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Tick infestation of birds across a gradient of urbanization intensity in the United States Great Plains

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Abstract
Migratory birds play an important role in large-scale movements of ticks and tick-borne pathogens, yet little is known about tick infestation of resident birds (e.g., non-migratory species and migratory species during the breeding season), especially in urban ecosystems. We captured birds during the breeding season in parks and greenspaces in Oklahoma City, Oklahoma, USA, to evaluate overall tick infestation patterns and to determine if urbanization influences infestation prevalence (the proportion of birds parasitized) and intensity (the number of ticks on infested birds). Of 459 birds, 111 (24.2%) had ≥ 1 tick, a high proportion of infestation compared with past North American studies. The most frequently infested species were Carolina Wren (*Thryothorus ludovicianus*; 56%), Brown Thrasher (*Toxostoma rufum*; 37%), and Northern Cardinal (*Cardinalis cardinalis*; 27%). The Lone Star Tick (*Amblyomma americanum*) comprised half (51%; n = 322) of all ticks on birds; other species sampled included Gulf Coast Tick (*A. maculatum*) (36%) and Rabbit Tick (*Haemaphysalis leporispalustris*) (13%). Urbanization intensity (i.e., the percentage of developed land around sites) was inversely related to infestation prevalence for all birds combined and for Carolina Wren, but intensity of infestation was unrelated to urbanization. Our results suggest that non-migratory and migratory birds during sedentary periods are important carriers of ticks in urban areas, and that tick infestation patterns can be influenced by the level of urbanization in the surrounding landscape. Clarifying how urban birds influence tick populations, and how urbanization shapes bird-tick interactions, will increase understanding of tick-borne disease ecology in urban ecosystems.

Keywords Avian · Parasite · Passerine birds · Tick-borne pathogen · Urban ecology · Vector-borne disease

Introduction

Ticks are parasitic vectors of many pathogens that cause disease in humans, wildlife, and domestic animals worldwide. Wildlife play a key role as hosts for tick-borne pathogens; tick populations, tick-host interactions, and thus spatiotemporal patterns of disease prevalence, are influenced by wildlife density, diversity, and species composition (Schmidt and Ostfeld 2001; Allan et al. 2010; Keesing et al. 2010; Hamer et al. 2012a; Silaghi et al. 2012; Pfäffle et al. 2013). Land-use and land cover changes greatly alter habitats of pathogens, vectors, and hosts, and thus the nexus of all three transmission components (Patz et al. 2000, 2004; Foley et al. 2005; Hornok et al. 2013). In particular, urbanization is increasing globally, changing almost all aspects of ecosystems (Grimm et al. 2008). These changes affect diseases through alteration of microclimates that influence vectors, hosts, and pathogens, reduction of host immune function via increased stress and pollutant exposure, and elevation of transmission rates due to greater host densities (Bradley and Altizer 2007). Consequently, urbanization has been linked to emergence and increased prevalence of many tick-borne diseases (Maupin et al. 1991; Steere 1994; Jobe et al. 2007; Schwan et al. 2009; Rydzewski et al. 2012; Blanton et al. 2014).

Understanding the emergence and increased prevalence of tick-borne diseases in urban areas requires research into the role of urban wildlife as carriers of ticks and pathogens. In suburban areas of the U.S. where Lyme disease is prevalent, populations of some wildlife reservoirs have been linked to increased risk of pathogen exposure in humans. For example,

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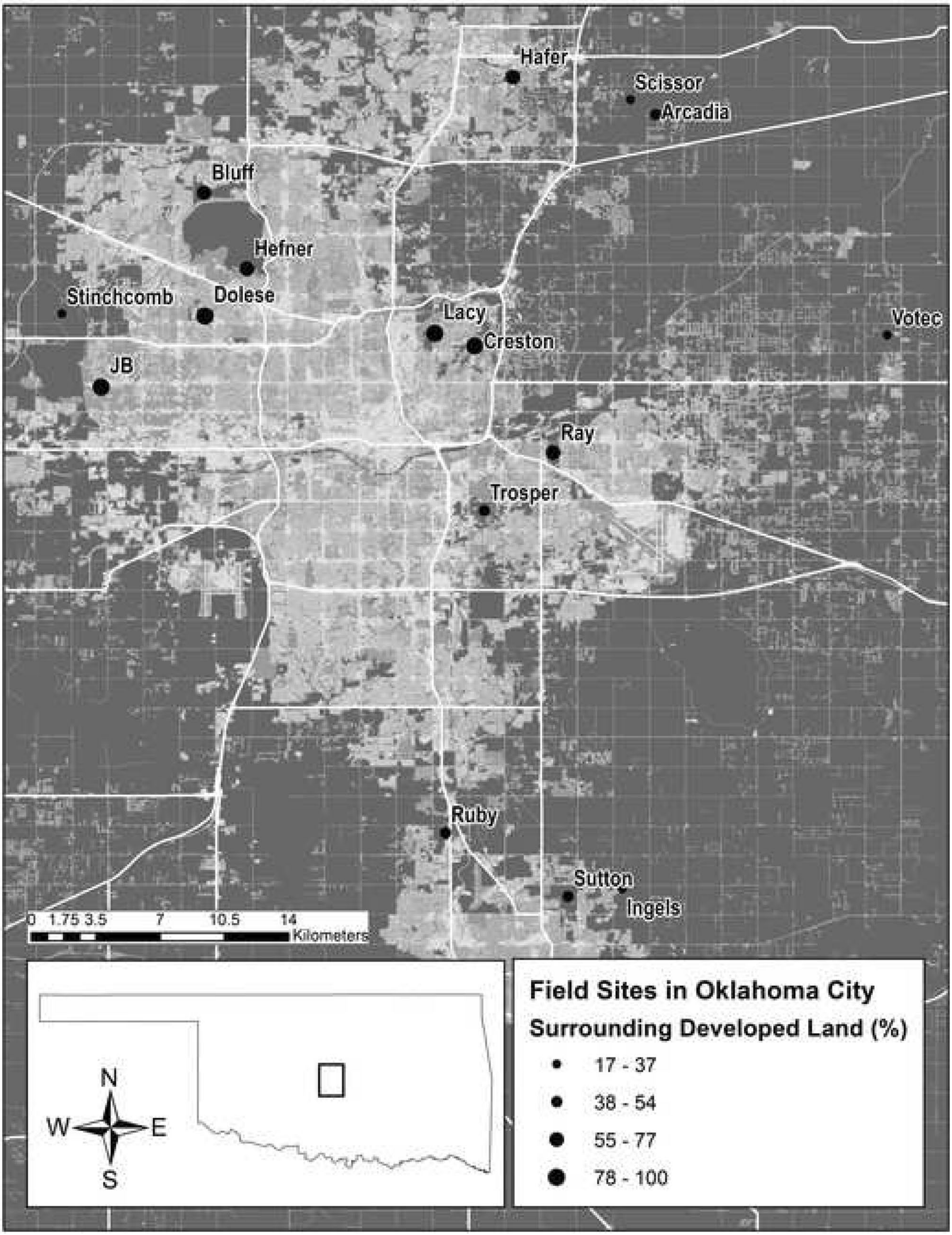

