Parasitology Research (2020) 119:2039–2045
https://doi.org/10.1007/s00436-020-06698-0

ARTHROPODS AND MEDICAL ENTOMOLOGY - ORIGINAL PAPER

Low host specificity and lack of parasite avoidance by immature ticks in Brazilian birds

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Received: 28 February 2020 / Accepted: 21 April 2020 / Published online: 7 May 2020

Abstract

Ticks are ectoparasites that feed on blood of a broad taxonomic range of terrestrial and flying vertebrates and are distributed across a wide range of environmental conditions. Here, we explore the biotic and abiotic factors on infestation probability of ticks of the genus *Amblyomma* and assess the degree of host specificity based on analysis of 1028 birds surveyed across Brazil. We show that tick infestation rates exhibited considerable variation across the 235 avian species analyzed and that the probability of an individual bird being parasitized by immature ticks (larvae and nymphs) increased with annual precipitation. Host phylogeny and two host ecological traits known to promote tick exposure (body mass and foraging behavior) did not predict infestation probability. Moreover, immature ticks displayed a low degree of host specificity at the family level. Lastly, tick occurrence in birds carrying infection with avian malaria and related parasites did not differ from those free of these haemosporidian parasites, indicating a lack of parasite avoidance by immature ticks. Our findings demonstrate that tick occurrence in birds across Brazilian biomes responds to environmental factors rather than ecological and evolutionary host attributes.

Keywords Avian malaria · *Amblyomma* · Co-infection · Hard tick · Parasite avoidance · Parasite specialization

Introduction

Parasitic organisms have evolved to maximize host exploitation using complex and diverse life history strategies to complete their life cycles (Poulin 2007). Birds can harbor a myriad of parasitic organisms, often with multiple parasites inhabiting the same individual host within the host community, thus creating the potential for multi-faceted interactions

Section Editor: Domenico Otranto

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00436-020-06698-0) contains supplementary material, which is available to authorized users.

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between the parasites and hosts (Cox 2001; Lutz et al. 2017). From the host perspective, it would be advantageous to detect and avoid parasites and pathogens due their detrimental effects, even if avoidance is costly to evolve (Sarabian et al. 2018). Competition between parasites within a coinfected host has led several parasites to evolve behavioral strategies and cues to avoid the presence of other conspecific or heterospecific parasitic and pathogenic organisms (Read and Taylor 2001; Poulin 2007). For instance, ticks can recognize previously infested hosts with acquired tick resistance, therefore avoiding the negative effect of parasitizing a host with increased numbers of protective immune cells, such as basophils (Eberle and Voehringer 2016). Host selection and host avoidance are important examples of behavioral and physiological adaptations that ensure parasite survival, reproduction, and eventual transmission (Izraylevich et al. 1995; Christe et al. 2007; Tinsley et al. 2020).

Parasites exhibit different degrees of host specificity, ranging from infecting closely related host species like avian malaria parasites (Fecchio et al. 2019a) to parasitizing a broad taxonomic range of vertebrate hosts as seen in immature hard ticks (Nava and Guglielmone 2013; Esser et al. 2016a). Ticks are ectoparasites that feed on the blood of terrestrial and flying vertebrates during all postembryonic stages of their life cycle (Nava et al. 2017). These hematophagous parasites display different strategies to encounter their hosts, seeking actively or waiting on vegetation (questing) to attach to their intermediate or definitive hosts (Godfrey et al. 2011; Ramos et al. 2017). During the stages of their life cycle when not on or attached to a host, ticks are exposed to a range of climatic conditions across variable landscapes. Hence, distribution and prevalence of some tick species may be constrained by adaptations to environmental conditions rather than adaptation to the host (Esser et al. 2016a).

