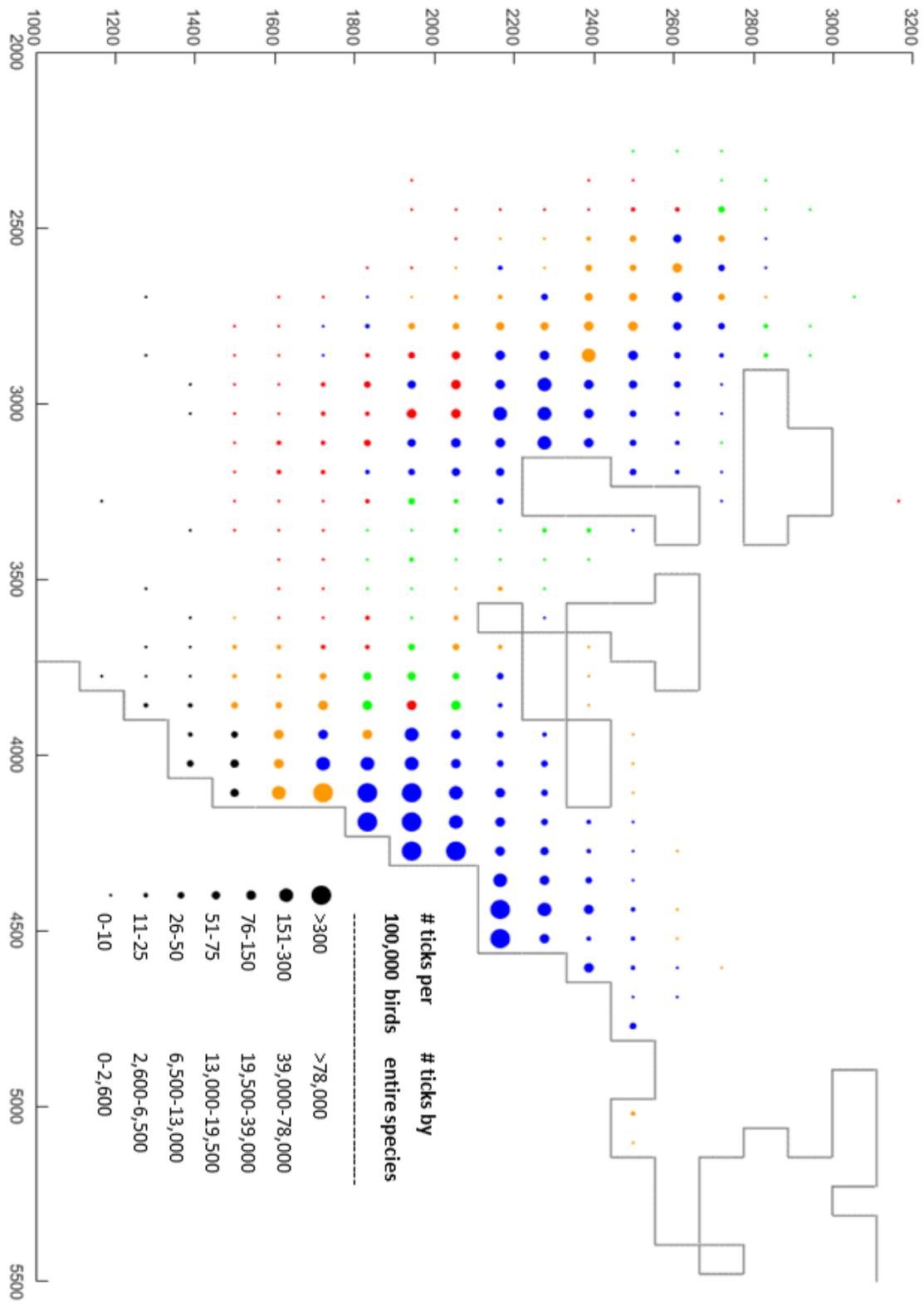


Figure 15. Frequency of bearings from attachment to detachment site for ticks dispersed by ovenbirds (A,B) and wood thrush (C,D) from areas west (A,C) and east (B,D) of the 86th meridian. Bearings are reported in a polar coordinate system. N = 18,095 ticks.

A)



B)