Hafer
Scissor
Arcadia
Bluff
Hefner
Stinchcomb
Dolese
Lacy
Creston
Votec
JB
Ray
Trosper
Ruby
Sutton
Ingels
0 1.75 3.5 7 10.5 14
Kilometers
N
W
E
S
Field Sites in Oklahoma City
Surrounding Developed Land (%)
17 - 37
38 - 54
55 - 77
78 - 100

◂**Fig. 1** Sixteen field sites used to sample birds in Oklahoma City, Oklahoma, USA, 2017–2018. Inset map indicates location of sampling area. Main map shows major highways in white and land cover categories (National Land Cover Database; Homer et al. 2015): light gray is human-developed land (including developed, open space; developed, low intensity; developed, medium intensity; developed, high intensity); dark gray is all other land-cover categories. Size of site labels indicates percent surrounding developed land within 1,000 m of the site's outer edge

increased forest fragmentation and biodiversity loss from urbanization increase proportional abundance of white-footed mice (*Peromyscus leucopus*), the main Lyme disease reservoir host, and thus prevalence of *Borrelia burgdorferi* spirochetes (causative agents of Lyme disease) in mice and ticks (Allan et al. 2003; LoGiudice et al. 2003). Yet, beyond Lyme disease, little is known about the role of wildlife in urban transmission of tick-borne diseases (Paddock and Childs 2003; Loss et al. 2016).

In addition to mammals, accumulating evidence indicates birds also play an important role in transmission of tick-borne pathogens. Birds, especially long-distance migrants, can move and establish tick populations in new areas (Ogden et al. 2008; Hamer et al. 2012a; Mukherjee et al. 2014; Cohen et al. 2015), and they may contribute to broad-scale expansion of tick-borne pathogens by carrying ticks harboring pathogens, such as *Anaplasma* spp., *Borrelia* spp., *Rickettsia* spp., and tick-borne encephalitis virus (Hornock et al. 2013; Schneider et al. 2015; Scott 2015). Moreover, both migratory and non-migratory birds are capable of serving as reservoir hosts necessary for local amplification of tick-borne pathogens (Comstedt et al. 2006). Despite increasing recognition that birds are key to the transmission of tick-borne diseases, little is known about their role in carrying ticks and tick-borne pathogens in urban areas, especially in North America. The limited research on birds in urban areas suggests that migratory species likely supplement existing urban populations of *Ixodes scapularis*, the primary Lyme disease vector in eastern North America, and may introduce neotropical tick species into temperate urban areas (Morshed et al. 2005; Hamer et al. 2012b; Cohen et al. 2015).

In addition to the above research gap, little is known about how urban land cover and development intensity influence the role of birds in carrying ticks. A study in the eastern U.S. found that birds in areas with extensive impervious surface (i.e. more urbanized areas) and water bodies were less likely to carry ticks, but percent imperviousness alone did not predict infestation (Heller et al. 2019). Pathogen prevalence in ticks carried by birds may also vary in relation to urbanization, as indicated by a study showing urban birds are less likely to carry *B. burgdorferi*-infected ticks (Hamer et al. 2012b). Most of these and other studies of tick infestation of birds have focused on long distance movements by migrating birds; however, a recent meta-analysis found that non-migratory birds carry more ticks and a greater proportion of pathogen-infected ticks (Loss et al. 2016). Resident birds, including non-migratory species and migratory species during relatively sedentary periods (e.g., breeding season), make many small-to-medium scale movements related to foraging, mating, territoriality, and dispersal (i.e., movements between successive breeding locations). This likely results in resident birds carrying large numbers of ticks up to at least tens of kilometers (Cox et al. 2016; Evans et al. 2017; Cooper and Marra 2020), and thus contributing to tick movement and tick-borne disease transmission across urban landscapes.

