Variation in Tick Load Among Bird Body Parts: Implications for Studying the Role of Birds in the Ecology and Epidemiology of Tick-Borne Diseases

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Abstract

Wild birds play important roles in the maintenance and dispersal of tick populations and tick-borne pathogens, yet in field studies of tick-borne disease ecology and epidemiology there is limited standardization of how birds are searched for ticks. We conducted a qualitative literature review of 100 field studies where birds were searched for ticks to characterize which parts of a bird's anatomy are typically sampled. To increase understanding of potential biases associated with different sampling approaches, we described variation in tick loads among bird body parts using field-collected data from 459 wild-caught birds that were searched across the entire body. The literature review illustrated a lack of clarity and consistency in tick-searching protocols: 57% of studies did not explicitly report whether entire birds or only particular body parts were searched, 34% reported concentrating searches on certain body parts (most frequently the head only), and only 9% explicitly reported searching the entire bird. Based on field-collected data, only 22% of ticks were found on the head, indicating that studies focusing on the head likely miss a large proportion of ticks. We provide tentative evidence that feeding locations may vary among tick species; 89% of Amblyomma americanum, 73% of Ambloyomma maculatum, and 56% of Haemaphysalis leporispalustris were on body parts other than the head. Our findings indicate a need for clear reporting and increased standardization of tick searching methodologies, including sampling the entire bird body, to provide an unbiased understanding of the role of birds in the maintenance and emergence of tick-borne pathogens.

Key words: bird, tick, tick-borne disease, sampling bias, sampling protocol

Wild birds are important hosts for many tick species of public health concern, as well as tick-borne pathogens responsible for disease in humans, domestic animals, and wildlife. Birds can establish new tick populations in previously un-colonized areas by dispersing them locally (Hamer et al. 2012, Schneider et al. 2015) and across continents as a result of their migratory movements (Ogden et al. 2008, Mukherjee et al. 2014, Cohen et al. 2015). Birds also contribute to the geographic expansion of tick-borne pathogens by transporting pathogen-infected ticks to new locations (Scott et al. 2015, Hornock et al. 2013), and they can serve as reservoir hosts necessary for the amplification of tick-borne pathogens (Comstedt et al. 2006, Brinkerhoff et al. 2011). Therefore, to understand most endemic and emerging tick-borne diseases, the role of wild birds must be considered, and sampling of birds for ticks must be conducted in an accurate and unbiased manner to avoid over- or under-estimation of their importance.

Historically, ticks have been sampled from wild birds using a variety of methods including: chemical removal, collection of ticks from dead birds (Brink et al. 1965), and transportation of wild birds to a laboratory setting for tick removal (Anderson et al. 1990). However, most researchers now perform visual tick searches in the field on wild birds that are temporarily restrained before being released (Hamer et al. 2012, Cohen et al. 2015). Despite the common use of this method, there appears to be little standardization in the approaches by which birds are visually searched for ticks. The use of standardized, repeatable, and minimally biased methodologies is a central hallmark of the scientific method and is likewise important for understanding the role of birds in tick-borne disease systems. The only study of which we are aware that assessed a factor biasing visual tick searches showed that inexperienced searchers find approximately one-third as many ticks as experienced searchers

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(Ogden et al. 2008). However, no studies have formally addressed other biases in the tick searching process. For example, although logistical efficiency may often require that tick searches be focused on particular bird body parts, such as the head and/or neck (e.g., Schneider et al. 2015, Di Lecce et al. 2018), no studies have quantified the frequency or potential biasing effect of this practice.

The goals of this study were to 1) conduct a qualitative literature review to describe which bird body parts are typically focused on during visual tick searches, and 2) to conduct a field study to quantify within-body variation of tick abundance and to estimate potential biases arising from focusing searches on particular bird body parts. Establishment of a standardized protocol to search birds for ticks will contribute to a more accurate representation of the importance of birds in the maintenance and dispersal of tick populations and tick-borne pathogens.

