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Ticks from the Brazilian Amazon: Species, Distribution and Host-Relations

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Abstract

Ticks are important ectoparasites and can transmit a wide variety of pathogens to animals and humans worldwide. These ectoparasites are the most important vectors of diseases causing pathogens in domestic and wild animals, and the second for man. In Brazil, Spotted Fever is the only disease transmitted to humans by ticks, while for animals we can highlight babesiosis, ehrlichiosis and anaplasmosis. Although ticks are found in all of Brazil's biomes, little is known about its diversity and host-relations in the Amazon biome. The existing gaps and the lack of research indicate that the diversity of ticks and their possible pathogens are underestimated in the Brazilian Amazon. Therefore, in order to guide the next studies in the Amazon biome, we present in this chapter a compilation of the records of hard ticks and soft ticks parasitizing wild and domestic animals, and humans. We present the general list of ticks for this biome, their distribution, hosts and importance for public health and veterinary. Finally, the ixodofauna found in the Brazilian Amazon and presented here does not match the vertebrate diversity of this biome, which is one of the largest on the planet. Therefore, more acarologists and epidemiologists are needed in this region.

Keywords: Ixodida, domestic animals, wild animals, humans, Amazon, Brazil

1. Introduction

The Amazon or Amazon Rainforest is the largest remnant of tropical forest in the world, occupying a region of approximately 6.7 million/km², covering nine countries in South America: Ecuador (\cong 2%), Suriname (\cong 2%), Bolivia (\cong 4%), Venezuela (\cong 4%), Guyana (\cong 3%), French Guiana (\cong 2%), Colombia (\cong 10%), Peru (\cong 13%), and Brazil (\cong 60%) (**Figure 1**) [1, 2]. In Brazil, the Amazon biome, also known as "Legal Amazon" occupies approximately 49% of its territory, covering the states of Acre, Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima, Tocantins and Maranhão (**Figure 1**). The Brazilian Amazon is known for its high richness of landscapes composed of 23 ecoregions, whose main domain is the humid rainforest (\cong 78%). Due to this heterogeneity, the Amazon has an immeasurable amount of essential habitats for the maintenance of flora and fauna, represented

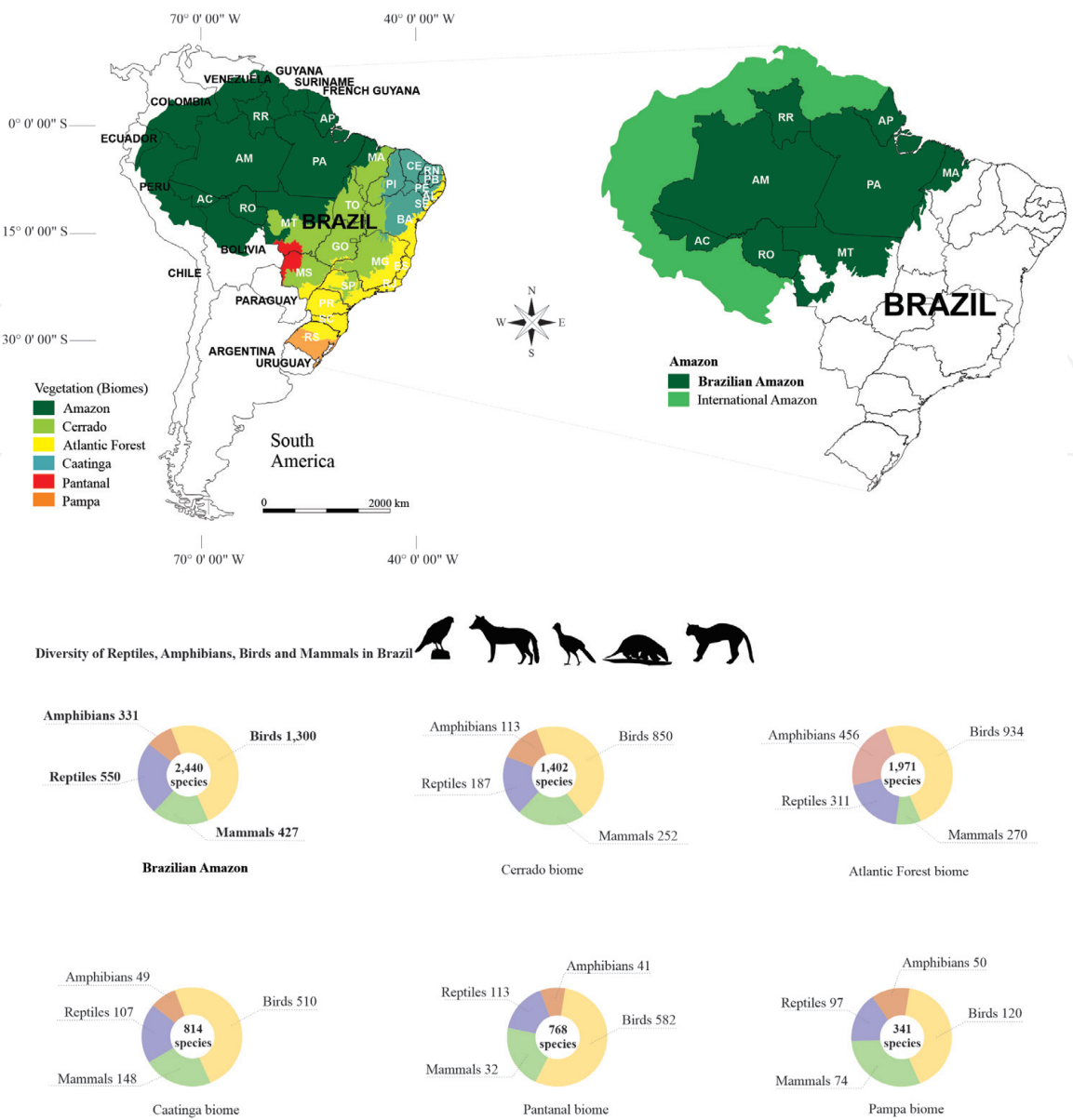


Figure 1.
Diversity of reptiles, amphibians, birds and mammals in Brazil, including the Brazilian Amazon.

with high biological diversity, which is regarded as the largest in the world [3, 4]. The Amazon has approximately 45,000 species of flora (39,474 species) and fauna (5,526 species) [2, 5]. However, even with this expressive diversity and the numerous faunal studies carried out in the region, there are still many gaps in the biological diversity of the Amazon. Due to its enormous extension and high degree of preservation (e.g., unexplored areas), new bioecological associations and new species are discovered every year. In the past 20 years, more than 1,200 new species have been described in the Amazon region from which we can highlight 16 birds, 39 mammals, 55 reptiles and $\cong 100$ amphibians [2]. However, anthropic action has negatively impacted the animal-forest relationships for decades, resulting in the extinction of ecologically demanding species and, at the same time, the appearance of opportunistic and/or generalist species [6].