To begin to evaluate the role of non-migratory and summer resident birds in carrying ticks and tick-borne pathogens in U.S. urban areas, and to test the overarching hypothesis that tick infestation of these birds is related to urban development intensity, we sampled birds for ticks at 16 parks and greenspaces surrounded by varying levels of urbanization in Oklahoma City, Oklahoma, USA. Despite high prevalence of several tick-borne diseases, including Spotted Fever Group rickettsiosis, ehrlichiosis, and tularemia (Biggs et al. 2016; Drexler et al. 2016; Heitman et al. 2016; CDC 2019), tick populations and tick-borne pathogens in this region are poorly studied (Paddock and Childs 2003; Loss et al. 2016; Springer and Johnson 2018). Related to our hypothesis, we predicted that both the proportion of all birds harboring ticks and the numbers of ticks on infested birds (i.e., infestation intensity) would decrease with increasing urbanization due to there being less favorable habitat for ticks, and thus fewer opportunities for ticks to parasitize birds, in and around parks in heavily urbanized areas. We also predicted that two different bird species (Carolina Wren [*Thryothorus ludovicianus*] and Northern Cardinal [*Cardinalis cardinalis*]) would show different infestation patterns relative to urbanization due to factors like species-specific habitat preferences, foraging behaviors, and movements differentially influencing tick acquisition across the urban-to-rural gradient.

Material and methods

Study area and design

Oklahoma City is the largest city in both population size and land area in Oklahoma (Fig. 1), with 655,057 people residing in 1,570 km^2 (United States Census Bureau 2019). The Oklahoma City metropolitan area consists of over 1.2 million residents in seven counties. The city is located in the U.S. Great Plains ecoregion (USEPA 2020), and the surrounding land cover is primarily grasslands and cultivated crops west of the city, and grasslands and deciduous forest with interspersed patches of pasture east of the city.

With a mild climate and mean annual temperature of 15.6 ℃ (Greater Oklahoma City 2020), tick activity occurs at least ten months of the year (Talley et al. 2017). Oklahoma has among the highest U.S. incidences of Spotted Fever Group rickettsiosis (> 60 per 1,000,000 persons per year in some counties) and ehrlichiosis (> 40 per 100,000 persons per year in some counties) (Biggs et al. 2016; Springer and Johnson, 2018), and high prevalence of tularemia (CDC 2019), making Oklahoma City an ideal study area for the purposes of our research. Other less-common tick borne diseases found in Oklahoma include Heartland virus and Bourbon virus (Dahlgren et al. 2015; OSDH 2020).

We used Google Earth and Google Street View to identify candidate study sites for bird and tick sampling in the Oklahoma City metropolitan area. We first identified all potential large areas (> 2 ha) of tick habitat, including parks, greenspaces, and vacant, abandoned, or otherwise uninhabited open land, with un-manicured understory vegetation, shrubs, savanna and/or woodland, but excluding areas dominated by manicured lawns. We manually digitized a polygon representing the boundaries of each candidate site and used ArcGIS 10.1 to calculate percentages of developed land and impervious surfaces in a 1,000-m buffer around each site's outer edge, with all land cover data from the national land cover database (NLCD; Homer et al. 2015). For developed land cover, we combined all NLCD cover classes representing human development (developed, open space; developed, low intensity; developed, medium intensity; developed, high intensity) and excluded all other cover types (e.g., water, forest, cultivated areas). Because percent surrounding impervious surface and percent surrounding developed land were strongly correlated (Pearson's r = -0.74), only percent developed land was used for the following stratified site selection approach. A preliminary analysis also showed that percent developed land within 1,000 m was strongly correlated with percent developed land within 500 m. We chose to use the larger buffer for our study to better capture a broad landscape surrounding study sites; use of buffers even larger than 1,000 m was determined to be inadvisable because these larger buffers would have overlapped among some study sites, resulting in non-independent measures. To capture a gradient of urban development intensity, we grouped sites into four categories based on percent developed land within 1,000 m—17–40%, 40–60%, 60–80%, 80–100% (17% was the minimum value across all candidate sites)—and randomly chose four sites from each category (n = 16). Sites were ground-truthed and assessed for safety and accessibility based on whether ownership of the site could be established, permission to sample could be obtained, and accessing the site was not considered dangerous due to potential illegal/criminal activity. Based on these logistical constraints, three sites had to be replaced with other randomly selected sites in the same land cover category. Final sites selected for inclusion are shown in Fig. 1.

Bird capture

At all 16 sites, we captured birds with mist nets, with sampling occurring twice between June and August in both 2017 and 2018 (4 total site visits), with the exception of one site we did not visit a second time in 2018 for safety reasons. These months were chosen to focus sampling on species that are non-migratory year-round residents, and on migratory species during their summer residency period (i.e., excluding most in-transit migratory birds, which primarily migrate before June and after August). In each year, site visits were roughly one month apart. For each visit, and at approximately sunrise, we set and opened 5–6 mist-nets (2.6 m in height, 12 m in length, 36 mm mesh, Avinet Inc., Dryden, NY) and captured birds until 1100 h, or earlier if temperatures were too warm to safely restrain birds in nets. We attached numeric aluminum bands to each bird (U.S. Geological Survey, Bird Banding Laboratory) and recorded species, sex, weight, and age class according to Pyle et al. (1997).

Tick searches

We followed the tick-searching protocol described in Roselli et al. (2020). Before release, each bird was searched visually for ticks by blowing apart feathers to see all skin surfaces. The whole body of each bird was searched, and we took special care to thoroughly search around thighs and wings due to the difficulty of viewing the folds of skin, bones, and hollows in these areas. When a tick was found, it was removed with fine-tip forceps, except when doing so posed a potential harm to the bird's safety (e.g., if the tick was inside the ear canal or close to the eye and/or if the bird showed signs of physical stress requiring us to release it before removing ticks). In all cases, even when ticks could not be removed, we recorded numbers and locations of ticks encountered on each bird sampled. Extracted ticks were immediately placed in 70% ethanol before later identifying them to species using pictorial keys (Keirans and Litwak 1989; Keirans and Durden 1998; Coley 2015; Dubie et al. 2017; Egizi et al. 2019). Because *A. maculatum* in the United States is indistinguishable from *Amblyomma triste* (Lado et al. 2018), all references to *A. maculatum* in this manuscript refer to the *A. maculatum* group.

