Original article

An individual-based model for the dispersal of *Ixodes scapularis* by ovenbirds and wood thrushes during fall migration

Benjamin A. Tonelli*, Donald C. Dearborn

Department of Biology, Bates College, Lewiston, ME, 04240, USA

ABSTRACT

Ixodes scapularis is responsible for the transmission of a variety of pathogens in North America, including *Borrelia burgdorferi* sensu stricto, *Anaplasma phagocytophilum* and *Babesia microti*. Songbirds have previously been described as agents of tick dispersal, and a combination of empirical data and modeling efforts have implicated songbirds in the range expansion of *I. scapularis* northward into Canada during spring bird migration. The role of fall bird migration has received comparatively less attention, particularly at a continental scale. The aim of the current research was to use a novel individual-based modeling approach (IBM) to investigate the role of southward migrating songbirds in the dispersal of *I. scapularis* within the continental United States. The IBM used in this research explicitly models dispersal by two extensively studied migrating songbird species, wood thrush *Hylocichla mustelina* and ovenbird *Seiurus aurocapillus*. Our IBM predicts the annual dispersal of more than four million ticks by *H. mustelina* and *S. aurocapillus*, notably into areas as far west as the Dakotas, and as far south as Central Alabama. Predicted dispersal locations include areas where the southern phenotype of *I. scapularis* dominates, suggestive of a possible mechanism for previously described unidirectional gene flow from north to south. In addition, the model demonstrates that three species-specific songbird traits – breeding range, migration timing, and propensity for tick attachment – each play a major role in the relative magnitude of tick dispersal by different songbird species. The pattern of *I. scapularis* dispersal predicted by this model suggests that migrating songbirds may have contributed to the range expansion of the tick historically, and may continue to do so presently and into the future, particularly as climate changes the geographic areas that are suitable for *I. scapularis*. Ultimately, widespread tick dispersal by migrating songbirds likely increases the human risk of Lyme disease and other tick-borne diseases in the United States.

1. Introduction

Lyme disease caused by *Borrelia burgdorferi* sensu stricto (s.s.) infection is the most commonly contracted vector-borne illness in the United States (Rosenberg et al., 2018). The causative agent is transmitted by the tick *Ixodes scapularis* (Burgdorfer et al., 1982; Steere et al., 2004). In addition to carrying *B. burgdorferi* s.s., *I. scapularis* has the potential to carry other human pathogens, including *Anaplasma phagocytophilum* and *Babesia microti* (Nelder et al., 2016). Although the present range of the tick stretches across most of the midwestern and eastern United States and parts of southern Canada, differences in nymphal host-seeking behavior currently lead to a lower risk of human bites in states south of 36°30′ (Arsnoe et al., 2015; Diuk-Wasser et al., 2010; Ogden et al., 2009; Pepin et al., 2012).

As our understanding of the current and historical biogeography of *I. scapularis* has developed (Dennis et al., 1998; Diuk-Wasser et al., 2006; Gatewood et al., 2009; Diuk-Wasser et al., 2010; Pepin et al., 2012; Eisen et al., 2016), one primary concern among public health officials is the increase in vector-borne illness that may result from future range expansion of the tick. *I. scapularis* dispersal, and subsequently range expansion, is dependent on the movement of hosts while ticks are attached. Migratory songbirds have been identified as an efficient dispersal agent of *I. scapularis,* and of other tick species, because of their capability of transporting parasites over long distances during migratory movements, particularly in comparison to other vertebrate hosts (Nicholls and Callister, 1996; Scott et al., 2001; Ogden et al., 2008a; Brinkerhoff et al., 2011; Scott and Durden, 2015). Previous mathematical models and field observations have predicted and demonstrated the role that northbound spring-migrating songbirds play in range expansion into Canada (Ogden et al., 2006b, b). Ticks have been found attached to humans in areas which lack an established tick population but where tick arrival via migratory songbirds is known to

occur (Ogden et al., 2006b), suggestive of a direct link between avian migration and vector-borne illness risk.

In addition to this important pattern of northward dispersal of ticks into Canada, ticks have also been collected on North American songbirds during the fall migration season, clearly implicating avian hosts as southward dispersal agents (Weisbrod and Johnson, 1989; Nicholls and Callister, 1996; Smith et al., 1996; Morris et al., 2007). While modeling methodologies have investigated the dispersal of *I. scapularis* northward by migratory songbirds, similar methods have not been used to explore the patterns and consequences of tick dispersal by southward migrants. Intuitively, warming climates of areas previously too cold for tick populations suggest that range expansion northward is likely of primary importance. However, the establishment of new *I. scapularis* populations in areas of equal or lower latitudes over the last few decades suggests that range expansion is not unidirectional (Eisen et al., 2016); additionally, the difference in host-seeking behavior between northern and southern *I. scapularis* (Arsnoe et al., 2015) heightens the importance of understanding the nature and scale of southward dispersal. Thus, songbird movements during fall migration are also important to explore when considering emergent health risks to human populations, particularly those within the United States.