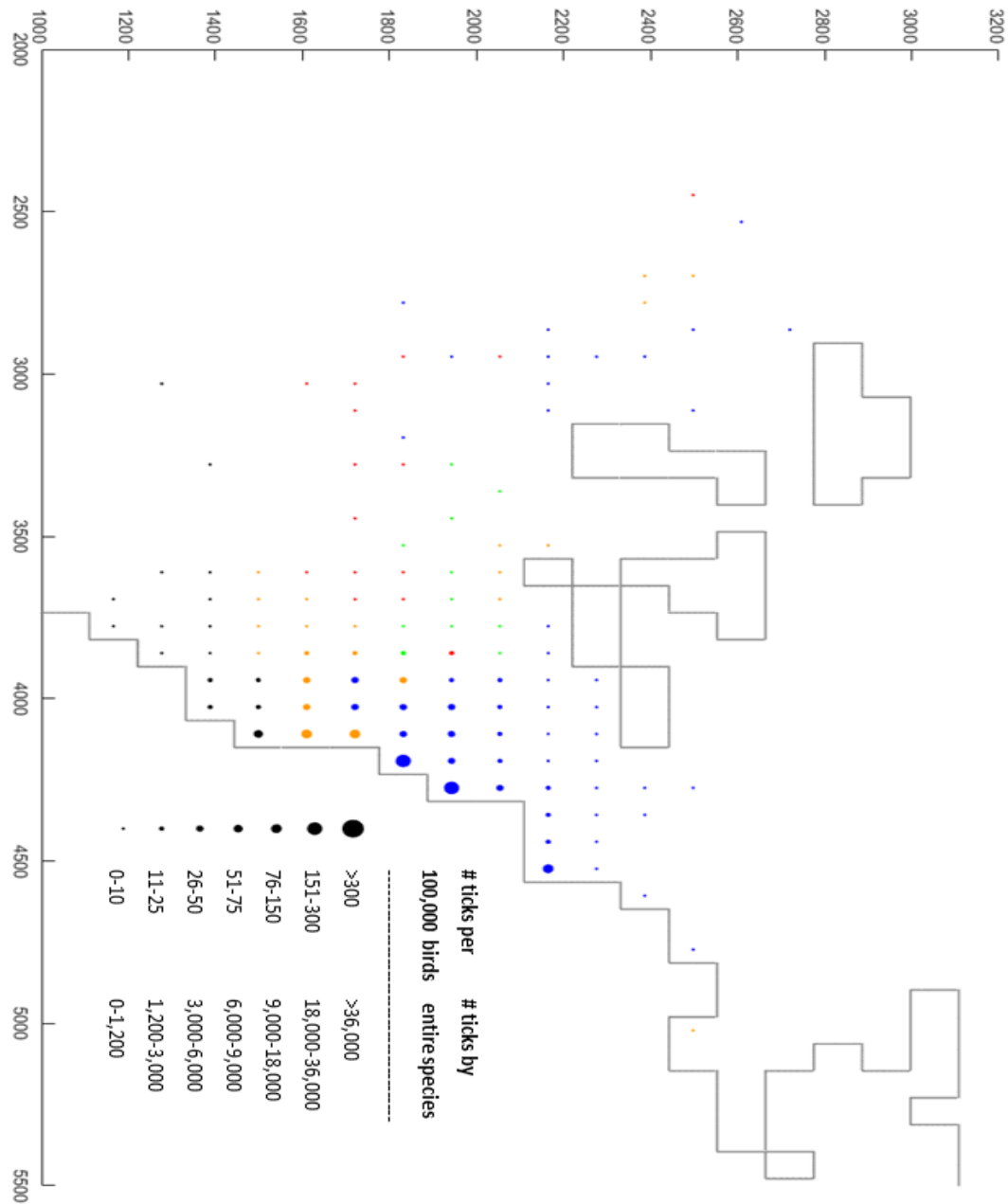
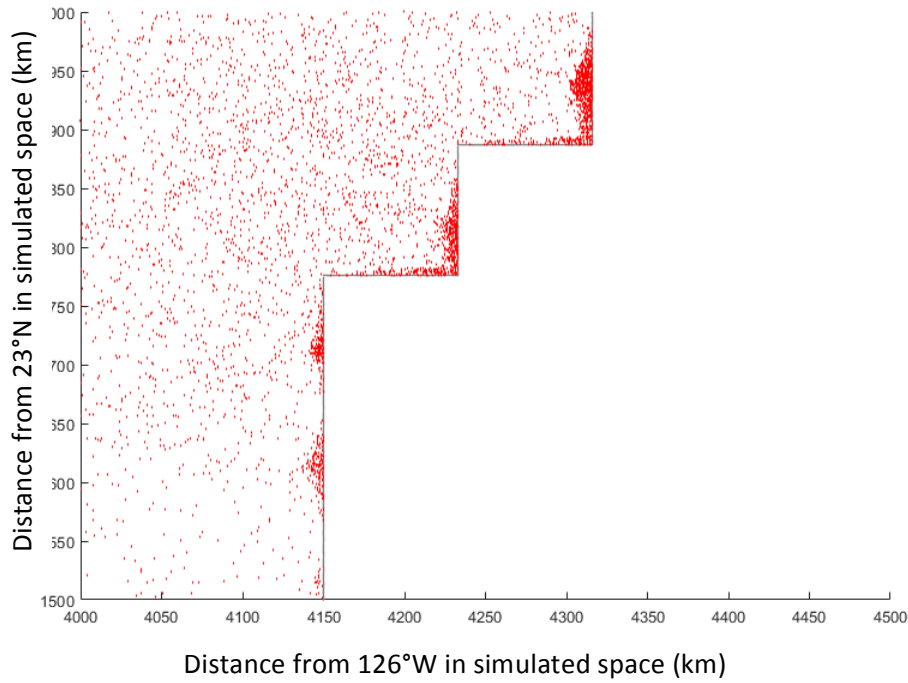


Figure 16. Total number of ticks predicted to detach from ovenbirds (A) and wood thrushes (B) within latitude-longitude cells. The number of ticks dropped is represented by the size of circles. The color of a dot indicates the climatic suitability of the cell for population establishment under present and predicted future conditions. Cells were categorized as areas where the northern tick genotype is already endemic (blue), where the southern genotype is endemic (black), where climate forecasts predict newly suitable conditions by the 2080s (red), where climatic conditions presently and by the 2080s are predicted to be suitable (orange), and where climate is not predicted to allow establishment, both currently and by the 2080s (green).

A)



B)