Prevalence, host specificity, and diversity of ticks may vary greatly across their definitive and intermediate hosts (Nava and Guglielmone 2013; Esser et al. 2016a, b). For example, immature ticks (larvae and nymphs) can feed opportunistically on several bird species in the same community (Luz and Faccini 2013). This indiscriminate feeding behavior could be interpreted as evidence that immature ticks are host-generalists capable of parasitizing a broad diversity of avian hosts in a given locality. On the other hand, adult ticks display a certain degree of specialization across their mammalian hosts and have also shown increased diversity when associated with large-bodied hosts (Esser et al. 2016a, b). Therefore, host attributes such as phylogenetic relatedness and body weight may also explain the interspecific differences in prevalence and specialization of ticks across bird communities.

Here, we tested whether climatic condition, avian ecological traits, and host phylogeny explain tick prevalence across avian species in four Brazilian biomes. Based on the theory of parasite avoidance (Read and Taylor 2001; Poulin 2007), we hypothesize that ticks will be more prevalent on birds that are not infected by avian haemosporidian parasites. We also measured the degree to which immature ticks are host-specific across 12 avian communities surveyed in Brazil, a megadiverse region supporting almost 2000 bird species (Piacentini et al. 2015) and 74 species of ticks (Martins et al. 2019).

Methods

Bird and parasite sampling

We collected 1028 individual birds from 12 avian communities spanning a latitudinal gradient of 0° to 27° S ≈ 3000 km (Fig. 1). The sampling sites were located in four biomes: Amazonia, Cerrado, Caatinga, and Atlantic Rain Forest. Detailed characterization of these sites including elevation, precipitation, temperature, and avian host community composition for each of the 12 avian communities can be found in Fecchio et al. (2019b, 2020) and Supporting Information Table S1. These sampling sites were surveyed as part of a long-term study on avian parasites across the New World, with part of the results on avian haemosporidians already published by Fecchio et al. (2019b) and Fecchio et al. (2020). Likewise, Martins et al. (2014) have published tick occurrence data from five Amazonian avian communities.

Netted birds were either ringed and released or euthanized and prepared as museum specimens in accordance with corresponding permits. In the field, each bird was examined for ticks through carefully checking the entire body. For detection of avian haemosporidian parasites approximately 50 μL of blood was collected from the brachial vein and stored either in 95% ethanol or on FTA cards. All birds were collected under appropriate Brazilian permits, and vouchers are deposited at Instituto Nacional de Pesquisas da Amazônia and the Ornithological Collection of Federal University of Mato Grosso, Brazil. Bird species nomenclature follows the BirdTree project (Jetz et al. 2012).

Ticks were removed with tweezers, stored in 95% ethanol, and identified using current taxonomic keys (Martins et al. 2010, 2013). Ticks collected in this study are deposited in the tick collection "Coleção Nacional de Carrapatos Danilo Gonçalves Saraiva" (CNC) of the Faculty of Veterinary Medicine of the University of São Paulo, Brazil.

Haemosporidian parasites from the genera *Haemoproteus*, *Leucocytozoon*, *Parahaemoproteus*, and *Plasmodium* were screened using a standard molecular barcoding approach. Briefly, DNA extracted from avian tissues underwent nested PCR-based detection targeting a 477 bp barcoding fragment of the cyt-*b* gene from the haemosporidian mitochondrial genome. Details on primers used, reaction protocols, and cycling

