

A quantitative synthesis of the role of birds in carrying ticks and tick-borne pathogens in North America

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Received: 27 January 2016 / Accepted: 9 September 2016
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Abstract Birds play a central role in the ecology of tick-borne pathogens. They expand tick populations and pathogens across vast distances and serve as reservoirs that maintain and amplify transmission locally. Research into the role of birds for supporting ticks and tick-borne pathogens has largely been descriptive and focused in small areas. To expand inference beyond these studies, we conducted a quantitative review at the scale of North America to identify avian life history correlates of tick infestation and pathogen prevalence, calculate species-level indices of importance for carrying ticks, and identify research gaps limiting understanding of tick-borne pathogen transmission. Across studies, 78 of 162 bird species harbored ticks, yielding an infestation prevalence of 1981 of 38,929 birds (5.1 %). Avian foraging and migratory strategies interacted to influence infestation. Ground-foraging species, especially non-migratory ground foragers, were disproportionately likely

to have high prevalence and intensity of tick infestation. Studies largely focused on *Borrelia burgdorferi*, the agent of Lyme disease, and non-migratory ground foragers were especially likely to carry *B. burgdorferi*-infected ticks, a finding that highlights the potential importance of resident birds in local pathogen transmission. Based on infestation indices, all “super-carrier” bird species were passerines. Vast interior areas of North America, many bird and tick species, and most tick-borne pathogens, remain understudied, and research is needed to address these gaps. More studies are needed that quantify tick host preferences, host competence, and spatiotemporal variation in pathogen prevalence and vector and host abundance. This information is crucial for predicting pathogen transmission dynamics under future global change.

Keywords Life history traits · Lyme disease · Passerine birds · Sampling biases · Vector-borne zoonotic diseases

Communicated by Hannu J. Ylonen.

Electronic supplementary material The online version of this article (doi:[10.1007/s00442-016-3731-1](https://doi.org/10.1007/s00442-016-3731-1)) contains supplementary material, which is available to authorized users.

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Introduction

Wild birds play crucial roles in the ecology of zoonotic diseases that impact human and domestic animal health, as well as wildlife populations (Hochachka and Dhondt 2000; Kilpatrick et al. 2006a; LaDeau et al. 2007; Robinson et al. 2010). Birds carry pathogens across neighborhoods and continents, both as hosts for infectious agents and by depositing infected arthropod vectors in previously uncolonized locations (Rappole et al. 2000; Ogden et al. 2008; Gaidet et al. 2010; Altizer et al. 2011). Birds also contribute to maintaining local transmission as reservoirs and amplifiers of pathogens that cause outbreaks in humans and animals (Weaver and Barrett 2004; Woodworth et al. 2005; Comstedt et al. 2006; Hamer et al. 2008).

Tick-borne pathogens comprise the most common vector-transmitted diseases of humans in North America [Centers for Disease Control (CDC) (2013a, 2015a)], and birds have been identified as important reservoirs for several of these pathogens (Brinkerhoff et al. 2009; Allan et al. 2010; Keesing et al. 2012; Pfäffle et al. 2013). Birds carry ticks infected with *Anaplasma* spp., *Borrelia* spp., *Rickettsia* spp., and tick-borne encephalitis virus (Hasle 2013), and bird movements contribute to expansion of tick-borne pathogens (Scott et al. 2012; Hornok et al. 2013; Schneider et al. 2015), even in the absence of primary vectors (Hamer et al. 2010, 2011). Birds also aid in importation and establishment of new tick populations (Ogden et al. 2008; Hamer et al. 2012a; Mukherjee et al. 2014; Cohen et al. 2015), thus creating new foci of disease risk. The role of birds in moving tick-borne pathogens will become even more crucial as climate change interacts with other anthropogenic processes (e.g., land use and land cover change) to open previously unfavorable areas for bird-assisted tick colonization (Harvell et al. 2002; Brinkerhoff et al. 2009; Wang et al. 2012; Robinson et al. 2015).

Research into the role of birds in carrying ticks and tick-borne pathogens has largely been descriptive and focused in small areas. These studies have improved the understanding of bird–tick interactions and pathogen transmission mechanisms. Individual studies have shown local tick infestation rates to be higher for ground-foraging bird species (Rand et al. 1998; Wright et al. 2006; Newman et al. 2015) and for birds in certain taxonomic groups and habitats (Newman et al. 2015). Large-scale studies have described tick–bird interactions and provided evidence for the above relationships across multiple study areas (Morshed et al. 2005; Ogden et al. 2008; Brinkerhoff et al. 2011; Scott et al. 2012). Other studies have quantified the importance of different bird species for carrying ticks in local areas (Battaly and Fish 1993) or across large scales for a single pathogen (Brinkerhoff et al. 2009).

Despite this research, a continental picture of the role of birds in tick-borne pathogen transmission in North America has not yet emerged. Individual studies provide valuable insights for particular locations and time periods. However, a comprehensive review of existing data is needed to synthesize knowledge, expand the scope of inference, assess range-wide importance of bird species for carrying ticks, and highlight research needs for understanding and predicting the dynamics of tick-borne pathogens under future global change. Furthermore, analyzing data under a common framework allows identification of and accounting for sampling biases and artifacts across studies. We conducted a continent-scale quantitative review of the role of birds in carrying ticks and tick-borne pathogens across North America to: (1) characterize bird life history correlates of the prevalence and intensity of tick infestation and

the prevalence of pathogen in bird-infesting ticks, (2) identify “super-carrier” bird species by calculating indices of infestation probability and overall numbers of ticks carried, and (3) identify sampling biases and research gaps limiting broad-scale understanding of the role of birds in carrying ticks and tick-borne pathogens. This study is novel in its quantitative approach to synthesizing the literature and in assessing sampling biases that emerge across the collective body of research.

