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EDITOR'S CHOICE

Migration and season explain tick prevalence in Brazilian birds

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Abstract. Neotropical birds are mostly parasitized by immature ticks and act as reservoir hosts of tick-borne pathogens of medical and veterinary interest. Hence, determining the factors that enable ticks to encounter these highly mobile hosts and increase the potential for tick dispersal throughout migratory flyways are important for understanding tick-borne disease transmission. We used 9682 individual birds from 572 species surveyed across Brazil and Bayesian models to disentangle possible avian host traits and climatic drivers of infestation probabilities, accounting for avian host phylogenetic relationships and spatiotemporal factors that may influence tick prevalence. Our models revealed that the probability of an individual bird being infested with tick larvae and nymphs was lower in partial migrant hosts and during the wet season. Notably, infestation probability increased in areas with a higher proportion of partial migrant birds. Other avian ecological traits known to influence tick prevalence (foraging habitat and body mass) and environmental condition that might constrain tick abundance (annual precipitation and minimum temperature) did not explain infestation probability. Our findings suggest that migratory flyways harbouring a greater abundance of migrant bird hosts also harbour a higher prevalence of immature ticks with potential to enhance the local transmission of tick-borne pathogens and spread across regions.

Key words. Acari, *Amblyomma*, avian migration, bird life history, hard tick, immature ticks, Ixodidae, migratory behaviour, migratory flyways, tick infestation.

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Introduction

Ticks are ectoparasites that depend on blood from terrestrial and flying vertebrates for development and reproduction (Guimarães *et al.*, 2001). These cosmopolitan hematophagous parasites are distributed across a wide range of vertebrate clades and environmental conditions (Guglielmone *et al.*, 2003; Nava *et al.*, 2017). Due to their feeding behaviour and use of humans, domestic and wild animals as intermediate and definitive hosts, ticks act as vectors for a broad diversity of pathogenic microorganisms that cause diseases at the human-wildlife interface, such as Lyme disease, Rocky Mountain spotted fever and tick-borne encephalitis (Piesman & Eisen, 2008; Stanek *et al.*, 2012).

Hard ticks belonging to the genus *Amblyomma* are the most diverse and common group of ticks parasitizing Neotropical vertebrates (Guglielmone *et al.*, 2003; Nava *et al.*, 2017). Although adult ticks display a certain degree of host specificity to large mammals (Esser *et al.*, 2016a), they are rarely found parasitizing avian hosts (Luz & Faccini, 2013; Martins *et al.*, 2014). Nonetheless, immature ticks (larvae and nymphs) can feed on birds and display host specificity at avian host family level (Luz & Faccini, 2013; Fecchio *et al.*, 2020a). Adult hard ticks have evolved different strategies to encounter their definitive hosts, ranging from actively seeking to waiting on vegetation (questing) to attach to their mammalian hosts. Whereas the behaviour and strategy that immature ticks use to encounter their intermediate avian hosts are unknown for most species of *Amblyomma* (Luz & Faccini, 2013; Ogrzewalska & Pinter, 2016). Therefore, determining the host traits that promote exposure to immature ticks and increase the potential for tick dispersal across regions is important for understanding spatial epidemiology of tick-borne pathogens.

Birds harbour several species of ticks and, in general, at lower prevalence across avian hosts (Luz & Faccini, 2013). Although host specialization is not a prominent aspect in the avian-tick association and evolutionary history, birds are known to act as reservoir hosts of several tick-borne pathogens of medical and veterinary importance (Piesman & Eisen, 2008; Stanek *et al.*, 2012). Because birds are highly mobile hosts and can fly long distances during migration, they have been implicated in the geographic range expansion of *Ixodes scapularis* in the Nearctic region (Ogden *et al.*, 2008; Hamer *et al.*, 2012; Schneider *et al.*, 2015). Moreover, migrating birds can potentially disperse tick-borne pathogens and spread zoonotic disease across host populations (Hasle, 2013). Migratory songbirds have played an important role in the transmission of Lyme Disease across North America (Ogden *et al.*, 2008; Hamer *et al.*, 2012; Schneider *et al.*, 2015). Thus, large-scale tick-bird surveys across avian migratory flyways can be useful to study spatial epidemiology and forecast the spread of tick-borne pathogens.