The aim of this research was to construct an individual-based model (IBM) to predict the patterns and magnitude of dispersal of *I. scapularis* by two neotropical migrant songbirds, wood thrush *Hylocichla mustelina* and ovenbird *Seiurus aurocapillus*. These species were chosen because of the existence of ample empirical research describing information critical for model parameterization. In addition, each species has been observed with high numbers of *I. scapularis* attached during the summer months (Stafford III et al., 1995), making it possible that these species could be efficient dispersal agents. We used an individual-based modeling approach due to its relevance and strength in describing how global patterns (e.g., patterns of traffic congestion in a traffic simulation) can emerge from a set of variables that define the behaviors of individuals (e.g., the decisions of individual drivers) (Railsback and Grimm, 2011). Specifically, we aimed to investigate the emergence of continental-scale patterns of *I. scapularis* dispersal that arise from individual-level characterization of bird and tick behavior. By comparing the dispersal patterns of the two avian species used in this model, we can also investigate the impact of bird species' life history characteristics (e.g., migration timing) on the magnitude of tick dispersal. This model has the potential to provide a foundation for future investigation of related questions, notably the dispersal of other tick species commonly found parasitizing songbirds, including *I. dentatus*, Haemaphysalis *leporispalustris*, and *Dermacentor variabilis* (Stafford et al., 1995; Smith et al., 1996). Ultimately, understanding the potential for rapid dispersal of this disease vector at a continental scale, both currently and in the future, can help to predict emergent public health risks due to numerous tick-borne diseases.

2. Methods

2.1. Purpose

This model was designed to predict patterns of larval and nymphal *I. scapularis* dispersal by fall songbird migrants in eastern North America; adult *I. scapularis* do not feed on songbirds. In addition, this model can provide a foundation, either in code or concept, for exploring related questions. Here we describe the methods using the ODD protocol, the standard for IBM description (Grimm et al., 2006, 2010). For an expanded description of model design see Supplement 1.

2.2. Entities, state variables and scales

The primary model and all sub-models were designed using MATLAB. 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 spatial parameters, including tick densities, questing behavior, and avian breeding locations. Although densities of questing ticks can vary over smaller distances (Pardanani and Mather, 2004), continent-wide tick density data are not available at such a fine-grained scale. This model encompasses the movements of ticks and birds from Northern Canada to the Gulf of Mexico between the 126th and 46th meridians W. Each cell is designed to have a constant height of 111 km and width of 83 km, ignoring distortion caused by the curvature of the earth. The simulation runs from May 30th to December 31st, a time period chosen in order to fully encompass tick attachments before, and detachments after, the fall migratory period. Migratory movements begin mainly between mid-August and late October for wood thrush and between late July and mid-September for ovenbirds (Appendix A). Time is represented using discrete daily time steps.

The agents described by the model are ovenbirds (*S. aurocapillus*), wood thrushes (*H. mustelina*), and deer ticks (*I. scapularis)*. These bird species were chosen because of the availability of extensive research detailing migration behavior, breeding densities, and interaction with *I. scapularis* ticks. For analysis, 100,000 birds of each species were simulated. Birds are described in space at all times throughout simulations, while ticks are modeled as agents only when attached to a host. At all times, densities of questing ticks are modeled using field surveys of tick densities (Diuk-Wasser et al., 2010) and tick questing phenology (Gatewood et al., 2009) in order to determine the probability of any discrete number of ticks attaching to a host within a certain area on a given day. In order to determine these values, a sub-model was built to recreate patterns of temporal songbird infestation rates described at a study site in Connecticut (Stafford III et al., 1995).

Life stage of both ticks and birds was represented. Only larvae and nymphs attach to songbird hosts (Stafford et al., 1995), and as a result attachment of adults was not modeled. Questing phenology of *I. scapularis* is dependent on life stage and geography (including pronounced differences between the Northeast and the Upper Midwest) (Gatewood et al., 2009). Consequently, the model uses different parameters to calculate, the independent probabilities of larval and nymphal attachment to a simulated host dependent on the location of the bird, as well as the date. Simulated songbirds are considered either hatch-year or adult birds, with the only difference between the two being their competency in flying closer to their goal heading during migration (Moore, 1984).