Materials and methods

Literature review and inclusion criteria

We located studies using key word searches of “bird tick” and “bird tick pathogen” in Web of Science and Google Scholar. To search for Spanish language studies from Mexico, we used the search term: “ave garrapata Mexico” (i.e., “bird tick Mexico”); however, only studies from Canada and the USA met the below inclusion criteria. Reference lists were also checked to locate additional studies. Two tiers of inclusion criteria were implemented. First-tier inclusion criteria applied to all analyses; titles, abstracts, and methods sections were reviewed, and studies were only included if they had original data on: (1) prevalence of infestation—the percentage of birds examined and found to be infested, (2) intensity of infestation—the total number of ticks observed divided by the number of infested birds (definitions 1 and 2 from Kahl et al. 2002), or (3) prevalence of infection—the number of bird-infesting ticks that tested positive for a pathogen divided by the total number of ticks tested. Summaries of earlier data and studies in offshore areas or of ticks in bird nests were excluded. We also excluded studies of tick-borne pathogens directly detected in bird tissues, because most of these studies used polymerase chain reaction (PCR)-based approaches. PCR results can be difficult to interpret because the presence of pathogen DNA in bird tissue does not necessarily indicate infectiousness to ticks, and absence of DNA does not necessarily confirm a negative result.

Second-tier inclusion criteria were designed to ensure that data portrayed all bird species carrying and not carrying ticks and all tick species on birds. These criteria were assessed at the study level, unless studies included two or more subsets of data (e.g., from different US states) with a different study design and/or data collection protocol for each, in which case we assessed second-tier criteria separately for each data set. As described below, second-tier inclusion criteria differed for infestation and pathogen analyses; however, many studies had data extracted for all analyses. For analyses related to prevalence and intensity of infestation, three criteria were implemented. First, studies

were only included if they captured birds under a systematic or randomized sampling approach with a large number of species having the potential to be captured (e.g., by mist netting). This excluded studies that compiled samples incidentally (e.g., wildlife rehabilitation submissions), did not provide information to determine the sampling scheme, and/or focused on one or a few bird species using a specialized trapping technique. Second, studies were only included if they reported data for all birds sampled, including those with no ticks. Third, studies were only included if they reported data for all tick individuals and species sampled. Of 59 studies reviewed, 11 (including 12 separate data sets, Online Resource 1) met criteria for infestation analyses (see Online Resource 2 for excluded studies/data sets).

For analyses of prevalence of infection, studies were only included if they presented testing results referenced to the bird species from which ticks were collected. We also included studies only if they tested individual ticks, because most studies that tested pools of ticks did not report numbers of ticks in each pool, thus our analyses would have been biased by varying sample size. All studies meeting these criteria either presented tick species-specific prevalence of infection or the data allowing us to calculate it. Not all studies presented this information for each tick life stage and bird species. In these cases, infection prevalence results were extracted across all tick stages and only data linked to bird species were included. Of 34 pathogen studies reviewed, only 1 (Mathers et al. 2011) was not also reviewed for the infestation analysis, and 20 studies met inclusion criteria. However, because 18 of these 20 studies (including 20 separate data sets) investigated *Borrelia burgdorferi*, we only used data for this pathogen (all included and excluded pathogen studies/data sets are in Online Resource 3).

Data extraction

For all accepted data sets—using data aggregated across all birds and by bird species—we extracted information about the number of birds sampled, prevalence of infestation, and intensity of infestation (for the latter, using data aggregated across all ticks and by tick species). For each infection prevalence record, we extracted either (by bird species and both across all ticks and by tick life stage): (1) the number of ticks tested and the number positive or (2) if presented directly, the prevalence of infection. Recaptures of individual birds were treated as separate events because most studies present data this way.

In some cases, not all data could be collected by direct extraction or calculation. For example, the numbers of infested birds could not be calculated if infestation prevalence was only provided by tick species and more than one tick species was found on a single bird species (e.g.,

a sample of ten birds with 50 % infestation prevalence for two different tick species could include between five and ten infested birds). Likewise, intensity of infestation could not always be calculated by bird species, because many studies presenting average numbers of ticks did not indicate if values were based on all birds sampled or only those with ticks. Finally, in a few cases when values in the text and tables of studies did not match, we used tabular data.

During the period when included studies were conducted (1986–2015), many taxonomic changes occurred. For ticks, *Ixodes dammini* is now considered con-specific with *I. scapularis*; all data for these ticks were merged. For birds, common and scientific names were based on the American Ornithologists' Union (AOU) Checklist of North American Birds (AOU 2015), and analyses were at the species level (i.e., sub-species and previously recognized species that have since been “lumped,” were grouped). For species with taxonomic splits, the location of sampling was combined with known distributions of new species to determine the species represented.