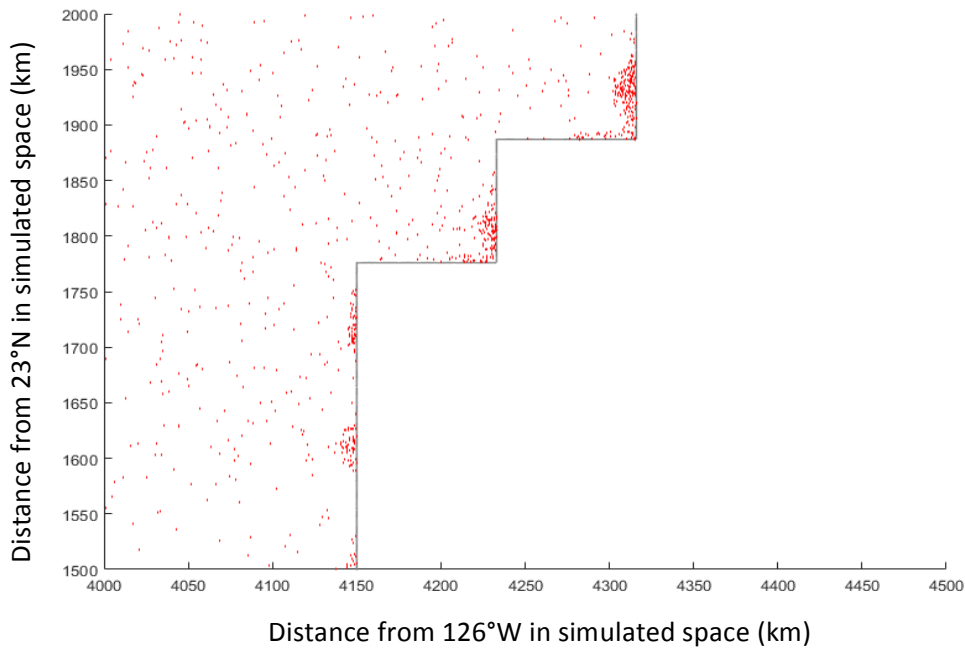


Figure 17. Ticks were dropped often near the Atlantic due to coastal landings of ovenbirds (A) and wood thrush (B) reorienting after ending flight phases over water. The above simulated space encompasses the Mid-Atlantic coast from North Carolina to Delaware.

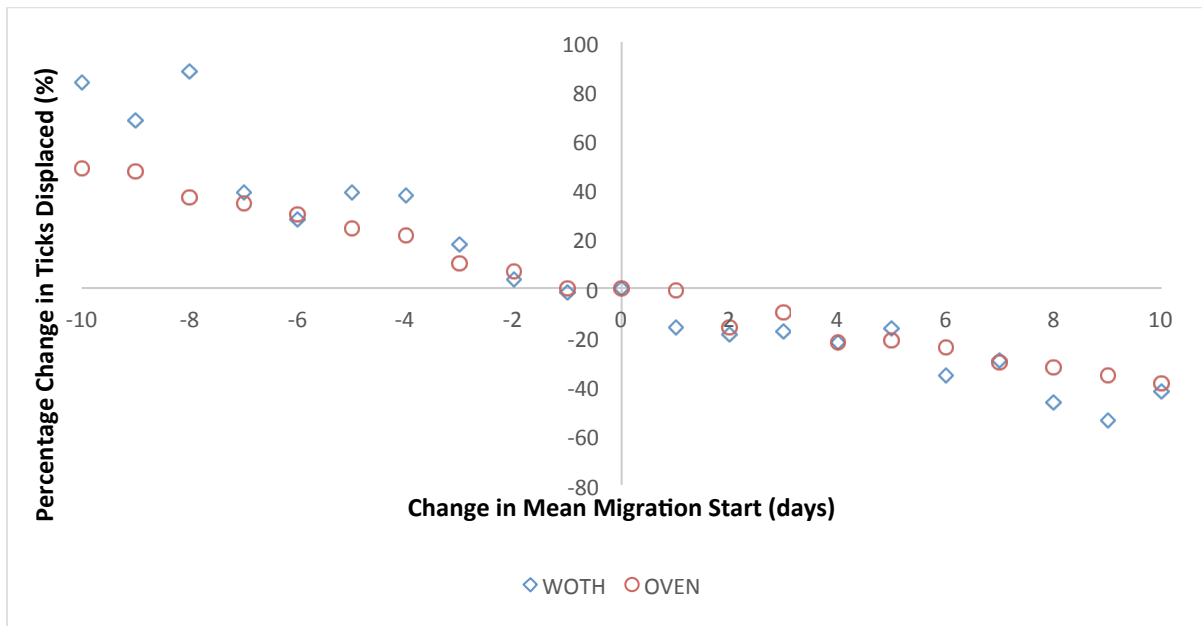


Figure 18. Percentage change in total ticks displaced by ovenbirds (blue) and wood thrush (orange) during fall migration season with changes to migration timing. Negative day values represent migration timing that has been advanced, with positive values representing delays to migration timing. N = 100,000 birds for control values (change of mean migration = 0). N = 10,000 for each species in all other simulations.

DISCUSSION

The expansion of areas climatically suitable for the population establishment of *I. scapularis*, the principal vector of Lyme disease in North America, has previously been mathematically predicted, and empirically observed. Dispersal on hosts is necessary for the establishment of the species in areas that lack endemic populations. Songbird species, especially those undergoing migratory movements, may play a role in dispersing ticks into areas with newly suitable climate conditions. The primary aim of this research was to use an individual-based model to investigate the impact of southward migratory movements of ovenbirds and wood thrushes on the dispersal of *I. scapularis*, and to qualitatively assess how songbird species may consequently contribute to the range expansion of the tick both presently and in the future. Understanding tick dispersal patterns occurring as a result of attachment to migratory songbirds will help to determine the risk from tick-borne pathogens to human populations, specifically in areas presently without established *I. scapularis* populations.

The model created for this analysis predicts the widespread dispersal of millions of ticks over hundreds of kilometers as a result of attachment to reservoir-competent ovenbirds and wood thrushes. Dispersed ticks detached in nearly all areas currently climatically suitable for the vector, and into the majority of areas predicted to be suitable by the 2080s. In addition, this model suggests that the impact of migrating songbirds on tick dispersal is dependent on a multitude of species-specific avian characteristics and behaviors. As a result, changes in avian and tick phenologies resulting from climate change will likely affect current patterns of *I. scapularis* dispersal by migrating songbirds.

Tick Dispersal, Range Expansion of *I. scapularis*, and Human Health Risks

The model created for this research predicts that individual *I. scapularis* are often displaced hundreds of kilometers from their point of attachment, and into areas where established populations of the tick do not exist. Dispersed ticks pose a significant risk to human health for two reasons. For one, ticks transported to areas without existing populations may molt and subsequently attach to human hosts. Ticks carrying *B. burgdorferi* dispersed via springtime migrants into areas without established populations have been collected after subsequently attaching to humans (Ogden, 2008a). Secondly, ticks dispersed into unestablished areas increase the likelihood that a reproducing population will become established. The range of *I. scapularis* overwhelmingly overlaps with rates of human Lyme infection, with human Lyme cases following the expansion in the range of the tick (Diuk-Wasser et al. 2006, Pepin et al. 2012). Both the introduction of molting ticks and the establishment of reproducing populations are important components when assessing human risk to certain tick-borne pathogens such as *B. burgdorferi*.