The probability of a bird being parasitized by ticks is highly variable across avian host species and changes throughout the seasons of the year. Spatial and temporal heterogeneity in tick prevalence can be explained by interacting avian host traits and tick phenology that enable host exposure (Hönig *et al.*, 2015). For example, the probability of an individual bird being infested with immature hard ticks was higher for resident birds that forage at ground level and during the transition between dry and wet season in the Brazilian Pantanal (Fecchio *et al.*, 2020b). This result is possibly because larvae and nymphs are more abundant in the leaf litter during the drier periods in the biome Pantanal (Ramos *et al.*, 2014, 2016), therefore, enhancing contact rates between birds and immature ticks prior to the avian breeding season (Fecchio *et al.*, 2020b). Furthermore, host body size is expected to impact tick prevalence because larger hosts can harbour a higher abundance and diversity of ticks (Mohr, 1961; Esser *et al.*, 2016b).

Spatial heterogeneity in infestation probability by ticks may not only result from variation in bird life history traits and tick life cycles but also from environmental conditions. Indeed, annual precipitation has been shown to increase tick prevalence across avian communities in Brazil (Fecchio *et al.*, 2020a). Because ticks are ectodermic parasites, temperature and humidity may also impact their activity and distribution (Estrada-Peña *et al.*, 2014; Nava *et al.*, 2017).

Here, we determine the impact of avian host life history and habitat conditions on tick prevalence across bird communities in five Brazilian biomes. Specifically, we tested the influence of biotic factors (migratory behaviour, host body mass and preferred foraging habitat) and abiotic factors (annual precipitation and minimum temperature) on tick prevalence. We also tested whether avian communities with higher proportion of migrant individuals harbour higher prevalence of ticks. We included season in our analysis because tick abundance and diversity are temporally variable in Brazil (Labruna *et al.*, 2009; Barbieri *et al.*, 2019; Fecchio *et al.*, 2020b). All of these variables are associated with tick exposure and thus can modulate, to some extent, variation in the prevalence of ticks in avian communities.

Material and methods

Bird and tick sampling

We analysed 9766 individual birds surveyed for ticks in Brazil, of which 6727 were published by Ogrzewalska *et al.* (2009, 2010, 2011), Martins *et al.* (2014), Lugarini *et al.* (2015) and Fecchio *et al.* (2020a, 2020b). The 59 sampling sites were located in five biomes: Amazonia, Atlantic Forest, Caatinga, Cerrado and Pantanal (Fig. 1). Detailed characterization of these sites including geographic coordinates, sampling size and tick prevalence can be found in the Tables S1–S3. Our dataset includes new and unpublished tick occurrence data for 3039 surveyed individual birds (see Table S1 and S2).

Netted birds were either ringed and released or euthanized and prepared as museum specimens. Less than 5% of the birds sampled were larger species, aquatic species and others not likely to be captured by mist nets and therefore we collected them using firearm or airgun in accordance with corresponding permits. Ticks were removed with tweezers, stored in ethanol and identified using current taxonomic keys (Martins *et al.*, 2010, 2013). Part of ticks collected and identified in this study have been 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. Ticks housed at the Academy of Natural Sciences of Drexel University, USA have not been identified to species. All birds were collected under appropriate Brazilian permits, and vouchers are deposited