Data analyses

We treated all captures (and recaptures) of individual birds as separate events. Although recaptures of a previously trapped bird are not truly independent samples, we used this approach because a small percentage of trapping events were recaptures (see "Results") and all recaptures occurred ≥ 14 days after the bird was previously sampled, a sufficient amount of intervening time for each successive capture event to represent a unique period of tick acquisition. All tick species were analyzed together due to limitations in sample size when considering the 16 sites as replicates; although *A. americanum* was found on birds at all 16 sites, *A. maculatum* and *H. leporispalustris* were only found at 50% (8 of 16) and 43.7% (7 of 16) of sites, respectively. We performed all analyses using R 3.2.2 (R Core Team 2016). We used *p*-values ($\alpha = 0.05$) to assess statistical significance of models described below.

We evaluated three predictions related to our overarching hypothesis that tick infestation of birds is related to urban development intensity. To address our first prediction (regarding variation in the proportion of birds that harbor ticks relative to urbanization intensity), the proportion of birds infested with ticks at each site was calculated by dividing the number of birds infested with at least one tick by the total number of birds sampled. To determine if the proportion of birds infested varied with urban development intensity (percent surrounding developed land), we used a generalized linear model (GLM) with a binomial error distribution that treated the number of birds with ≥ 1 tick as the number of "positive" outcomes out of a sample of binomial trials represented by the number of birds sampled. We treated site as the unit of replication (n = 16), total prevalence of infestation (across all bird species at each site) as the dependent variable, and percent surrounding developed land as a fixed effect. To address prediction 2 (regarding variation in the intensity of tick infestation relative to urbanization intensity), intensity of tick infestation was calculated for each site by dividing the total number of ticks observed on all birds by the total number of birds infested with ticks. To determine if intensity of tick infestation varied with urban development intensity, we used a GLM with a gamma error distribution (because values of the dependent variable were positive non-integers, and distributions of values were generally left-skewed), site as the replicate, total intensity of infestation (i.e., across all bird species at a site) as the dependent variable, and percent surrounding developed land as a fixed effect.

To address our third prediction (regarding bird species-specific associations between urbanization intensity and infestation prevalence and intensity), we calculated proportion infested and intensity of infestation at each site (described above) for the two most commonly captured bird species: Northern Cardinal and Carolina Wren. For each species, we used a GLM with site as the replicate, proportion infested (binomial error distribution) or intensity of infestation (gamma error distribution) as the dependent variable, and percent surrounding developed land as a fixed effect.

Results

Descriptive summary of bird and tick sampling

We conducted 459 tick searches on 432 individual birds (i.e., 27 searches [5.9%] were of recaptures) representing 31 species (Table 1). Northern Cardinal and Carolina Wren comprised 56.6% (n = 260) of all captures; American Robin (*Turdus migratorius*) and Painted Bunting (*Passerina ciris*) were also caught more than 30 times. More tick searches were conducted in 2017 (n = 282, 61.4%) than 2018 (n = 177, 38.6%) despite roughly equal mist-netting effort at all sites in each year (except for the single site that was not sampled a second time in 2018 for safety reasons). The most commonly sampled bird age class was after hatching year (i.e., birds hatched during the previous calendar year or before; 71.2% of capture events/tick searches), followed by hatching year (i.e., birds hatched earlier in the same calendar year; 22.7%), and unknown (i.e., age could not be determined or aging was not attempted; 6.1%). Most hatching-year individuals could not be reliably sexed; of after-hatching-year birds, 39.8% were female, 37.9% were male, and 22.3% were of unknown sex (i.e., individuals of species with sexually monomorphic feather plumages and no discernable sex-specific anatomical characteristics).

A total of 111 birds representing ten species was infested with 495 total ticks. The prevalence of infestation (percentage of all birds parasitized by at least one tick) was 24.2%, and the mean intensity of infestation (mean number of ticks on infested birds) was 4.46 ticks per bird. Carolina Wren had the highest prevalence of infestation (55.9%), followed by Brown Thrasher (*Toxostoma rufum*, 37.5%) and Northern Cardinal (27.1%). Of 495 ticks, 322 were removed for identification. Among this sample, we found three tick species—*Amblyomma americanum* (51%), *Amblyomma maculatum* (36%), and *Haemaphysalis leporispalustris* (13%)—with all individuals representing either larval (69%) or nymphal (31%) life-stages (Table 1). Of 164 *A. americanum*, a nearly equal number were larvae (80; 48.8%) and nymphs (84; 51.2%), whereas most *A. maculatum* (109 of 116; 93.4%) and *H. leporispalustris* (34 of 42; 81%) were larvae.

Tick infestation of birds relative to urbanization intensity

There was a statistically significant inverse association between the percent of surrounding developed land and prevalence of tick infestation for all birds species combined ($p < 0.001$; $\beta \pm$ standard error [SE] = -0.016 ± 0.005; 95% confidence interval [CI] of β = -0.026, -0.007; Fig. 2) and for Carolina Wren ($p < 0.001$; $\beta \pm SE = -0.050 \pm 0.015$; 95% CI = -0.082, -0.023; Fig. 3). However, there was no statistically significant association between surrounding

Table 1 Numbers and species of birds sampled for ticks, prevalence of infestation (i.e., proportion of birds with at least one tick), and numbers of ticks of each species and life stage, based on field sampling in Oklahoma City, Oklahoma, USA, Jun-Aug 2017–2018