Each simulated bird is considered to have a discrete breeding location, a flight distance capacity, an innate pre-determined date of migration start, and a migratory 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). This goal point changes for ovenbird individuals during migration according to location, to simulate the observed pattern of migration in which birds breeding in parts of Canada move east towards the Great Lakes before turning south (Hallworth et al., 2015). For wood thrushes, goal points simply represent the wintering site of individuals. Individuals of either species have an identical starting flight capacity, and the same rate of flight capacity replenishment during stopover days. All state variables are parameterized using evidence in the literature, a complete description of which can be found in Appendix A and Supplement 1.

2.3. Scheduling

During each day from May 30th to December 31st, birds die, ticks attach and detach, and migratory movements occur. Bird death occurs first, and is determined probabilistically using values that recreate average mortality rates. The death of a bird results in the detachment of all attached ticks, and removal of the bird from the modeled population.

Next, the model simulates the detachment of ticks. All ticks that

attach to songbirds detach after a period of time based on observed attachment durations in other endothermic hosts (Hu et al., 1997). Attachment occurs based on the spatio-temporal patterns of tick questing phenology described above. Birds in a given location pick up a number of ticks drawn from a unique Poisson distribution, which is determined by the date and local tick density.

After ticks attach and detach, all birds that have begun migration enter the movement phase for that day. During migration, each bird's current flight capacity causes it to initiate or continue a stopover or to fly a distance drawn from a normal distribution according to theoretical and observed patterns (Alerstam et al., 2007; McKinnon et al., 2017). The bearing at which each individual travels is determined by sampling a normal distribution with the mean as the 'ideal heading' towards the bird's goal point. Initial migratory movement that leads an individual overwater triggers a second migratory step, with the bird reorienting towards the nearest land and flying until it reaches land or runs out of energy and dies, with the exception of birds flying over the Gulf of Mexico. These birds are assumed to be making their flight to wintering grounds in either the Caribbean or the Yucatan peninsula, and are no longer tracked by the model. The initiation of a stopover is more likely as flight capacity diminishes. Stopover period length is determined by the number of days required for the bird to replenish fuel reserves. Flight capacity increases at a constant rate during stopover, independent of location or date.

2.4. Design concepts

2.4.1. Basic principles
The goal of this model is to predict the continental-level patterns of tick dispersal by migrating songbirds. An IBM is uniquely relevant as a tool to predict dispersal patterns in comparison to field-based methods.

2.4.2. Emergence
Dispersal patterns resulting from interactions between ticks and songbirds are the main emergent result of the model. Relatedly, migration behavior of simulated birds is an emergent phenomenon based on variables such as orientation direction, fuel capacity, and flight speed. Individual migration paths are the output of interactions between a multitude of stochastic factors, each of which serves as basic governing rules that eventually lead to predicted patterns of dispersal.

2.4.3. Sensing
Sensing describes the internal and environmental variables that the individual actors in the model are assumed to be able to sense and thus respond to. In this model, simulated birds have the ability to orient themselves based on their location in the model space. This affects their orientation towards a predetermined goal point. All birds are considered to know their exact location at all times, including when over water.

2.4.4. Interaction
Interaction between ticks and songbirds occurs in the Northeast and Midwest during the summer and fall months when tick populations are locally questing. After ticks attach, they are monitored within the model to measure movement, which is dictated by the movement of hosts.

2.4.5. Stochasticity
Stochasticity of individual parameters is the norm in this model, and distributions have been estimated from the literature for breeding ranges, migration start timing, flight distances, flight bearings, tick attachment time, and probability of death. Because of this stochasticity, different runs of the model using small samples (i.e., few individual birds whose behavior is modeled and tracked) might yield different results regarding the overall magnitude and pattern of tick dispersal; to explore this, we validated the model using different sample sizes to

determine a sample size that creates reproducible results (Supplement 2 Fig. 1).

2.4.6. Observation
To ensure that the model was working according to design and to create a record of results, two master matrices were collected for each model run. The first records the various states of each simulated bird in the model on each given day, including position and flight capacity. The second of the two matrices recorded the day that each tick attached and detached, and the bird that it attached to. By accessing the information in these two matrices simultaneously, information regarding model functionality is accessible, and records of tick dispersal are available.