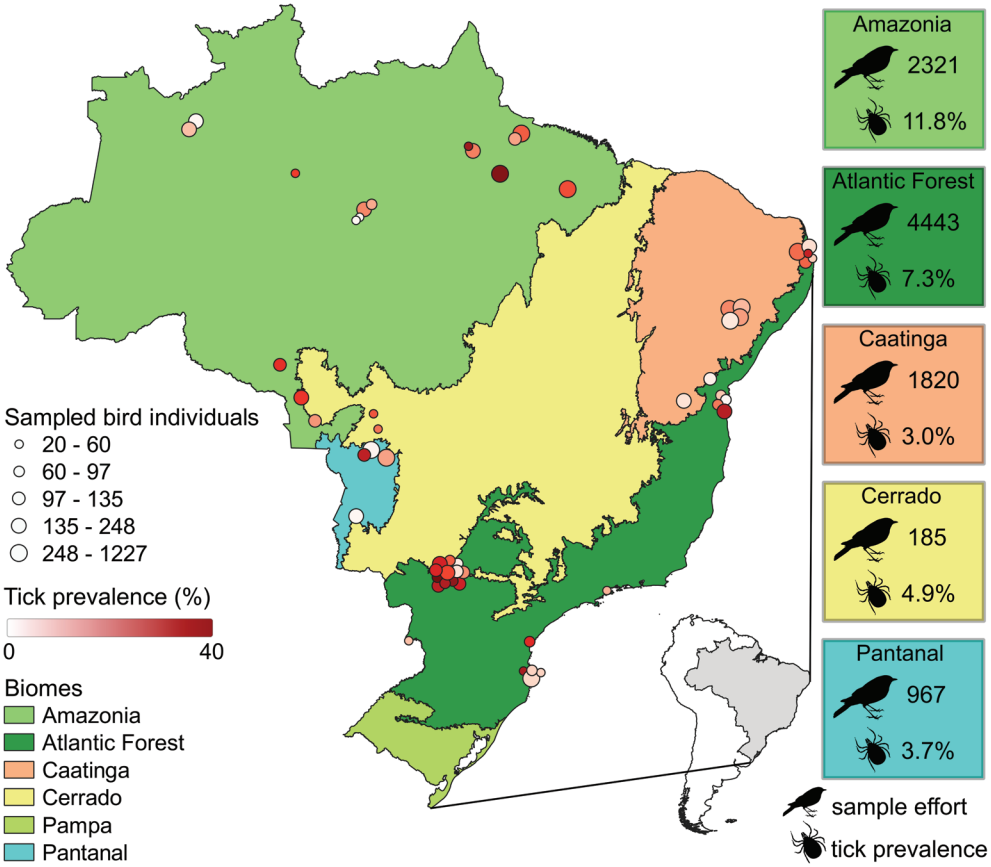

Fig. 1. Bird and tick sampling sites across Brazilian biomes. A total of 9736 individual birds from 584 species were surveyed from the 55 avian communities. Water foragers are included in the prevalence values. The four avian communities where we sampled less than 20 birds were omitted from the map.

at Instituto Nacional de Pesquisas da Amazônia, Ornithological Collection of Federal University of Mato Grosso, Coleção de Aves Heretiano Zenaide in the Federal University of Paraíba, Ornithological Collection of Federal University of Pernambuco, Museu Paraense Emilío Goeldi, The Field Museum of Natural History, and Academy of Natural Sciences of Drexel University. Bird species nomenclature follows the BirdTree project (Jetz *et al.*, 2012).

Phylogenetic signal and spatial autocorrelation

All analyses were conducted in R version 4.0 (R Core Team, 2020). Tick prevalence may be more similar among phylogenetically close avian hosts and therefore, 'phylogenetic signal' would create non-independence among bird species in the comparative analysis. To estimate the phylogenetic signal for tick prevalence, we downloaded a full avian phylogeny file from the AllBirdsHackett1.tre website (https://birdtree.org/) and used the 'treeman' package (Bennett *et al.*, 2017) to create a treeman file containing all trees from the original file and then extracted a consensus tree to account for phylogenetic uncertainty. We eliminated all bird species that were not present in our dataset and we matched the species between the tree and our dataset. We used these trees to calculate Pagel's lambda (λ) to evaluate phylogenetic signal for tick prevalence (Pagel, 1999). Values of λ can range between 0 and 1, where 1 indicates that the trait of interest has evolved consistently with a Brownian motion model with trait values similar among related species, and where 0 indicates that trait values are unrelated to phylogenetic relatedness among species.