				A. americanum		*A. maculatum*		*H. leporispalustris*	
Species[a]	Number of searches[b]	Number of ticks observed[c]	Proportion infested	Larvae	Nymphs	Larvae	Nymphs	Larvae	Nymphs
American Robin (*Turdus migratorius*)	34	13	0.12	1	8			2	2
Bewick's Wren (*Thryomanes bewickii)*	4	15	0.5	2	2	7			
Blue Jay (*Cyanocitta cristata*)	3	0							
Brown Thrasher (*Toxostoma rufum*)	16	10	0.38		3			1	2
Carolina Chickadee (*Poecile carolinensis*)	17	0							
Carolina Wren (*Thryothorus ludovicianus*)	68	143	0.56	40	22	14	2	18	2
Common Grackle (*Quiscalus quiscula*)	3	0							
Downy Woodpecker (*Picoides pubescens*)	4	0							
Eastern Bluebird (*Sialia sialis*)	1	1	1		1				
European Starling (*Sturnus vulgaris*)	4	0							
Great Crested Flycatcher (*Myiarchus crinitus*)	5	0							
Gray Catbird (*Dumetella carolinensis*)	4	0							
House Sparrow (*Passer domesticus*)	7	0							
Indigo Bunting (*Passerina cyanea*)	15	37	0.2	1		44			
Least Flycatcher (*Empidonax minimus*)	4	0							
Northern Cardinal (*Cardinalis cardinalis*)	192	257	0.27	34	47	31	2	13	2
Northern Mockingbird (*Mimus polyglottos*)	5	0							
Painted Bunting (*Passerina ciris*)	32	16	0.09	2		13	1		
Tufted Titmouse (*Baeolophus bicolor*)	12	1	0.08		1				
White-eyed Vireo (*Vireo griseus*)	13	0							
Yellow-billed Cuckoo (*Coccyzus americanus*)	3	2	0.33				2		
Total	459[d]	495	0.25	80	84	109	7	34	8

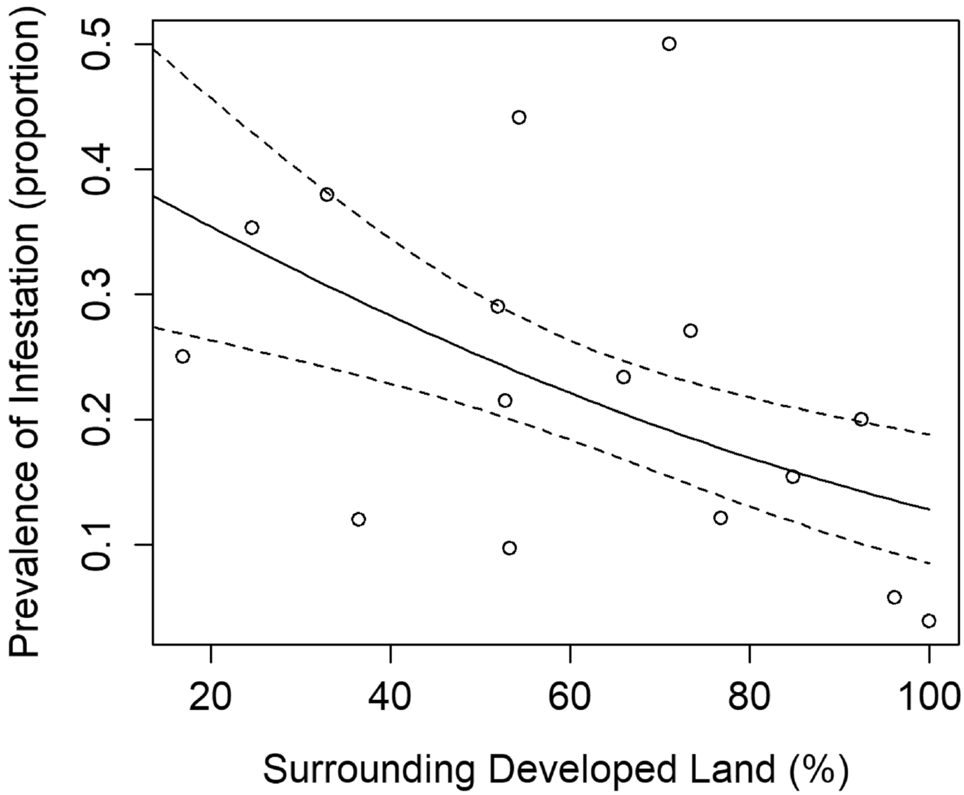
[a]Species common names follow American Ornithological Society (Chesser et al. 2018)

[b]All bird captures, including recaptures of the same individual (n = 27), were considered as unique capture events (see text for rationale)

[c]Counts of each tick species are based only on the 322 ticks that were removed for identification