2.5. Initialization

Initialization defines the initial state of the model at time zero. Our model begins with 100,000 birds of each species (a mix of adults and hatch-year birds; see Appendix A and Supplement 1) with full fuel stores at breeding grounds in North America on May 30. No ticks are attached to simulated birds at this time. Simulated birds are stationary initially, awaiting an individualized, predetermined migratory start date.

2.6. Submodels

For a brief description of tick attachment/detachment, migration, and death submodels, please refer to "Scheduling." For a full description of submodel design, implementation, and current limitations, please refer to Supplement 1.

2.7. Validation

Individual and population-level dynamics of simulated migration movement were qualitatively similar to those recorded by geolocators and by citizen-science sighting data. Similar to tracks of wood thrushes in the wild, simulated birds followed both coastal and inland routes during migration (Supplement 2 Fig. 2). At the population level, shifting densities throughout the migration period for both species generally matched density estimates compiled and reported by EBird (Supplement 2 Fig. 3). In addition, migration behavior recreated the empirically observed 'coastal effect' (Supplement 2 Fig. 4), a pattern defined as an increased proportion of juveniles near coastal regions due to orientation mishaps leading them to the edge of migratory flyways (Ralph, 1978). Emergence of this phenomenon lends credence to the strength of the model in reproducing natural migration patterns. In all, simulated migration movements reproduced realistic patterns at both the individual and population level. For an extended written explanation of model validation, see Supplement 2.

3. Results

The model predicts the total annual dispersal of approximately 4.5 million larval and nymphal *I. scapularis* by wood thrush and ovenbird populations during fall migration (Table 1, Fig. 1). Approximately 4% and 11% of simulated ticks dispersed by ovenbirds and wood thrushes, respectively, detached below 36°30′ north latitude – areas where the southern tick phenotype dominates. Out of all ticks dispersed by simulated wood thrushes, 97% attached within the Northeast. In comparison, roughly 70% of all ticks dispersed by simulated ovenbirds attached in the Northeast (Table 1). Direction of dispersal varied according to attachment location and host species, with ticks attaching in the northeast being dispersed most often to the south-southwest (ovenbirds: mean = 193°, SD = 74° wood thrush: mean = 189°, SD = 66°), and those attaching in the Midwest being dispersed most often to the southeast (ovenbirds: mean = 173°, SD = 47° wood thrush:

Table 1

Frequency of *I. scapularis* dispersal by simulated ovenbirds and wood thrushes, by date and geographic region of attachment. Values per month and values summed across all months and regions are the number of ticks dispersed per 10,000 simulated birds per host species. The final column scales up to estimate the total tick dispersal by the entire population of ovenbirds and wood thrushes (26 million and 12 million, respectively; Rosenberg et al., 2016). Standard errors were computed from replicate runs of the simulation.

			Month (ticks per 10,000 birds)					Total (ticks per 10,000 birds ± SE)	Ticks by Entire Host Population (± SE)
			June	July	August	September	October		
Ovenbird	Larvae	Northeast	0	62	840.3	211.2	1.6		
		Midwest	0.1	68.2	340	33.3	0.1	1,556.8 ± 15.9	4,047,680 ± 41,340
	Nymphs	Northeast	0	5.1	30.8	4.3	0.1		
		Midwest	0	5.9	32.9	2.2	0	81.3 ± 2.4	211,380 ± 6,240
								1,638.1 ± 17.3	4,259,060 ± 44,980
Wood Thrush	Larvae	Northeast	0	1.3	62.9	73.4	2.5		
		Midwest	0	0.1	1.3	0.7	0	142.2 ± 3.8	170,640 ± 4,560
	Nymphs	Northeast	0	1.1	18.9	13.1	0.2		
		Midwest	0	0.1	1.5	0.2	0	35.1 ± 2.2	42,120 ± 2,640
								177.3 ± 4.4	212,760 ± 5,280

mean = 156°, SD = 63°). The effect of host species on dispersal direction is partly a consequence of overall migratory route and partly a consequence of migratory timing in relation to local tick questing phenology - i.e. at what location during migration the host is most likely to encounter a questing tick.

Simulated ticks were dispersed an average of 277 (interquartile range (IQR) = 187–361) and 309 (IQR = 224–388) kilometers from point of attachment by ovenbirds and wood thrushes, respectively; within a host species, mean dispersal distance for larvae versus nymphs differed by less than 15 km. The predicted distribution of dispersal distances was multimodal, roughly corresponding to the number of migratory days that the tick was attached. For both host species, the maximum dispersal distance of a single simulated tick was greater than 800 km.