Many avian species are competent reservoir hosts for *B. burgdorferi*, meaning that transmission of the Lyme-causing bacteria between avian hosts and ticks can occur during attachment. Importantly, songbirds have the ability to transport ticks much farther than the non-reservoir competent white-tailed deer (Scott et al. 2001), the host often implicated in the range expansion of the tick (Madhav et al 2004). High tick infestation rates in songbird populations during the summer months suggest a large percentage of songbirds are exposed to the spirochete in areas where *I. scapularis* is established. If a tick is infected after attachment to a migratory host, the disease may continue to persist in a newly established population elsewhere. However,

even if a newly established population of *I. scapularis* does not carry *B. burgdorferi* initially, it is still possible for that population of ticks to become carriers of the bacteria in the future.

The dispersal of ticks by songbirds migrating northward has been suggested to be responsible for the population establishment of *I. scapularis* in Canada, although the number of transported ticks needed to establish a reproducing population at a specific site is currently unknown (Ogden, 2008a). The probability of establishment of a new population varies temporally and spatially depending on a variety of abiotic and biotic factors, including climate, host availability, and number of ticks brought to an area. Because of this, and along with the likely underestimation of the number of ticks dispersed on migrating birds by this model, it is not feasible to speculate where, and if, the two species simulated here have the capacity to cause the establishment of new populations. Although this model is not targeted to model range expansion, it does conclusively suggest that the first step of the establishment process, the dispersal of large numbers of ticks to non-endemic and climatically suitable areas, is occurring presently.

The combination of previous research confirming reservoir competency of numerous songbird species with the widespread dispersal patterns predicted by this model suggest that fall migrants play a critical role in the dispersal of *I. scapularis*, and subsequently *B. burgdorferi* and other tick-borne pathogens. According to the model used in this analysis, Iowa, Minnesota, North Carolina and Virginia are predicted to experience the highest rate of dispersal among non-endemic areas. According to climate models, the current risk of population establishment of the vector in these areas is high (Brownstein et al., 2005). The model predicts that tick dispersal occurs widely throughout the Eastern United States, albeit at varying frequencies. Depending on tick survival rates in dispersal locations, ticks may molt and subsequently quest again. These ticks may pose an immediate risk to humans as they seek future hosts. As a result, current and

future human risk to tick-borne illness across the Eastern United States is likely increased by the dispersal of ticks by fall migrants.

Differences between Songbird Species

An avian-centered model allows for the analysis of how species-specific behaviors can lead to varying patterns of *I. scapularis* dispersal. Despite a similar rate of infestation during the summer months as observed by Stafford et al. (1995), the model predicts that the entire population of ovenbirds transport nearly twenty times the number of ticks than that of wood thrushes. This evidence indicates that the differences in tick dispersal potential of migrating birds cannot solely be ascertained from summer infestation rates. The difference in simulated dispersal potential of songbirds is the result of two other major factors: breeding/migration range and migration timing. The impact of tick attachment rates, breeding and migratory densities, and timing of migration on the magnitude of simulated dispersal suggests that an avian-centered approach is critical in accurately predicting the role of songbirds on the dispersal and range expansion of *I. scapularis*. Each of these factors is explored in detail below.

Tick Attachment Rates – Difference between Species

The difference in rates of tick attachment between species is likely due to differences in avian feeding behavior, with time spent foraging on the ground serving as a predictor for attachment likelihood. However, ticks have been found attaching to individuals belonging to numerous songbird species with varying foraging strategies (Brinkerhoff 2009). As a result, infestation rates may be tied to other species-specific characteristics such as preening behavior and habitat associations (Ogden 2008a). Infestation rates have been shown to vary between species, and

these reported rates are important in assessing the magnitude of expected tick dispersal. In this model, ovenbirds are parameterized to disperse more ticks based on higher rates of attachment observed throughout the summer and fall (Stafford et al. 1995).

Breeding and Migratory Densities

The breeding and migratory densities of populations passing through the Upper Midwest and Northeast, two of the foci of *I. scapularis*, differ between ovenbirds and wood thrushes.

Although the breeding range of wood thrushes and ovenbirds both encompass the Northeast and upper Midwest, ovenbird population size in the Midwest is far greater than that of wood thrush (Fig. 6). A greater number of birds breeding in regions of high tick density results in a greater percentage of birds departing from their breeding grounds with ticks attached. In addition, ovenbirds that breed in western Canada pass through the Great Lakes region during migration, further increasing the number of ovenbirds exposed to ticks in the Midwest compared to wood thrushes. As a consequence, the model predicts more tick dispersal from the Midwest by ovenbirds than wood thrushes.

The impact of wood thrush as a species on tick dispersal is also limited by the high density of the population breeding below latitudes at which the tick vector is found (Fig. 6). Because individual migration paths orient these birds south, birds breeding at latitudes below the northern range of the tick are unlikely to disperse ticks during the migration season. In contrast, the majority of ovenbirds breed at latitudes within, or north of, the range of the tick. In all, the difference in species-specific breeding densities is a critical factor for predicting the effect of *I. scapularis* dispersal by songbird hosts.

Timing of Migration

Because tick questing phenology peaks during the summer months, earlier migration timing of songbird species leads to higher rates of tick transport. The departure timing of simulated ovenbirds, which is parameterized to occur a month earlier than wood thrushes on average, in part led to the much higher rate of tick transport events observed in the simulation. Tick questing phenology peaks earlier in the Midwest compared to the Northeast, and attachment to migrating wood thrush hosts in the Midwest is subsequently unlikely given late migration timing. By experimentally altering the average departure date in a series of simulations, the model predicts that the magnitude of the dispersal of ticks is sensitive to the timing of migration of avian hosts.