Methods

Literature Review

We conducted a literature review in Google Scholar to locate studies that searched birds for ticks; we used the search terms 'bird tick' or 'bird tick "<continent>" with no limitations on the publication year. The literature review was conducted by three of the authors, each focusing on different geographic regions to avoid any overlap in studies reviewed. Reference lists of articles retrieved from this search were also reviewed to locate additional eligible studies. Studies were only included if they involved capturing wild birds and visually searching them for ticks while alive in the field; studies were excluded if birds were killed or transported to a laboratory setting prior to searching them and/or if chemicals were administered to remove ticks. Any study that met these criteria was included in calculating the descriptive statistics presented in the results. Studies were placed into one of three categories based on information provided in the methods section describing the portion of the bird searched for ticks: 1) whole-body search, 2) concentrated search (i.e., only a portion of the bird was searched), and 3) unspecified search area (i.e., no explicit details about whether a whole-body or concentrated search was conducted). If the study fell into category 2, we also recorded the specific bird body part(s) on which searches were focused. We note that some studies in category 3 likely included whole-body searches. For example, a general description such as 'birds were searched for ticks' could have been meant to imply whole-body searches. However, without explicit reporting as such, we could not confirm these were whole-body searches and thus treated these studies as unspecified.

Bird Capture

We captured birds using mist nets in 16 parks and green spaces in Oklahoma City, Oklahoma, USA. Each site was visited twice from June to August in both 2017 and 2018 (i.e., four total site visits, with the exception of one site, which was only visited once in 2018 due to safety reasons). We sampled during these months as part of a larger study that focused on nonmigratory and summer resident birds; therefore, few in-transit migratory birds were captured and sampled. Within each year, site visits were roughly 1 mo apart. At approximately sunrise, we used five to six mist-nets (2.6 m in height, 12 m in length, 36 mm mesh, Avinet Inc., Dryden, NY) to capture birds at a site until 11 a.m. or earlier if temperatures became too warm to safely restrain birds in nets. We also attached alphanumeric aluminum bands to each bird (U.S. Department of Interior, bird banding laboratory) and recorded species, sex, weight, and age class according to Pyle, 1997. All bird handling was permitted under a U.S. federal bird banding permit (#23929) and State of Oklahoma wildlife collection permit (#6963); bird handling was also approved by the Institutional Animal Care and Use Committee at Oklahoma State University (protocol #AG-14–6).

Tick Searches

Before release, each bird was visually searched for ticks by blowing apart feathers to see all skin surfaces. The whole body of each bird was searched, and special care was taken to thoroughly search around the thighs and wings due to the difficulty of viewing the folds of skin, bones, and hollows in these locations. When conducting tick searches, we held the bird in the bander's grip (Fig. 1a) and lifted the wing via the humerus to search all fleshy and feathered portions of the wing, flank, and axilla, and each leg was also lifted to examine all areas around the thigh. When necessary to fully view the bird's body, we also used the photographer's grip (Fig. 1b) to search a birds' nape, back, and/or rump. When a tick was found, it was removed with fine-tip tweezers, 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 that required us to release it before tick removal). We recorded descriptive locations of where each tick was found according to bird anatomical definitions (Fig. 2), and extracted ticks were immediately placed in 70% alcohol before later being identified to species using pictorial keys (Keirans and Litwak 1989, Keirans and Durden 1998, Coley 2015, Dubie et al. 2017).

Data Analysis

For the literature review, descriptive statistics were used to quantify percentages of studies that conducted different visual tick searching protocols. For the field study, we estimated within-body variation in total tick loads (i.e., numbers of all tick species combined); specifically, percentages of ticks on each bird body part were calculated by summing all ticks found on that part across all birds sampled and dividing by the total number of ticks found across all body parts for the entire sample of birds. All recaptures of individual birds were treated as separate events; although recaptures are not truly independent samples, there is strong precedent for this approach in the literature (Loss et al. 2016). In addition to quantifying within-body variation in total tick loads, we used similar calculations to quantify variation in feeding locations for each of three tick species (see Results for species found). For this analysis, we were only able to use a subset of ticks (n = 156) that (1) could be removed from field-captured birds for identification to the 143 species level (i.e, we excluded ticks that were not removed and identified due to abovementioned concerns about bird welfare) and (2) had information about the body part on which they were found (i.e., we excluded multiple ticks from a single bird that were placed in a single vial and therefore could not be assigned to a particular body part). All data visualization was done in R v3.2.2 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Literature Review

We reviewed a total of 100 studies matching our inclusion criteria; our search strategy returned results from 36 countries representing 5 continents (a list of all studies is given in Supp Materials [online only]; Table 1). Of these, 57% of studies had unspecified search areas (i.e., they did not explicitly report whether a whole-body or concentrated search was conducted), 34% of studies reported using

concentrated searches focused on certain bird body parts, and only 9% of studies explicitly reported using a whole-body search methodology (Fig. 3a). Of the 34 studies with concentrated searches, 100% included searches of the head (including the eyes, bill, and ears), 29.4% included searches of the throat and/or nape, 8.8% included searches of the vent (i.e., the area around the cloaca), and 8.8% included searches of the abdomen (Fig. 3b).