Birds were sampled in multiple localities across Brazil, which can potentially create another source of non-independence and/or bias. To evaluate the impact of proximity among localities, we determined the spatial autocorrelation for tick prevalence among localities in our dataset by calculating the Moran Index value. Index values range between −1.0 and +1.0, with 0 indicating no spatial autocorrelation and −1.0 or +1.0 high spatial autocorrelation.

Environmental variables

We used annual precipitation (variable BIO15) and minimum temperature (variable BIO6, °C) as predictors in the Bayesian models as temperature and precipitation are known to impact tick occurrence and phenology (Estrada-Peña *et al.*, 2014; Nava *et al.*, 2017). We extracted these climate variables from the

WORLDCLIM database (https://worldclim.org/version2) and then selected the data with 10 min resolution for the 55 localities included in our dataset.

Avian host traits

Avian host species traits previously shown to be associated with tick prevalence in New World birds (Dingler *et al.*, 2014; Newman *et al.*, 2015; Miller *et al.*, 2016; Fecchio *et al.*, 2020b) were extracted from the ELTONTRAITS v. 1.0 database (Wilman *et al.*, 2014) and Dufour *et al.* (2020). The selected traits included foraging behaviour, host species' average body mass and migratory strategy (resident and partial migrants). We considered body mass as a continuous variable and foraging behaviour and migratory strategy as categorical variables. The foraging behaviour category was extracted from Elton 1 (Wilman *et al.*, 2014), which presents the relative importance of each stratum category. Here we divided birds into four categories based on the foraging stratum information (water, ground/understory, midhigh/canopy/aerial and multiples strata (reference level = ground/understory).

Bayesian analyses

We constructed two Bayesian models using the 'brms' package (Bürkner, 2017) to evaluate whether partial migratory species harbour higher prevalence than residents and whether communities with more partial migrants are more infested by ticks. In both models, we created a matrix with phylogenetic distances between bird species and used bird phylogeny covariance matrixes as random variables to account for phylogenetic influence on tick prevalence. By controlling for bird phylogeny, and because most host traits are phylogenetically conserved, our models took into account the possible effects of various host traits on parasite prevalence. This was an important step in the present analyses as we observed considerable phylogenetic signal (0.42) in our dataset. However, we did not observe strong spatial autocorrelation (Moran Index value = 0.2).

For the first model, we analysed tick prevalence as a function of host migratory category (resident or partial migrant, reference level = resident). Infestation status of individual birds was our dependent variable (binary response: 0 for non-infested, 1 for infested), and migratory strategy as our independent variable. Minimum temperature, precipitation, season, average body mass and foraging behaviour (reference level = ground/understory) were also retained as fixed factors, whereas community, biome and phylogeny were considered random factors. We employed the Bernoulli distribution family, using 4 chains with 4000 total iterations per chain (2000 for warmup, 2000 for sampling). Priors were obtained using the function 'get_priors' from 'brms' package in R.

In our second Bayesian model, we analysed the tick infestation on each bird among localities to test whether tick prevalence is related to the presence of partial migrant birds. We used the local number of infested birds out of the total sample for each locality as our dependent variable, and local proportion of partial migratory individuals (i.e., proportion of partial migrant birds out of all individuals sampled in a locality) as our independent variable. The proportion of partial migrant individuals in an area was based on our captured bird dataset. For this model, we also retained minimum temperature, precipitation, average body mass, season and foraging behaviour (reference level = ground/understory) as fixed factors and community, biome and phylogeny as random factors. We again employed the Bernoulli distribution family, using 4 chains with 4000 total iterations per chain (2000 for warmup, 2000 for sampling). Priors were obtained using the function 'get_priors' from 'brms' package in R. For these two Bayesian models, we considered only avian communities with 20 or more bird individuals sampled. We excluded 54 individuals classified as foraging on water surface from the analyses due to the low sample size for this category. Thus, our dataset of tick occurrence consists of 9682 individual birds from 572 species and 54 families surveyed across 55 avian communities in Brazil (Tables S1–S3, Fig. 1).