The model predicts that, as a species, ovenbirds disperse 20 times the number of ticks than wood thrushes (Table 1). Timing of dispersed tick detachment events differed between modeled host species, with those attached to wood thrush occurring later than ovenbirds (Table 1).

4. Discussion

This model predicts that the fall migratory movements of two commonly parasitized neotropical songbird species is likely causing the widespread dispersal of millions of ticks annually, including movement of northern ticks into areas where the southern phenotype of *I. scapularis* currently predominates. Based on simulated patterns of dispersal, songbird migrants have likely contributed to previously observed range expansion of the tick, and may continue to do so in the future. In addition to the mechanistic validation provided by this model, this research also lends insight into the impact of songbird life history characteristics and climate change on tick dispersal and gene flow.

4.1. Gene flow

This model predicts that the majority of ticks dispersed will remain within the region in which they attached, suggesting that songbirds contribute to *I. scapularis* gene flow mainly within both the Northeast and Midwest foci. However, a small minority of ticks was transported from these two northern foci of the tick into areas below 36°30′ N latitude in which the southern phenotype is dominant. Ticks dispersed by songbirds into these southern areas may be responsible for the observed unidirectional gene flow between northern and southern genotypes (Van Zee et al., 2015). These two genotypes differ in questing behavior, with the southern population primarily remaining below the leaf litter, and often found attached to reptilian hosts (Arsnoe et al., 2015; Diuk-Wasser et al., 2010; Steere et al., 2004). As a result, host-seeking behavior by ticks in southern populations would not lead to significant

dispersal into the Midwest and Northeast from the southern foci during spring bird migration, because the ticks would be less likely to attach to birds.

The public health consequence of immigration of northern individuals to the southern foci is currently unknown. Immigration of northern individuals could lead to breeding between northern and southern genotypes (Oliver et al., 1993), possibly increasing the southern use of endothermic hosts, including humans. Recent research has demonstrated lower nymph survival for offspring of crosses between northern and southern *I. scapularis*, but non-significant differences between survival rates of newly emerged northern larvae under southern and northern climatic conditions (Ginsberg et al., 2017). In addition, northern nymphs artificially translocated into various states in the American South continue to quest above the leaf litter (Arsnoe et al., 2015), suggestive of the possibility for increased risk to human populations with an influx of ticks naturally translocated by migrating birds.

4.2. Impact of host species characteristics on dispersal

Through comparing the differences between the simulated dispersal of the two explicitly modeled species, ovenbirds and wood thrushes, this IBM allows for a qualitative examination of the role of avian life history traits on the magnitude and patterns of dispersal of *I. scapularis*. This model demonstrates that the dispersal potential of various songbird species is largely dependent on unique life history traits, including breeding range, migration timing, and the propensity of a member of a given species to pick up ticks. Earlier songbird migration timing and a strong overlap of breeding range with northern *I. scapularis* ranges appear to favor an increased magnitude of tick dispersal during the fall season. Our model also reinforced the importance of variation among songbird species in tick attachment rates, likely due to differences in avian feeding behavior (Weisbrod and Johnson, 1989) (though nesting location might affect tick attachment rates earlier in the season).

We chose ovenbirds and wood thrushes as focal host species in part because they are so well studied that we could devise realistic parameter distributions for the model. Similar details are not currently available for all songbird species. Consequently, it is difficult to estimate the cumulative impact of all migrating songbirds on *I. scapularis* dispersal in North America. However, the results of our work with ovenbirds and wood thrushes suggest that the dispersal potential of all migrating songbird species could be ecologically important (Fig. 2). The continental population size of ovenbirds and wood thrushes is 26 million and 12 million, respectively. Our model suggests that together these two species disperse nearly 4.5 million ticks. With hundreds of migrating landbird species in North America, with individuals totaling in the billions (Rosenberg et al., 2016), the total dispersal potential by

A)