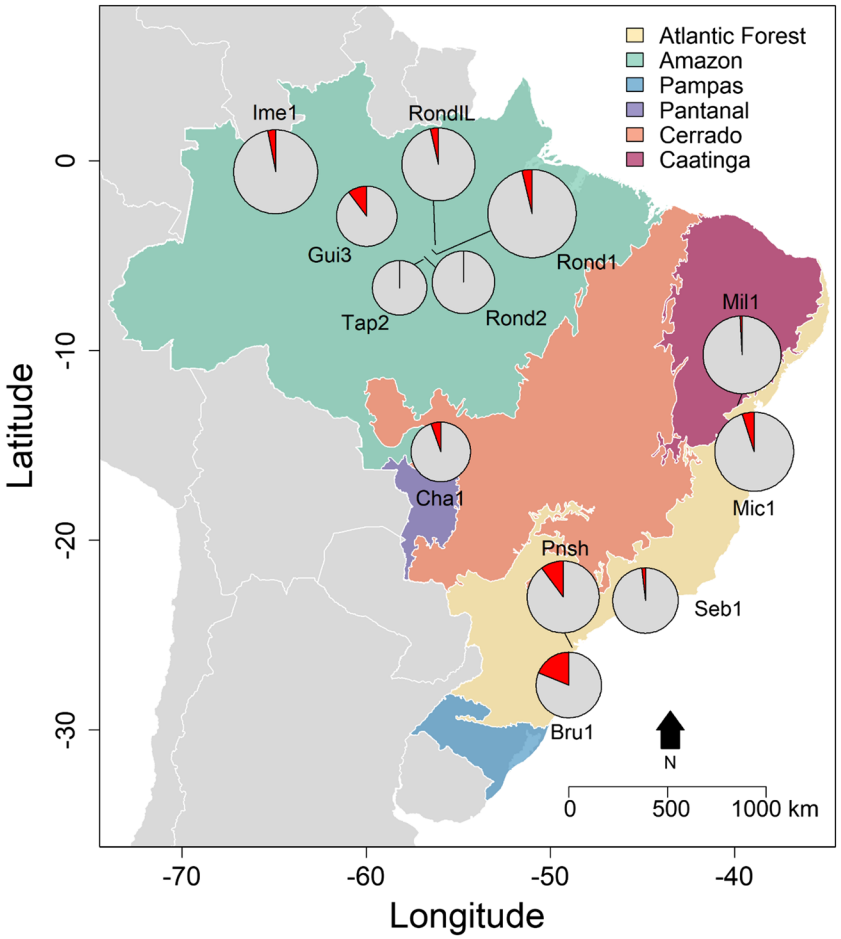

Fig. 1 Map of Brazil showing the 12 sampling locations. Size of pie charts indicates the number of birds sampled at each location. The largest circle represents 214 individuals and the smallest circle represents 27 individuals. The pie charts indicate the proportion of birds with (red) and without (gray) ticks

conditions can be found in Hellgren et al. (2004) and Bell et al. (2015).

Statistical analysis

Avian host species traits that may influence exposure to ticks (revision in Newman et al. 2015) were extracted from the EltonTraits v. 1.0 database (Wilman et al. 2014). The selected traits included the relative proportion of time that a given bird species spends foraging in lower and upper level canopies and the species' average body mass. We considered body mass as a continuous variable and foraging behavior as categorical variable. Foraging strata are given by the EltonTraits database (Wilman et al. 2014) as a semiquantitative trait, informing the relative importance of each category. We created four categories based on the foraging stratum information (water, ground/understory, midhigh/canopy, and multiples strata; the latter for species that forage proportionally in more than two strata; i.e., score of ≤ 50 in all the other categories).

We fitted a Phylogenetic Generalized Linear Mixed Model (Ives and Garland 2014; Ives 2018) using the function *MCMCglmm* from the package "MCMCglmm" (Hadfield 2010) to investigate the influence of abiotic factors (annual mean temperature, mean diurnal temperature range, annual precipitation) and biotic factors (host foraging stratum, host body weight, and the presence or absence of blood parasites) on the probability of tick occurrence across avian communities. The function creates a linear mixed model using Bayesian Markov Chain Monte Carlo to account for the influence of the phylogeny (Hadfield 2012). We used a phylogeny based on the Hackett backbone (Hackett et al. 2008) obtained from the Birdtree project (http://birdtree.org, Jetz et al. 2012) as a random effect to control for phylogenetic nonindependence and categorical mixed model using the logit link function and set largely uninformative priors. To ensure model convergence, we ran the model for 1000,000 iterations, with a 1000 burn-in period, and stored samples every 100 interactions. The model resulted in comparable effective sample size for all factors (~1000). Data for all numeric predictor variables were log transformed. We excluded information from two individuals classified as foraging on or just below water surface from the original dataset due to the low sample size for this category.

To investigate the degree of tick host specialization we used the package "bipartite" (Dormann et al. 2008) to calculate two ecological metrics for the tick-host network. Bipartite

networks represent the associations between species belonging to two different trophic levels. We calculated the network specialization index H_2 for the entire bipartite network. Higher values of H_2 indicate more selective species for the web (Blüthgen et al. 2006). We also calculated the Kullback–Leibler distance d, which estimates the degree of specialization at the species level, evaluating how a given species deviates from a random association with the hosts available (Dormann 2011). Both H_2 and d values are normalized and range from 0 (lowest specificity) to 1 (highest specificity; Blüthgen et al. 2006).

Finally, we tested the entire network specialization index against null models based on 10,000 randomized networks with the method "r2dtable" (Dormann et al. 2009). The null model was based on the algorithm that randomly assigns the interactions across the species in the network while keeping the totals for columns and rows identical to the observed dataset (Patefield 1981). The tick larvae found on bird species were not considered for the calculation of the network metrics because they could not be identified to species. All analyses were undertaken using the software R (version 3.6.1, R Development Core Team 2020).

Results

We analyzed 1028 individual birds surveyed across 12 avian communities in Brazil (Fig. 1). These individuals belong to 235 avian species, 31 families, and 11 orders (see raw data for sample size, prevalence, and tick species found by avian taxa, time of year, and location in Supporting Information Table S1). Overall tick prevalence was 4.7%, with heterogeneity across sampling sites (Fig. 1). The highest prevalence was observed in an area of Atlantic Forest in Southern Brazil where ticks were found on 18.9% of individual hosts, whereas no ticks were found in two out six areas in the Amazon (Fig. 1). Without considering Falconidae where the single sampled individual was parasitized, the most parasitized family was Turdidae, with ticks found on 16.7% of individuals ($n = 42$). Within Turdidae, the highest prevalence was observed in the pale-breasted thrush (*Turdus leucomelas*; $n = 4$) and in the rufous-bellied thrush (*Turdus rufiventris*; $n = 4$) with 25.0% of the sampled individuals parasitized. However, the highest overall prevalence was observed in the sooty grassquit (*Tiaris fuliginosus*; $n = 3$) with ticks found on 66.6% of sampled individuals. A single individual white-shouldered antshrike (*Thamnophilus aethiops*) was parasitized by two different species of ticks (*Amblyomma calcaratum* and *Amblyomma longirostre*).

When evaluating the effects of the predicting variables on the probability of tick infestation, annual precipitation of the sampling area was positively associated with a high probability of an individual bird being infested by ticks (Table 1). In other words, ticks were more likely to be found parasitizing birds in areas with a higher annual precipitation. The prevalence of ticks found on birds infected by blood parasites was 3.2%, whereas the prevalence of ticks on birds without blood parasites was 5.3%. Despite the trend of lower probability of tick infestation in birds harboring blood parasites, this difference was not statistically significant in our model (Table 1). We did not find any effect of foraging stratum, host body weight, annual mean temperature, or mean diurnal temperature range on the probability of tick infestation (Table 1).

Only immature tick stages were found on avian hosts. Nymphs were the most commonly found, and were observed on 29 individual hosts, whereas larvae were observed on 19 individual hosts. Ticks were found on individual hosts from 13 bird families with an apparent level of specificity for some tick species (Fig. 2). However, the network specialization index was generally low for the overall tick-host association ($H_2 = 0.31$). Consequently, the tick-host association did not differ significantly from random network models ($P = 0.272$).

The most common tick species in the sampled areas was *Amblyomma longirostre*, which we found parasitizing 16 individual hosts. Tick specialization in the network varied among tick species. *Amblyomma calcaratum* showed the highest level of specificity ($d = 0.43$), followed by *Amblyomma nodosum* ($d = 0.31$) and *Amblyomma longirostre* ($d = 0.26$). The other tick species found parasitizing birds (*Amblyomma sculptum*, *Amblyomma coelebs*, *Amblyomma geayi*, and *Amblyomma humerale*) were considered generalists (all $d = 0.14$).

