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Article

Higher probability of tick infestation reveals a hidden cost of army ant-following in Amazonian birds

Alan Fecchio, Thiago F. Martins, Maria Ogrzewalska, Fabio Schunck, Jason. D. Weckstein and Raphael I. Dias

A. Fecchio ✉ (alanfecchio@gmail.com), Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade, Universidade Federal de Mato Grosso, Cuiabá, MT, Brazil. – AF and J. D. Weckstein, Dept of Ornithology, Academy of Natural Sciences of Drexel Univ., Philadelphia, PA, USA. – T. F. Martins, Depto de Laboratórios Especializados, Superintendência de Controle de Endemias – SUCEN, Secretaria de Estado da Saúde de São Paulo, São Paulo, SP, Brazil; and, Depto de Medicina Veterinária Preventiva e Saúde Animal, Faculdade de MedicinaVeterinária e Zootecnia, Univ. de São Paulo, São Paulo, SP, Brazil. – M. Ogrzewalska, Laboratório de Vírus Respiratórios e Sarampo, Inst. Oswaldo Cruz – IOC, Fundação Oswaldo Cruz – FIOCRUZ, Rio de Janeiro, RJ, Brazil. – F. Schunck, Brazilian Committee for Ornithological Records – CBRO. – JDW, Dept of Biodiversity, Earth and Environmental Sciences, Drexel Univ., Philadelphia, PA, USA. – R. I. Dias, Faculdade de Ciências da Educação e Saúde, Centro Univ. de Brasília, Brasília, DF, Brazil.

The foraging specialization of army ant-following birds has long intrigued ecologists and provided numerous questions such as why, how and when did this foraging guild specialization arise and evolve. Many of the answers to these questions have focused on ecological interactions such as predation and competition, whereas little has been done to study the potential effects of host–parasite interactions among members of this foraging guild. Using 1177 Amazonian birds from 187 species, we studied the probability of tick infestation in relation to attendance of birds at army ant swarms. We demonstrate that the probability of tick infestation was higher among professional and occasional ant-followers than in bird species that do not follow army ants to prey upon leaf-litter flushed arthropods. Moreover, occasional ant-followers harbored a greater diversity of nymphal ticks. We argue that although the evolutionary transition toward specialized ant-following behavior has a genetic basis, a trade-off between the cost of evolution of this trait and its fitness benefits might exist. In this case, the cost is in the form of higher parasite pressure. Therefore, parasites may impose a selective pressure not only during foraging but also through the allocation of resources for an immunological response. Our results of an analysis of tick parasitism on Amazonian birds emphasizes the importance of parasitic organisms on ecology and evolution of behavioural traits of their hosts. Considering the effects imposed by parasite pressure is essential for understanding the evolution and maintenance of behavioral and life-history traits.

Keywords: antbirds, feeding behavior, foraging strategies, host–parasite interaction, Ixodidae, tick prevalence

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Introduction

Although being in a group during foraging can constitute an anti-predatory strategy and enhance the energy intake of individual participants (Terborgh 1990, Beauchamp 2010), it may also increase the risk of acquiring parasites and pathogens because of the proximity and physical contact among group members (Altizer et al. 2003). Some empirical evidence supports the prediction that parasite transmission increases with increasing group size for a broad range of vertebrate hosts and parasitic organisms with different modes of transmission. For example, passerine birds living in groups were more infested by feather mites (a contact-transmitted ectoparasite) than solitary species (Poulin 1991). At an intraspecific level, prevalence of gastrointestinal parasites was positively correlated with group size of African bovids (Ezenwa 2004). In Neotropical primates, malaria prevalence (a vector transmitted pathogen) increased with host group size (Davies et al. 1991). Specialized African ant-following birds, which regularly form flocks with several individuals of many species while tracking raids of army ants, were 10 times more infected by nematode microfilariae and *Trypanosoma* than non-ant-following birds (Peters 2010).