B)
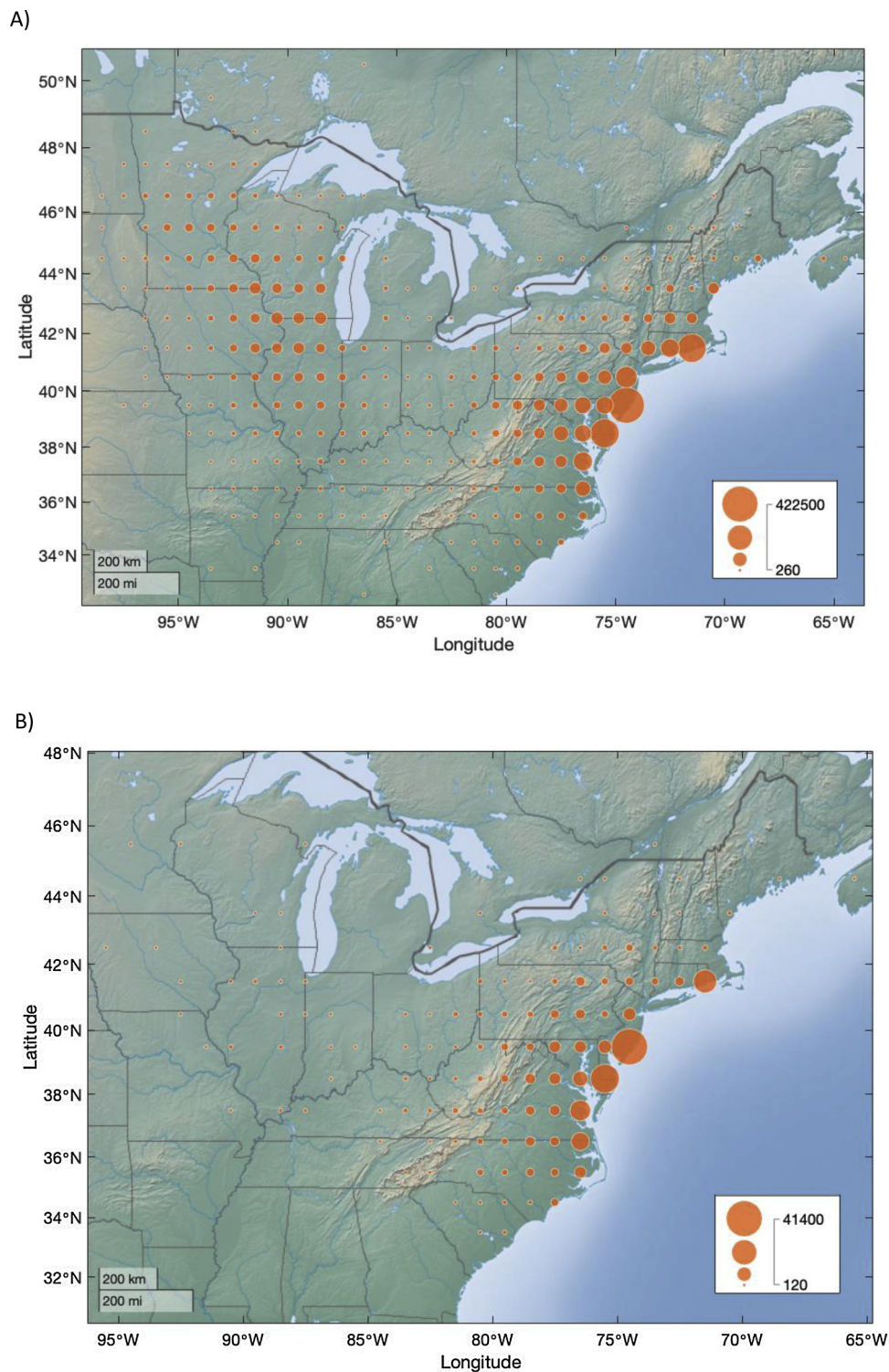
Fig. 1. Total number of simulated *I. scapularis* detaching in 1-degree latitude-longitude cells, based on dispersal by the entire host population of 26 million ovenbirds (A) and 12 million wood thrushes (B). The area dominated by the southern phenotype of *I. scapularis* is south of 36°30′ north latitude, which corresponds roughly to the northern borders of Arkansas, Tennessee, and North Carolina.

migratory birds is certainly greater than that explicitly modeled here. Although the precision of this model should not be overestimated, as it depends heavily on the accuracy of a number of parameters derived from other research efforts and exhibits a degree of stochasticity across trials, this model strongly suggests that southward dispersal of ticks by songbirds is likely to be ecologically significant.

A total estimate of *I. scapularis* dispersal by all migrating songbirds

would require a more taxonomically detailed understanding of avian migration. However, because of the insights provided by this IBM, it is possible to identify avian species that likely disperse ticks in relatively high numbers. Considering rates of tick attachment, breeding range and migration timing, we suspect that at least three additional host species are likely responsible for the dispersal of a similar magnitude of *I. scapularis* as wood thrushes and ovenbirds: veeries *Catharus fuscescens,*

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. scapularis* 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. Accesible via birdsna.org	Cornell Lab of Ornithology. Accesible via birdsna.org	Stafford et al., 1995	Stafford et al., 1995	Cornell Lab of Ornithology. Accesible via birdsna.org	Cornell Lab of Ornithology. Accesible via birdsna.org	Rosenberg et al., 2016	Estimated by author

Fig. 2. Comparisons of migratory and tick-related characteristics of various North American songbird species. Colors represent the potential impact of species-specific characteristics on magnitude of dispersal in relation to modeled host species (red = high, orange = moderate, green = low). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

common yellowthroats *Geothlypis trichas*, and house wrens *Troglodytes aedon* (Fig. 2).