Results

We found ticks on 700 avian hosts out of 9766 surveyed individuals across the 59 sampled communities in Brazil (Fig. 1). These infested individuals belong to 192 avian host species, 35 families and 14 orders (see Table S3 for sample size and tick prevalence per avian host species). Overall tick prevalence was 7.17%, with heterogeneity across sampling sites (Fig. 1). The highest prevalence was observed in avian communities from Amazonia and Atlantic Forest biomes (Fig. 1). Only larvae and nymphs were found in Brazilian birds. The most common tick species was *Amblyomma nodosum* found on 174 individuals from 42 host species, followed by *Amblyomma longirostre* found on 142 individuals from 58 host species, *Amblyomma parvum* found on 29 individuals from 18 host species, *Amblyomma auricularium* found on 22 individuals from 17 host species, *Amblyomma calcaratum* found on 15 individuals from 10 host species, *Amblyomma humerale* found on 15 individuals from eight host species, *Amblyomma sculptum* found on 13 individuals from 11 host species, *Amblyomma coelebs* found on 12 individuals from nine host species, *Amblyomma geayi* found on nine individuals from seven host species, *Amblyomma ovale* found on five individuals from four host species, *Amblyomma parkeri* found on four individuals from three host species, *Amblyomma varium* and *Amblyomma triste* found on two individuals from two host species, and *Haemaphysalis juxtakochi* found on two individuals from two host species.

In our first Bayesian model, with which we analysed whether partial migrant individuals are more frequently infested by ticks than residents, we observed that migration strategy was negatively related to tick infestation, with partial migrant hosts less frequently parasitized than residents (Table 1, Fig. 2). The phylogenetic signal was significant for this model, indicating that the probability of tick infestation is influenced by bird phylogenetic relationships (Table 1). In our second model, with which we analysed whether the number of migrants in a given avian community impacts tick prevalence, we show a positive relationship between proportion of migratory birds and tick infestation probability, with avian communities harbouring a higher proportion of partial migrants hosts also harbouring a higher prevalence

Table 1. Parameter estimates, standard errors and confidence intervals (CIs) for the Bayesian model testing the difference in tick prevalence in relation to traits including host migratory strategy, minimum temperature, precipitation, body mass, foraging strata and season.

	Estimate	Standard error	95% CI	
			Lower	Upper
Intercept	−2.27	1.24	−4.67	0.22
Migratory strategy	−0.81	0.39	−1.60	−0.07
Minimum temperature	−0.01	0.01	−0.01	0.01
Annual precipitation	−0.01	0.00	−0.01	0.01
Body mass	0.01	0.00	−0.01	0.01
Foraging strata: Mid-high/ Canopy/Aerial	−0.14	0.16	−0.45	0.18
Foraging strata: Multiple	−0.26	0.23	−0.72	0.19
Season	−0.39	0.14	−0.67	−0.12
Phylogenetic variance	1.42	0.18	1.08	1.81

of ticks (Table 2, Fig. 3). The phylogenetic variance was considerable in this model, indicating that the probability of tick infestation in each community was influenced by bird phylogenetic composition (Table 2). Annual precipitation, minimum temperature, foraging behaviour and body mass, in both models, did not explain tick prevalence (Tables 1 and 2). Season also influenced tick prevalence with birds in dry season more prone to tick infestation (Tables 1 and 2, Fig. 4).

Discussion

Current human-induced changes in land cover and climate are altering the migratory flyways, onset of migration and population density of migrant birds (Visser *et al.*, 2009; Howard *et al.*, 2020). This in turn, might disrupt the ecological and evolutionary relationships between migratory birds and the ticks and tick-borne pathogens they disperse, therefore impacting the transmission and spread of tick-borne diseases into new areas. We showed that avian hosts are at greater risk of being infested by immature ticks during the dry season in Brazil. More importantly, we provide some of the first evidence that tick prevalence is correlated with proportion of migrant birds across migratory flyways in Brazil and not correlated with environmental conditions or other avian traits thought to drive tick infestation in bird populations.