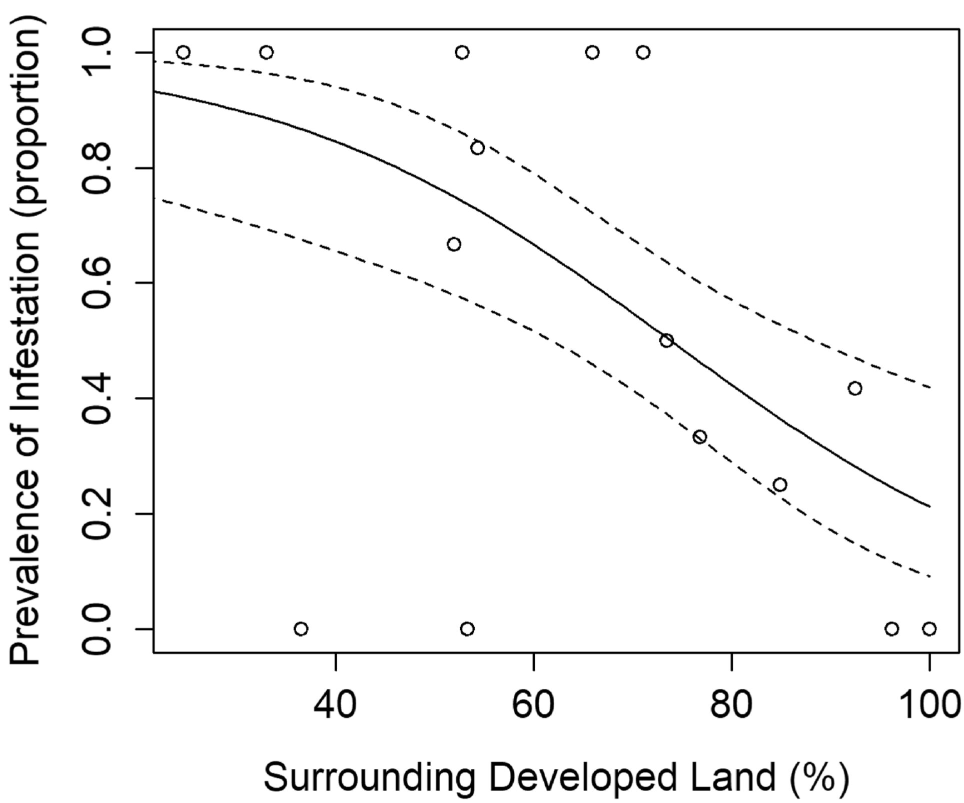
[d]Total includes 9 unlisted bird species with < 3 captures (13 individuals across 10 species); species not shown include American Goldfinch (*Spinus tristis*), Bell's Vireo (*Vireo bellii*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Brown-headed Cowbird (*Molothrus ater*), Eastern Phoebe (*Sayornis phoebe*), Eastern Wood-Pewee (*Contopus virens*), Louisiana Waterthrush (*Parkesia motacilla*), Red-eyed Vireo (*Vireo olivaceus*), and Summer Tanager (*Piranga rubra*) (we also sampled an unidentified *Empidonax* flycatcher)

Fig. 2 Relationship between percentage of developed land in a 1,000-m radius around study sites and prevalence of infestation (i.e., proportion of birds carrying at least one tick) for all bird species captured in Oklahoma City, Oklahoma, USA, Jun–Aug 2017–2018 (Points indicate observed values, solid line indicates fitted relationship from a generalized linear model (GLM) with a binomial error distribution, and dotted lines indicates 95% confidence interval for fitted model)



developed land and prevalence of tick infestation for Northern Cardinal ($p = 0.125$; $\beta \pm SE = -0.011 \pm 0.007$; 95% CI = -0.025, 0.003). For intensity of infestation, there was no significant association with amount of surrounding developed land when considering all bird species combined ($p = 0.217$; $\beta \pm SE = 0.003 \pm 0.002$; 95% CI = -0.001, 0.007),

Fig. 3 Relationship between percentage of developed land in a 1,000-m radius around study sites and prevalence of infestation (i.e., proportion of birds carrying at least one tick) for Carolina Wrens captured in Oklahoma City, Oklahoma, USA, Jun–Aug 2017–2018 (Points indicate observed values (we did not sample any Carolina Wrens at 1 of the 16 sites), solid line indicates fitted relationship from a generalized linear model (GLM) with a binomial distribution, and dotted lines indicate 95% confidence interval for the fitted model)



Northern Cardinal ($p = 0.550$; $\beta \pm SE = 0.005 \pm 0.007$; 95% CI = -0.010, 0.019), or Carolina Wren ($p = 0.121$; $\beta \pm SE = 0.005 \pm 0.003$; 95% CI = -0.001, 0.010).

Discussion

We found a high proportion of birds to be infested with ticks in a large metropolitan area of the U.S. Great Plains, a region where little is known, including in urban areas, about the importance of birds as carriers of ticks and tick-borne pathogens. About one-quarter of birds had one or more ticks, suggesting that non-migratory species, and migratory species during their breeding season, are important carriers of ticks and may be contributing to increased prevalence of tick-borne diseases in urban areas. We also found support for our overarching hypothesis that tick infestation of birds is related to urban development intensity. In agreement with our first prediction, we found that prevalence of tick infestation for all birds combined declined with increasing urbanization intensity. However, contrary to our second prediction, intensity of infestation was unrelated to urbanization, suggesting that other factors (e.g., tick questing behavior, abiotic conditions, vegetation) influence numbers of ticks on infested birds. Related to our third prediction that focused on tick infestation of individual bird species, prevalence of infestation decreased with increasing urbanization for Carolina Wren, but not for Northern Cardinal, and intensity of infestation was unrelated to urbanization for both species.

Importance of resident birds as carriers of ticks in urban areas

The U.S. Great Plains has high prevalence of several tick-borne diseases, including Spotted Fever Group rickettsiosis, ehrlichiosis, and tularemia (Biggs et al. 2016; Drexler et al. 2016; Heitman et al. 2016; CDC 2019); however, the role of birds in carrying ticks was previously unknown in this region (Loss et al. 2016). We found that in Oklahoma City, birds were parasitized by *A. maculatum*, *H. leporispalustris*, and most commonly, *A. americanum*. The greater frequency of parasitism by *A. americanum* could result from the aggressive feeding habits of this species, which may enhance its host-preference for ground-foraging birds (Goddard and Varela-Stokes 2009), or is related to how abundant this tick is in our study area (Roselli 2019). *H. leporispalustris*, the least commonly observed tick, was found only on four species that all forage on or near the ground: American Robin, Brown Thrasher, Carolina Wren, and Northern Cardinal. This finding could reflect that these bird species were sampled most frequently, and a larger sample of other species would lead to observations of *H. leporispalustris* on additional bird species. In a study in Chicago, USA, of > 6,000 birds sampled, *H. leporispalustris* was found on 12 species (5 that we captured in the present study) (Hamer et al. 2012b). A second explanation is that *H. leporispalustris* is more likely to parasitize ground-foraging species (Comstedt et al. 2006; Cohen et al. 2015; Loss et al. 2016). We also observed species-specific differences in which tick life stages were most often found on birds. On birds we sampled, a roughly equal number of *A. americanum* were larvae and nymphs, but the majority of *A. maculatum* and *H. leporispalustris* were larvae. This finding supports the observation that *A. maculatum* (Barker et al. 2004) and *H. leporispalustris* (Kollars and Oliver 2003) nymphs have less host-preference for small animals, whereas *A. americanum* nymphs may not have such differential preferences. Our results provide foundational information for understanding tick host preferences in urban areas of the U.S. Great Plains.

Most previous studies have focused on long-distance transport of ticks and pathogens by migratory birds (Kinsey et al. 2000; Morshed et al. 2005; Hamer et al. 2012a; Mukherjee et al. 2014; Cohen et al. 2015), but a recent meta-analysis showed infestation to be greatest for non-migratory bird species (Loss et al. 2016). Our study, which was designed to focus on bird species that are year-round, non-migratory residents and migratory species during their breeding season, further supports the importance of resident birds in influencing tick populations, and potentially, transmission of tick-borne pathogens. The earlier meta-analysis, which included many studies that sampled birds during migration periods, found an overall prevalence of infestation of 5.1% for 38,929 birds across 11 studies. Focusing on non-migrants, we found a much higher overall infestation percentage of 24.2%, suggesting birds may be more important for localized movement of ticks than previously thought, even in urban areas. Further support for this conclusion is provided by a complementary study that included extensive tick collection at the same 16 sites using carbon dioxide traps and tick flags (Roselli 2019). Using flagging and trapping, that study did not find *A. maculatum* at one highly urbanized site; however, we sampled one *A. maculatum* from a bird captured at that site. This suggests that birds can transport ticks within urban areas, and potentially deposit them into previously uncolonized areas where they may become established if they find suitable host populations.

In addition to our exclusion of migrating birds, the location of our study in the U.S. Great Plains, where no studies have previously been conducted, could contribute to the exceptionally high infestation observed. Specifically, the high proportion of infestation appears to be driven by *A. americanum*, which is the dominant tick species in the region but is less commonly found and studied in the north-eastern and western U.S despite recent abundance increases in parts of the eastern U.S. (Jordan and Egizi 2019; Raghavan et al. 2019). Results of one study in the south-eastern U.S. are contrary to this explanation, as overall tick infestation of birds was found to be similar in areas with and without *A. americanum* (Kinsey et al. 2000). Another explanation for the high proportion of infestation relates to methodology. While many previous studies focused searching effort only on the head and neck of birds, we searched the entire body, and this approach results in significantly more ticks being found (Roselli et al. 2020).

Tick infestation of birds relative to urbanization intensity

We found a significant inverse association between urban development intensity and prevalence of tick infestation for all birds combined and for Carolina Wren, but not for Northern Cardinal. Thus, urbanization may decrease prevalence of tick infestation for many, but not all, bird species. The decrease of infestation prevalence with increasing urban development in the surrounding landscape could reflect bird movement or behavior changes caused by urbanization (Jokimäki et al. 2011). Specifically, for Carolina Wren, a species highly sensitive to urban development (Evans et al. 2015), intense urbanization may change foraging, territoriality, and/or dispersal movements and behaviors in ways that make this species less susceptible to tick infestation (e.g., changes in preening behavior or the amount of time spent near the ground and/or in vegetation types with large numbers of ticks). Tick community changes may also influence variation in infestation prevalence. For example, Carolina Wrens were found to be infested by relatively high numbers of all three tick species, and an urbanization-related change in abundance of one or more of these species could cause an overall change in tick infestation (notably, we lacked sufficient replication to separately assess infestation patterns for individual tick species on each bird species). The lack of effect of urbanization on infestation prevalence for Northern Cardinal, the species we captured most frequently (> 41% of total captures), suggests that urbanization levels may have less influence on the behaviors, habitat conditions, and/or tick populations relevant to the infestation of this species. Future research should explore how effects of urbanization on tick infestation are mediated by factors like species-specific traits of birds, vegetation and abiotic conditions, and tick populations and communities.

Unlike prevalence of tick infestation, intensity of infestation was unrelated to urbanization. Previous studies show a link between large-scale land use and ticks, hosts, and pathogens (Allan et al. 2003; LoGiudice et al. 2003; Heller et al. 2019). Our results suggest that even if the proportion of birds carrying at least one tick is influenced by urbanization, numbers of ticks carried by infested birds can be more consistent across an urban-to-rural gradient. One explanation for this finding relates to the questing behavior of larvae, the tick life stage most often found on birds in this and most other studies. For most tick species, larvae quest in groups to prevent desiccation (Nicholson et al. 2019); for birds that encounter such a cluster of larvae, numbers of ticks acquired may be relatively consistent. An effect of urbanization on the number or density of tick larvae clusters could result in the patterns we observed, specifically, a lower proportion of birds encountering a cluster and being parasitized in more-urbanized areas, but similar numbers of ticks acquired if a cluster is encountered, regardless of urbanization intensity.

A complementary explanation for the lack of relationship between urbanization and infestation intensity is that factors other than large-scale urbanization may influence the number and activity of ticks in an area, and thus the number of ticks on birds. For example, in the Lyme disease transmission system, tick infestation of white-footed mice depends on many factors, including presence of top-level and meso-predators (Levi et al. 2012), acorn mast (Ostfeld et al. 2006), forest fragmentation (Allan et al. 2003), invasive plant presence (Williams and Ward 2010), and host diversity (Ostfeld and Keesing 2000). Urbanization changes almost all aspects of ecosystems from large to small spatial scales, including temperature, humidity, vegetation structure/composition, wildlife communities, and landscape-scale habitat fragmentation, heterogeneity, and connectivity (Hage 1975; Kim 1992; Savard et al. 2000; Arnfield 2003; Kowarik 2008; Chaves et al. 2011; Ramalho and Hobbs 2012). Thus, numbers of ticks encountered by birds in our urban study system is likely driven by a similarly complex suite of factors. In particular, landscape-scale habitat connectivity and heterogeneity influence both host populations (e.g., deer [*Odocoileus virginianus*] and birds; Walter et al. 2011; Kang et al. 2015) and vector populations, including ticks (Estrada-Peña 2003; Chaves et al. 2011; Uspensky 2014). Urbanization-associated changes in habitat connectivity and heterogeneity may affect host movements, populations, and/or communities in ways that influence infestation for birds and other hosts. We encourage future urban studies to consider the entire community of potential wildlife hosts for ticks and tick-borne pathogens, as well as other abiotic and biotic factors that operate across multiple scales to influence the unique ecology of each tick-borne disease system.

Future research into bird movements and study limitations

Several movement-related mechanisms could drive how resident urban birds contribute to establishment and maintenance of tick populations and emergence and transmission of tick-borne diseases. Resident birds do not make the long-distance movements typical of migrating birds, but they do make frequent, smaller-scale movements with likely implications for ticks and tick-borne diseases. These include movements within and among breeding territories to forage, mate, and defend against predators and conspecifics (movements ranging from tens/hundreds of meters to a few kilometers for the passerines/songbirds comprising most of our sample; Cox et al. 2016; Evans et al. 2017). Natal and breeding dispersal also entail large numbers of birds moving between breeding attempts (Greenwood and Harvey 1982). Dispersal is likely most relevant to movement of ticks across urban areas when it occurs within one breeding season (e.g., for non-migratory or summer resident species moving among two or more breeding locations in the same season). Dispersal-related movements of ticks may also occur with single-brooded migratory birds; for example, before they migrate out of an area, some species appear to "prospect" for future breeding sites by making breeding season movements up to tens of kilometers in length (Cooper and Marra 2020). Further research tracking these types of movements, while simultaneously quantifying tick infestation of the birds studied and tick populations in areas moved through, would improve understanding of mechanistic links between bird movements, tick infestation of birds, and tick-borne pathogen transmission in urban areas.

The broad applicability of our results is uncertain, as our study was heavily focused on passerines (i.e., perching birds/songbirds) and limited in sample size (459 total bird searches), seasonal coverage (June–August), and geographic area (one city in the central U.S). Nonetheless, most of the bird and tick species sampled have relatively large geographic distributions, potentially making these results widely generalizable. For example, most bird species captured, including the two species most commonly sampled (Northern Cardinal and Carolina Wren) have geographic distributions spanning at least the eastern half of the U.S. Two of three tick species collected (*A. americanum* and *H. leporispalustris*) also range across the eastern half of the U.S., as well as much of Mexico and southern Canada (Brown et al. 2005; Springer et al. 2015). Although our results may be applicable across much of North America, additional research is needed in other regions, during seasons other than summer, and with a variety of tick species and non-passerine birds, to elucidate whether exceptions exist to the patterns documented or if these patterns exist across wider geographic areas.

Conclusions

We documented a high proportion of tick infestation of birds in a large U.S. urban area, suggesting a key role of birds as carriers of ticks in cities. We also observed species-specific patterns of tick infestation prevalence relative to urbanization. These findings provide novel insight, especially for interior North America, into bird-tick interactions and the ecology of tick-borne diseases in urban ecosystems. This information is relevant for urban wildlife ecology and management because it suggests that efforts to manage for birds and their habitats across urban-to-rural gradients have implications for tick-borne disease transmission, in addition to benefiting bird populations and providing aesthetic value for humans. Findings are also relevant for public health and veterinary efforts to predict and manage tick-borne disease risk in humans and domestic animals in cities. The percentage of earth's population living in urban areas continues to grow (United Nations 2014), and tick-borne diseases continue to emerge and increase in prevalence in U.S. urban areas (Jobe et al. 2007; Schwan et al. 2009; Blanton et al. 2014). Further, climate change and other changes like habitat conversion to urban and agricultural uses (Ogden et al. 2006; Porretta et al. 2013) are greatly altering conditions on the landscape, in some cases facilitating tick colonization in previously inhospitable areas (Brownstein et al. 2005). Thus, more of the human population than ever before will be at risk for contracting tick-borne diseases in urban areas (Ogden et al. 2014). Understanding the role of birds and other highly-mobile animals as carriers of ticks in cities is essential to predicting and managing tick-borne disease transmission and emergence.

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Authors' contributions All authors conceived and designed the study and developed its methods. M.A.R. led fieldwork and data collection, managed and analyzed data, and drafted the manuscript. B.H.N. and S.R.L. provided feedback and edits on manuscript drafts.

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Availability of data and materials Data are available within this manuscript and can be provided by the authors upon request.

Code availability All analyses were conducted using standard code within existing R packages; however, code can be provided by the authors upon request.

Declarations

Ethics approval All applicable national, state, and institutional guidelines for the care and use of animals were followed. Handling of wild birds was permitted under a U.S. federal bird banding permit (#23929) and State of Oklahoma Scientific Collector's Permit (#6963); bird handling was also approved by the Institutional Animal Care and Use Committee at Oklahoma State University (protocol #AG-14–6).

Consent to participate Not applicable.

Consent for publication Not applicable.

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