Bird Captures

We conducted 459 tick searches on 432 individual birds (27 recaptures) representing 31 species (Table 1). Northern cardinal (*Cardinalis cardinalis*) and Carolina wren (*Thryothorus ludovicianus*) comprised 56.6% (260) of total captures. More tick searches were conducted in 2017 (282, 61.4%) than 2018 (177, 38.6%), despite approximately equal mist-netting effort at all sites in both years (except for the single site sampled only once in 2018 due to safety concerns).

Tick Location

A total of 111 birds representing ten species were infested with 495 total ticks (321 ticks could be removed for identification; Table 1). The three species with the most ticks included Northern Cardinal (257 ticks across 52 individuals), followed by Carolina Wren (143 total ticks across 38 individuals), and Indigo Bunting (*Passerina cyanea*; 37 ticks across 3 individuals). Three species of ticks, *Amblyomma americanum* (n = 164), *Amblyomma maculatum* (n = 115), and *Haemaphysalis leporispalustris* (n = 42) were collected. Although

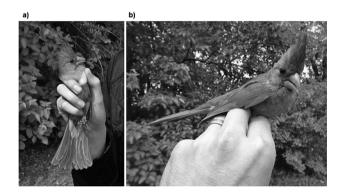


Fig. 1. A Northern Cardinal in the (a) bander's grip and (b) photographer's grip. These grips are commonly used in bird banding, and are useful when performing tick searches.

we encountered most ticks as individuals (42% of birds with only 1 tick found), a few birds were heavily parasitized (20 birds with >5 ticks), and in these cases, some clustering of ticks occurred on particular body parts (e.g., one Northern Cardinal with 32 total ticks, 31 of which were on the ear). Ticks were found on 11 different bird body parts (Table 1, Fig. 4a). Among the 495 ticks found, the most frequent body part on which they were located was around the thigh (28.5%), followed by the axilla (i.e., the 'armpit' area under the wing; 13.3%) and neck (12.7%). Notably, 78% of all ticks were found on a body part other than the head, which includes the eyes, ears, and bill (Fig. 4b), and which our literature review indicated is the most common location of concentrated searching in past studies (Fig. 3b). Further, 58% of all ticks were found on a body part other than the head or the neck/nape, the latter of which is the second most common location of concentrated searching in past studies (Fig. 3b).

Of the 156 ticks used to assess species-specific variation in tick feeding locations, 98 were *A. americanum*, 26 were *A. maculatum*, and 32 were *H. leporispalustris*. For *A. americanum*, individuals were most commonly found on the thigh (51%), axilla (15%), and wing (12%), and only 11% of individuals were located on the head. For *A. maculatum*, 27% of individuals were on the head, 27% were on the neck, and 27% were on the wing, and 19% were on the thigh. For *H. leporispalustris*, 44% of individuals were on the head, 56% were on the neck.

Discussion

Knowledge regarding the role of birds in the ecology and epidemiology of tick-borne pathogens has been greatly benefited by several decades of important studies that included sampling of ticks from birds. Nonetheless, our literature review demonstrates limitations regarding clear reporting and consistency of methods used in past studies to visually search birds for ticks in the field. Over half of reviewed studies did not explicitly state whether the entire bird or only specific body parts were searched, and one-third of studies focused searches on the head, which appears to hold only ~22% of all ticks, as indicated by our field data.