Bird species were classified by migration strategy, nesting location, and foraging strategy (Sibley 2014; Cornell University 2015a). For migration strategy, two categorization schemes were used: (1) migratory versus non-migratory, and (2) non-migratory, short-distance migratory, and long distance migratory. Species with more than one migration strategy were classified into the longest distance movement category known to occur. Irruptive species (i.e., those with noncyclical, variable-length movements) were classified as either short- or long distance migratory using a more comprehensive life history database (Cornell University 2015b). Elevational migrants were treated as non-migratory because all those in our database move within small regions. For nesting location, two categorization schemes were developed: (1) ground nester versus all other nesting locations, and (2) ground, cavity, shrub, tree, building, cliff, and burrow nesting. For foraging strategy, two categorizations were used: (1) ground forager versus all other strategies and (2) ground forager, aerial dive, aerial forager, bark forager, fly-catching, foliage gleaner, and hovering.

Comparisons by bird life history strategy

All analyses were conducted in R (R Core Team 2013). Descriptive summaries were compiled (by bird species, family, and life history strategy) for prevalence and intensity of tick infestation and for prevalence of *B. burgdorferi* infection. Bird species was the unit of replication for all analyses (i.e., there was one associated value of each predictor variable for each species). Two types of statistical models were used. For rate variables (prevalence of infestation and *B. burgdorferi* infection), generalized linear

Table 1 Model selection results for analyses of life history characteristics affecting prevalence and intensity of tick infestation on birds and prevalence of infection with *B. burgdorferi* in bird-infesting ticks; a preliminary ranking of single-variable models is in Online Resource 4

Model ^a	K^b	ΔAIC_c^c	ω_i^d	Model ^a	K^e	ΔAIC_c^c	ω_i^d
Prevalence of tick infestation				Intensity of total tick infestation			
Migratory strategy * foraging strategy	4	0.000	1.000	Migratory strategy * foraging strategy	5	0.000	0.577
Foraging strategy	2	37.388	0.000	Foraging strategy	3	1.914	0.222
Nesting location * foraging strategy	4	40.560	0.000	Nesting location * foraging strategy	5	2.140	0.198
Migratory strategy * nesting location	4	203.910	0.000	Migratory strategy	3	11.100	0.002
Migratory strategy	2	228.093	0.000	Migratory strategy * nesting location	5	14.166	0.000
Nesting location	2	249.826	0.000	Null model	2	15.905	0.000
Null model	1	260.532	0.000	Nesting location	3	16.274	0.000
Model ^a	K^e	ΔAIC_c^c	ω_i^d	Model ^a	K^b	ΔAIC_c^c	ω_i^d
Intensity of larval tick infestation				Prevalence of <i>Borrelia burgdorferi</i> infection			
Migratory strategy * foraging strategy	5	0.000	0.440	Migratory strategy * foraging strategy	4	0.000	0.961
Foraging strategy	3	0.308	0.377	Migratory strategy	2	7.267	0.025
Nesting location * foraging strategy	5	1.780	0.181	Migratory strategy * foraging strategy	4	8.573	0.013
Migratory strategy	3	11.474	0.001	Foraging strategy	2	43.508	0.000
Migratory strategy * nesting location	5	14.635	0.000	Nesting location * foraging strategy	4	44.050	0.000
Null model	2	15.028	0.000	Nesting location	2	44.857	0.000
Nesting location	3	16.242	0.000	Null model	1	48.371	0.000

^a Variables included in each candidate model; models with interaction terms also included individual additive effects (e.g., migratory strategy * foraging strategy is equivalent to migratory strategy + foraging strategy + (migratory strategy* foraging strategy))

^b Number of parameters in the logistic regression model (includes intercept parameter)

^c Difference in AIC_c value between model and the most strongly supported model

^d AIC weight—relative strength of support for the model

^e Number of parameters in the negative binomial model (includes intercept and overdispersion parameters)

models (glm function in package lme4) with a binomial error structure and logit link were used. For count variables (intensity of total and larval tick infestation), negative binomial models (glm.nb function in MASS package) were used because infestation intensity data were overdispersed and therefore not well fit by a Poisson model (likelihood ratio results for negative binomial model compared to the Poisson model for total and larval tick infestation, respectively: $\chi^2 = 1190.63$; $p < 0.01$ and $\chi^2 = 2163.61$; $p < 0.01$). Despite a preponderance of zero values in the data set, zero-inflated negative binomial models did not improve upon negative binomial models (likelihood ratio results for both total and larval tick infestation: $\chi^2 < 0.001$; $p > 0.99$), so we did not include zero-inflation terms.

For all variables, we conducted a preliminary analysis to determine which life history categorization scheme best fit the data using Akaike's information criteria, corrected for small sample sizes (AIC_c , Burnham and Anderson 2002). We compared ΔAIC_c values, which capture the trade-off between model fit and parsimonious model structure ($\Delta AIC_c = 0$ indicates “best” model) and AIC weights (ω_i), which indicate the relative model support ($\omega_i = 1$ indicates maximum support). For all life history traits, the scheme

with fewest categories received greatest support. The simplest categorizations were therefore used for subsequent analyses. For each dependent variable, we first considered an intercept-only (i.e., null) model and three single-variable models, one each with migration strategy, nesting location, and foraging strategy as independent variable. For each dependent variable, one model received overwhelming support among this initial model set ($\omega_i \geq 0.98$ for all best models; Online Resource 4); therefore, no rationale existed for assessing additive multiple variable models. However, to consider potential interacting effects of independent variables, we also ranked models with two-variable interaction terms (Table 1).