4.3. Climate change

Climate change has been implicated as one possible driving force behind the ongoing range expansion of *I. scapularis* (Brownstein et al., 2005), in conjunction with suitable habitat and sufficient populations of rodents and deer (Guerra et al., 2002). If tick populations increase and more ticks come to seek hosts annually, attachment to and dispersal by songbirds is likely to increase, and subsequently contribute to range expansion. Tick life stage phenologies are predicted by some models to shift depending on changes to local climate conditions, although the overall effect of climate change on questing phenology is unclear (Ogden et al., 2006a).

Importantly, climate is also implicated in the shifting of breeding ranges and migration timing of North American songbirds. Generally, songbird breeding ranges are expected to shift northward (Hitch and Leberg, 2006), while climate-related shifts in migration timing have been shown to differ between species in both magnitude and directionality (Van Buskirk et al., 2009; Barton and Sandercock, 2018). Migration timing is not currently well understood, and the sheer number of species and their uniqueness in this regard complicates comprehensive research efforts. The potential impact that changes to songbird phenology and life history characteristics will have on the magnitude of *I. scapularis* dispersal is currently unclear. Future research in these areas could be focused to answer questions that allow for parameterization of an IBM that predicts tick dispersal patterns under future climate conditions.

4.4. Conclusions

Research efforts to predict large-scale dispersal patterns of *I.*

scapularis by migrating songbirds have focused mainly on northward migrating songbirds. However, current and future areas of suitable tick habitat exist in regions that are traversed by southbound migrating birds in the fall. This model synthesizes research detailing songbird and tick phenologies and biogeography to create a predictive individual-based model to explore the likely patterns of tick dispersal by two songbird species during fall migration. In all, this model predicts that ovenbirds and wood thrushes migrating southward during the fall months disperse millions of ticks, many into areas where no record of an established tick population exists; of additional interest is the dispersal of northern *I. scapularis* into the geographic range of the southern phenotype. Given that numerous songbird species have life history traits that likely make them effective dispersal agents of *I. scapularis*, migration of infested songbirds has likely played a role in the range expansion of the tick in the past, and likely has the potential to continue to do so into the near future. Research into currently cryptic aspects of migration behavior could allow for the design of a more accurate IBM. Possible expansions of the model could explicitly incorporate local variation in tick densities, different species of ticks, the influence of explicitly modeled local weather conditions on migratory behavior and energetics, and changes of avian life history characteristics in response to climate change.

Appendix A. Model parameter values and sources. For additional details on model methods and validation, see Supplements 1 and 2, respectively

Parameter	Description	Sources
Spatial tick density	Mean spatial densities reported by Diuk-Wasser et al. from flagging data spanning the Midwest and Atlantic Coast were calculated for latitude and longitude cells by the authors (2010). 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.	Diuk-Wasser et al. (2010)
Tick questing phenology	The authors calculated best-fit unimodal normal functions to explain relative temporal questing frequency of nymphal and larval forms of *I. scapularis* in the Northeast and, separately, the Midwest using host seeking data reported by Gatewood et al. (2009) and Diuk-Wasser et al. (2010). N.E. larvae: μ = July 26, σ = 23.4 days; N.E. nymphs: μ = June 20, σ = 26.3 days; M.W. larvae: μ = July 7, σ = 24.6 days; M.W. nymphs: μ = June 29, σ = 26.0 days.	Gatewood et al. (2009); Diuk-Wasser et al. (2010)