The absence of clear reporting and standardization of ticksearching methodologies not only compromises repeatability of individual studies but may also limit conclusions that can be drawn from the collective and growing body of research into the role of birds in carrying ticks and tick-borne pathogens. Notably, some studies classified in the 'unspecified' search category of our literature review may have indeed included whole-body searches. General statements

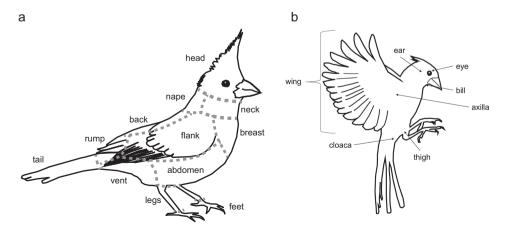


Fig. 2. A profile view of Northern Cardinal both (a) at rest and (b) in flight with relevant anatomical locations labeled.

| Species | No. of captures | No. ticks collected | No. of ticks found in each location | | | | | | | | | | |
|-------------------------------|--------------------|------------------------|-------------------------------------|------|--------|-----|-----|-------|------|------|------|-------|------|
| | | | Ax- illa | Bill | Cloaca | Ear | Eye | Flank | Head | Nape | Neck | Thigh | Wing |
| American Robin | 34 | 13 | 2 | 4 | | | | 1 | | | | 6 | |
| Bewick's Wren | 4 | 15 | 2 | | | | | | 9 | | 3 | | 1 |
| Blue Jay | 3 | 0 | | | | | | | | | | | |
| Brown Thrasher | 16 | 10 | | | | | 1 | 1 | 1 | | 2 | 5 | |
| Carolina Chickadee | 17 | 0 | | | | | | | | | | | |
| Carolina Wren | 68 | 143 | 21 | 17 | | 3 | 2 | 7 | | 18 | 32 | 22 | 21 |
| Common Grackle | 3 | 0 | | | | | | | | | | | |
| Downy Woodpecker | 4 | 0 | | | | | | | | | | | |
| Eastern Bluebird | 1 | 1 | | | | | | | | | | 1 | |
| European Starling | 4 | 0 | | | | | | | | | | | |
| Great-crested Fly- catcher | 5 | 0 | | | | | | | | | | | |
| Gray Catbird | 4 | 0 | | | | | | | | | | | |
| House Sparrow | 7 | 0 | | | | | | | | | | | |
| Indigo Bunting | 15 | 37 | | | | 6 | 1 | | | 13 | 15 | 2 | |
| Least Flycatcher | 4 | 0 | | | | | | | | | | | |
| Northern Cardinal | 192 | 257 | 41 | 7 | 1 | 48 | 3 | 19 | 5 | 1 | 8 | 100 | 24 |
| Northern Mockingbird | 5 | 0 | | | | | | | | | | | |
| Painted Bunting | 32 | 16 | | 1 | | | 1 | | | 3 | 3 | 2 | 6 |
| Tufted Titmouse | 12 | 1 | | | | | | | | | | 1 | |
| White-eyed Vireo | 13 | 0 | | | | | | | | | | | |
| Yellow-billed Cuckoo | 3 | 2 | | | | | | | | | | 2 | |
| Total | 459* | 495 | 66 | 29 | 1 | 57 | 8 | 28 | 15 | 35 | 63 | 141 | 52 |

Table 1. Numbers and species of bird capture events with visual tick searches conducted, and location where ticks were found; resultsare based on field sampling in Oklahoma City, Oklahoma, USA, June–August 2017–2018 (Species' common names follow the AmericanOrnithologists Society 2018, Chesser et al. 2018)

*Total includes 9 unlisted bird species with a sample size of captures <3 (13 total individuals across the 9 species) and no ticks found. Species excluded are: American Goldfinch, Bell's Vireo, Blue-gray Gnatcatcher, Brown-headed Cowbird, Eastern Phoebe, Eastern Wood-pewee, Louisiana Waterthrush, Red-eyed Vireo, Summer Tanager, *Empidonax* spp. (unidentified flycatchers in the *Empidonax* genus).

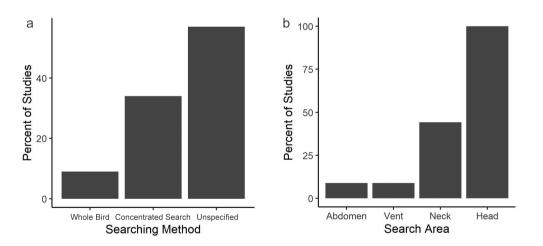


Fig. 3. (a) Percentage of all reviewed studies (n = 100) implementing each approach to search birds for ticks including: 1) whole bird (i.e., a whole-body search explicitly reported), 2) concentrated search (only a portion of the bird was searched), and 3) unspecified (i.e., no explicit reporting of whether a whole-body or concentrated search was conducted); b) among studies implementing a concentrated search approach (n = 34), percentage concentrating on specific bird body parts.

about tick searches being conducted, without explicit reporting of whether they included the whole bird or only particular body parts, could have been meant to imply whole-body searches. However, the nontrivial proportion of studies explicitly noting a focus on particular bird body parts (34%) supports our classification approach and suggests that such general descriptions cannot automatically be assumed to represent whole-body searches (Lydecker et al. 2019). Unclear or differing methodologies can limit direct comparisons of results generated in different locations or during different time periods, and they also contribute uncertainty and/or bias to synthetic analyses that combine data from multiple studies in assessing large-scale variation or drivers of the role of birds in tick-borne disease transmission (e.g., Brinkerhoff et al. 2011, Loss et al. 2016). Perhaps most importantly, our understanding of the role of birds in

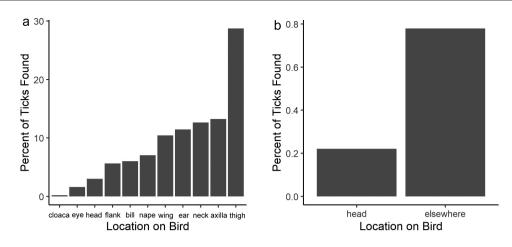


Fig. 4. For field-sampled wild birds from Oklahoma City, Oklahoma, USA, June–August 2017–2018, (a) Percentage of all ticks (*n* = 495 total ticks on *n* = 111 birds) found on each bird body part, and (b) Percentage of ticks found on the head (includes head, eye, ear, and bill categories from Fig. 2a) versus elsewhere (includes all other categories).

tick-borne pathogen transmission may be incomplete. Concentrating search effort on a bird's head and/or neck may sometimes be required for logistical efficiency, but it must also be recognized that the tradeoff of this efficiency may be a dramatic underestimation of the prevalence and intensity of tick infestation of birds, with associated implications to our understanding of disease transmission systems. Our field data suggest searching the entire bird for ticks will yield approximately 4.5 times more total ticks than searching only on the head and 2.5 times more ticks than searching the head and neck. This suggests that the proportion of birds carrying ticks, the average number of ticks on each bird, and thus the importance of birds in maintaining and dispersing tick populations and tick-borne pathogens, may be greater than previously thought.

Whether our results related to the distribution of ticks on birds' bodies are broadly generalizable remains uncertain, as our study was heavily focused on passerines (perching birds like cardinals, wrens, and thrashers) and was fairly limited in sample size (n = 459 total)bird searches), seasonal coverage (June-August), and geographic area (one city in the central United States). Nonetheless, most of the bird and tick species sampled have relatively large geographic distributions, potentially making these results widely applicable. For example, most of the bird species captured, including the two most commonly sampled species (Northern Cardinal and Carolina Wren) have geographic distributions that span at least the eastern half of the United States. Two of the three tick species collected (A. americanum and H. leporispalustris) also range across the eastern half of the United States, as well as much of Mexico and southern Canada (Brown et al. 2005, Springer et al. 2015), transmitting pathogens such as Ehrlichia spp. and Francisella tularensis that widely cause diseases in humans, domestic animals, and wildlife. Although our results may be more broadly applicable, additional research is needed in other regions, countries, and continents, during seasons other than summer, and with a variety of tick species and nonpasserine birds, to elucidate whether exceptions exist to the patterns we documented.

Our data for individual tick species tentatively suggest the possibility of interspecific variation in tick foraging locations on birds. Whereas 89% of *A. americanum* and 73% of *Ambloyomma maculatum* were on body parts other than the head, but roughly half (44%) of *H. leporispalustris* individuals were found on the head. This finding suggests that the pattern of ~78% of all ticks occurring on locations other than the head could be driven by *A. americanum*, the most abundant tick in our sample. However,

we note that the subsample of ticks used for the species-level analysis was small (e.g., 26 A. maculatum; 32 H. leporispalustris) and may be biased in terms of what bird body parts are represented; specifically, we may have removed and identified more ticks from the head simply as a result of greater detectability of ticks on this body part (discussed further below). Although we found single ticks on most infested birds, clustering of ticks may further limit our analysis, as multiple ticks found on one bird and/or within a group clustered on a particular part of an individual bird's body part are not necessarily statistically independent replicates. Notably, we did not detect any Ixodes spp., the tick genus that transmits Borrelia burgdorferi and is the primary focus of many studies that investigate the importance of birds as hosts for ticks and tick-borne disease in the United States (Loss et al. 2016) and Europe (Rizzoli et al. 2014). We are unaware of any peer-reviewed studies documenting whether Ixodes spp., or any other tick species, preferentially feed on particular bird body parts. Therefore, it is unclear if the biases suggested by our study would also be expected when searches for these other tick species focus on birds' heads. Although we recommend whole-body tick searches whenever possible, we encourage future studies to quantify species-specific patterns of tick feeding locations on birds, as such information can help clarify if there are certain circumstances when focused tick searches are warranted (e.g., if the study is focused on particular tick species with a clearly documented pattern of feeding location preference). Such information would also allow testing of hypotheses related to mechanisms of species-varying infestation patterns (e.g., interspecific competition for space on birds).

We did not formally quantify whether tick foraging locations differed among bird species due to lack of replication for most species. However, such variation may be expected because bird species have varying habitat associations and foraging behaviors—which likely influences the species of ticks encountered—and different preening behaviors, which may influence which ectoparasites, including ticks, are removed and which remain attached (Hodgson et al. 2001). A descriptive summary of our data (Table 1) suggests such variation among bird species is possible. For example, whereas the thigh was the most parasitized location for Northern Cardinal (~39% of ticks on this species) and 5 other species, the most parasitized body part for most other species was on or near the head (including the bill, ear, eye, head, nape, and neck categories in Fig. 1). The large number of cardinals captured (192, 42% of all birds

sampled), the large number of ticks from this species (257, 52% of all ticks sampled), and the high rate of tick infestation on body parts other than the head, likely played an important role in the overall tick infestation patterns we documented. Further research with greater replication of individuals for different bird species would allow more formal modeling of the independent and interactive effects of bird species and tick species on the location where ticks are found.

Conducting whole-body searches of birds for ticks will reduce bias by ensuring birds are searched similarly across studies; however, this approach will not account for individual observer variation in tick detection rates or other factors influencing tick detection. We encourage additional studies to test and refine hypotheses regarding these potential biasing factors. For example, tick size, life stage, state of engorgement, and location on the bird's body could affect detectability; specifically, we hypothesize that smaller tick species and life stages, as well as less-engorged ticks, may be systematically under-represented in the literature. Related to the location of ticks on birds, we hypothesize that tick detection may be easiest on the bird's head, especially near the eye and bill where feathers are scarce relative to the rest of the body. Characteristics of birds may also influence tick detection, including plumage and skin coloration, size, body condition (which influences the shape of the body), and docility (which influences the difficulty of restraining birds during tick searches). In particular, the pattern and stage of feather molt, which affect the density and distribution of feathers on individual birds, are likely to affect tick detection because observers visually search by blowing bird feathers apart. Finally, factors related to observers are also expected to influence tick detection. Observer experience in conducting tick searches has been shown to influence numbers of ticks found (Ogden et al. 2008), and other factors, such as visual ability and experience in handling and restraining birds, may also play a role.

Despite the above potential limitations in the geographic, seasonal, and taxonomic scope of our conclusions, we argue that this study provides more than sufficient evidence indicating that-in the absence of information suggesting otherwise-researchers sampling birds for ticks should search the entire bird's body and explicitly report this approach to sampling. Ticks typically move no more than a few meters in their entire lifetime and primarily depend on hosts, including birds, for long-distance movements (Estrada-Pena 2003, Pfäffle et al. 2013). Further, as climate change, land cover change, and other global changes continue to make previously inhospitable areas suitable for tick colonization (Brownstein 2005; Ogden et al. 2006; Porretta et al. 2013), birds and other mobile hosts may become even more important in dispersing ticks and tick-borne pathogens. Thus, it will be essential to thoroughly and accurately sample birds and other hosts for ticks in order to understand and better predict tick-borne disease transmission and emergence in the future. The whole-body searching strategy that we propose here, and that is described in the methodology of this paper, will contribute to the accurate representation of the importance of birds in maintaining and dispersing tick populations and tick-borne pathogens.

Supplementary Material

Supplementary data are available at Journal of Medical Entomology online.

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