Peters (2010) examined the infection rates of blood protozoan parasites (genera *Plasmodium*, *Haemoproteus*, *Leucocytozoon* and *Trypanosoma*) and microfilarie larvae of nematodes, based on the findings reported by Sehgal et al. (2005) and Beadell et al. (2009) for African birds, and demonstrated that *Trypanosoma*, microfilaria and *Plasmodium* parasites were more frequently found in ant-followers than in other birds. A surprising result discussed by Peters (2010) was that one evolutionary lineage of *Trypanosoma* was only shared among four phylogenetically unrelated host species, all of which specialized on following army ant swarms. Based on the findings reported by Sehgal et al. (2001), Peters also suggested that for *Trypanosoma* transmission a coevolutionary relationship arose between the vectors and specialized ant-followers, and that this blood parasite may be successfully transmitted not only among individuals of the same ant-following species, but also among those of different bird species that attend swarms of army ants.

Army ants are cooperative foragers in tropical forests that evolved to become a social predator (Gotwald 1995). Raids are formed by hundreds of thousands of carnivorous ants that forage over the forest floor searching for arthropod prey (Willis and Oniki 1978, Gotwald 1995). To escape predation, arthropods and small vertebrates flee away from the leaf litter or lower vegetation when the ant swarm is approaching (Willis and Oniki 1978, Gotwald 1995, Peters 2010). Some bird taxa in Neotropical and Afrotropical rain forests have specialized on following army ants where they capture arthropods flushed by the swarms and these ant-following bird species exhibit behavioral adaptations that help them to locate army ants (Willis and Oniki 1978, Swartz 2001, Willson 2004, Peters et al. 2008). Although these foraging strategies and extreme social behavior provide foraging advantages for the ant-following birds, one potential cost is that through social interactions and perhaps foraging close to the ground they may be more prone to infestation by hard ticks.

Here, we analyzed the infestation probability of hard ticks on Amazonian birds to test whether parasite pressure is indeed higher among New World ant-following birds. This parasite–host bird system in Amazonia differs from the African system analyzed by Peters (2010). Unlike the groups of vector transmitted blood parasites studied in Africa, ticks are ectoparasites in which immature stages (larvae and nymphs) feed on the blood of a broad range of bird taxa and display host specificity only at higher taxonomic levels in the Neotropical region (Barros-Battesti et al. 2006, Nava et al. 2017).

Material and methods

Bird and tick sampling

We collected birds with mist-nets, firearms and airguns in 10 bird communities surveyed across the Brazilian Amazon (Fig. 1). Sampling sites included in this study were surveyed either as part of a long-term study on avian parasites in Amazonia or through research programs that were part of the National Biodiversity Research System (Sisbiota) and the Biodiversity Research Program (PPBio) in Brazil, from which tick occurrence data has already been published (Ogrzewalska et al. 2010, Martins et al. 2014, Fecchio et al. 2020a). Birds collected by firearm were less than five percent of sampled individuals, but this collection method allowed for capturing avian taxa from the forest canopy where mist-nets are difficult to use. Netted birds were either ringed and released or euthanized and prepared as museum specimens. In the field, each bird was visually examined for ticks through carefully checking the entire body. Ticks were removed with tweezers, stored in 95% ethanol, and identified using taxonomic keys for South American ticks (Martins et al. 2010, Nava et al. 2017). All birds were collected or banded and released under appropriate permits in Brazil, and for those specimens that were collected, vouchers are available at Institute Nacional de Pesquisas da Amazônia, Museu Paraense Emílio Goeldi and The Academy of Natural Sciences of Drexel University. Bird species nomenclature follows the BirdTree project (Jetz et al. 2012).