Tick attachment to avian hosts	A Poisson distribution with μ dependent on Julian date, tick density of cell, and a species constant was used to determine probability of tick attachment to both wood thrushes and ovenbirds. The species constants were determined by fitting sub-model rates of infestation to those reported by Stafford et al. (1995). Attachment of nymphs and larvae is determined independently. See Supplement 1 for relevant equations and further discussion.	Gatewood et al. (2009); Diuk-Wasser et al. (2010), Stafford et al. (1995)
Tick attachment time	Non-normal distribution derived directly from data reported by Hu et al. (1997) describing attachment time for nymphs and larvae. Larvae detached roughly 61-120 hours after attachment. Nymphs detached roughly 37-120 hours after attachment. The majority of both larvae and nymphs detached between 49-96 hours after attachment.	Hu et al. (1997); Bontemps-Gallo et al. (2016); Couret et al. (2017); Goddard et al. (2015); Hodzic et al. (1998); Nakayama and 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. For the purpose of the model, hatch-year wood thrushes were considered to make up 22.5% of the population of the species. Ovenbird juveniles are considered to constitute 33% of hatch-year individuals.	Michel et al. (2006)
Population sizes	Whole population size has been estimated as 26 million for ovenbirds and 12 million for wood thrushes.	Rosenberg 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 and Wikelski (2005); Emlen and Demong (1978); Åkesson and Bianco (2016); Chapman et al. (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). σ = 55.1°	Moore (1984); Woodrey (2000)
Flight length - wood thrush	Single night flight length of wood thrush tracked by geolocators was 253 km per day. Wikelski found single spring night flights to range from 1-8 hours in a small sample of northward migrating thrushes. Similarly, Cochran et al. (1967) measured spring flight time of thrushes lasting 4-8 hours. We used a flight length of 5 hours ± 1 hr SD based on this data and then incorporated differences in spring and autumn flight speeds. μ = 253 km, σ = 50.6 km	Stutchbury et al. (2009); McKinnon et al. (2013); Yong and Moore (1997); Newton (2007); Cochran et al. (1967); Wikelski et al. (2003)
Flight length - ovenbird	Single night flight length of ovenbirds was derived from theoretical fight 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 = 198.8 km, σ = 39.76 km	Alerstam et al. (2007); Moore and Kerlinger (1987)
Goal headings - wood thrush	Goal points are initialized at the start of each simulation and drawn from a uniform distribution on the 23rd parallel between the 83rd and 86th meridian. Wintering locations were estimated from geolocator data reported by Stanley. Goal headings were updated every day for each bird.	Stanley et al. (2015); Thorup et al. (2007)
Goal headings - ovenbird	Goal headings for ovenbirds was determined relative to location in the simulated space, based on published migration route analysis. Goal points are updated as birds pass into new regions, and are governed by general flyway patterns.	Hallworth et al. (2015); Thorup et al. (2007)
Death rates	Probability of death is based on continental apparent survival estimates and considered to be constant throughout the migration period and equal for all birds, regardless of age. A daily death rate was experimentally determined by calibrating the model to recreate a decrease in wood thrush and ovenbird populations by 23.5% and 18.8% during the migration period, respectively.	Michel (2006), Sillett and Holmes (2002)
Departure date - wood thrush	A normal distribution for departure dates for wood thrush was approximated from observed departure dates. μ = September 18, σ = 16 days. Timing of migration was not considered to be dependent on breeding latitude or distance to wintering grounds.	Stanley et al. (2012)
Departure date - ovenbird	A normal distribution for departure dates was experimentally determined by measuring the date of trans-gulf flights in ovenbirds. These dates were compared to published mean arrival dates to the Yucatan measured by mist-netting. Standard deviation was experimentally determined to simulate the earliest arrivals to wintering grounds around the same date as those observed in the wild. μ = August 19, σ = 13 days. Timing of migration was not considered to be dependent on breeding latitude or distance to wintering grounds.	Deppe and Rotenberry (2005); Sanders and Mennill (2014); Taylor (1972); Thobaben 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 % 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. See Supplement 1 for relevant equations and further discussion.	Estimated by authors; see Supplement 1
Energy uptake - wood thrush	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 126.5 km/day spent in stopover. See Supplement 1 for relevant equations and further discussion.	Hussell and Lambert (1980)
Energy uptake - ovenbird	Energy uptake during stopover has been measured as 0.87 grams/day and in the model was considered to remain constant throughout the migration period and equal between individual birds. Considering the rate of mass loss per hour of	Moore and Kerlinger (1987); Hussell and Lambert (1980)

	flight, the calculated flight potential increase is equal to 172.96 km/day spent in stopover. See Supplement 1 for relevant equations and further discussion.	
Starting/maximum energy - wood thrush	Starting flight potential and the flight potential limit used to determine a 100 % chance of migratory flight, was estimated by Yong and Moore (1997) to be 1200 km. This was considered to be the same for all individual wood thrush.	Yong and Moore (1997)
Starting/maximum energy - ovenbird	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 1590 km.	Hussell and Lambert (1980); Taylor (1972)

Appendix B. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ttbdis.2019.05.012.

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