Avian traits such as the preferred foraging habitat can influence rates of tick exposure for a given host, and in turn, predicts tick prevalence (Eisen *et al.*, 2004; Hasle, 2013; Dingler *et al.*, 2014; Loss *et al.*, 2016; Fecchio *et al.*, 2020b). Host seeking and questing behaviour for most hard tick species found in Brazilian birds are not recorded (Luz & Faccini, 2013; Nava *et al.*, 2017). For example, information on whether the larvae and nymphal stages disperse horizontally on the ground or vertically through the vegetation is lacking for most hard tick species found in Brazil. Whether larval and nymphal hard ticks might have specialized on parasitizing avian hosts or evolved cues to find these vertebrate hosts needs additional research. Moreover, tick life history information at the species level (e.g., breeding location) is necessary to determine whether birds are exposed to ticks while in the nest or only during foraging through the environment (e.g., on the ground or across different forest strata).

Traits that constrain resource allocation to mount host immune response and potentially restrict parasite invasion, such as migratory behaviour (Altizer *et al.*, 2011), might be more influential in modulating the probability of an avian host being infested by ticks. Previous studies used migratory behaviour,

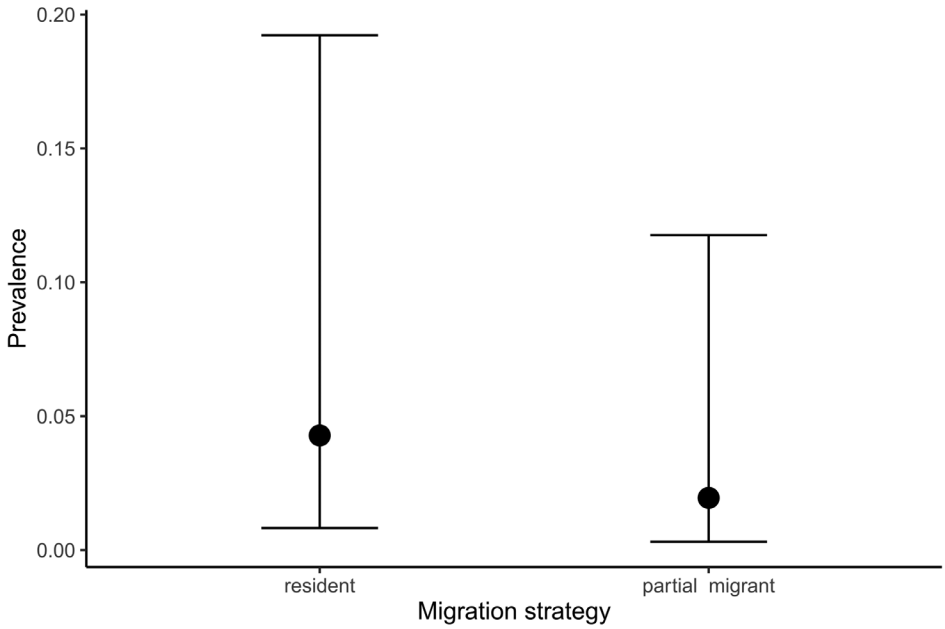

Fig. 2. Mean (±standard error) tick prevalence for each host migratory strategy.

Table 2. Parameter estimates, standard errors and confidence intervals (CIs) for the Bayesian model testing the variation in local number of birds infested by ticks as a function of the proportion of migratory birds out of all individual birds sampled per locality, minimum temperature, precipitation, body mass, foraging strata and season.

	Estimate	Standard error	95% CI	
			Lower	Upper
Intercept	−3.01	1.38	−5.74	−0.29
Proportion of migrants	0.06	0.02	0.01	0.11
Minimum temperature	0.01	0.01	−0.01	0.01
Annual precipitation	−0.01	0.00	−0.01	0.01
Body mass	0.01	0.00	−0.01	0.01
Foraging strata: Mid-high/ Canopy/Aerial	−0.21	0.16	−0.54	0.10
Foraging strata: Multiple	−0.29	0.24	−0.76	0.16
Season	−0.36	0.14	−0.64	−0.08
Phylogenetic variance	1.46	0.19	1.12	1.86

among other avian life history traits, to explain tick parasitism and found that this host trait has been identified as a determinant of increased tick infestation and infection probability by *Borrelia burgdorferi* (Dingler *et al.*, 2014) or had no effect on tick prevalence in the same region (Newman *et al.*, 2015). We showed that partial migrants were less infested than resident birds, possibly because migrant birds have developed better immune function to cope with higher parasite pressure during their annual cycle (Buehler *et al.*, 2008). Alternatively, heavily infested migratory birds may be debilitated and not able to complete the migration (migratory stalling, Peacock *et al.*, 2018) or may die before the end of migration (migratory culling, Altizer *et al.*, 2011). Both mechanisms could diminish the number of parasitized individuals in a host population after the breeding season, therefore, explaining lower tick prevalence across partial migratory birds. In accordance with our results from Brazilian birds, Neotropical–Nearctic migratory birds were less parasitized than resident species across Panama (Miller *et al.*, 2016). In addition, a study with Nearctic bird communities demonstrated that non-migratory birds were more often parasitized by ticks and more likely to carry ticks infected by *Borrelia burgdorferi* (Loss *et al.*, 2016).

By estimating the effect of avian phylogenetic relationships, we find that barriers to avian host encounters with ticks are influenced by host phylogeny, not by host ecological similarity (e.g., similar preferred foraging habitat or body mass), indicating that most ticks in the dataset infest avian hosts that are, on average, phylogenetically similar within the community. Whether partial and long-distance migratory species that breed in Brazil have the potential to disperse their ticks and spread tick-borne pathogens across their wintering sites in North America and Southern South America has yet to be assessed. Although resident avian host species might play a critical role in acquiring ticks locally and thus contribute to both tick population persistence, recruitment and pathogen maintenance in a local host community (Loss *et al.*, 2016), areas concentrating higher proportions of partial migrant hosts might play an important role in tick-borne transmission and pathogen spillover by harbouring more infested avian host individuals.

Time of year is expected in drive tick prevalence and infestation rates across hosts populations because tick development

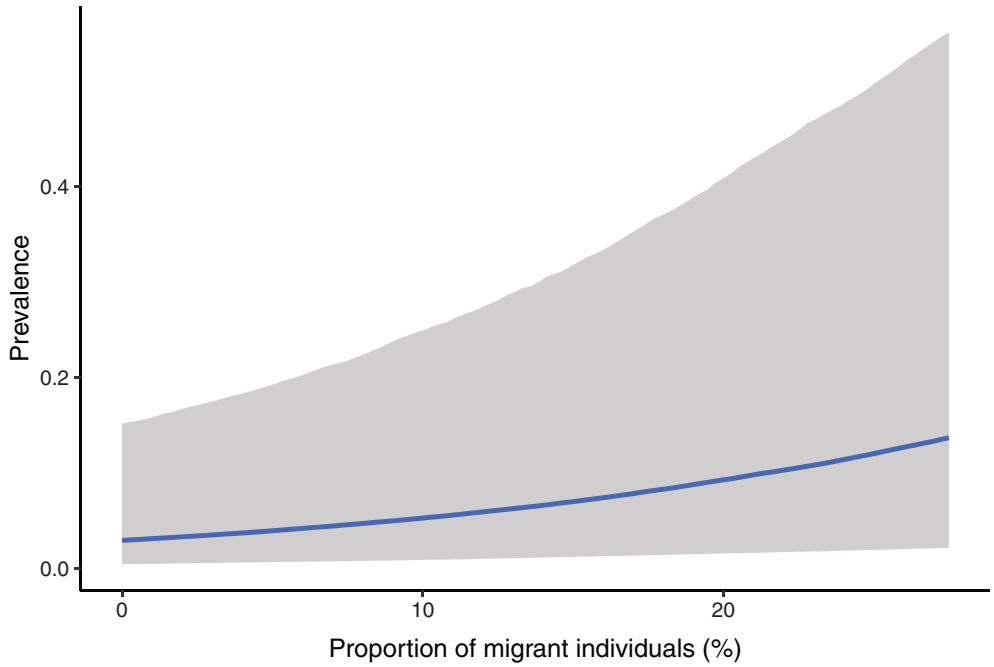

Fig. 3. Predicted model relationship (±95% confidence intervals) between tick prevalence and proportion of partial migrants in an avian community.

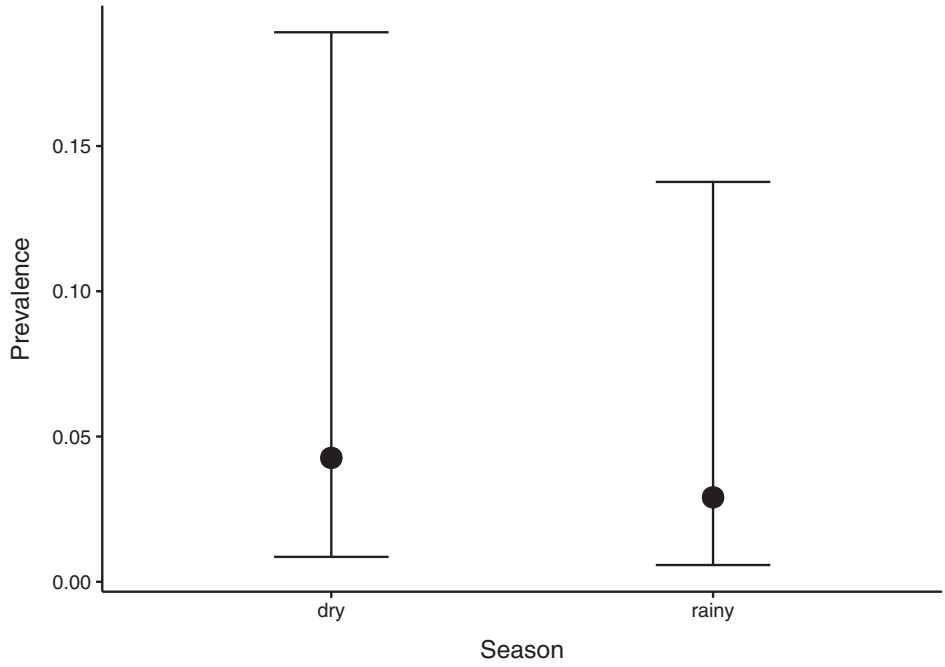

Fig. 4. Mean (±standard error) of tick prevalence for dry and rainy season.

and host-seeking behaviour are often seasonal. Hard tick larvae are more abundant in the environment between March and July (Labruna *et al.*, 2009). Whereas nymphs are more common between July and November (Labruna *et al.*, 2009) when most passerine birds are more actively defending territories and building or attending nests. The higher abundance of larvae and nymphs during the dry season and increased avian host movement prior to the breeding season might explain the higher prevalence of ticks found during this time of year in Brazil. Whether immature hard ticks have evolved to adjust their life cycles with avian host phenological cycle to assure transmission has yet to be investigated. Nevertheless, we show that avian hosts inhabiting sites with more migratory birds during the dry season are more likely to be infested by ticks.

Recognizing that tick prevalence on avian hosts is a labile trait that changes according to the number of migrant individuals in a host community can provide useful leverage for outlining prediction of tick-borne disease risk. Translating this framework to other host-parasite systems would help to identify habitat conditions other than climate conditions and host composition, such as number of migrating hosts that increase risks for pathogenic disease emergence and parasite spillovers across regions (de Angeli Dutra *et al.*, 2021).

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1: Raw dataset and associate metadata.

Table S2: Dataset summary detailing information per sampling site: total number of bird individuals and ticks found per community, geographic coordinates, biome, and data source. The four avian communities with less than 20 sampled birds were omitted from the table.

Table S3: Number of sampled individuals and infested individuals per avian host taxon: species (italic) and avian family (bold).

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Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Author contributions

AF and DdAD conceived the idea and designed the research. DdAD analysed the data. AF wrote the manuscript. The remaining authors contributed with tick collection, curating the data

and funding field expedition. All authors contributed critically to the manuscript drafts and gave final approval for publication.

Data availability statement

The raw dataset used in this study will be published as Supporting Information.

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