Infestation probability index

The number of tick-infested birds found for each species is driven by true variation in infestation prevalence and sampling-related variation in the availability of bird species for capture. To reduce bias associated with studies oversampling particular regions and abundant and/or easily captured bird species, we followed the approach of Loss et al. (2014), a study that identified which bird species are

disproportionately likely to collide with buildings (“super-colliders”). By replacing numbers of building-killed birds with numbers of tick-infested birds, we were able to identify bird species disproportionately likely to be infested. Three components of bird sampling availability were accounted for: (1) population size (i.e., common species are more likely to be captured and have more individuals found to be infested), (2) the degree of range overlap with the sampling area (i.e., species with a large number of sampling sites within their range are more likely to be captured and have more individuals found to be infested), and (3) the sample size of birds in each study (i.e., studies with more captures are more likely to find high numbers of infested birds). Bird sampling availability was assumed to indirectly reflect tick availability. Variation in tick sampling availability arises because different tick species have different seasonal activity patterns. Incomplete information on the phenology of different tick species across their distributional ranges prevents a comprehensive comparison of the timing of bird sampling relative to tick seasonal activity. However, all studies in the analysis sampled in the spring, summer, and/or fall (Online Resource 1), the months ticks are generally most active.

To account for population size, we used North American population estimates from the Partners in Flight Population Estimates Database Version 2.0 (Blancher et al. 2013). These estimates are based on US Breeding Bird Survey data, have been updated to reflect various recommendations and critiques (e.g., Thogmartin et al. 2006), and remain the only available continental estimates of bird population sizes in North America. To account for range overlap, we used range maps (Sibley 2014) to count the number of included study sites that overlap with each species’ breeding, wintering, and/or migration range. To account for sample size, individual data sets were standardized by multiplying the observed infestation proportions for each bird species to the largest single site total of 1662 infested birds (Hamer et al. 2011) and summing standardized counts for each species across all studies. This analysis was conducted for two regional clusters of sites characterized by different bird assemblages (California, $n = 2$ sites; east of Mississippi River, $n = 10$ sites; hereafter, “West” and “East”, respectively). Species with no population estimates available were excluded, and only bird species that were sampled at least ten times across all studies (and in two different studies for the East analysis) were included.

Using species as replicates, the $\log_{10}(x + 1)$ -transformed counts of tick-infested birds was regressed on \log_{10} (population size) and \log_{10} (range overlap). Coefficients were fixed to 1, residuals were calculated and, to calculate the infestation probability index, 10 was raised to the power of the absolute value of residuals (Loss et al. 2014). This assumes a tenfold increase in bird abundance

or range overlap results in a tenfold increase in the number of infested birds. The index thus indicates the factor by which a species has a greater probability (positive residuals) or smaller probability (negative residuals) of being infested with at least one tick compared to an average species. Infestation probability index was also estimated for taxonomic groups and life history strategies by averaging residuals across species occurring in at least two studies.

Infestation importance index

An index of relative importance that approximates the total number of ticks carried across all individuals of a bird species was also calculated. Each bird species’ estimated population size was multiplied by estimated tick mean density—i.e., the total number of ticks found on infested birds divided by the total number of birds sampled, including birds with no ticks (Kahl et al. 2002). As with the infestation probability index, only species with sample sizes ≥ 10 across all studies were included. Because many studies do not present the numbers of ticks on each bird species and instead present only presence/absence data, there were a limited number of species (45) for which the infestation importance index could be calculated.

Results

Summary of extracted data

Among studies meeting inclusion criteria for infestation analyses, two were in California and nine were east of the Mississippi River with only one site in Canada. This sample roughly matches the geographic coverage of all studies (Fig. 1a), but western Canada and the US Great Plains were not represented due to exclusion of all studies from these regions. Many infestation studies also tested ticks for pathogens; therefore, geographic coverage of infection prevalence studies is similar (Fig. 1b). Only 2 of 20 studies meeting inclusion criteria (and 6 of 34 total studies) investigated a pathogen other than *B. burgdorferi*, and only 1 study tested for any pathogen between the Mississippi River and west coast.

Across included studies, 78 of 162 bird species had at least one individual with at least one tick; the overall prevalence of infestation was 1981 of 38,929 birds (5.1 %). For species sampled ≥ 10 times, 8 of 115 (7.0 %) had infestation prevalence ≥ 20 % (Online Resource 5). Intensity of infestation was variable with a maximum of 151 ticks/infested bird for Carolina Wren (*Thryothorus ludovicianus*). For most species, larvae comprised the vast majority of ticks. Birds were infested by 27 tick species in 6 genera (Online Resource 6), but 7 species comprised



Fig. 1 Data sources for North American analysis of the role of birds in carrying ticks and tick-borne pathogens, including **a** studies of tick infestation of birds and **b** studies of pathogen infection prevalence in bird-infesting ticks. Most circles represent a single study, but some

white circles represent greater than one excluded study in the same location, and in some cases, included studies are directly overlaid on excluded studies in the same location

>99 % of all ticks for which counts were provided (*Amblyomma americanum*, *A. maculatum*, *Dermacentor variabilis*, *Haemaphysalis chordeilis*, *H. leporispalustris*, *I. dentatus*, *I. scapularis*). The most commonly encountered tick species on birds in the studies we reviewed are generally considered host generalists—feeding on small, medium and large mammals, birds, and sometimes reptiles (*A. americanum*, *A. maculatum*, *D. variabilis*, and *I. scapularis*)—but also include two species that feed almost exclusively on birds and rabbits (*H. leporispalustris*, *I. dentatus*) and one species that is an avian specialist (*H. chordeilis*) (Sonenshine 1979).