Data analyses

We selected ecological traits that may influence avian exposure to ticks (Newman et. al. 2015, Fecchio et al. 2020b) from the EltonTraits v. 1.0 database (Wilman et al. 2014) including avian species' average body mass and the relative proportion of time that a given species spends foraging in a given forest stratum. We did not include diet because this trait was associated with both foraging stratum and ant-following behavior in the species studied. Migratory behavior was also not included because all species sampled for this
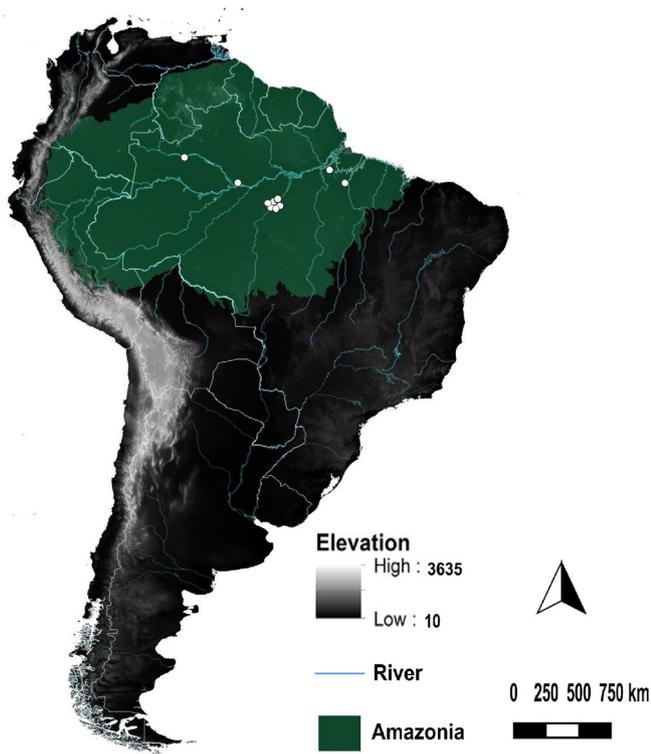
Figure 1. Sampling locations in the Brazilian Amazonia. Coordinates for each of the 10 sites, number of birds captured and tick prevalence are available as Supporting information.

study were tropical residents. Here we created three categories of foraging strata: 1) ground/understory, which includes bird species that forage on the ground or below two meters in the forest understory, forest edges, bushes and shrubs; 2) midheight/canopy for bird species that forage two meters or higher in trees or high bushes up to tree canopy; and 3) multiple strata, for species that forage in more than two strata. These three foraging strata categories are derived from the EltonTraits v. 1.0 database which classifies the relative proportions of each stratum's usage for each species (Wilman et al. 2014). Ant-following behavior for each species was determined based on data presented in Oniki (1972), Oniki and Willis (1972), Willis and Oniki (1978), Willis (1983a, b, c, 1984a, b, c), Willson (2004), Brumfield et al. (2007) and Birds of the World (Billerman et al. 2020) and we classified ant-following behavior into three categories: 1) non-follower, when the bird species has never been observed associating with ant swarms; 2) occasional follower, when the bird species was rarely or infrequently observed associating with ant swarms; and 3) professional follower, when the bird species was commonly and frequently observed associating with ant swarms, which includes both obligate and facultative ant-followers. We included season in our analysis, because tick abundance and diversity are temporally variable (Nava et al. 2017, Fecchio et al. 2020b). We considered only body mass as a continuous variable. Season and the other two host traits were scored as categorical variables.

Statistical analyses

To evaluate how body mass, foraging stratum, ant-following behavior and seasonality affect the probability of tick infestation (denoted hereafter as the probability of an individual bird being parasitized by ticks), we fitted a phylogenetic generalized linear model (PGLMM) with binomial error distribution (Ives and Garland 2014, Ives 2018). We chose this approach because species traits are frequently phylogenetically dependent (Felsenstein 1985). We used a subset of the whole dataset to evaluate whether the same explanatory variables also influence the number of ticks found on individual birds. For this analysis, we only included the parasitized birds. For both analyses we used the function MCMCglmm from the package 'MCMCglmm' (Hadfield 2010) to create a linear mixed model using Bayesian Markov Chain Monte Carlo (Hadfield 2012). To account for phylogenetic effects, we used 100 randomly selected phylogeny trees based on the Hackett backbone (Hackett et al. 2008) obtained from the Birdtree project (<http://birdtree.org>; Jetz et al. 2012). We fitted the models to each of the trees and then extracted the mean density of the combined posterior distribution using the package mulTree (Guillerme and Healy 2014). In both models we included the study sites and bird phylogeny as random terms. To test the effects of the explanatory variables on the probability of host infestation, we fitted a categorical mixed model using the logit link function. To investigate the influence of the explanatory variables on the number of ticks found on each bird, we fitted a Poisson model with log link function. We set uninformative priors for both fixed and random effects of both models. To ensure model convergence, we ran each model for 500 000 iterations, with burnin set at 10 000 and stored samples every 100 iterations. The model resulted in comparable effective sample size for all factors (~1000). Fixed effects were considered statistically significant when the 95% credible interval did not overlap zero. For each model, we calculated the percentage of variance explained by each of the fixed effects only and the combination of fixed and random effects, using marginal and conditional R^2, respectively (Nakagawa and Schielzeth 2013).

We also estimated tick diversity found on the avian hosts. We used the function 'estShannonf' to estimate the Shannon index for the tick communities on birds in relation to the host's ant-following behaviors. We also constructed confidence intervals by bootstrapping with the function sbdiv to test for differences in diversity between groups. We used the method 'WYht' with 2000 bootstrap replicates. Both functions are from the package *simboot* (Scherer and Pallmann 2017). All the analyses were performed using R (ver. 4.0.2, <www.r-project.org>).

Results

A total of 1177 birds from 187 avian species belonging to 34 families were searched for ticks. Antbirds and woodcreepers, the two avian clades where obligate ant-following behavior

arose, comprised 52% of sampling. Overall tick prevalence was 17.3% in the sampled birds (see raw data for sample size, capture date, prevalence and tick species found by avian taxon and location in Supporting information). The avian host families with highest prevalence were Falconidae (50.0% infested; n=2 individuals), Conopophagidae (36.4%; n=11), Dendrocolaptidae (35.4%; n=237), Strigidae (33.3%; n=3) and Turdidae (30.0%; n=20). Ticks were not found on birds from 14 avian families (Caprimulgidae, Cathartidae, Coerebidae, Cracidae, Cuculidae, Emberizidae, Hirundinidae, Icteridae, Jacanidae, Psittacidae, Psophiidae, Trochilidae, Trogonidae and Vireonidae).

When we excluded avian species with a single sampled individual, the prevalence was higher for woodcreepers, including Brigida's woodcreeper (*Hylexetastes brigidai*, 83.3%; n=6 individuals), Amazonian barred woodcreeper (*Dendrocolaptes certhia*, 75.0%; n=4) and Hoffmanns's woodcreeper (*Dendrocolaptes hoffmannsi*, 72.1%; n=43). These three host species are obligate ant-followers. In fact, the two avian host families with the most ant-following species exhibited elevated overall tick prevalence (Dendrocolaptidae, 35.4%; n=237 individuals and Thamnophilidae, 16.2%; n=377; Fig. 2) in comparison to non-ant-following birds. Yet, by including only the avian species for which ant-following behavior is frequently observed, we found that the

prevalence was even higher for both of these host families (Dendrocolaptidae, 56.3%; n=96 and Thamnophilidae, 22.2%; n=135). All 16 investigated species from the family Dendrocolaptidae were occasional or professional ant-followers. For Thamnophilidae, 82.9% of the species sampled (n=41 species) were occasional or professional ant-followers. Ant-following behavior was uncommon among all other studied families, where most species are non-followers (83.0%, n=130) and those species that follow are classified as occasional ant-followers.

We found that ant-following behavior was associated with tick parasitism (marginal $R^2=0.08$, conditional $R^2=0.49$). After accounting for phylogeny, both occasional and professional ant-followers exhibited a higher probability of tick infestation in comparison to birds where ant-following behavior was never documented (Fig. 3). We did not observe any effect of body mass, foraging stratum and seasonality on the probability of host infestation (Table 1). The phylogenetic signal was strong in the data (total variance explained=42%), suggesting that the probability of tick infestation is influenced by bird phylogenetic relationships.

Only larval and nymphal ticks were found on the birds. Parasitized birds usually had a higher number of larvae than nymphs. In 124 cases individual hosts harbored more larvae than nymphs, in 25 cases individual hosts had more nymphs
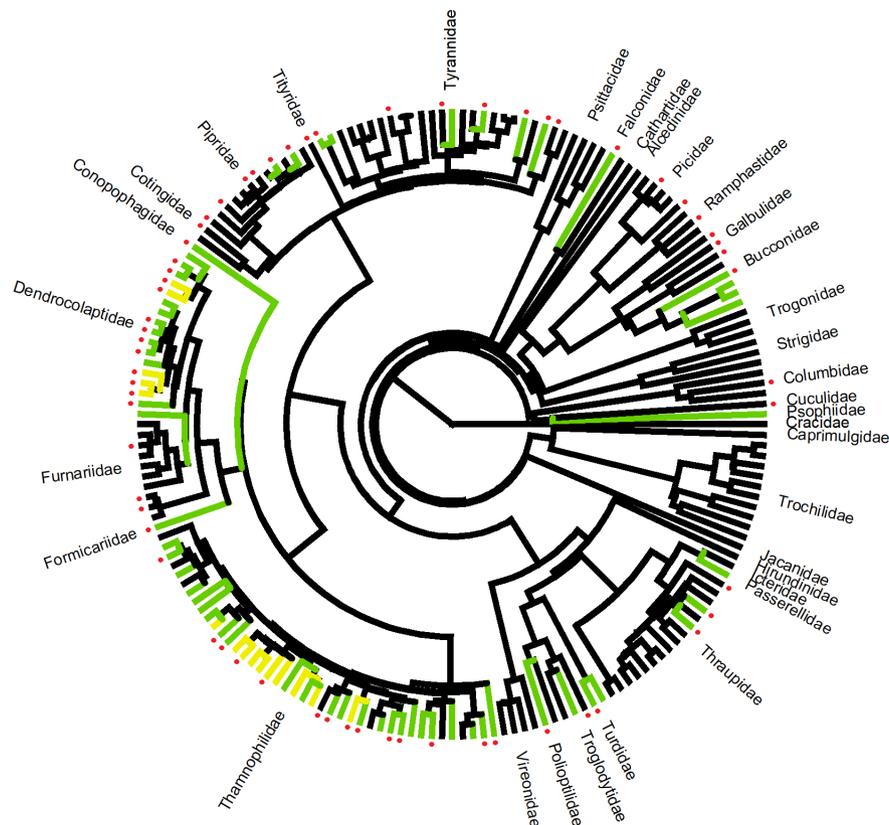

Figure 2. Phylogenetic relationships of ant-following behavior and tick parasitism in Amazonian birds. Branches for avian taxa never recorded following army ants are colored black, occasional ant-followers are colored green and professional ant-followers are colored yellow. The red dot associated with some of the terminal branches indicates hard tick occurrence on that avian host species.
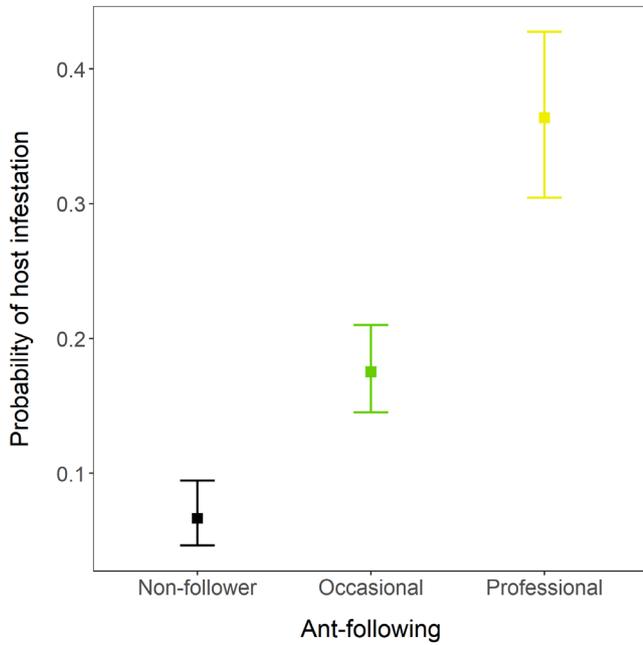
Figure 3. Effect of ant-following behavior on the probability of tick infestation on Amazonian birds. The squares represent the probability of tick infestation with 95% confidence intervals based on the 1,177 individual birds sampled. Phylogenetic position and color scheme for the three categories of ant-following behavior are shown in Fig. 2.

bird (marginal $R^2 = 0.05$, conditional $R^2 = 0.43$; Table 2), we did not find any significant effect after controlling for phylogeny. The estimation of phylogenetic signal demonstrated that the number of ticks found on the birds was influenced by the phylogenetic relationships of avian hosts (total variance explained = 38%).

Six tick species were found in eight out of 10 bird communities that we sampled across Amazonia (no ticks were detected in two communities). Five species belonged to the genus *Amblyomma* (*A. calcaratum*, *A. coelebs*, *A. geayi*, *A. humerale* and *A. longirostre*), and we have also recorded infestations of *Haemaphysalis juxtakochi*. The most common tick species was *A. longirostre*, found in 71 birds, followed by *A. humerale*, which was found in 15 birds. *A. longirostre* was also the most abundant tick found on parasitized birds with 1.69 ± 1.55 ticks per host individual (mean ± SD; range: 1–11 ticks). Considering ant-following behavior exclusively, we observed that tick diversity estimated by Shannon's index was estimated as 0.56 ± 0.03 (mean ± variance) for avian species where ant-following was never recorded, 1.22 ± 0.01 (mean ± variance) for occasional ant-followers and 0.85 ± 0.01 (mean ± variance) for professional ant-followers. Bootstrapping indicated that the diversity of ticks found on occasional ant-followers was higher than that observed on professional ant-followers (p = 0.033). No difference was observed between the other pairwise comparisons (all p > 0.05).

Discussion

Our results provide strong evidence that Amazonian ant-following birds are more often parasitized by hard ticks than bird species that do not attend army ant swarms to obtain

than larvae and in five cases the number of nymphs and larvae were the same. On average, the parasitized individuals hosted 3.30 ± 5.04 larvae (mean ± SD; range: 1–37) and 1.15 ± 0.43 nymphs (mean ± SD; range: 1–3). When investigating the factors that may result in a higher number of ticks per

Table 1. Results from a phylogenetic generalized linear mixed model with a binomial error distribution and logit-link function to evaluate the effects of ecological and behavioral characteristics on the probability of tick infestation in Amazonian birds. The references for the categorical variables included in the model were: non-follower (ant-following), ground/understory (foraging stratum) and dry (season). Black circles indicate the mean of the estimate produced by averaging 100 models and the error bars (grey shading) show the lower and upper 95% and 50% credible intervals (CI).

Variable	Estimate	95% CI		Posterior distribution
		Lower	Upper	
Ant-following: occasional	1.01	0.30	1.75	
Ant-following: professional	1.75	0.68	2.75	
Body mass	−0.10	−0.62	0.23	
Foraging stratum: midhigh/canopy	−0.37	−1.02	0.29	
Foraging stratum: multiples	−0.13	−1.07	0.86	
Season: wet	−0.09	−3.04	3.19	
Phylogenetic variance	2.86	0.44	8.83	
Residual variance	3.39	0.84	10.99	

Table 2. Results from a phylogenetic linear mixed model with a Poisson error structure to evaluate the effects of ecological and behavioral characteristics on the number of ticks in Amazonian birds. The references for the categorical variables included in the model were: non-follower (ant-following), ground/understory (foraging stratum) and dry (season). Black circles indicate the mean of the estimate produced by averaging 100 models and the error bars (grey shading) show the lower and upper 95% and 50% credible intervals (CI).

Variable	Estimate	95% CI		Posterior distribution
		Lower	Upper	
Ant-following: occasional	−0.00	−0.78	0.78	
Ant-following: professional	0.29	−0.70	1.28	
Body mass	0.38	−0.56	1.34	
Foraging stratum: midhigh/canopy	0.1	−0.55	0.80	
Foraging stratum: multiples	0.20	−0.58	0.98	
Season: wet	−0.04	−1.76	1.74	
Phylogenetic variance	0.44	0.11	1.36	
Residual variance	0.66	0.13	2.46	

their food. Our models also revealed that the probability of a bird being parasitized by ticks is unaffected by time of year and two other host ecological traits known as predictors of tick prevalence and diversity, namely foraging stratum and body mass, respectively. Moreover, host phylogenetic relationships had an important role in determining the probability of a bird being parasitized by ticks in Amazonia, possibly because ant-following behaviour is a conserved trait that increases exposure to parasites in the two most diverse clades of Amazonian understory birds, namely, Dendrocolaptidae and Thamnophilidae.

Several host life history strategies can explain parasite infection risk, such as sociality, migratory propensity and breeding strategy (Alexander 1974, Tella 2002, Altizer et al. 2003). For example, Tella (2002), showed that the evolutionary transition from solitary to colonial breeding strategy was accompanied by an increased prevalence and diversity of blood parasites in colonial bird species, possibly because bird aggregation during reproduction attracts more vectors, leading to higher parasite transmission. Furthermore, parasitism is a cost associated with sociality (Alexander 1974). This demonstrates that the increased risk of acquiring and accumulating parasites and pathogens could be a result of the host's propensity for increasing exposure to parasites, such as increased prevalence of ectoparasites caused by animal aggregations (Alexander 1974, Altizer et al. 2003). Ant-following in Neotropical antbirds (Thamnophilidae) is an ancient and phylogenetically conserved behavioral trait that likely followed a progression from least to most specialized (Brumfield et al. 2007) and has multiple evolutionary origins across Amazonian bird clades (Fig. 2). Notably, the vulnerability to coextinction, an evolutionary consequence hypothesized to accompany specialization, was not observed in army ant-following antbirds (Brumfield et al. 2007). Conversely, such specialization in foraging behavior has been implicated in increasing the infection risk for vector-transmitted blood

parasites in African ecological counterparts (Peters 2010). Higher tick infestation probability on Amazonian ant-following host groups is largely consistent with empirical evidence and theoretical expectations of higher parasite prevalence and increased transmission of infectious diseases as a major cost of ant-following behavior (Peters 2010). We demonstrate that specialization in ant-following behavior in Amazonian birds is currently associated with a cost of greater prevalence of immature ticks in professional ant-followers as well as higher diversity of nymphal ticks in occasional ant-followers. Therefore, higher parasitism rates found in ant-following birds might be an ecological consequence of the evolution of this behavioral trait.

Parasitism by ticks can negatively affect the avian host through erythrocyte depletion (Heylen and Matthysen 2008) or inoculation of tick-borne pathogens such as bacteria from the genera *Anaplasma*, *Borrelia*, *Ehrlichia* and *Rickettsia* or RNA viruses from the genus *Flavivirus* (Barros-Battesti et al. 2006, Dantas-Torres et al. 2012, Machado et al. 2012, Ogrzewalska and Pinter 2016). Moreover, tick infestation may impact host behavior and foraging, and in extreme cases may cause host death from anemia and weight loss when the parasite burden is high (Hart 1990). Parasitism by ticks and tick-borne pathogens may trigger different components of the avian host immune defense, which is costly for the host. Infestations by blood-sucking ectoparasites, such as immature ticks, have a major impact on bird inflammatory responses and immune counterattacks for preventing blood loss (Heylen and Matthysen 2008). Besides acquired immunological resistance against ticks (Heylen et al. 2020), avian hosts infected with tick-borne pathogens will be under selective pressure to develop and activate effective defenses against microorganisms. The costs of general functioning of the acquired immune system and simultaneous activation for acquisition and expression of immunity (e.g. cellular and humoral response) to cope with the increased parasite

pressure on ant-following hosts might be compensated by the increased daily intake of leaf-litter arthropods. If the cost of boosting the components of the immune system defending against these parasites and pathogens is mediated by nutrient limitation (Gershwin et al. 1985, Hutchings et al. 2003), then ant-following birds might be maximizing this foraging trait for defense against parasites and pathogens.

The higher diversity of nymphs found on occasional ant-followers may be explained by the broader diversity of habitats and forest stratum where these birds forage when not attending army ant swarms. Alternatively, the lower diversity of nymphs found on professional ant-followers may indicate that specialization of this foraging behavior might release these avian hosts from infestation by a broader diversity of nymphal ticks, as tick nymphal stages can disperse vertically through the environment. Conversely, this also suggests that larval ticks might have specialized on parasitizing professional ant-followers, as tick larval stages disperse horizontally through the environment (Barros-Battesti et al. 2006, Nava et al. 2017) where professional ant-followers are most common. Tick life history information at the species level (e.g. host seeking behavior and breeding location) is necessary to quantify the detrimental effects that these parasites impose on their avian hosts and to confirm that higher parasite pressure from ticks is energetically costly in terms of host foraging efficiency (energy intake) and resources spent on immunological responses to cope with higher tick parasitism.

A significant phylogenetic signal in probability of tick infestation supports previous findings that host evolutionary history predicts parasitism, either because an ecological trait promotes higher parasite exposure (Davies et al. 1991, Ezenwa 2004, Fecchio et al. 2020b) or because host susceptibility and resistance to parasites and pathogens are phylogenetically conserved (Barrow et al. 2019). Ancestry may explain the complexity of intra- and interspecific interaction while attending army ant swarms or perhaps army ant-following as a trait is phylogenetically conserved among antbirds (Brumfield et al 2007). Whether evolution and maintenance of ant-following behavior were accompanied by the diversification of genes of the adaptive immune response has yet to be investigated. Because host species in a clade may share a trait that promotes exposure and resistance through common ancestry, one might predict that obligate ant-followers should diversify their immune genes to cope with increased parasite pressure. If increased parasite pressure is a major cost of ant-following behavior then we would expect to observe a higher diversity of immune genes, such as MCH and Toll-Like receptors, among the species that regularly attend swarms of army ants.

Author contributions

Alan Fecchio: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (supporting); Writing – original draft (lead); Writing – review and editing (lead). **Thiago Martins**: Data curation (supporting); Methodology (equal); Writing – review and editing (equal). **Maria Ogrzewalska**: Data curation (equal); Funding acquisition (equal); Methodology (equal); Writing – review and editing (equal). **Fabio Schunck**: Conceptualization (equal); Data curation (equal); Methodology (equal); Project administration (equal); Writing – review and editing (equal). **Jason Weckstein**: Conceptualization (equal); Data curation (equal); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (equal); Writing – review and editing (supporting). **Raphael Dias**: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Investigation (lead); Methodology (supporting); Project administration (supporting); Writing – original draft (lead); Writing – review and editing (lead).

Transparent Peer Review

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Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi:10.5061/dryad.fttdz08sn> (Fecchio et al. 2021).

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