Many domestic and wild animals are responsible for the maintenance and dispersion of ticks in nature. In addition, vertebrates act as amplifiers and/or reservoirs for viruses, protozoa and bacteria transmitted by these ectoparasites. The anthropic action affects the population dynamics of both ticks and their wild hosts directly or indirectly, and consequently, the epidemiology of tick-borne diseases once restricted to wild fauna can reach domestic animal and humans interfaces [7]. Ticks are responsible for more than 100,000 cases of diseases in humans and animals

worldwide [8], therefore a concern for public health professional. In Brazil, ticks are vectors of diseases such as babesiosis, ehrlichiosis, anaplasmosis and rickettsioses, including Brazilian Spotted Fever (BSF) [9, 10].

Ticks belong to the Sub-Class Acari, Super-Order Parasitiformes, Order Ixodida, and four families: Ixodidae, Argasidae, Nuttalliellidae and Deinocerotonidae [11, 12], the latter extinct. Of these, only the Ixodidae and Argasidae families occur in Brazil, with nine genera and 75 species [11, 13–16]. Ixodidae family is the most diverse with 51 species and five genera: *Amblyomma* (33 species), *Ixodes* (12 species), *Rhipicephalus* (two species), *Haemaphysalis* (three species) and *Dermacentor* (one species). Argasidae family is represented by 24 species and four genera: *Ornithodoros* (18 species), *Antricola* (three species), *Argas* (one species) and *Nothoaspis* (two species). In general, the immature stages (larvae and nymphs) of two or three host ticks feed on small mammals and birds, while adults exploit medium to large-sized hosts [17]. One-host species *Dermacentor nitens* and *Rhipicephalus microplus*, complete the life cycle mainly on large animals such as horses and cattle, respectively. Second Esser et al. [18] the diversity of ticks increases with the increase of diversity of hosts, inasmuch as these hematophagous arthropods rely on the hosts to complete their life cycles. Therefore, if we take into account the high diversity of hosts living in this biome and the amount of unexplored ecoregions, it is reasonable to infer that the diversity of ticks in the Amazon biome is insufficiently addressed. Thus, a review on the subject is necessary to point out the existing gaps and encourage new studies on ticks in the Brazilian Amazon.

2. Hard ticks associated with amphibians and reptiles

The class Amphibia includes the orders Anura, Caudata, Gymnophiona, whereas the class Reptilia includes the orders Squamata, Testudines and Crocodylia. There are 331 amphibian and 550 reptile species in the Brazilian Amazon (**Figure 1**), although that faunal records are far from complete [2, 19]. Brazil has witnessed an increasing number of reports on tick parasitism of amphibians and reptiles over the past few years [20–24]. However, knowledge of this tick fauna as their hosts remains incomplete. To date, major tick-amphibian associations reported in Brazil are the ixodids *Amblyomma dissimile*, *Amblyomma rotundatum*, *Amblyomma humerale*, *Amblyomma fuscum* and *Amblyomma goeldii* [20–24], and the argasids *Ornithodoros saraivai* and *Ornithodoros faccinii* associated with species *Cycloramphus boraceiensis* and *Thoropa miliaris*, respectively [25, 26]. Occasional records on reptiles have also been reported for *Ornithodoros mimon* and *Ornithodoros rietcorraei* [22]. However, none of these argasids have been reported in the Amazon biome. Although the Brazilian Amazon has a high diversity of amphibians and reptiles, studies on ticks in association with these hosts are still rare, with a dominance of species *A. dissimile*, *A. rotundatum* and *A. humerale* [21–23, 27, 28].

The tick *A. dissimile* is constantly misidentified with the morphologically similar *A. rotundatum*. Recently, the distribution of *A. dissimile* in the country was reorganized, showing that this tick is restricted to the Pantanal and Amazon biomes [28]. Therefore, reports outside these biomes are considered misidentifications and must be viewed with caution. Most publications on this species are simple records of occurrence with some authors including data on prevalence and intensity of infestation both in the Amazon biome and elsewhere. According to Luz et al. [29] 12 (54.5%) out of 22 *Rhinella marina* toads captured in Amapá state, were parasitized by a total of 97 ticks (6 males, 39 females, 31 nymphs, 21 larvae) and mean intensity of 8.1 ticks per infested toad. In the Amazonian biome, *A. dissimile* is common on *R. marina* (Anura) and Boidae (Squamata) (**Table 1**). The experimental life cycle

Host	Specie	<i>A. dissimile</i>			<i>A. rotundatum</i>		
		L	N	A	L	N	A
Amphibian (Anura)							
Bufonidae	<i>Rhinella marina</i>	37	12M; 16F	164	133F	[23, 29–33]	
	<i>Rhinella major</i>		2F	15	2F	[33–35]	
	<i>Rhaebo guttatus</i>			1	1F	[23]	
	<i>Rhinella margaritifera</i>			3	1F	[23]	
	<i>Rhinella gildae</i>			1		[36]	
Leptodactylidae	<i>Leptodactylus pentadactylus</i>				1F	[23]	
Reptile							
Boidae	<i>Boa constrictor</i>	1703	723M; 1346F	12	1M; 77F	[23, 30, 32–34, 36–40]	
	<i>Corallus hortulanus</i>	3	1M			[31, 34]	
	<i>Eunectes murinus</i>	305	21M; 3F			[31, 40]	
Viperidae	<i>Bothrops atrox</i>	4	11	24M; 14F	1M; 2F	[32, 33, 36, 37]	
	<i>Crotalus durissus</i>			1M; 1F		[34]	
	<i>Lachesis muta</i>	1				[34]	
Elapidae	<i>Micrurus averyi</i>			3F		[31]	
	<i>Micrurus lemniscatus</i>			12M; 9F		[31]	
Colubridade	<i>Leptophis ahaetulla</i>				3	[33]	
	<i>Chironius multiventris</i>				3	[33]	
	<i>Chironius scurrulus</i>			1M; 1F		[34]	
	<i>Chironius laevis</i>	12	15M; 6F			[31]	
	<i>Mastigodryas boddaerti</i>				1	[33]	
	<i>Hydrodynastes gigas</i>				1	7F	[30]
	<i>Helicops polylepis</i>	1				[34]	
	<i>Leptodeira annulata</i>	1				[34]	
	<i>Phimophis guerini</i>			1F		[34]	
	<i>Erythrolamprus reginae</i>	1				[34]	
	<i>Spilotes pullatus</i>	72	42M; 9F			[31]	
	<i>Erythrolamprus reginae semilineatus</i>	1				[34]	
Dipsadidae	<i>Xenodon severus</i>		8			[40]	
Testudinidae	<i>Chelonoidis denticulatus</i>		3M	3	2M; 42F	[31, 41]	
	<i>Chelonoidis carbonaria</i>	1	1M; 1F	11		[32, 39]	
Podocnemididae	<i>Podocnemis expansa</i>				1F	[39]	
	<i>Podocnemis unifilis</i>			1		[39]	
	<i>Trachemys dorbigni</i>			2	12F	[39]	
Kinosternidae	<i>Kinosternon scorpioides</i>				2F	[42]	