Emergence and Conclusion

Overall, the model suggests that ovenbirds transport a greater number of ticks into more areas at risk for population establishment than wood thrushes. Interestingly, other patterns seen in the simulation indicate that individual infected wood thrushes may be a more effective host than ovenbirds. Despite a lower rate of dispersal, wood thrushes tended to transport ticks farther from point of attachment than ovenbirds due to a greater average flight distance (Table 3). As a percentage of ticks transported, those detaching from migrating wood thrushes tended to do so at a higher rate in areas currently climatically suitable for tick population establishment. These nuances suggest that correctly parameterizing seemingly secondary species characteristics, such as flight speed, is important to assessing dispersal patterns.

In all, the pattern of dispersal by both ovenbirds and wood thrushes suggests that greater attention to species-specific migration-related behaviors and characteristics is necessary in order to understand the relative impact of certain species, and subsequently songbirds as a whole, on the dispersal of *I. scapularis*. This model demonstrates that three species-specific characteristics play a dominant role in the number of ticks transported by a given species: breeding/migration range, migration timing, and infestation rates. In addition, less obvious factors such as flight speed may also play a more cryptic role in dispersal patterns. With the impact of these avian factors on the dispersal patterns of *I. scapularis* elucidated, it is possible then to understand the role of songbird species not represented explicitly in this model (Fig 1). Qualitatively comparing characteristics of ovenbirds and wood thrushes to other songbird species can give a sense of the role on dispersal of North American migrant populations as a whole.

Certain songbird species not represented in this model can be expected to transport ticks at similar rates to ovenbirds and wood thrushes. Seven other migratory songbird species where sufficient research exists were qualitatively compared to ovenbirds and wood thrushes based on migration timing, breeding densities and tick attachment (Fig. 19). Out of the seven songbird species analyzed, I predict that veery, common yellowthroat and house wren populations each disperse ticks at a magnitude similar to, or greater than, that of wood thrush. Notably, veeries are earlier migrants than both species modeled, have been observed with greater infestation rates than ovenbirds (Stafford et al. 1995), and have large breeding populations in the Midwest and Northeast. Because of these factors, veeries may disperse a greater number of ticks during fall migration than both species examined explicitly by this model. The table presented does not provide an exhaustive list of all species that likely disperse ticks during the fall (Fig. 19). The aim of qualitatively comparing other songbird species to those in the model is to suggest the

cumulative role of migratory species in the dispersal of ticks during fall migration. With more time, and a stronger foundation of field research related to migratory behavior, future inclusion of other migrating songbirds into the model will further explain the ultimate impact of songbirds on the dispersal of *I. scapularis*.

Impact of Climate Change

Climate change patterns have been implicated as the central cause for the increasing number of suitable areas and the growing population sizes of *I. scapularis* in the U.S. and Canada (Eisen et al. 2016, Ogden et al. 2006a, Ogden et al. 2008b, Ogden et al. 2016). As a result, climate change is hypothesized to be driving the increasing rate of tick-borne illnesses in humans (Brownstein et al. 2005, Ogden et al. 2016). Within the simulation, increasing tick densities and a broadening range would lead to an increase in the magnitude of dispersal by avian hosts. Therefore, it is logical to predict that tick dispersal by fall migrants will increase under current warming climate conditions. In addition to rising densities and range expansion of *I. scapularis*, certain characteristics of tick and songbird phenologies are predicted to shift as a result of climate change. Understanding these changes is critical to understanding the role of fall migrants on the dispersal of *I. scapularis*.

Climate Change and Tick Phenology

Various aspects of *I. scapularis* phenology are affected by climate conditions, with changes differing depending on life stage (Moore et al. 2014). With warming climates, questing behavior of larvae is predicted by one model to peak earlier than it does currently, with peak questing of

nymphs occurring later (Ogden 2006a). Because this could lead to changes in temporal overlap with songbird migration, these changes will affect the number of ticks displaced, and the proportion of ticks brought into each area belonging to each life stage. Less intuitive changes in avian-tick interactions may occur as a result of these nuanced phenology changes, and further investigation of the impact of this is a future application of this model. Updating this model with predicted changes in questing behavior as a result of climate change would be a valuable resource for addressing the future role of songbirds in transporting ticks during fall migration.

Avian Behavior

As explored above, one of the strengths of an avian-oriented model is exploration of the role of songbird behavior on the dispersal of tick vectors. Avian behavior is dependent on climate conditions, with breeding ranges and migration timing being among the factors affected. Other models predict that climate change will shift the breeding ranges of many songbird species to more northern latitudes (Langham et al. 2015). This general trend is similarly predicted for both ovenbirds and wood thrushes. A breeding range shift of these two species may coincide with the northern range expansion of *I. scapularis*, leading to greater levels of tick dispersal in Canada during the fall months. Migratory surveys also suggest a general advancement in the timing of fall migration with changing climate patterns, although these changes have been shown to be widely variable between species (Mills 2005, Van Buskirk et al. 2009). To the knowledge of the author, conclusive field evidence of a shift in migration timing of ovenbirds and wood thrushes does not exist. Further evidence for climate related shifts in migration timing of these two species, and other species likely to transport ticks, is critical for assessing the changing relationship between songbirds and tick populations. Advances of migration timing in species

that play a role in dispersal could greatly increase the number of ticks transported during this time.

Conclusion

Behavioral patterns of ticks and songbirds are dependent on environmental cues, and are likely to change in the future. As climate patterns change across North America, the role of songbirds in the dispersal of ticks will be affected as a result. Overall, this model suggests that future climate conditions will greatly increase the number of ticks dispersed by fall migrants by increasing the range of the tick and enlarging tick populations. The framework of this model could be used to investigate the more cryptic effect of changes to tick questing and migrant phenology on the patterns and magnitude of tick dispersal.

Implications for Gene Flow

Dispersal of ticks over hundreds of kilometers may contribute to gene flow within, and between, wide geographical areas. The foci of tick populations in the Midwest, Northeast and South are generally geographically isolated (Eisen et al. 2016). A high percentage of simulated ticks remained within the endemic area from which they originated, suggesting a high rate of gene flow within, but not between, the Midwest and Northeast (Table 5). Current research suggests that, generally, genetic homogeneity characterizes northern tick populations, and that southern and northern populations are genetically distinct (Araya-Anchetta et al. 2015, Van Zee et al. 2015). The finding of the current research is concurrent with studies detailing gene flow among *I. scapularis* populations.

Based on genetic analysis, Van Zee et al. suggest that gene flow is occurring unidirectionally from northern to southern *I. scapularis* populations (2015). The model used in this research predicts that roughly 2% and 9% of ticks transported by ovenbirds and wood thrushes, respectively, detach in areas where the southern tick population is endemic. As spring migrants passing through southern *I. scapularis* populations experience much lower rates of attachment due to the reptilian-host seeking behavior of ticks in this area, the impact of avian species on gene flow would be restricted from north to south. This model suggests that the unidirectional gene flow observed between *I. scapularis* populations can be explained by the overwhelmingly unidirectional dispersal of ticks attached to migrant songbirds.

Future range expansion leading to geographic overlap of these distinct foci may result in an increase in gene flow between currently isolated populations. The model predicts a large amount of tick detachments from avian hosts in the coastal Southwest, an area that may act as a bridge between the Northeast and Southwest foci of the tick. Longitudinal spread into Ohio and southward expansion from both the Midwest and Northeast foci may lead to a fully continuous range over the next century. The potential for gene flow between currently isolated *I. scapularis* populations could have consequences for the spread and maintenance of tick-borne pathogens, and lead to an increase in rates of human diseases. Ticks being dispersed into climatically suitable southern populations that exhibit mammalian host seeking behavior could lead to the emergence of a new center for Lyme and other tick-borne illnesses.

Limitations of, and Improvement to, Current Model Parameters

The current model is parameterized from a wide base of available evidence in the literature detailing avian and tick behavior. Within this foundational research, considerable shortcomings

in the investigation and knowledge of these behaviors remain. It is important to consider that, as a result of the gaps in the existing knowledge, parameters of this model likely encode varying levels of inaccuracies. To mitigate this effect, parameters used in this model that were calculated from field research with a high degree of uncertainty were intentionally designed to avoid overestimation of tick dispersal. It is likely then that updating parameters based on the inclusion of future research may increase the predicted impact of songbirds on tick dispersal.

Intensity of Infestation

One of the most likely inaccuracies in the model pertains to the underestimation of the number of ticks attached to simulated songbirds. As addressed in the methods, this model accurately reproduces observed infestation rates, but consistently underestimates mean intensity rates. The probability distribution used to determine the number of ticks attaching each day to each bird is based on the assumed independent nature of tick attachment events. The underestimation produced by the model is likely indicative that tick attachment events may not be independent, that attachment rates may vary among individuals within a species, or that other behavioral patterns such as preening play a significant role in intensity rate. This is a critical subject for future research. In a survey of ticks attached to ovenbirds in an area without an established population during fall migration, infested individuals were reported to have an average of more than 4 ticks attached. In addition, the number of ticks attached to infested ovenbirds ranged from 1-16, indicating significant variability between individuals (Morris et al. 2007). Within the model, the average number of ticks attached to each infested ovenbird during the migration period is just above 1. Given the scale of this difference, and the impact that this difference may have on the underestimation of the number of ticks dispersed during fall migration, the

importance of the accuracy of this parameter cannot be overstated. Future research that measures and reports the number of ticks attached to each individual bird during the summer and fall months will help inform the use of a probability distribution that will adequately recreate infestation and intensity rates within this model.

Spatial Tick Densities

Extensive field data from Diuk-Wasser et al. has provided for recreation of tick densities across the United States (2010). Partially because of the lat-long cell method of representing these densities used in the current research, and partially due to the limitation of sampling sites within certain areas, densities within some regions where *I. scapularis* is endemic are parameterized as having a density value of zero in the simulation. Comparison of the spatial densities represented within the model used in the current research with county-scale reported presence of *I. scapularis* suggests that cells with non-zero densities may be underrepresented in this model (Eisen et al. 2016). In addition, no sites in Canada were parameterized to have an established population. Future versions of this model could be improved by using a smoothing function to estimate more spatially robust density values from the combination of field-gathered densities in the United States and Canada.

Further Applications and Expansion of the Model

This model provides a foundational step for addressing a myriad of questions relating to songbirds and ticks that are not directly addressed within this research. One of the most obvious expansions of this model is including the representation of tick dispersal during spring migration.

Considerably more research examines northward dispersal (Elias et al. 2011, Leighton et al. 2012, Ogden et al. 2006a-b), and re-parameterization of this model based on spring migration could be time-effective and fruitful. One of the major considerations when expanding this model to include spring migration would be to re-examine the questing phenology parameters used currently, which seem to overestimate infestation rates during the early spring months in comparison to data from Lyme, Connecticut (Stafford et al. 1995). In addition, parameterization of spring migratory behavior would require the recreation of homing of individuals to breeding sites. Despite these hurdles, simulating tick dispersal by springtime migrants is a relevant component in assessing the risk of range expansion of the vector, and a clear first step for model expansion.

The spatial scale of certain parameters is one important and improvable aspect of this model. The spatial scales used in this model were chosen for simplicity of design, availability of research detailing necessary parameters, and in order to minimize costly computational problems. One spatial component of this model is the geographic variance in tick densities. Other researchers have created models for habitat suitability for *I. scapularis* populations at a continental scale (Brownstein et al. 2003, Diuk-Wasser et al. 2006). Expanding these population models to include varying densities over small spatial scales would give the current model a greater degree of spatial precision. Modeled approaches to estimate tick populations at a smaller spatial scale would likely be based on variation in habitat types. In addition to radically augmenting the ability of this model to simulate realistic tick density patterns, the inclusion of habitat type data could also lead to more realistic simulations of stopover densities of migrating birds, representing the range of avian densities present within a small reference frame. In all, a

finer spatial representation of habitat types could illuminate specific areas at risk for an influx of ticks on fall migrants.

Another potential improvement in this model could come from the inclusion of temporal weather data, a factor that influences both tick and avian behavior. Inclusion of wind data in the model could inform realistic flight displacements, although inclusion of this factor would be dependent on adequate understanding of the movement of birds in flows. Bird behavior in displacement due to wind is a topic that has been explored extensively (Chapman et al. 2011, Goto et al. 2017, Horton et al. 2016), but is likely age and species-specific. This would make parameterization difficult given the current available research in the field. In contrast, inclusion of weather data may be more readily applied to parameters relating to simulated ticks. Classical models describe the dependency of tick populations on climate conditions and host availability (Madhav 2004, Ogden et al. 2008b). Inclusion of climate data could allow for analysis of the variability in tick dispersal as a result of songbirds between years according to historical data and future weather models.

Inclusion of other species of ticks and songbirds is another direction for expansion of this model that may be easily done given the current state of the research. Within the current framework of the model, the inclusion of other birds would provide for a clearer picture of the total role of songbirds in the dispersal of *I. scapularis*. Future inclusion of other ticks species such as *Haemaphysalis leporispalustris* and *Amblyomma americanum* would be contingent on adequate information regarding density and rates of attachment to avian hosts, but could provide valuable information regarding dispersal patterns as a result of attachment to avian hosts. Inclusion of other tick species could answer questions related to vector range expansion and disease risk of other tick-borne pathogens.

This model can be used in the future to investigate other questions related to *I. scapularis* dispersal through the expansion and update of certain parameters. As an author, my focus on the intended question has often been clouded by the numerous opportunities to expand the model to investigate others. The myriad of new parameters that could be encoded in this model to answer novel research questions is exciting, but equally treacherous. With new parameters comes added uncertainty. Any potential edits or expansions of this model must be accompanied by consideration of whether or not these new parameters add unnecessarily to the complexity of this model without providing more accurate answers to the research questions being examined (see Railsback and Grimm 2011 for summary).

Conclusions

This model lends support to the theory that migrating songbirds disperse millions of ticks over hundreds of kilometers, and therefore may impact the future range expansion of the Lyme disease vector *I. scapularis* in the United States. Simulated birds within the model framework displaced ticks from their origins in the Upper Midwest and Northeast into the majority of areas predicted to be suitable for the establishment of tick populations both currently, and into the 2080s. Importantly, tick dispersal patterns differed between the two species simulated in this model as a result of differing species characteristics. Comparing ovenbirds and wood thrush with other songbirds, it is likely that other species may disperse similar numbers of ticks.

Tick dispersal as a result of attachment to avian hosts is likely to lead to increased human risk of tick-borne illness across the United States. Ticks attached to reservoir-competent songbirds may harbor, or become infected by, the causative agent of Lyme disease, and may be dispersed into areas that do not have established tick populations. Risk for human tick bites in

these areas can increase if a reproducing population becomes established, or simply due to an influx of ticks that molt and survive to subsequently quest again. Further expansions of the current model, or other similar avian-centered individual-based models, have the potential to answer additional questions relating to risks to human health as a result of tick dispersal by migrating songbirds.

Species	Migration timing compared to ovenbird	Migration timing compared to wood thrush	Attachment rate compared to ovenbird	Attachment rate compared to wood thrush	Breeding/migrating population in Midwest	Breeding/migrating population in Northeast	Population Size	Author-estimated level of <i>L. scapularis</i> dispersal
Veery	Earlier	Earlier	Less	Greater	Large	Large	12 million	Very High
Ovenbird*	Equivalent	Earlier	Equivalent	Greater	Large	Large	26 million	High
Wood Thrush*	Later	Equivalent	Less	Equivalent	Small	Large	12 million	Medium
Common Yellowthroat	Later	Later	Less	Greater	Large	Large	81 million	Medium
House Wren	Later	Equivalent	Less	Less	Large	Large	42 million	Medium
Hooded Warbler	Earlier	Earlier	Less	Greater	None	Small	5.2 million	Low
Northern Waterthrush	Later	Later	Less	Less	Large	Large	18 million	Low
Gray Catbird	Later	Later	Less	Less	Large	Large	29 million	Low
Song Sparrow	Later	Later	Less	Less	Large	Large	22 million	Low
Sources	Cornell Lab of Ornithology. Accessible via birdsna.org	Cornell Lab of Ornithology. Accessible via birdsna.org	Stafford et al., 1995	Stafford et al., 1995	Cornell Lab of Ornithology. Accessible via birdsna.org	Cornell Lab of Ornithology. Accessible via birdsna.org	Rich, 2016	Estimated by author

Figure 19. Comparisons of migratory and tick-related characteristics of various North American songbird species. All species listed here have been shown to serve as reservoir-competent hosts of *B. burgdorferi* (Brinkerhoff et al. 2009, Giardina et al. 2000)

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Appendix A: Outline of Parameters and Sources

	<u>Description</u>	<u>Source(s) *</u>
Spatial tick density	Spatial densities reported by Diuk-Wasser from flagging data spanning the Midwest and Atlantic Coast were grouped by latitude and longitude by the author (2010).	Diuk-Wasser 2010
Tick questing phenology	Temporal frequency of host seeking derived from same flagging dataset as reported in Diuk-Wasser (2010). Different distributions were determined for nymphs and larvae in both the Midwest and Northeast foci.	Gatewood et al. 2009
Tick attachment to avian hosts	A Poisson distribution with μ dependent on Julian date, tick density of cell, and species constant was used to determine probability of tick attachment to both wood thrushes and ovenbirds. The species constant was determined by fitting sub-model rates of infestation to those reported by Stafford et al. (1995). Attachment of nymphs and larvae is determined independently.	Diuk-Wasser 2010, Gatewood et al. 2009, Stafford et al. 1995
Tick attachment time	Distribution derived directly from data reported by Hu et al. Attachment time is different for nymphs and larvae.	Hu et al. 1997, Bontemps-Gallo et al. 2016, Couret et al. 2017, Goddard et al. 2015, Hodzic et al. 1998, Nakayama & Spielman, 1989
Breeding ranges	Breeding Bird Survey data was used to create a probability map detailing the chance each bird would occupy a given cell during the breeding season. Breeding location of each bird is randomly determined at the start of each simulation.	Sauer et al. 2017
Age demographics	Monitoring Avian Productivity and Survivorship data on the age of birds captured only once during breeding season was used to determine the overall percentage of juveniles in the populations of both species.	Michel et al. 2006
Population sizes	Rich et al. provide estimates of whole population sizes of both ovenbirds (26 million) and wood thrushes (12 million).	Rich et al. 2016

Bird flight headings - Adult	Flight headings are derived from radar tracking studies, and supported by other methodologies including Emlen funnel experiments. μ = goal heading (described below) σ = 36.73°	Cochran 2005, Demong and Emlen 1978, Akesson and Bianco 2016, Chapman 2011, Goto et al. 2017, Horton et al. 2016
Bird flight headings - Juvenile	Emlen funnel experiments suggest the standard deviation of orientation headings to be 1.5x that of adults in juvenile birds; likely due to reasons reviewed by Woodrey et al. (2000).	Moore 1984; Woodrey 2000
Flight length - WOTH	Single night flight length of wood thrush tracked by geolocators was 253km per day. Wikelski found single spring night flights to range from 1-8 hours in a small sample of northward migrating birds. Similarly, Newton references an early study done by Frank Moore measuring spring flight time of thrushes lasting 4-8 hours. The mean and standard deviation of flight length (5 hours with a standard deviation of 1 hour) was estimated by the author based on this data, and consideration of differences in spring and autumn flight speeds. μ =253km σ = 50.6km	Stutchbury et al. 2009, McKinnon et al. 2013, Moore and Kerlinger 1987, Newton 2007
Flight length - OVEN	Single night flight length of ovenbirds was derived from theoretical flight estimates for kilometers traveled per hour. Flight time was estimated using data referenced above, with a mean of five hours of flight and standard deviation on one hour. μ =198.8km σ = 39.76km	Alerstam et al. 2007, Moore and Kerlinger 1987
Goal headings - WOTH	Goal points are initialized at the start of each simulation and drawn from a uniform distribution between on the 23rd parallel between the 83rd and 86th meridian. Breeding locations were estimated from geolocator data reported by Stanley, and updated every day for each bird.	Stanley et al. 2015, Thorup et al. 2007
Goal headings - OVEN	Goal headings for ovenbirds was determined based on location in the simulated space, based on migration route analysis by Hallworth. Goal points are updated as birds pass into new regions, and are dependent on general flyway patterns.	Hallworth et al. 2015, Thorup et al. 2007
Death rates	Probability of death is considered to be constant throughout the migration period and equal for all birds, regardless of age. A daily death rate was experimentally determined by matching death rates in the model to those expected according to available research.	Michel et al. 2006, Sillet and Holmes 2002
Departure date - WOTH	A normal distribution for departure dates for wood thrush was approximated from observed departure dates. μ =Sep. 18th σ = 16 days	Stanley et al. 2012

Departure date - OVEN	A normal distribution for departure dates was experimentally determined by measuring the date of trans-gulf flights in ovenbirds. These dates were compared to mean arrival dates to the Yucatan measured by mist-netting reported by Deppe & Rotenberry. Standard deviation was experimentally determined to simulate the earliest arrivals to wintering grounds around the same date as those observed in the wild. μ = Aug 19th σ = 13 days	Deppe and Rotenberry 2005 , Sanders et al. 2014, Taylor 1972, Thobaban et al. 1987
Chance of stopover	Chance of stopover was parameterized as being linear and negatively correlated with energy stores. The relationship was parameterized so that a bird has a 100 percent chance of stopover if it has a flight capacity equal to or less than the ability to fly one more long flight (3 SDs from the mean) before depleting energy stores. When current flight stores are equal to or greater than initial flight stores, a bird has a 0% chance of stopping over.	
Energy uptake - WOTH	Energy uptake during stopover for wood thrush was estimated according to the days spent in stopover for the species. Wood thrush spent two-thirds of the migratory period in stopover, suggesting that the energy gained in two days of stopover were needed for each day of migratory flight. The calculated flight potential increase is equal to 126.5km/day spent in stopover.	Hussell and Lambert 1980
Energy uptake - OVEN	Energy uptake during stopover was measured by Hussell and Lambert to be .87 grams/day and considered to remain constant throughout the migration period and equal between birds. Considering the rate of mass loss per hour of flight, the calculated flight potential increase is equal to 172.96km/day spent in stopover.	Moore and Kerlinger 1987
Starting/maximum energy - WOTH	Starting flight potential and the flight potential limit used to determine a 100% chance of migratory flight, was estimated by Yong and Moore to be 1200km. This was considered to be the same for all individual wood thrush.	Yong and Moore 1997
Starting/maximum energy - OVEN	Starting flight potential was calculated using measured energy losses during flight, flight speed estimates, and the range of body masses seen in migratory ovenbirds. From this, the flight potential of a migratory ovenbird was estimated to be 1,590km.	Hussell and Lambert 1980 , Taylor 1972

***Bold type** indicates primary sources used for parameterization. Non-bold citations are supporting sources.