Discussion

The low prevalence of ticks found in the present study (4.7%) and heterogeneity across host species are consistent with previous studies across Brazilian biomes surveyed in undisturbed areas (Ogrzewalska et al. 2011; Martins et al. 2014; Lugarini et al. 2015). Our models reveal that the probability of a bird being parasitized by ticks is higher in avian communities from rainy regions across Brazil. The model estimates that an increase of 500 mm of annual precipitation would result in a 1.91 increase in a bird's odds of being parasitized by immature ticks (Table 1). This finding is puzzling considering that ticks are not dependent on water for reproduction and development. However, wetter regions in South America also support higher vertebrate diversity (Borregaard et al. 2020). The indirect correlation between annual rainfall and diversity of both intermediate and definitive vertebrate hosts may explain the heterogeneity in tick prevalence across avian communities. It is important to mention that regions with higher precipitation also correlate with higher plant diversity and biomass. Tree cover may also explain the occurrence of ticks as these parasites are sensitive to direct solar radiation while questing for their hosts.

Table 1 Phylogenetic generalized linear mixed model, using MCMCglmm, evaluating the effect of the presence of blood parasites (present or absent), annual mean temperature (logarithmic scale (°C)), mean diurnal range (logarithmic scale (°C)), annual precipitation (logarithmic scale (°C)), foraging strata (ground/understory, midhigh/canopy or multiples), and body mass (logarithmic scale (g)) on the probability of tick infection on birds from a latitudinal gradient in Brazil

		95% CI		
Variable	Estimate	Lower	Upper	pMCMC
Intercept	− 3.42	− 19.83	11.91	0.672
Blood parasites: present	− 0.93	− 2.05	0.05	0.064
Annual mean temperature	− 1.36	− 3.63	1.04	0.264
Mean diurnal range	− 1.69	− 3.78	0.34	0.110
Annual precipitation	1.60	0.24	2.98	**0.007**
Foraging stratum: midhigh/canopy	0.62	− 0.43	1.64	0.242
Foraging stratum: multiples	0.13	− 0.82	1.01	0.783
Body mass	0.52	− 0.09	1.16	0.110

Therefore, we suggest that tree cover jointly with precipitation and vertebrate diversity might explain the occurrence of ticks across Brazil and future studies should explore this premise by including adult ticks and other groups of vertebrates into statistical modeling.

The immature ticks identified to species showed no host selection across avian host communities as they parasitized a broad taxonomic range of avian hosts and displayed low degrees of host specificity. This lack of avian host specificity for the larvae and nymphs of *Amblyomma* ticks is consistent with previous studies of ticks parasitizing vertebrates in the Neotropics (Luz and Faccini 2013; Nava and Guglielmone 2013; Esser et al. 2016a) and highlights the generalist and opportunistic feeding behavior of immature ticks on vertebrate hosts at lower taxonomic levels. The broad spectrum of distantly related avian host species used by *Amblyomma* ticks could be interpreted as evidence that immature ticks are host-generalists capable of parasitizing an enormous diversity of vertebrate hosts at a given locality. However, specificity does exist among species of *Amblyomma*, but it is constrained to higher taxonomic levels. For example, some species display specificity for classes of vertebrates such as amphibians, reptiles, and birds (Barros-Battesti et al. 2006; Nava and Guglielmone 2013).

Host phylogeny and host foraging behavior although previously identified as strong predictors of tick prevalence across avian communities (revision in Newman et al. 2015) did not predict the probability of a bird being parasitized by ticks across the Brazilian biomes analyzed for the present study. Moreover, our results do not support previously

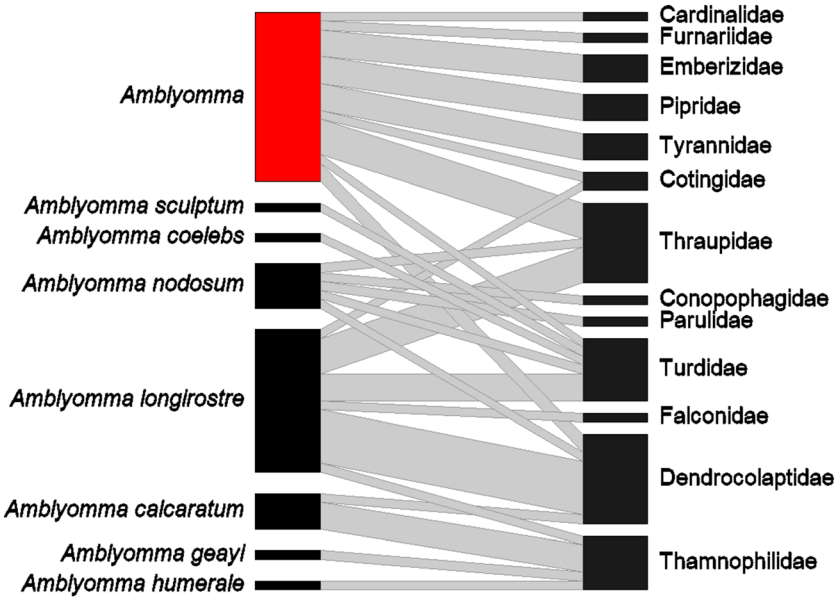

Fig. 2 Network of ticks (left nodes) and their host bird family (right nodes) from a large latitudinal gradient in Brazil. Interactions are indicated by lines connecting taxonomic boxes. Box size and line width indicate the frequency of the interactions. Red box consists of *Amblyomma* larvae not identified to species

published findings indicating an increase in tick infestation and prevalence in large-bodied avian hosts (Brinkerhoff et al. 2019). This suggests that environmental rather than ecological and historical factors may play a more significant role in the distribution of immature ticks among their intermediate avian hosts across Brazilian biomes.

Numerous examples of interactions between micro- and macro-parasites and parasites and pathogens that might affect the outcome of parasitic infections and therefore parasite prevalence across host populations were summarized and debated by Cox (2001). Since then, the literature on the multi-faceted interactions between co-infecting vector transmitted pathogens, their hosts, and the environment has expanded dramatically. Here, we report for the first time, an interaction between an ectoparasite that feeds on blood and a ubiquitous group of blood protozoan parasites, both of which use avian hosts during part of their life cycle. Contrary to our expectation, we found that immature ticks were parasitizing birds carrying haemosporidian infections with a frequency similar to those observed on birds free of these common and diverse blood parasites, indicating that immature ticks of the genus *Amblyomma* do not avoid attaching to and feeding on birds harboring chronic avian malaria parasite infections. Alternatively, ticks may not recognize immunological host response caused by pathogens and parasites not transmitted by other arthropods, such as mosquito transmitted blood parasites. Nevertheless, the presence of haemosporidians in avian hosts could influence tick occurrence by altering bird movement, and therefore tick encounter rates. For example, birds during the acute phase of haemosporidian infection might be less active, foraging less, and therefore causing lower tick prevalence in avian species more susceptible to avian haemosporidian infections. Future studies with controlled experimental designs may confirm whether avian malaria parasites can have indirect effects on tick occurrence and dispersal due reduced flight ability, which could impact the transmission of the tick-borne agents (e.g., *Borrelia* and *Rickettsia*) of public health and veterinary interest.

Funding information This work was funded by US National Science Foundation grants DEB-1503804 to JDW and DEB-1120734 to VVT. Field collection was supported in part by grant from the Instituto Nacional de Ciências e Tecnologia em Áreas Úmidas (INAU). During the project, AF was supported by a postdoctoral fellowship (PNPD scholarship) and GMT by a PhD scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

Compliance with ethical standards

Both the American Ornithologist's Union and University of North Dakota Animal Care and Use Committee guidelines (Project No. 1402-1) for ethically collecting avian blood and tissue samples were strictly followed.

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

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