Host	Specie	A. dissimile			A. rotundatum		
		L	N	A	L	N	A
Chelidae	<i>Platemys platycephala</i>						5F [32]
Tropiduridade	<i>Uranoscodon superciliosus</i>				7		6F [33]
	<i>Tropidurus</i> sp.						1M [38]
Teiidae	<i>Ameiva ameiva</i>		4				1F [31, 34]
Iguanidae	<i>Iguana iguana</i>		31	118M; 69F			2F [31, 36, 39, 40]
Dactyloidae	<i>Norops auratus</i>		1				[34]
Gekkonidae	<i>Hemidactylus mabouia</i>		1				[34]
Alligatoridae	<i>Paleosuchus trigonatus</i>			9M; 15F	4		12F [31, 32]
	<i>Caiman crocodilus</i>		3				[31, 39]
Total		4	2189	983M; 1496F	221		307F

Table 1.
Hosts of *Amblyomma dissimile* and *Amblyomma rotundatum* in the Brazilian Amazon.

including pre-attachment periods for each parasitic stage lasts approximately 350 days, as reported by Schumaker et al. [43] who started a colony from one engorged female collected from the Amazonian biome. Ogrzewalska et al. [37] reported *Rickettsia bellii* and ‘*Candidatus Rickettsia colombianensi*’ in ticks collected from *Bothrops atrox* from Pará state. Luz et al. [29] reported ‘*Ca. R. colombianensi*’ in ticks collected on *R. marina* from Amapá state.

The tick *A. rotundatum* is an obligate parthenogenetic species, although there are six reports of adult males, two males in the laboratory [44] and six in the Amazon region parasitizing *Tropidurus* sp., *Boa constrictor*, *Iguana iguana*, *Chelonoidis denticulatus* and *B. atrox* [30, 36, 44–47]. Most publications on *A. rotundatum* are simple records of its occurrence with some additional data on prevalence and intensity of infestation in the Cerrado, Atlantic forest and Amazon biomes [22, 23, 31, 34, 48]. In the Brazilian Amazon, the families Bufonidae (Amphibian) and Boidae (Reptilia) are the most frequently parasitized by *A. rotundatum*, but there are reports on other species of Amphibian and Reptiles (Table 1). Recently, Gianizella et al. [31] reported *A. rotundatum* in different municipalities of the Amazonas state, on *B. constrictor* and several unknown hosts. The bioecology of this species under quasi-natural environment demonstrated a peak of larvae and nymphs in the dry season and females in the rainy season; however, there is a hypothesis of the absence of seasonality in this tick [48, 49]. Although *A. rotundatum* is a three-host tick on amphibians, it can behave as a two-host tick when feeding on snakes [50]. The complete experimental life cycle, including pre-attachment periods for each parasitic stage, ranged from 126 to 228 days on toads [51] or 56 to 163 days on snakes [50] and ulcerative lesions and hemorrhages after *A. rotundatum* feeding [48] were reported for ticks collected on toads from the Cerrado biome. Transmission of the hemogregarine *Hemolivia stellata* by *R. marina* collected in Belém, state of Pará was reported by Petit et al. [52]. This tick has also been found infected with *R. bellii* in the state of Amazon in the municipalities of Cacaupê and Monte Negro, in the state of Rondônia; in the municipalities of Amapá (Ilha de Maracá) and Santana, in the state of Amapá; and in the municipality of Rio Branco, in the state of Acre [29, 53, 54].

Most reports of *A. humerale* mention the adult stage parasitizing species of tortoises, namely the “yellow-footed tortoise” *C. denticulatus* and the “red-footed tortoise” *Chelonoidis carbonarius* [27, 55]. There is also a record of *A. humerale* on *Rhinoclemmys punctularia* in central Amazon [56]. Labruna et al. [27] collected 215 adult ticks from six *C. denticulatus* and nine *Chelonoidis* sp. from state of Rondônia, with mean infestation of 14.3 ± 12.0 ticks per tortoise. In addition, seven engorged nymphs were collected on lizards. Morais et al. [57] collected 120 adult ticks from 18 (75%) out of 24 *C. denticulatus* captured in a transitional area between the biomes Cerrado and southwestern Amazon rainforest, in the state of Mato Grosso. The mean intensity of infestation was 6.7 ticks/tortoise. In both surveys, male ticks were mostly attached in clusters on the carapace whereas females were found attached to the tortoise skin. The sex ratio (males:females) for *A. humerale* were different in both surveys, 10.3:1 [27] and 1.1:1 [57]. There is one additional record of two nymphs on *Paleosuchus trigonatus* (Crocodylia) [32]. The life-cycle in the laboratory, including pre-feeding periods for each of the parasitic stages, could be completed in an average period of ca. 200 days [58]. *Rickettsia bellii* and *Rickettsia amblyommatis* have been detected in *A. humerale* [42, 53]. The records of *A. fuscum* in association with amphibians and reptiles are rare in Brazil. Dantas-Torres et al. [59] collected one male tick in one out of 490 caimans (*Caiman latirostris* and *Paleosuchus palpebrosus*) trapped in the Atlantic rainforest biome in Pernambuco state, north-eastern Brazil. *Amblyomma goeldii* has been recorded only in the Amazonas state. Martins et al. [60] reported two males collected on *B. constrictor* and recovery of ≈ 100 (20%) engorged larvae out of ≈ 500 unfed larvae experimentally infested on a *B. constrictor*.

3. Hard ticks associated with wild birds

The importance of birds to maintain biodiversity and ecological balance of nature is notorious [61]. Due to migration, wild birds are of concern to human and animal health worldwide [62] because they can carry infected ticks over long distances, directly influencing the epidemiology of tick-borne diseases in animals and humans. In addition, wild birds themselves can be reservoirs of *Borrelia burgdorferi* sensu lato, and potentially to *Anaplasma phagocytophilum* and *Rickettsia* spp. [62, 63]. Wild birds play an important role in maintaining and dispersing immatures (larvae and nymphs) of several tick species into new locations [61, 64].

Of the total genera of ticks described in Brazil, five have at least one species recorded in association with wild birds. The most common are the hard ticks of the genera *Amblyomma*, *Haemaphysalis* and *Ixodes* [61, 64]. There are also occasional reports of the genera *Rhipicephalus* and *Ornithodoros*. Ticks of the genus *Amblyomma* are the most common on wild birds in the Brazil including the Amazon biome, exclusively for the larvae and nymphs [61, 64]. Adult ticks are only occasionally found on wild birds, with the exception of *Ixodes paranaensis* and *Ixodes auritulus*, which have the entire cycle synchronized with birds [65]. In Brazil, there are no reports of wild birds as a source of pathogens transmitted by ticks to humans, but they can serve as disperser hosts for vectors of Brazilian Spotted Fever (BSF) as *Amblyomma sculptum*, *Amblyomma aureolatum* and *Amblyomma ovale*, in the larvae and nymph stages [64]. Therefore, wild birds act indirectly in the epidemiology of BSF by dispersing and maintaining their vectors in nature.

Over more than 1,900 birds recorded in Brazil, approximately 1,300 reside in the Brazilian Amazon, with a 20% of endemism [66] (**Figure 1**). Of these, approximately 7% are migrants from the northern hemisphere and southern South America, including migrations from other Brazilian biomes [67]. To date, 86 bird species

of Brazilian Amazonian have been recorded in association with at least one tick species (**Table 2**). This is equivalent to approximately only 7% of bird species found in this biome and 5% of the total birds recorded in Brazil (**Table 2**). Similar to other studies regarding tick-bird associations in Brazil [73–75], Passeriformes birds were the most parasitized in the Amazon biome, including 14 families and 72 species (**Figure 2** and **Table 2**). In this group, the greatest diversity of parasitized birds was *Thamnophilidae* (20 species) followed by *Dendrocolaptidae* (16 species) and *Tyrannidae* (10 species) (**Figure 2**). The least parasitized families were *Conopophagidae*, *Furnariidae*, *Xenopidae*, *Tityridae*, *Cardinalidae*, *Columbidae*, *Cuculidae*, *Momotidae*, *Capitonidae*, *Ramphastidae*, *Psittacidae*, *Accipitridae* and *Falconidae* with only one species of parasitized bird each (**Figure 2** and **Table 2**). Non-Passerines were represented by 10 different orders and 11 families, with

Hosts		Ticks		References	
		Species	Stages		
			LL	NN	
Passeriformes	Thamnophilidae	<i>Thamnomanes schistogynus</i>	<i>A. humerale</i>	1	[68]
			<i>A. nodosum</i>	1	
		<i>Thamnophilus doliatus</i>	<i>A. nodosum</i>	2	[68]
		<i>Thamnophilus schistaceus</i>	<i>A. nodosum</i> <i>Amblyomma</i> sp.	2 2	
		<i>Thamnophilus aethiops</i>	<i>A. calcaratum</i>	5	[68]
			<i>A. longirostre</i>	1	
		<i>Myrmelastes hyperythrus</i>	<i>A. nodosum</i>	9	[68]
		<i>Sciaphylax hemimelaena</i>	<i>A. nodosum</i>	1	
		<i>Schistocichla leucostigma</i>	<i>A. humerale</i>	4	[69]
			<i>Amblyomma</i> sp.	5	
		<i>Phlegopsis nigromaculata</i>	<i>A. coelebs</i>	1	[68, 69]
			<i>A. longirostre</i>	1	
			<i>A. nodosum</i>	24	
			<i>Amblyomma</i> sp.		
		<i>Hypocnemis subflava</i>	<i>Amblyomma</i> sp.	3	[70]
		<i>Hylophylax naevius</i>	<i>H. juxtakochi</i>	1	
			<i>A. humerale</i>	3	[69]
			<i>A. longirostre</i>	1	
			<i>A. calcaratum</i>	8	
			<i>Amblyomma</i> sp.		
		<i>Hylophylax punctulatus</i>	<i>Amblyomma</i> sp.	1	[69]
		<i>Thamnomanes caesius</i>	<i>A. geayi</i>	1	
			<i>A. longirostre</i>	3	[69, 71]
			<i>A. humerale</i>	4	
			<i>Amblyomma</i> sp		
		<i>Hylophylax poecilinotus</i>	<i>A. geayi</i>	1	[69]
			<i>A. humerale</i>	1	
			<i>A. longirostre</i>	3	
			<i>Amblyomma</i> sp.	22	
			<i>H. juxtakochi</i>	1	
		<i>Myrmornis torquata</i>	<i>Amblyomma</i> sp.	3	[69]

Hosts		Ticks		References	
		Species	Stages		
	<i>Myrmotherula hauxwelli</i>	<i>Amblyomma</i> sp.	1	[69]	
	<i>Myrmotherula longipennis</i>	<i>A. longirostre</i>	3	[69]	
		<i>Amblyomma</i> sp.	3		
	<i>Pyriglena leuconota</i>	<i>A. coelebs</i>	1	1	[69]
		<i>A. humerale</i>	1		
		<i>A. longirostre</i>	9		
		<i>Amblyomma</i> sp.	4		
	<i>Myrmoborus myotherinus</i>	<i>A. longirostre</i>		1	[69]
	<i>Epinecrophylla leucophthalma</i>	<i>A. longirostre</i>		1	[71]
	<i>Willisornis poecilinotus</i>	<i>A. calcaratum</i>		1	[71]
Conopophagidae	<i>Conopophaga aurita</i>	<i>Amblyomma</i> sp.		1	[69]
Scleruridae	<i>Sclerurus cf. rufigularis</i>	<i>A. humerale</i>		1	[68]
	<i>Sclerurus caudacutus</i>	<i>A. humerale</i>		1	[69]
Furnariidae	<i>Automolus paraensis</i>	<i>Amblyomma</i> sp.		1	[69]
Dendrocolaptidae	<i>Dendrocincla merula</i>	<i>A. longirostre</i>	7	1	[68, 69, 71]
		<i>Amblyomma</i> sp.	34		
	<i>Dendrocincla fuliginosa</i>	<i>Amblyomma</i> sp.	10		[31, 70]
	<i>Deconychura longicauda</i>	<i>A. longirostre</i>	4	1	[69, 71]
		<i>Amblyomma</i> sp.	39		
	<i>Deconychura stictolaema</i>	<i>A. longirostre</i>	1	1	[69]
		<i>Amblyomma</i> sp.	1		
	<i>Dendrocolaptes hoffmannsi</i>	<i>A. calcaratum</i>	1	2	[69]
		<i>A. geayi</i>	2	1	
		<i>A. humerale</i>	4	3	
		<i>A. longirostre</i>	39		
		<i>Amblyomma</i> sp.	59		
	<i>Dendrocolaptes certhia</i>	<i>A. longirostre</i>		1	[71]
	<i>Glyphorhynchus spirurus</i>	<i>A. longirostre</i>		1	[71]
	<i>Glyphorhynchus spirurus</i>	<i>A. geayi</i>	1	1	[69]
		<i>A. longirostre</i>	6	2	
		<i>Amblyomma</i> sp.	16		
	<i>Hylexetastes brigidai</i>	<i>A. geayi</i>	1	2	[69]
		<i>A. longirostre</i>	6		
		<i>Amblyomma</i> sp.	21		
	<i>Sittasomus griseicapillus</i>	<i>A. humerale</i>	2	1	[70]
	<i>Xiphorhynchus guttatus</i>	<i>Amblyomma</i> sp.			
		<i>A. longirostre</i>		2	[68]
	<i>Xiphorhynchus guttatoides</i>	<i>A. nodosum</i>		1	
		<i>A. humerale</i>	1	2	[70]
	<i>Xiphorhynchus elegans</i>	<i>Amblyomma</i> sp.			
		<i>A. longirostre</i>	3	2	[69]
		<i>Amblyomma</i> sp.	2		

Hosts		Ticks		References	
		Species	Stages		
Xenopidae Pipridae Rhynchocyclidae Tyrannidae	<i>Xiphorhynchus ocellatus</i>	<i>A. calcaratum</i>	1		[71]
	<i>Xiphorhynchus pardalotus</i>	<i>Amblyomma</i> sp.	3		[31]
	<i>Dendroplex picus</i>	<i>A. longirostre</i> <i>A. nodosum</i>	3 3		[68, 70]
	<i>Xenops minutus</i>	<i>A. nodosum</i>	2		[69]
	<i>Pipra filicauda</i>	<i>A. geayi</i> <i>Amblyomma</i> sp.	1		[68, 70]
	<i>Pipra fasciicauda</i>	<i>A. longirostre</i> <i>A. nodosum</i> <i>Amblyomma</i> sp.	1 8	7	[68]
	<i>Machaeropterus pyrocephalus</i>	<i>A. longirostre</i>	1		[68]
	<i>Dixiphia pipra</i>	<i>A. geayi</i> <i>A. longirostre</i>	1 1	1 1	[69]
	<i>Lepidothrix nattereri</i>	<i>Amblyomma</i> sp.	1		[71]
	<i>Leptopogon amaurocephalus</i>	<i>A. geayi</i>	1		[68]
	<i>Rhynchocylus olivaceus</i>	<i>A. geayi</i> <i>A. humerale</i> <i>A. longirostre</i> <i>A. nodosum</i> <i>Amblyomma</i> sp.	1 1 4	2 1 17	[68]
	<i>Todirostrum maculatum</i>	<i>A. nodosum</i>	1		[68]
	<i>Poecilatriccus latirostris</i>	<i>A. nodosum</i> <i>Amblyomma</i> sp.	6	3	[70]
	<i>Hemitriccus flammulatus</i>	<i>Amblyomma</i> sp.	1		[70]
	<i>Myiozetetes similis</i>	<i>A. nodosum</i>	1		[68]
	<i>Empidonax alnorum</i>	<i>A. nodosum</i> <i>A. longirostre</i>	4	1	[68]
	<i>Platyrinchus saturatus</i>	<i>Amblyomma</i> sp.	1		[69]
	<i>Hemitriccus minor</i>	<i>A. longirostre</i>	1		[69]
	<i>Mionectes macconnelli</i>	<i>A. longirostre</i> <i>Amblyomma</i> sp.	4 5		[69]
	<i>Attila spadiceus</i>	<i>A. geayi</i> <i>Amblyomma</i> sp.	1 3		[69]
	<i>Myiobius barbatus</i>	<i>A. longirostre</i>	3		[69]
	<i>Onychorhynchus coronatus</i>	<i>A. longirostre</i> <i>Amblyomma</i> sp.	3 6		[69]
	<i>Ramphotrigon megacephalum</i>	<i>A. nodosum</i> <i>Amblyomma</i> sp.	1	3	[70]
	<i>Knipolegus poecilocercus</i>	<i>Amblyomma</i> sp.	1		[71]

Hosts			Ticks		References	
			Species	Stages		
	Troglodytidae	<i>Pheugopedius genibarbis</i>	<i>A. nodosum</i> <i>Amblyomma</i> sp.	363 1		[68]
		<i>Microcerculus marginatus</i>	<i>Amblyomma</i> sp.	3		[69]
	Tityridae	<i>Schiffornis turdina</i>	<i>A. longirostre</i> <i>Amblyomma</i> sp.	3 14		[69]
		<i>Turdus hauxwelli</i>	<i>A. longirostre</i>	2		[68]
	Turdidae	<i>Turdus sanchezorum</i>	<i>A. longirostre</i>	1		[68]
		<i>Turdus ignobilis</i>	<i>A. geayi</i> <i>A. nodosum</i> <i>A. longirostre</i> <i>Amblyomma</i> sp.	2 1 1 1		[68]
		<i>Turdus amaurochalinus</i>	<i>Amblyomma</i> sp.	1		[70]
		<i>Turdus albicollis</i>	<i>A. longirostre</i> <i>A. coelebs</i> <i>Amblyomma</i> sp.	2 3 3		[31, 69]
	Thraupidae	<i>Ramphocelus carbo</i>	<i>A. nodosum</i> <i>A. longirostre</i> <i>Amblyomma</i> sp.	44 15 4		[30, 68, 70, 71]
		<i>Tachyphonus surinamus</i>	<i>A. humerale</i> <i>A. longirostre</i> <i>Amblyomma</i> sp.	1 1 5		
	Cardinalidae	<i>Cyanoloxia cyanooides</i>	<i>Amblyomma</i> sp.	1		[71]
Columbiformes	Columbidae	<i>Columbina talpacoti</i>	<i>A. nodosum</i>	1		[68]
Cuculiformes	Cuculidae	<i>Crotophaga major</i>	<i>A. nodosum</i>	1		[68]
Coraciiformes	Momotidae	<i>Momotus momota</i>	<i>A. longirostre</i> <i>A. humerale</i>	1 1		[68, 70]
Piciformes	Capitonidae	<i>Capito auratus insperatus</i>	<i>A. nodosum</i> <i>A. longirostre</i>	2 1		[68]
		<i>Ramphastidae</i> <i>Ramphastos vitellinus</i>	<i>A. geayi</i>	3		[31]
		<i>Pteroglossus bitorquatus</i>	<i>A. longirostre</i>	1		[30]
Galbuliformes	Bucconidae	<i>Monasa nigrifrons</i>	<i>Amblyomma</i> sp.	1		[70]
		<i>Malacoptila rufa</i>	<i>Amblyomma</i> sp.	1		[69]
		<i>Galbula cyanicollis</i>	<i>Amblyomma</i> sp.	2		[69]
Psittaciformes	Psittacidae	<i>Primolius maracana</i>	<i>A. dissimile</i>	1		[72]
Accipitriiformes	Accipitridae	<i>Harpia harpyja</i>	<i>A. cajennense</i> <i>H. juxtakochi</i>	16 1		[41]
		<i>Cariamidae</i> <i>Cariam cristata</i>	<i>A. cajennense</i>	5		[39]
Galliformes	Cracidae	<i>Penelope superciliaris</i>	<i>A. cajennense</i>	1 1		[42]
Falconiformes	Falconidae	<i>Micrastur ruficollis</i>	<i>A. longirostre</i>	1		[71]
Total				884 184		

Table 2.
Ticks identified on wild birds in the Brazilian Amazon biome.

emphasis on *Bucconidae* with three species (**Figure 2** and **Table 2**). To date, approximately 1,068 specimens of ticks have been collected from birds in the Brazilian Amazon, in the stages of larvae (884/83%), nymphs (184/17%) and no adults (**Figure 3**). These are included in the genera *Amblyomma* and *Haemaphysalis*. The genus *Amblyomma* was the dominant with eight species (**Table 2**). The greatest diversity of ticks was reported for the *Thamnophilidae* family with seven species: *A. longirostre*, *A. nodosum*, *A. humerale*, *A. calcaratum*, *A. geayi*, *A. coelebs* and *Haemaphysalis juxtakochi*. The *Dendrocolaptidae* family was the second with five

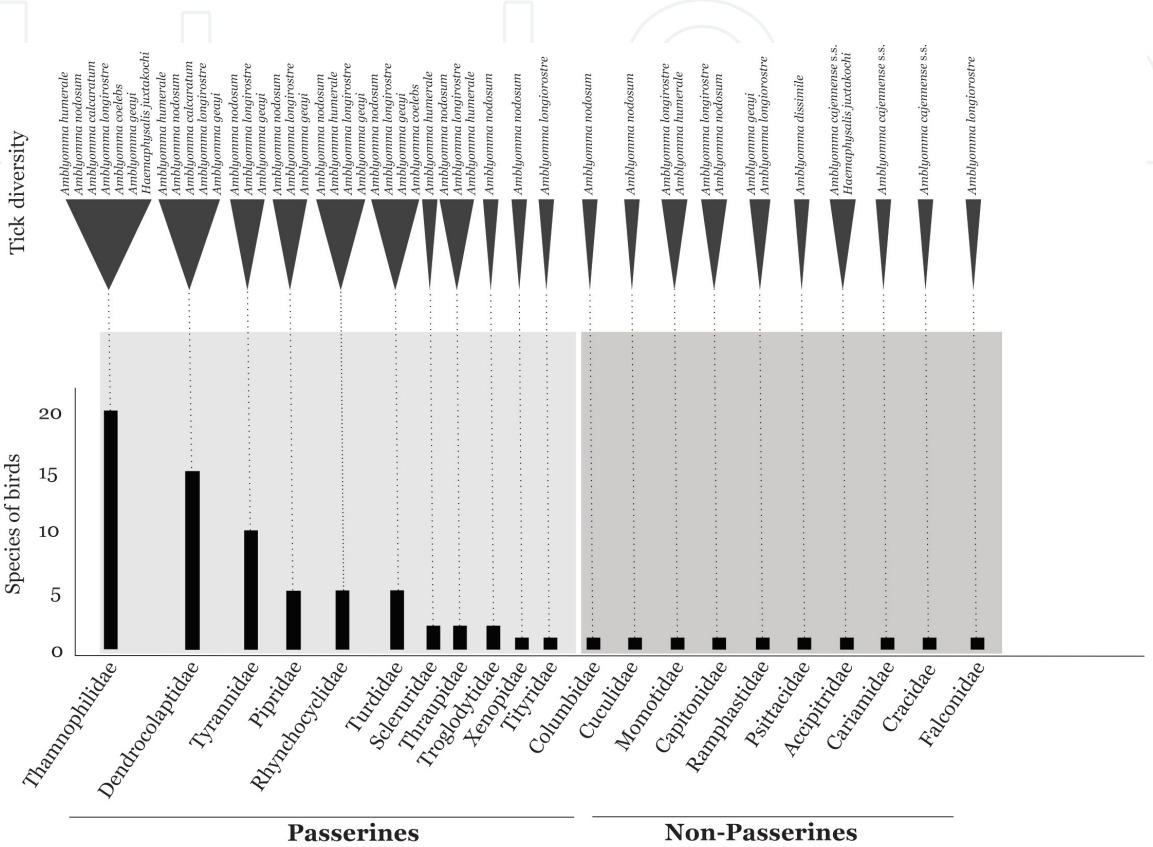


Figure 2.
Diversity of hard ticks parasitizing wild birds from the Brazilian Amazon.

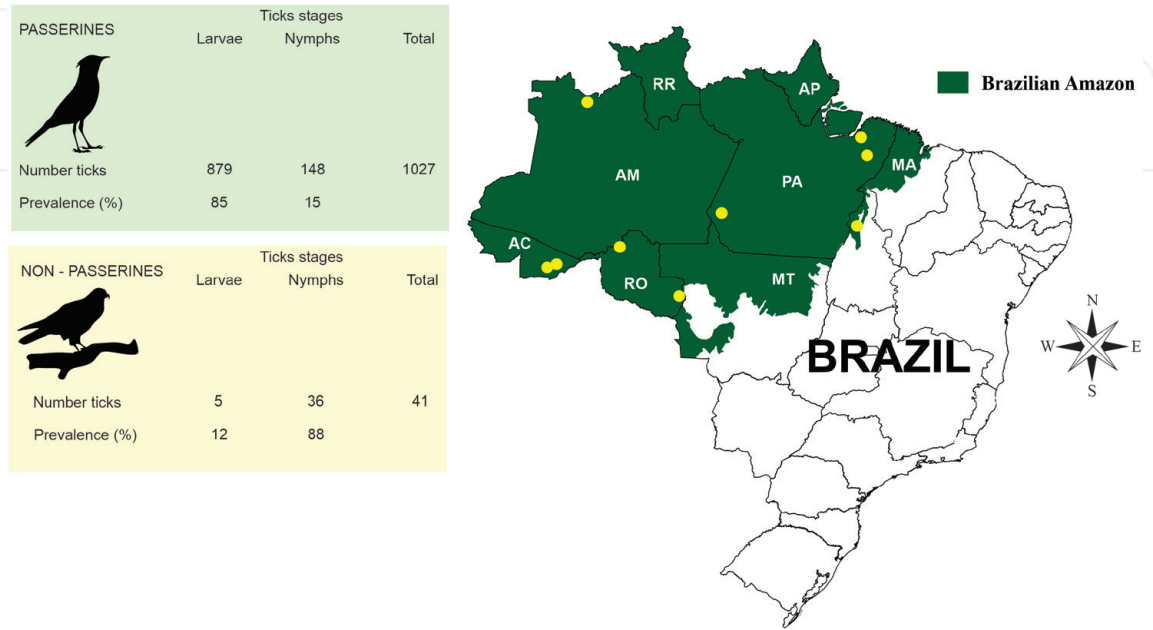


Figure 3.
Distribution of studies reporting the association of hard ticks on wild birds from the Brazilian Amazon.

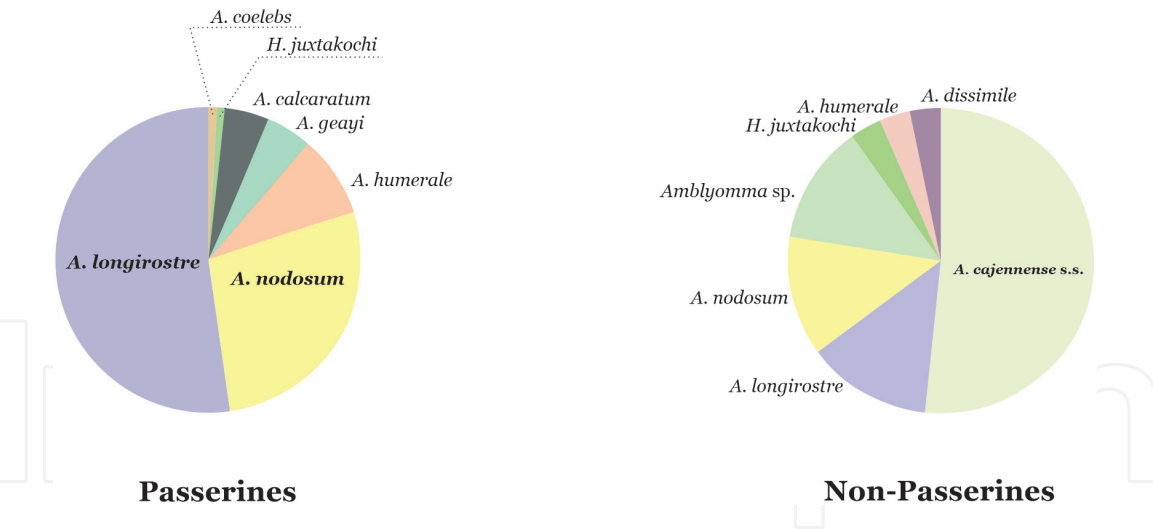


Figure 4.
Hard tick species parasitizing wild birds from the Brazilian Amazon.

species: *A. longirostre*, *A. nodosum*, *A. humerale*, *A. calcaratum* and *A. geayi* (Figure 2 and Table 2).

Overall, *A. longirostre* and *A. nodosum* are the two most common species on wild birds in the Brazilian Amazon [68–71] (Figure 4 and Table 2). The tick *A. longirostre* was the most common, recorded in 12 families and 40 species of birds (36 Passerines and 4 non-Passerines) (Figure 2). *Amblyomma longirostre* has been treated as an arboreal tick, with immatures parasitizing birds and adults parasitizing rodents Erethizontidae (e.g., *Sphiggurus* spp.) [73, 76]. This tick was also the most abundant with 110 larvae and 39 nymphs. *Amblyomma longirostre* was found in co-infestation with the following species: *A. calcaratum*, *A. nodosum*, *A. coelebs*, *A. humerale*, *A. geayi* and *H. juxtakochi* (Table 2). In addition, as it is frequent on birds, *A. longirostre* is popularly known as “bird tick” or “bird earring” [77]. *Amblyomma nodosum* was the second most common species collected on 12 families and 22 species of birds. This tick was recorded in co-infestation with *A. longirostre*, *A. coelebs*, *A. humerale* and *A. geayi* (Table 2 and Figures 2 and 4). The birds most infested by *A. nodosum* were *Rhynchocyclus olivaceus* and *Ramphocelus carbo* with 17 and 15 nymphs, respectively. These birds inhabit the forest understory and visit the soil occasionally [67]. As Xenartha mammals (*Myrmecophaga tridactyla*, *Tamandua tetradactyla*) are the primary hosts of *A. nodosum* [17], it is believed that the low areas of the understory are a major source of infestation. Interestingly, *T. tetradactyla* may have arboreal habits [78], which helps to explain the presence of *A. nodosum* also on birds of different forest strata.

To date, of the total of ticks collected, 736 (70%) were larvae identified as *Amblyomma* sp. due to lack of reliable tools for larval identification, thus, indicating that the diversity of ticks on birds of the Amazon may be underestimated. Luz et al. [75], using molecular biology, identified more than 90% of the larvae collected from birds in the Atlantic Forest biome, reporting the greatest diversity of ticks on birds in a single study in Brazil and description of the new tick *Amblyomma romarioi* [14]. Therefore, the identification of all larvae by molecular biology in addition to morphological identification is extremely important to ascertain the diversity of ticks in the Amazon biome.

4. Hard ticks associated with wild and domestic mammals

The fauna of wild mammals in Brazil is quite diverse and more than half lives in the Amazon biome [79]. Like birds, amphibians and reptiles, mammals play an

important role in preserved or anthropized ecosystems. Therefore, the knowledge of the local diversity of wild mammals, and their relationship with ticks is considered an important tool for public conservation policies and consequently for public health. The alteration of wild habitats can determine changes in the patterns of parasitic specificity, inducing tick species to seek new groups of hosts, increasing the risk of disease transmission [79, 80]. Some wild mammals (small, medium and large) are directly or indirectly involved in the transmission cycles of many tick-borne pathogens worldwide, including *Anaplasma* spp., *Babesia* spp., *Borrelia* spp., and *Rickettsia* spp. [80, 81]. In Brazil, the main zoonosis transmitted by ticks is Brazilian Spotted Fever caused by the bacterium *Rickettsia rickettsii*, which has the rodent *Hydrochoerus hydrochaeris* as its main amplifier. In addition, there is evidence that marsupials and small rodents can serve as amplifier hosts for *R. rickettsii* in nature [82].

In Brazil there are approximately 755 species of mammals distributed in all its six biomes, including the Amazon biome [78, 79]. Of the total mammal species, 41% (\cong 311 species) occur in the Amazon biome (**Figure 1**) [2, 76]. These vertebrates are distributed in 11 orders, 51 families and 249 genera [78, 79]. Among the families, Cricetidae is the most diverse, with 144 species [78, 79]. The vast majority of tick species, including all life stages, in Brazil have records on wild mammals of different sizes [17]. In general, small mammals of the orders Rodentia and Didelphimorphia are those that have a greater number of studies in association with ticks, especially the families Cricetidae and Didelphidae [17, 82]. In general, medium and large mammals are parasitized by ticks in all stages (larva, nymph and adult), while in small mammals the stages of larva and nymph are more common. In this last group of hosts we can highlight the cricetids *Akodon* spp., *Calomys* spp., *Oligoryzomys* spp. and *Nectomys* spp. as the most parasitized by immature ticks in nature.

Nine orders and 24 families of wild mammals have representatives in association with ticks in the Brazilian Amazon (**Figure 5**). Rodentia was the most diverse with 16 species of mammals, followed by the orders Carnivora (13 species) and Didelphimorphia (12 species) (**Figure 5**). However, it was the family Didelphidae that presented a greater number of parasitized species, followed by Dasyproctidae (seven species) and Mustelidae (four species). These records corroborate with numerous studies of tick parasitism on wild animals from South America, with emphasis on the orders Rodentia and Didelphimorphia [17, 82, 83].

Hard ticks parasitizing wild mammals in the Brazilian Amazon are represented by five genera: *Amblyomma*, *Ixodes*, *Haemaphysalis*, *Dermacentor* and *Rhipicephalus*. Of these, the genus *Amblyomma* was more frequently recorded with 23 species (**Figure 5**). The orders Rodentia, Pilosa and Didelphimorphia are hosts for highest diversity to *Amblyomma* species 17, 15 and eight, respectively. All these species are also recorded on a variety of wild mammals in Brazil [83–87], except for *A. rotundatum* and *A. dissimile*, which are more specific ticks of cold-blooded animals (Amphibians and Reptiles), although there are occasional reports on mammals in South America [20, 83]. *Amblyomma humerale*, of which the adult stage is more specific to tortoises, immature stages have been found on a variety of small mammals, reptiles and birds [17, 68, 71, 83].

The second most common genus in the Amazon is *Ixodes*, with six reported species: *Ixodes amarali*, *Ixodes bocatorensis*, *Ixodes lasallei*, *Ixodes luciae*, *Ixodes schulzei* and *Ixodes spinosus* (**Table 3**). Although there are two exclusive species on birds in Brazil [65], all species recorded in the Brazilian Amazon parasitize mainly wild mammals [13, 16, 31, 32, 88, 99, 102]. *Ixodes* spp. were found on families Didelphidae, Dasyproctidae, Cricetidae, Myrmecophagidae, Bradypodidae and Cyclopedidae (**Figure 5** and **Table 3**). In general *Ixodes* ticks mainly parasitize

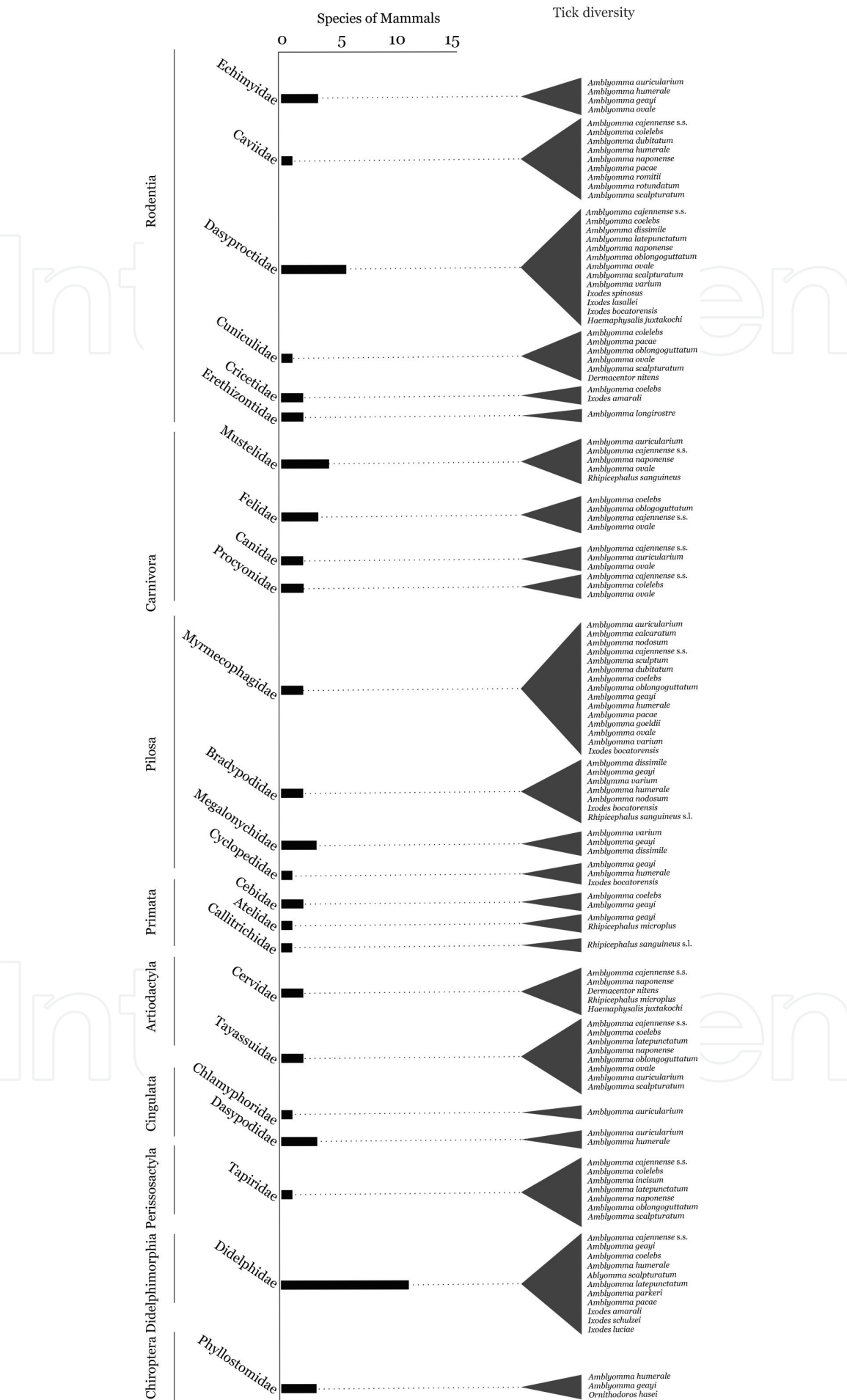


Figure 5. Diversity of hard ticks parasitizing wild mammals from the Brazilian Amazon.

Tick species	Domestic mammals	Wild mammals	States	References
<i>Amblyomma auricularium</i>		<i>Cabassous unicinctus</i> ⁴ , <i>Dasypus novemcinctus</i> ^{4,5,7} , <i>Dasypus septemcinctus</i> ^{4,9} , <i>Euphractus sexcinctus</i> ^{4,9} , <i>Galactis cuja</i> ^{4,9} , <i>Galictis vittata</i> ⁴ , <i>Lycalopex vetulus</i> ⁹ , <i>Myrmecophaga tridactyla</i> ⁹ , <i>Pecari tajacu</i> ⁹ , <i>Tamandua tetradactyla</i> ⁴ , <i>Thrichomys inermis</i> ⁴	MA ⁴ , MT ⁵ , RO ⁷ , TO ⁹	[30, 32, 36, 39]
<i>Amblyomma cajennense sensu stricto</i>	<i>Equus caballus</i> ^{4,5,6,7,8,9} , <i>Sus scrofa</i> ^{4,9} , <i>Canis familiaris</i> ^{4,9} , <i>Bubalus bubalis</i> ