Research Article

Urbanization and Tick Parasitism in Birds of Coastal Southeastern Virginia

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ABSTRACT One of North America's major avian migratory pathways occurs along a large anthropogenically modified coastal region of southeastern Virginia, USA. Because hundreds of avian species migrate along the east coast of North America, understanding factors affecting birds and their health is of ecological and conservation interest. Within southeastern Virginia, 14 tick species have been documented, all of which may serve as vectors of vertebrate pathogens. We tested 5 hypotheses to understand how varying levels of urbanization within an urban matrix of a coastal region affected avian parasitism rates. We sampled resident and migratory birds for ticks across an urbanization gradient at 5 permanent and 6 *ad hoc* sites from August 2012 to August 2014 and determined parasitism rates at the landscape and site scales. At the landscape scale, the proportion of birds parasitized by ticks was reduced at more urbanized sites. Urbanized sites were largely associated with higher water and impervious surfaces in the surrounding area, which may have prevented dispersal of ticks or hosts to isolated urban locations, and lower tree cover, which likely reduced tick survival because of decreased leaf litter. At the site scale, properties associated with being on or near the ground (i.e., foraging guild and age) were the best predictors of tick parasitism. These findings demonstrate that the effects of urbanization are neither uniform nor straightforward. In addition to affecting avian species composition, anthropogenic changes to the landscape are affecting the relationship between avian hosts and their parasites, a finding that has important implications for avian conservation efforts and management practices. © 2019 The Wildlife Society.

KEY WORDS environmental constraint, foraging guild, host age, host sex, impervious surface.

Urbanization, or the alteration of natural habitats into anthropogenic communities, is common in the modern era (Hamer and McDonnell 2009). Between 1970 and 2000, the quantity of developed land within the United States grew approximately 1.6%/year (Theobald 2005). This increase in urbanization, and the consequent movement of human populations to more urban areas, has caused the displacement of wildlife as suitable habitat is degraded and has resulted in the loss of vertebrate taxa from areas inhabited previously, restricting extant ranges to fragments within urban matrices (Bradley and Altizer 2006). Consequently, urbanization often reduces species diversity and richness for most taxa, including highly vagile organisms like birds (Marzluff 2001),

forcing them into smaller and potentially less suitable habitats over time (Melles et al. 2003).

Concomitant with the exclusion of vertebrate hosts from natural habitats has been a decline in ectoparasites, such as ticks, that parasitize wildlife (Wilson et al.1988, Lane et al. 1991). Ticks are the most common agent of vector-borne diseases in North America (Spach et al. 1993) and are the most common agents of vector-borne diseases affecting wild and domestic vertebrates globally (de la Fuente et al. 2008).

Because most tick species require a minimum threshold of humidity and moisture to prevent desiccation, the loss of vegetation and leaf litter required to maintain suitable microclimates in urban areas likely limits tick presence and abundance in general (Alberti 2015). Urban areas often exhibit a high proportion of impervious and impermeable surfaces and limited vegetative cover (Pauleit and Duhme 2000, Pauleit et al. 2005, Grimm et al. 2008). Forested areas with high edge cover, for example, typically provide more suitable habitat for most tick species than manicured yards or open fields (Maupin et al. 1991, Ostfeld et al. 1996, Peters 2009). Likewise, areas comprising fragmented forested lots with a variety of understory vegetation support higher numbers of ticks and their vertebrate hosts (Brownstein et al. 2003).

Habitat fragmentation and an increase in urbanization have resulted in a decline in forest cover and vertebrate diversity (Melles et al. 2003). Because most terrestrial vertebrates are affected negatively by urbanization, understanding how tick parasitism of such vertebrates varies across an urban-rural gradient has important implications for wildlife diseases and the life histories, conservation, and management of vertebrate hosts (McKinney 2008). Because most birds can fly, they have a greater potential role as dispersal agents of ticks than do mammalian, reptilian, or amphibian hosts, who likely disperse ticks over much shorter distances (Scott et al. 2001, Ogden et al. 2008). Additionally, because most birds can travel long distances relatively quickly, they have the propensity to spread pathogens to novel areas (Anderson and Magnarelli 1984, Scott et al. 2001, Hamer et al. 2012b, Hasle 2013). Pathogenic diseases have only recently been associated with habitat degradation and biodiversity loss (Pongsiri et al. 2009; Keesing et al. 2009, 2010); thus, migratory taxa may be particularly vulnerable if stopover sites along migratory flyways are degraded by urbanization (Smith and McWilliams 2010, Altizer et al. 2011).

Fourteen species of hard-bodied ticks occur in coastal southeastern Virginia, USA (Sonenshine 1979), a highly urbanized area intermixed with fragmented agricultural and forested areas within a major avian flyway, making it an ideal site to study host-parasite ecological relationships across urban gradients. Our objective was to identify what landscape characteristics associated with levels of urbanization influence tick occupancy and to determine what avian life-history traits predict tick parasitism. To do this, we tested 5 hypotheses: impervious surface, environmental constraint, foraging guild, host age, and host sex (Table 1).

STUDY AREA

We conducted this study year-round (Aug 2012 to Aug 2014) at 5 permanent and 6 ad hoc sites that varied from 0.8 ha to 410.5 ha in the coastal southeastern region of Virginia, centered around Norfolk, Virginia (36.8508° N, 76.2859° W; Fig. 1). We defined season as follows: winter (Dec–Feb, day-of-year [DOY] 335 to 365 and 1 to 59), spring (Mar–May, DOY 60 to 152), summer (Jun–Aug, DOY 153 to 243), or autumn (Sep–Nov, DOY 244 to 334). Permanent sites included Weyanoke, Paradise, Hoffler, Jacobson, and Stephens. Ad hoc sites included Hidden Cove, Virginia Zoo, Kiptopeke, Suffolk, York, and Blackwater (Fig. 1). On average, we sampled permanent sites every other week year-round (Aug 2012–Aug 2014) and ad hoc <10 times throughout the duration of the study. To represent a continuum of degrees of urbanization (i.e., urban, suburban, rural), we chose all sites from a larger list of sites used as part of other tick-related studies by our research group. Urban sites included areas heavily modified by anthropogenic factors, containing large buildings and ≥ 2.6 people/km^2 (U.S. Bureau of the Census 1993, Imhoff et al. 1997). Suburban sites were areas within, surrounding, or bordering single-family occupancies (Moos and Mendez 2014). Rural sites were areas comprising expansive forests or forests and pastures with little to no human infrastructure (Cooke 1980).

The study area is characterized by relatively flat topography ranging in elevation from 0.0 to 3.0 m (Titus and Wang 2008). Vegetation varied by site but generally consisted of mixed hardwood-conifer forests where the dominant species included loblolly pine (Pinus taeda), white oak (Quercas alba), red maple (Acer rubrum), and sweet gum (Liquidambar styraciflua). Common understory species included shorebay (Persea borbonia), greenbrier (Smilax spp.), poison ivy (Toxicodendron radicans), and southern wax myrtle (Morella cerifera). Climate in the region is temperate, with mean maximum daily temperatures in Norfolk ranging from 9.8°C in December to 28.8°C in July. Mean annual precipitation for Norfolk was 118.4 cm (U.S. Climate Data 2018). Dominant land uses included naval yards, agriculture, and urban or suburban developments.

Table 1. The 5 hypotheses tested to identify which landscape characteristics associated with levels of urbanization influence tick occupancy and which avian life-history traits predict tick parasitism in southeastern Virginia, USA, August 2012–August 2014.

Hypothesis	Description
Landscape characteristics	
Impervious surface	Impervious surface, including water, is related negatively to tick parasitism of birds (Hoch et al. 1971, Semtner et al. 1971), and areas with more impervious surfaces tend to be more urban (Arnold and Gibbons 1996). Because ticks are typically not found in areas with high percentages of developed land (Noden et al. 2017) or in areas with reduced vegetative cover where they are prone to desiccation (Stafford 1994, Schulze et al. 1995), birds that occupy areas that have high impervious and impermeable surface cover (i.e., more urbanized) should be less likely to be parasitized by ticks than those in more rural areas.
Environmental constraint	Birds in more urbanized areas exhibit lower tick burdens than those in less urbanized areas (Arnold and Gibbons 1996). The lack of suitable tick habitat and vertebrate hosts in urban areas limits the number of ticks that can survive, reducing potential tick burdens on birds (Bradley and Altizer 2006).
Avian life-history traits	
Foraging guild	Ticks are more likely to parasitize ground-foraging birds than birds within other foraging guilds (e.g., foliage, aerial; Anderson and Magnarelli 1984). Because ticks quest close to the ground, their ability to parasitize birds that forage above the ground is limited (Rand et al. 1998, Peters 2009).
Host age	Juvenile birds spend more time near the ground during their fledgling stage and are therefore more likely to be parasitized by ticks than adult birds (Soler 1994). This increased time on the ground increases contact time with potential tick habitat and therefore increases the likelihood of a bird being parasitized (Semtner et al. 1971, Anderson and Magnarelli 1984).
Host sex	Male birds are more likely to be parasitized by ticks than females. Males often spend more time defending territories and foraging than females, particularly during the breeding season (Hau et al. 2000). If males are more likely to forage, defend territories, or engage in aggressive encounters near the ground, they are more likely to come in contact with ticks than their female counterparts (Matysiokova and Remes 2014).

Figure 1. Permanent (1–5) and *ad hoc* (6–11) field sites in coastal, southeastern Virginia, USA, 2012–2014. We sampled permanent sites consistently year-round, and *ad hoc* sites <10 times. 1 = Weyanoke Bird and Wildlife Sanctuary, 2 = Paradise Creek Nature Park, 3 = Hoffler Creek Wildlife Preserve, 4 = Jacobson Tract, 5 = Stephens Tract, 6 = Hidden Cove, 7 = Virginia Zoo, 8 = Kiptopeke State Park, 9 = Suffolk Landfill, 10 = York, 11 = Blackwater Ecological Preserve. Image from Google Earth (Google, Mountain View, CA, USA).

METHODS

We caught birds at the 11 sites using ≤10 mistnets (12 m long × 2.5 m high) erected for approximately 4 hours after sunrise and before sunset, facilitating avian capture during the most active times of day (Daan and Aschoff 1975, Karr 1981, Deslauriers and Francis 1991). We sampled the Hoffler and Stephens sites from August 2012 to August 2014, Weyanoke and Paradise from November 2012 to August 2014, and Jacobson from June 2013 to August 2014 (Fig. 1). We identified and banded all birds with standard United States Geological Survey (USGS) aluminum bands, and sexed and aged them, where possible, based on plumage or other morphological characteristics. Some taxa could not be reliably aged or sexed outside of the breeding season because plumage or morphological characters were indistinguishable among ages or between sexes (Pyle 2008). We removed all ticks from birds using forceps and later identified each to species using morphological and molecular methods (Heller et al. 2016).

We obtained all necessary state (Virginia Department of Game and Inland Fisheries Wildlife Salvage permit 044737, Virginia Department of Game and Inland Fisheries Scientific Collection permit 044735, Virginia Department of Conservation and Recreation Research and Collecting permit FLKPYR-RCP-030512, Virginia Department of Conservation and Recreation Division of Natural Heritage Natural Area Preserve Research and Collecting permit DNH MTR01-12) and federal (Department of the Interior Federal Bird Banding permit 23803 and U.S. Fish and Wildlife [USFWS] permit MG71673A-0) permits. All animal handling was approved under Old Dominion University's Institutional Animal Care and Use Committee protocols 12-006 and 13-018.

Land Cover

To quantify urbanization, we used the National Land Cover Database (NLCD) to determine land cover types at each site (USGS 2011, Homer et al. 2015; Table S1, available online in Supporting Information). We used a handheld global positioning system (GPS; Garmin Montana 650t, Garmin International, Olathe, KS, USA) to delineate each of the field sites and quantified landscape features using the Gap Analysis Program (GAP) USGS National Land Cover Map for Virginia (GAP 2011, Homer et al. 2015; Table S1) in ArcGIS 10.3 (version 10.3.1, Environmental Systems Research Institute [ESRI], Redlands, CA, USA).

Additionally, we created fixed-distance buffer zones around the centroids of each site at 100 m, 500 m, 1,000 m, and 1,500 m. The 100-m buffer was relevant at the scale of the mistnets used to capture birds, whereas we used the 1,500-m buffer to represent the approximate scale of local bird movements within and around the study sites (Haskell et al. 2002). We quantified the number of pixels of each land cover type present at each of the 11 sites and used mean percent impervious cover to determine the relative urbanization level of each site (Table S1). For analyses, we used combinations of the 3 vegetation covers (tree, ground,

all) with the 2 impervious surface covers (water, impervious surface). We consolidated these 5 categories from the list of cover types used by the NLCD, though we did not incorporate all cover types within the database (USGS 2011, Heller 2015), and then used 2 methods to quantify relative urbanization among sites: mean percent impervious surface cover (Arnold and Gibbons 1996) and a qualitative assessment of each site (urban vs. suburban vs. rural; Table S1).

Statistical Analyses

We predicted tick parasitism relative to landscape-scale and site-scale factors. The landscape analyses attempted to determine which landscape variables predicted tick occupancy, whereas we used the site-scale analyses to predict which life-history attributes made birds more predisposed to being parasitized at sites where ticks occurred.

To determine which variables associated with level of urbanization, phenotypic traits, and season were the best predictors of tick parasitism (coded as a binary variable [yes or no]), we used an information-theoretic approach by building an *a priori* candidate set of models and ranked candidate models using Akaike's Information Criterion for small sample sizes (AIC_c), with lower AIC_c values indicating better-supported models, using the R package MuMIn (Burnham and Anderson 2002, R Core Team 2017). We report all models with $\Delta AIC_c < 2$, though we disregard models where the additional variable(s) received little support, based on little deviance reduction from the top-ranked model (Arnold 2010). We used only permanent sites in these analyses because we sampled *ad hoc* sites irregularly, resulting in insufficient phenological data for analyses. We did, however, use *ad hoc* sites for comparative purposes when examining urbanization patterns across the full complement of sites. To standardize predictor variables, we subtracted the mean from all observations and divided all values by the standard deviation.

Variables for AIC_c analyses included year, percent impervious surface cover, percent water cover, percent tree cover, percent ground vegetation cover, percent all vegetation cover, avian species richness, temperature (°C), percent humidity, foraging guild (ground, foliage, aerial), host age (juvenile, adult, unknown), host sex (male, female, unknown), and season (winter, spring, summer, autumn). We included season to address any seasonal variation in tick parasitism rates. We quantified landscape features (% impervious surface cover, % water cover, % tree cover, % ground vegetation cover, and % all vegetation cover) using the GAP USGS National Land Cover Map for Virginia (GAP 2011, Homer et al. 2015) in ArcGIS 10.3 (version 10.3.1, ESRI).

Our model set included 74 candidate models with varying combinations of predictor variables within the 4 buffer zones (100, 500, 1,000, and 1,500 m). We first ran these models using all 5 permanent field sites to determine abiotic landscape-scale factors associated with tick occupancy and then again using only the 3 permanent sites where we consistently found ticks (i.e., Hoffler, Jacobson, and Stephens) to determine which biotic variables predicted whether a bird would be parasitized. We tested multicollinearity for all predictor variables using variance inflation factor (VIF) in the CAR package in R (Fox and Weisberg 2011). Multicollinearity was represented by models with variance inflation factors >2.5 or variables that were correlated >0.7 or <-0.7 (Anderson et al. 2001). We removed any models with multicollinearity issues among variables from the candidate set.

Based upon the best-supported models ($\Delta AIC_c < 2$), we used logistic regression and odds ratios (OR) in R (version 3.4.1) to determine statistically significant relationships ($P < 0.05$) between the probability of tick presence and the predictor variables. We checked data to ensure that they met the assumptions for logistic regression. To avoid pseudoreplication, we included only an individual's first capture in the analyses, if we caught the bird >1 time.

RESULTS

We captured 1,187 unique individuals representing 66 species (Table S2, available online in Supporting Information) at the 5 permanent sites. We captured most birds in summer (32.2%), followed by spring (25.0%), autumn (24.8%), and winter (18.0%). The 5 species captured most commonly across all sites were northern cardinal (*Cardinalis cardinalis*, $n = 183$), white-throated sparrow (*Zonotrichia albicollis*, $n = 113$), Carolina wren (*Thyrothorus ludovicianus*, $n = 93$), gray catbird (*Dumetella carolinensis*, $n = 86$), and yellow-rumped warbler (*Setophaga coronata*, $n = 69$).

Over the duration of the study, we collected 455 hard-bodied ticks from the 1,187 birds caught at permanent sites. Of these birds, 10.5% were parasitized by ≥ 1 tick. Jacobson had the highest proportion of avian species parasitized, followed by Stephens (Fig. 2). The bird species most commonly parasitized were brown thrasher (*Toxostoma rufum*, 42.0%, $n = 50$), eastern towhee (*Pipilo erythrophthalmus*, 40.0%, $n = 15$), Carolina wren (35.5%, $n = 93$), white-throated sparrow (15.9%, $n = 113$), and common yellowthroat (*Geothlypis trichas*, 10.5%, $n = 57$). Of ticks collected, the majority were rabbit ticks (*Haemaphysalis leporispalustris*, 74.5%, $n = 339$), followed by bird ticks (*Ixodes brunneus*, 12.1%, $n = 55$), *Ixodes dentatus* (5.7%, $n = 26$), blacklegged tick (*Ixodes scapularis*, 4.9%, $n = 22$), *Ixodes affinis* (2.4%, $n = 11$), and lone star tick (*Amblyomma americanum*, 0.4%, $n = 2$).

Using all permanent sites, we found that the model containing water plus impervious surface plus tree cover at the 500-m buffer, as a predictor of reduced tick parasitism in birds, was best supported (Table S3, available online in Supporting Information). No other models were supported ($\Delta AIC_c > 2$). As percent water plus impervious surface cover within the 500-m buffer increased, the proportion of birds parasitized decreased, supporting the impervious surface hypothesis (OR = 0.43, CI = 0.32–0.55, $P \leq 0.001$; Fig. 3). We compared the best-supported model from the 5 permanent sites at the 500-m buffer size with data from the 6 *ad hoc* sites and found that *ad hoc* sites generally exhibited a similar pattern in that parasitism rates increased
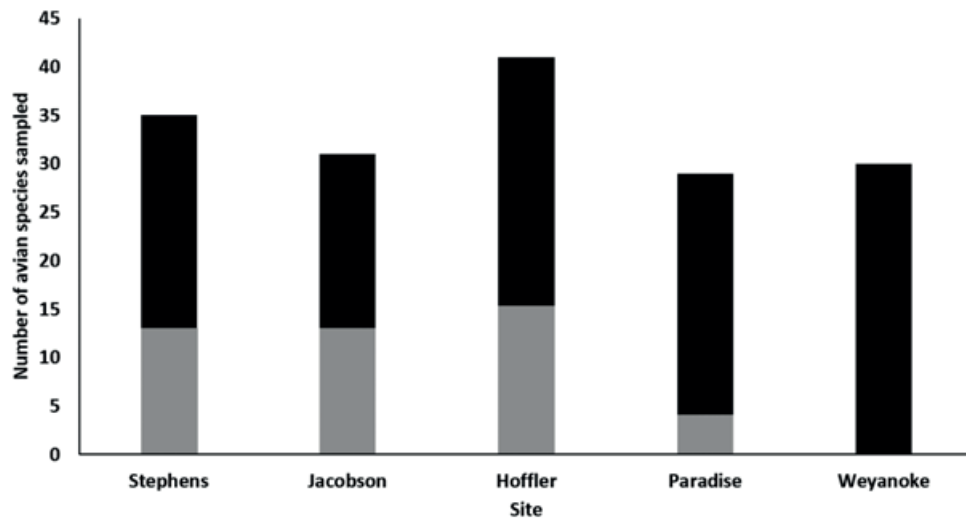
Figure 2. The number of avian species caught at each of the 5 permanent sites in coastal, southeastern Virginia, USA, 2012–2014. Species parasitized by ticks are indicated in gray. Sites are listed in order of increasing urbanization.

with decreasing water plus impervious surface cover at 500 m (Fig. 3). The outliers along the model-predicted curve were Kiptopeke, York, Suffolk, and Blackwater (all *ad hoc* sites). These sites exhibited higher proportions of birds parasitized relative to percent water plus impervious surface cover at 500 m than expected. Additionally, as percent tree cover within the 500-m buffer increased, the proportion of birds parasitized increased, though there was high variability beyond 50% tree cover, supporting the environmental constraint hypothesis (OR = 2.57, CI = 1.86–3.66, $P \leq 0.001$; Fig. 4). The outliers along the model-predicted curve were Kiptopeke and Blackwater (*ad hoc* sites). These sites exhibited higher proportions of birds parasitized relative to percent tree cover at 500 m than expected.

To address whether birds in urban areas were less likely to be parasitized by ticks than those found in rural areas, we used 2 approaches. The first considered only bird species where ≥10 individuals were caught at each site and ≥1 individual was parasitized at each of the 5 permanent sites, to exclude potential bias of species that were never parasitized.

This limited the analyses to 3 species: northern cardinal, Carolina wren, and white-throated sparrow. Birds were parasitized more frequently at rural and suburban sites than urban sites: rural-urban comparison (OR = 62.79, CI = 18.69–391.37, $P \leq 0.001$), rural-suburban comparison (OR = 1.89, CI = 1.06–3.44, $P = 0.03$), and suburban-urban comparison (OR = 33.17, CI = 9.56–209.55, $P \leq 0.001$).

The second approach examined all bird species where ≥10 individuals were caught among all sites. At least 1 individual for each species had to have been parasitized; however, this approach did not require that each individual species occur at all sites, as was required in the first approach. This limited analyses to 12 species: American robin (*Turdus migratorius*), brown thrasher, Carolina wren, common yellowthroat, dark-eyed junco (*Junco hyemalis*), gray catbird, hermit thrush (*Catharus guttatus*), northern cardinal, northern mockingbird (*Mimus polyglottos*), song sparrow (*Melospiza melodia*), white-throated sparrow, and yellow-rumped warbler. Again, birds were parasitized more frequently at rural and suburban sites than at urban sites: rural-urban comparison (OR = 14.49,
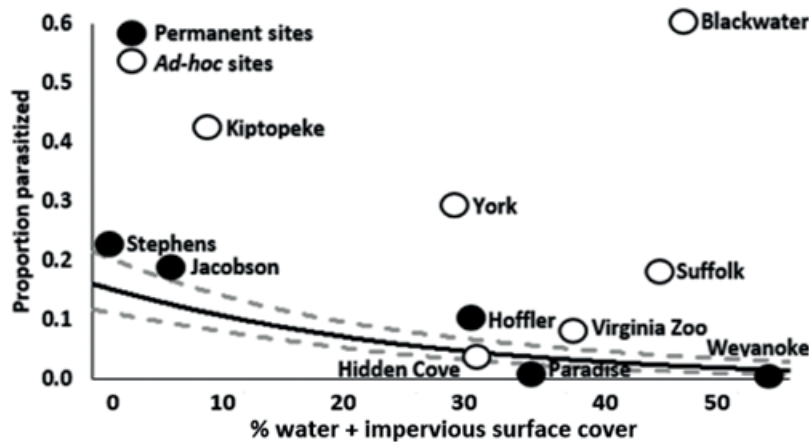

Figure 3. Model-predicted proportion of birds parasitized by ticks relative to percent water plus percent impervious surface cover at the 500-m buffer for permanent and *ad hoc* sites in coastal, southeastern Virginia, USA, 2012–2014. Dotted lines indicate unconditional standard errors around predictions. Permanent sites are represented by solid black circles; *ad hoc* sites are represented by open white circles.
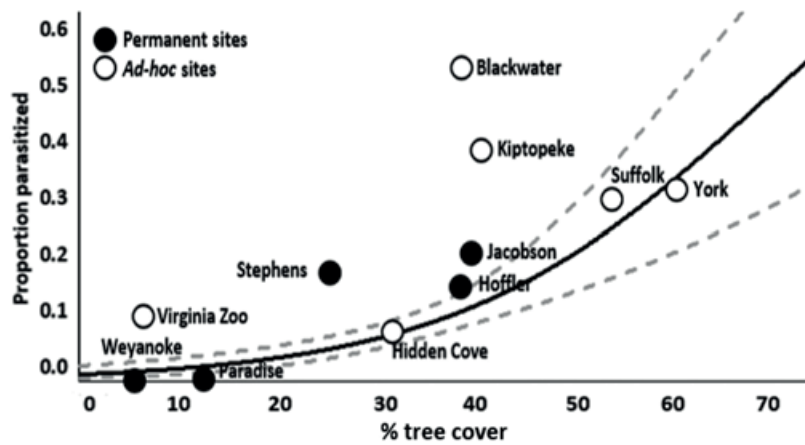
Figure 4. Model-predicted proportion of birds parasitized by ticks relative to percent tree cover at the 500-m buffer for permanent and *ad hoc* sites in coastal, southeastern Virginia, USA, 2012–2014. Dotted lines indicate unconditional standard errors around predictions. Permanent sites are represented by solid black circles; *ad hoc* sites are represented by open white circles.

CI = 6.98–35.26, $P \leq 0.001$), rural-suburban comparison (OR = 1.75, CI = 1.12–2.79, $P = 0.01$), and suburban-urban comparison (OR = 8.25, CI = 3.80–20.62, $P \leq 0.001$). Both approaches, thus, supported the environmental constraint hypothesis.

To focus on life-history characteristics of birds at sites where ticks occurred regularly, we eliminated the urban sites where ticks were either infrequently found (we collected only 3 ticks from birds caught at Paradise over the study) or not found at all (Weyanoke) for a second set of analyses. Based on 711 birds, we found that the best-supported model contained bird age, bird sex, and foraging guild as predictors of tick parasitism (Table S4, available online in Supporting Information). We deemed bird sex to be an uninformative parameter based on little change in deviance from the more parsimonious model (age + foraging guild $\Delta AIC_c = 1.55$); thus, we considered only foraging guild and bird age as having support as predictors of tick parasitism (all other models $\Delta AIC_c > 3$).

To determine which individuals were most likely to be parasitized based on foraging guild and age, we examined only those birds where age was known and excluded aerial foragers ($n = 7$) because none were parasitized. Within this subset of birds ($n = 631$), 8.3% ($n = 422$) of ground-foraging birds and 5.7% ($n = 209$) of foliage-foraging birds were parasitized. There was a highly significant overall effect of foraging guild on tick parasitism, with ground-foraging birds being more likely to be parasitized than those that forage among foliage (OR = 6.22, CI = 3.47–12.17, $P \leq 0.001$), supporting the foraging guild hypothesis. Additionally, 27.5% ($n = 274$) of juvenile and 14.6% ($n = 357$) of adult birds were parasitized (OR = 2.25, CI = 1.52–3.36, $P \leq 0.001$), supporting the host age hypothesis.

DISCUSSION

The predictors of tick parasitism acted at 2 scales. At the landscape scale, the more water and impervious surface and the less tree cover within the 500-m buffer, the less likely it was for a bird to be parasitized, supporting both the

impervious surface and environmental constraint hypotheses. More urban areas typically contain more impervious surface cover and lower tree cover (Alberti 2015). Areas with more impervious surface and water cover likely act as barriers to dispersal because ticks are unable to survive long-term in dry conditions, underwater, or in areas with little understory vegetation (Hoch et al. 1971, Semtner et al. 1971, Maupin et al. 1991, Anderson 2002). The patterns observed at the 5 permanent sites were generally supported by the patterns observed at the *ad hoc* sites, suggesting that an increase in water and impervious surface cover at 500 m ultimately reduced tick parasitism on birds within the urban matrix (Fig. 3). Birds at the *ad hoc* sites of Kiptopeke, York, Suffolk, and Blackwater were more heavily parasitized than predicted (Fig. 3), but this finding may be an artifact of the timing of sampling; we sampled these sites primarily during autumn migration when most birds sampled were migrants that may have been parasitized elsewhere.

An increase in percent tree cover at the 500-m buffer was associated with higher proportions of birds being parasitized by ticks (Fig. 4). Ticks require adequate vegetative cover and leaf litter to prevent desiccation; thus, areas with higher tree cover likely provided more suitable microclimates for ticks (Alberti 2015). The model-predicted proportion of birds parasitized relative to percent tree cover at the 500-m buffer exhibited high variability above 50% cover. This finding is likely a bias associated with the limited data we collected at *ad hoc* sites, like Kiptopeke and Blackwater, where percent tree cover was generally higher than at permanent sites, coupled with a high proportion of migrant birds that may have been parasitized prior to arriving at these stopover sites.

Relative to other buffer sizes, these relationships were likely strongest for the 500-m buffer because it was more representative of the site's characteristics without encompassing large portions of surrounding areas. The 100-m buffer included only a small fraction of most sites and therefore likely underestimated the effects of water plus impervious surface and tree cover, whereas the 1,000-m and 1,500-m buffers typically extended beyond site boundaries

and thus included a variety of land cover types found outside of the areas sampled.

The predictors of parasitism were different when examined at the site scale. Once we eliminated sites with few to no ticks (i.e., Paradise, Weyanoke), the model that included bird age and foraging guild was best supported. By limiting our examination to sites where ticks were present, we were able to contrast landscape-scale predictors with phenotypic characteristics as predictors of parasitism. Ground-foraging birds were more likely to be parasitized than foliage foragers, likely because ground foragers spend most of their time in microhabitats where ticks quest, providing support for the foraging guild hypothesis. Because most ticks quest near the ground, their ability to parasitize birds that forage above the ground is limited. Thus, taxa that forage close to the ground were likely more susceptible to being parasitized than taxa within other foraging guilds (Anderson and Magnarelli 1984, Rand et al. 1998).

Juvenile birds were more commonly parasitized than adults, possibly because young birds often spend more time on the ground as fledglings where they are more likely to encounter ticks (Semtner et al. 1971, Soler 1994). Although bird sex appeared in the top-ranked model with bird age and foraging guild, this parameter was dismissed as an uninformative parameter (Arnold 2010). Thus, the host sex hypothesis was not supported in this study, yet sex could be an important determinant of parasitism for some avian taxa at particular times of year (Holmes 1986).

Overall, we found that percent water plus impervious surface, percent tree cover, foraging guild, and bird age were associated with tick parasitism of birds, suggesting a 2-step process whereby environmental variables predict tick occupancy at the landscape scale, but life-history characteristics ultimately influence parasitism within sites where ticks are present at the site scale.

Urbanization is increasing globally, and coastal southeastern Virginia is no exception. Wildlife and their associated ectoparasites are displaced, leading to species extirpation (Bradley and Altizer 2006), decreases in host species diversity, and increases in pathogen prevalence because of a reduction of pathogen-competent hosts (Melles et al. 2003, Bradley and Altizer 2006, Swaddle and Carlos 2008). Thus, studying how urbanization affects wildlife in different ways is imperative to our understanding of how faunal communities respond to habitat alteration (De Silva and Marshall 2012).

Birds may be susceptible to various tick-borne pathogens and some taxa are unique in their abilities to travel thousands of kilometers in a relatively short period of time, having the potential to spread pathogens more efficiently than other vertebrate hosts (Anderson and Magnarelli 1984; Scott et al. 2001; Hamer et al. 2012b, c); therefore, investigating species-specific susceptibility and the environmental and phenotypic factors that may influence relationships between ticks and their hosts are paramount to understanding avian population dynamics and human health risks. Resident birds may also play an important role in host-pathogen relationships because residents likely serve as reservoirs for pathogens and therefore may affect the spread of pathogens to vertebrates, including humans (Brinkerhoff et al. 2011; Hamer et al. 2012a).

Because ticks are obligate parasites and often host-specific (McCoy et al. 2013), the expectation is that tick abundance and diversity should decline concomitant with host declines (Wilson et al. 1988, Lane et al. 1991, Krasnov et al. 2004) attributed to increasing levels of urbanization (Marzluff 2001). Changes in vertebrate host species richness can also affect pathogen transmission rates (Kurtenbach et al. 2002, Hernandez-Lara et al. 2016), where a decrease in host diversity may increase the proportional abundance of reservoir-competent hosts, a concept that forms the basis of the dilution effect (Bradley and Altizer 2006, Swaddle and Carlos 2008). Moreover, reservoir competence, or the ability of an individual to support and transmit infection to a feeding vector, varies within and among taxa (LoGiudice et al. 2003, Brinkerhoff et al. 2011). Thus, the relationships among vectors, hosts, and pathogen transmission are multifaceted, further complicating vector-host relationships.

This study was limited in that we did not sample all species of birds present at each study site, primarily because of biases associated with method of capture. For example, we did not sample waterfowl, game birds, or those taxa that are high-flying because they were either too large to catch in mistnets or were species that do not regularly fly close to the ground, where mistnets were erected. Additionally, we did not survey sites to determine which species were present relative to those caught in mistnets. There is also the likelihood that we may have overlooked some parasitizing ticks because we were unable to wait for ticks to feed to repletion and fall off hosts, a method commonly used with mammals but that requires several days of monitoring (Schmidt and Ostfeld 2001). Therefore, we likely did not exhaustively sample all ticks found on birds and thus may have misclassified some individuals as being tick-free when they were not.

The interaction between landscape-scale effects of urbanization and host-parasite dynamics is not straightforward. What determines whether an area should be considered urban versus rural is idiosyncratic and largely dependent upon relatively arbitrary criteria, as is any relative metric of what constitutes high or low levels of various surface covers (e.g., impervious and impermeable surfaces). The variability in life-history characteristics of avian and tick taxa further exacerbates such relationships. Although this study demonstrates that urbanization may affect the relationships between hosts and their parasites, it is imperative to understand that these relationships are complex because birds tend to be more vagile than other hosts and therefore may be more likely to disperse ticks over long distances (Hasle 2013). This suggests that birds may play an important role in transporting ticks and tick-borne pathogens into novel areas, potentially increasing both tick and pathogen ranges (Melles et al. 2003). During autumn and spring migrations, this complication is amplified, as numerous migratory species of birds travel through Virginia on their way to wintering or breeding grounds, respectively (Hinshaw et al. 1985). Thus, we are unable to be certain that the capture site of each bird was where the parasitism initially took place. This issue is

particularly relevant for migratory taxa, species that can travel >250 km in 1 night (Stutchbury et al. 2009).

Although we do not present these data here, we did recapture many resident birds that were parasitized by ticks on multiple occasions. These recaptures occurred ≥2 weeks after the previous capture, enough time for any ticks that may have been missed to fall off because of feeding repletion (Anderson 2002, Anderson and Magnarelli 2008), suggesting that these birds were parasitized locally. Moreover, most birds were parasitized in the late spring and summer, a period during which birds establish territories and nest (Semtner et al. 1971, Holmes 1986). We, thus, suspect that most birds that were parasitized outside of the migratory periods were parasitized locally. Further study on the migratory tendencies of hosts and their movement patterns may help elucidate the timing and frequency of parasitism, particularly for migratory taxa (Schaub et al. 2001).

MANAGEMENT IMPLICATIONS

The relationships between ticks and their avian hosts is a function of the matrix of landscape habitats and the life history of hosts. As the landscape becomes more urbanized, the complex relationships among ticks and their hosts change. Ultimately, management strategies, particularly in stopover areas that provide habitat to millions of birds each migratory season, should focus on the prevention of further urban sprawl and habitat fragmentation. Providing more suitable natural habitat for both resident and migratory birds may reduce the potential for ticks, and hence tick-borne pathogens, from disproportionately affecting particular vertebrate hosts, including humans, within fragmented and urbanized habitat.

We demonstrated that habitat patches surrounded by impervious and impermeable cover are less likely to harbor ticks. Whether this pattern is a function of dispersal limitation by ticks or reduced density of potential hosts is unknown. We are not advocating that impervious buffers be created to lessen the likelihood of tick occupancy, as any increase in impervious or impermeable surfaces likely has important negative consequences for wildlife that may depend on continuous habitat for dispersal. Moreover, we did not sample non-avian vertebrate hosts; therefore, it is possible that we have uncovered only a portion of the overall pattern of vertebrate host parasitism at the sites we sampled. Future studies should focus on sampling all tick life stages both on and off potential vertebrate hosts to obtain a more accurate assessment of true occupancy and parasitism patterns attributed to increasing urbanization.

ACKNOWLEDGMENTS

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Associate Editor: Robin E. Russell.

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