Across studies included for the prevalence of infection analysis, 11 tick species, 3617 larvae, 1744 nymphs, and at least 6947 total ticks (including larvae, nymphs, and ticks not identified to life stage) were tested (Online Resource 7) from 89 bird species (Online Resource 8). Most studies did not report the numbers of birds corresponding to the ticks tested, so the total number of birds represented is unknown. The overall prevalence of infection for *B. burgdorferi* was 13.0 % (10.4 and 22.1 % for larvae and nymphs, respectively). For bird species with ≥ 10 ticks tested, 12 of 46 (26.1 %) carried ticks with infection prevalence ≥ 20 %.

Comparisons by bird life history strategy

For all dependent variables, the most strongly supported model contained an interaction between migratory strategy and foraging strategy (Table 1). The single-variable foraging strategy model also received strong support for the analyses of intensity of total tick infestation and intensity of larval tick infestation. For prevalence of tick infestation, ground-foraging birds were more likely to be infested than other foraging groups, but this difference was more pronounced for non-migratory species (based on odds ratios, tick infestation 8.53 times more likely for ground foragers relative to other foraging groups) than for migratory species (tick infestation 5.11 times more likely for ground foragers relative to other foraging groups). For intensity of total tick infestation and larval tick infestation, ground foraging birds carried more ticks on average, and, again, this difference was greater for non-migratory species (an average of 75.26 and 80.79 more total ticks and larval ticks, respectively, on ground foragers relative to other foraging groups) than for migratory species (an average of 6.42 and 11.09 more total ticks and larval ticks, respectively, on ground foragers relative to other foraging groups). For *B. burgdorferi* prevalence, non-migratory birds were more likely than migratory birds to carry ticks infected with *B. burgdorferi*, and this difference was more pronounced for ground foragers (infection 2.98 times more likely for non-migratory species relative to migratory species) than other

foraging groups (infection 1.53 times more likely for non-migratory species relative to migratory species).

Infestation probability and infestation importance indices

Five species comprised ≥ 50 % of the 1981 infested bird records used to calculate the infestation probability index: Northern Cardinal (*Cardinalis cardinalis*), American Robin (*Turdus migratorius*), Song Sparrow (*Melospiza melodia*), Hermit Thrush (*Catharus guttatus*), and Gray Catbird (*Dumetella carolinensis*). As expected, there was a strong positive correlation between counts of infested birds and bird population size ($r = 0.29$, $df = 119$, $p = 0.001$), but there was no relationship between infestation counts and range overlap ($r = 0.12$, $df = 104$, $p = 0.178$).

After accounting for sample size, population size, and range overlap, the infestation probability index was highly variable across species, with species ranging from (for the East) 137 times more likely than average (Canada Warbler, *Cardellina canadensis*) to 104 times less likely than average to carry ticks (Red-eyed Vireo, *Vireo olivaceus*) (Online Resource 9). For the east, all species with the top 25 infestation probability indices were passerines (Table 2). The west analysis was limited by sample size (two total studies) and should be interpreted with caution. Nonetheless, there was substantial variation in the estimated infestation probability indices for the western species (Table 2; Online Resource 10). For families represented by at least two species, the mimic thrushes (*Mimidae*), wrens (*Troglodytidae*), tits (*Paridae*), and thrushes (*Turdidae*) had the highest indices, while kinglets (*Regulidae*), vireos (*Vireonidae*), woodpeckers (*Picidae*), and tyrant flycatchers (*Tyrannidae*) had the lowest (Online Resource 11). Non-migratory species had the highest infestation probability indices of all migratory strategies, and ground foragers had the highest indices of all foraging strategies (Online Resource 12). Results for nesting location were ambiguous, as shrub, ground, and cavity nesters all had above average infestation probability indices, and only tree nesters had below average infestation probability indices.

When considering tick mean density and total bird population size, the Northern Cardinal, American Robin, Brown-headed Cowbird (*Molothrus ater*), Carolina Wren, and Eastern Towhee (*Pipilo erythrophthalmus*), were estimated to carry more total ticks than any other bird species (e.g., a minimum of 110 million ticks for Northern Cardinal and 82 million ticks for American Robin, species with estimated continental populations of 91 and 300 million, respectively) (Table 3). The 20 species with the highest infestation importance index were passerines. Because the importance index could only be calculated for 45 bird species, comparisons should not be made beyond species in our analysis (Online Resource 13).

Table 2 Species with highest index of tick infestation probability in eastern and western North America after accounting for population abundance and degree of range overlap with study locations

Species	Sites ^a	Infestation probability index ^b	Species	Sites ^a	Infestation probability index ^b
East			West ^c		
Canada Warbler	5	137.3	Oak Titmouse	2	2095.1
Gray Catbird	9	89.3	Lazuli Bunting	2	806.3
Prairie Warbler	3	66.5	Bewick's Wren	2	522.0
Blue Jay	10	64.8	Wrentit	2	405.7
Black-throated Blue Warbler	6	55.7	California Towhee	2	401.5
Brown Thrasher	7	39.9	California Quail	1	188.3
Palm Warbler	6	38.7	Golden-crowned Sparrow	2	131.8
Mourning Warbler	4	38.6	White-breasted Nuthatch	2	63.5
Blue-winged Warbler	3	38.4	Orange-crowned Warbler	1	49.9
Rose-breasted Grosbeak	8	34.0	Chipping Sparrow	2	19.0
Wood Thrush	6	32.7	Hermit Thrush	2	13.2
Hermit Thrush	5	28.3	Bushtit	1	3.1
House Wren	7	27.7	Purple Finch	2	1.1
Tufted Titmouse	6	27.3			
Common Yellowthroat	9	20.2			
Northern Cardinal	9	18.7			
Swainson's Thrush	9	15.9			
Northern Waterthrush	7	15.9			
Northern Parula	4	14.7			
Field Sparrow	3	13.5			
Black-capped Chickadee	5	12.7			
Northern Mockingbird	5	12.1			
Carolina Wren	7	11.2			
Ovenbird	9	11.1			
Veery	6	11.1			

^a Number of sites in which species was sampled (out of ten included studies for east and two included studies for west)

^b Index values indicate the factor by which species are more likely to be infested with ticks compared to average species

^c For the west, all species with positive residuals are shown (i.e., those more likely to be infested than average species)

Discussion

By compiling data from across North America, we have expanded the scope of inference regarding the role of birds in carrying ticks and tick-borne pathogens. We found that bird foraging and migratory strategies interact to influence tick infestation and *B. burgdorferi* prevalence in ticks. Ground-foraging bird species, especially non-migratory ground foragers, are disproportionately likely to have high prevalence and intensity of tick infestation. Non-migratory species, especially those that are ground foragers, are disproportionately likely to carry *B. burgdorferi*-infected ticks. Indices of infestation probability and importance highlight many super-carrier bird species, with many bird species especially likely to carry ticks (e.g., thrushes, sparrows, many warblers) and others—due to large populations—collectively carrying large total numbers of ticks (e.g., American Robin, Brown-headed Cowbird, Eastern Towhee).

Some species are both likely to be infested and carry large tick loads [e.g., Northern Cardinal, Carolina Wren, Ovenbird (*Seiurus aurocapillus*)]. Our synthesis also reveals that vast interior regions of North America are largely unstudied, along with associated pathogens, vectors, and hosts.

Comparisons by bird life history strategy

Several studies have shown that ground-foraging birds experience greater tick infestation than other species (Battaly et al. 1987; Magnarelli et al. 1992; Morshed et al. 2005; Wright et al. 2006; Mitra et al. 2010). The single study of which we are aware that compared infestation between migratory and non-migratory species found greater mean tick loads on migratory birds (Dingler et al. 2014). Our synthesis provides additional nuance by illustrating an interaction between avian foraging and migratory strategies. Ground-foraging status was always associated with greater

Table 3 Indices of species importance for carrying ticks based on the estimated minimum number of ticks (millions) carried across all individuals of a species

Species	Sites ^a	Index of species importance ^b
Northern Cardinal	9	110.43
American Robin	8	82.04
Brown-headed Cowbird	6	69.55
Carolina Wren	7	60.63
Eastern Towhee	8	47.38
Ovenbird	9	33.65
Song Sparrow	7	21.88
Swamp Sparrow	7	21.58
Wood Thrush	6	18.26
Veery	6	15.82
Indigo Bunting	9	15.81
Common Yellowthroat	10	14.28
House Wren	7	10.58
Chipping Sparrow	8	6.59
Eastern Bluebird	5	6.56
Northern Waterthrush	7	6.55
Red-winged Blackbird	6	5.96
Northern Mockingbird	5	4.62
Swainson's Thrush	9	2.77
White-throated Sparrow	7	2.55

^a Number of sites in which bird species was sampled

^b Importance index calculated by multiplying species' estimated continental population size by mean tick density (i.e., total number of ticks found divided by number of birds sampled)

prevalence and intensity of infestation, but non-migratory ground foragers were especially likely to be infested and carry large tick loads. This finding is somewhat unexpected because the greater physiological expenses associated with bird migration could be expected to reduce avian anti-parasite vigilance and therefore increase tick infestation. We hypothesize that the observed interaction could arise if non-migratory ground foragers spend a greater proportion of their annual cycle on or near the ground than migratory ground foragers. This hypothesis requires further testing but is generally supported because migratory birds not only traverse a greater geographic area and breadth of habitat types, but also tend to display greater foraging niche variation throughout the year (e.g., Hutto 1981). Thus, non-migratory ground foragers may spend more total time in near-ground micro-habitats associated with a high probability of tick acquisition. The lack of support for nesting location in our analysis suggests that spending time on the ground per se does not influence tick acquisition; rather, the specific behavior of ground foraging is most important (Newman et al. 2015). Studies have suggested that other foraging strategies can be associated with elevated tick

infestation (e.g., bark-foraging, Dingler et al. 2014), but these factors did not emerge at the scale of our analysis.

Non-migratory birds were also more likely to carry *B. burgdorferi*-infected ticks, and infection was especially likely for ticks on non-migratory ground foragers. Elevated tick infection rates have been previously found for ground-foraging birds (Rand et al. 1998; Elfving et al. 2010). However, the finding that ticks from non-migratory species have greater infection prevalence than those from migratory species is unexpected. Numerous studies highlight the role of migratory birds in the long distance dispersal of ticks and the introduction of ticks and pathogens into previously uncolonized locations (Ogden et al. 2008; Brinkerhoff et al. 2009; Hasle 2013; Mukherjee et al. 2014). However, our results suggest that resident species could be more important than previously thought for acquiring and dispersing ticks locally and contributing to tick population persistence and local pathogen maintenance. Brinkerhoff et al. (2009) suggested a role for non-migratory birds in dispersing nymphal *I. scapularis* and expanding the range of *B. burgdorferi* in the northeast USA. Other studies illustrate high *Borrelia* infection rates in ticks and tissues from non-migratory species (Magnarelli et al. 1992; Wright et al. 2000; Hamer et al. 2012b; Scott et al. 2010, 2012). However, the contribution of non-migratory birds to tick-borne pathogen transmission remains relatively understudied.

Seasonal sampling biases could influence comparisons of infestation and infection between migratory and non-migratory species—and thus contribute to our finding of interactions between migratory strategy and foraging strategy—if they result in some species being disproportionately sampled during periods of high infection probability. For example, non-migratory birds sampled during summer may be more likely to carry ticks because this is the peak feeding period for larvae and nymphs of many tick species. The studies we used sampled during a variety of seasonal periods (Online Resource 3). We were unable to compare capture dates for infected and uninfected migratory and non-migratory birds because most studies do not report this information for all ticks. We found high overall prevalence of *B. burgdorferi* infection, a finding in agreement with Brinkerhoff et al. (2009) and suggestive of a sampling bias toward Lyme disease-endemic regions during peak transmission periods (Fig. 1). However, we detected no clear biases toward non-migratory species in our data set.

The infection prevalence analysis was limited to *B. burgdorferi*, because few North American studies have addressed the role of birds in carrying other tick-borne pathogens. Those that have indicate that birds can carry ticks infected with *Anaplasma phagocytophilum*, the agent of granulocytic anaplasmosis (Dingler et al. 2014); *Rickettsia rickettsii*, the agent of Rocky Mountain Spotted Fever (RMSF) (Sonenshine and Clifford 1973); other *Rickettsia* species

imported from Central and south America (Mukherjee et al. 2014); and *B. andersonii*, and *B. miyamotoi* (Hamer et al. 2012b; Scott et al. 2010). Studies in Europe also document a role for birds in carrying multiple tick-borne pathogens, particularly *Borrelia* genospecies and *Rickettsia* spp. (Dubska et al. 2009; Elfving et al. 2010; Socolovschi et al. 2012; Hornok et al. 2013). Our continental review therefore reveals that additional research is needed to determine the importance of different bird species for the transmission of pathogens other than *B. burgdorferi*. This research need is especially acute in regions that have received little research (Fig. 1) and have high incidence of human tick-borne disease, such as the US Interior Southeast and Southern Great Plains, areas with high incidence of RMSF, ehrlichiosis, and tularemia (Oppenshaw et al. 2010; Dahlgren et al. 2011; CDC 2013b, 2015b), as well as newly emerging tick-borne pathogens (Heartland virus and Bourbon virus, McMullan et al. 2012; Kosoy et al. 2015).

Infestation probability and infestation importance indices

The infestation probability index suggests that several bird families (mimic thrushes, wrens, tits, thrushes, cardinaline finches) and species [e.g., Canada Warbler, Gray Catbird, Prairie Warbler (*Setophaga discolor*), Blue Jay (*Cyanocitta cristata*)] have exceptionally high tick infestation probability. The infestation importance index indicates that several bird species carry, at minimum, tens to hundreds of millions of ticks. These super-carrier species may be contributing disproportionately to the overall movement of ticks and maintenance and amplification of tick-borne pathogen transmission. Species- and family-level infestation probability indices could partially reflect life history strategies that lead to elevated infestation probability. Many top-ranked species are ground foragers, and some top-ranked families (e.g., thrushes) include multiple ground-foraging species. A comparison of average probability indices (Online Resource 12) supports that ground foragers and non-migratory species are disproportionately likely to be infested. However, these indices also suggest the importance of traits not documented in the above statistical comparisons of avian life history traits. For example, shrub- and tree-nesting species are, respectively, estimated to be 4.9 and 5.7 times more likely than average to be infested. The difference between this finding and the above statistical comparison may arise because the probability index was corrected for sampling availability. Most studies sampled birds with mist nets, a method biased toward ground foragers (Remsen and Good 1996). Comparisons of life history strategies that do not correct for sampling availability could be biased toward indicating the importance of ground-foraging status to the exclusion of other foraging strategies.

Our estimates of prevalence and intensity of infestation are likely to be conservative because some ticks are not detected during sampling. Ogden et al. (2008) showed that inexperienced members of bird netting crews found roughly one-third as many ticks as experienced searchers, and this underdetection bias may be widespread. However, the bias would not be expected to affect our analysis unless the rate of underdetection varied systematically among bird species or life history groups. Several components of sampling availability may have influenced the index of infestation probability. We accounted for abundance and range overlap for species captured in at least one study; however, we could not account for these factors for species that were: (1) available for sampling in at least one study but were never captured and (2) unavailable based on lack of range overlap with sampling locations. Other factors also dictate bird availability for sampling, such as capture location relative to season, time of day, and vegetation structure (Dunn and Ralph 2004). Further, because there were little data from western North America, probability indices for western species should be considered working estimates from which to develop, test, and refine hypotheses with future studies. As a result of entire regions and pathogens remaining unstudied, entire ecosystems (e.g., prairie, shrubland, and western mountain ecosystems) and bird species groups (e.g., grassland and wetland birds and migratory species that only migrate through central North America) are also understudied. We hypothesize that abundant species that inhabit undersampled regions and are similar to super-carrier species based on life history may be most likely to be infested and carry large numbers of ticks [e.g., the ground-foraging Harris's Sparrow (*Zonotrichia querula*) and Dickcissel (*Spiza americana*) in grasslands/shrublands of the Great Plains].

Toward increased understanding of the role of birds in tick-borne pathogen transmission

Additional infestation and pathogen infection studies are needed to gain a basic understanding of tick-borne pathogens, especially for understudied regions and pathogens. However, substantial conceptual advances in the ecology of tick-borne pathogens also require a move beyond descriptive studies of infestation and infection toward a holistic assessment of pathogen transmission systems. For example, many tick-borne pathogens are multi-host systems, and the diversity and species composition of host communities may influence transmission dynamics (Keasing et al. 2006; Wang et al. 2016). Information about the role of birds in tick-borne pathogen transmission must be integrated with data for other relevant groups of animal hosts. Heterogeneity in tick behavior, host preference, and host reservoir competence must also be considered because these factors can

drive pathogen transmission dynamics and determine the importance of different host species (Kilpatrick et al. 2006b; Hamer et al. 2009). Although different tick species are likely to have different host preferences, quantifying host feeding patterns for ticks that are not attached to hosts (e.g., using blood meal analysis) is more challenging than for other arthropods, such as mosquitoes (Hamer et al. 2015). Preference estimates based on sampling ticks from hosts are biased due to the difficulty of sampling the entire community of vertebrate hosts, biases inherent to different capture techniques, and the challenges of linking highly mobile vertebrate hosts to tick populations.

Population genetic and phylogeographic modeling approaches for infectious agents and tick species will also be useful for providing historic and dynamic perspectives on the distribution and diversity of ticks and tick-borne pathogens (Ogden et al. 2013). Patterns of genetic diversity may help elucidate when tick populations and pathogens are rapidly expanding across long distances—and therefore more likely to be driven by migratory birds—and when populations and pathogens are comparatively stationary with maintenance likely to be reliant on more sedentary hosts, including non-migratory birds. For example, in Europe, the population structure of different *Borrelia* species is associated with the mobility of hosts; pathogen species that use migratory birds as reservoirs have limited population structure relative to those that use small mammals (Vollmer et al. 2011).

Intensive local studies that generate time series of tick infestation data will also be useful for testing whether key environmental variables influence tick populations and for understanding differences between observed and actual tick populations, information that is central to understanding tick–host interactions (Dobson 2014). As discussed above, our study reveals several sampling biases, and less biased sampling approaches must be developed and implemented to characterize spatial heterogeneity in the distribution of ticks, hosts, and infectious agents. These approaches should account for heterogeneity in the detectability of host and vector species to reduce bias in the estimation of population sizes (Yoccoz et al. 2001; Williams et al. 2002). Specific promising methods include repeated sampling, occupancy modeling, and the wide variety of other hierarchical modeling approaches that account for observer error and are already widely used in animal ecology research (McClintock et al. 2009).

Conclusion

Birds play a crucial role in the ecology of tick-borne pathogens in North America and globally. Our quantitative synthesis provides greater statistical power and a more nuanced

understanding of how interactions between avian foraging and migratory strategies influence prevalence and intensity of tick infestation. We also highlight the importance of non-migratory birds for carrying infected ticks, and potentially for contributing to local pathogen transmission dynamics. Finally, this review spotlights several research needs that must be addressed to gain increased conceptual understanding of the ecology of tick-borne pathogens (e.g., additional research for understudied regions and pathogens; sophisticated analyses that characterize pathogen dynamics and account for uncertainty and observation error). Assessing the role of birds in local transmission and long distance dispersal of pathogens is necessary given the rapid emergence of new pathogens and uncertainty associated with future global changes. Describing relationships among birds, ticks, and tick-borne pathogens—along with correlates of these relationships—will provide a fundamental basis upon which to predict future reservoir–host interactions and their consequences for pathogen transmission and human and animal health.

Acknowledgments We thank Faithful Williams for assistance with literature review and data management. SRL and BHN were funded by NIFA/USDA Hatch Grant funds through the Oklahoma Agricultural Experiment Station (for SRL: OKL-02915; for BHN: OKL-02902).

Author contribution statement All authors conceived and designed the idea and developed the methodology. SRL conducted statistical analyses and wrote the manuscript. BHN, GLH, and SAH provided feedback and edits on the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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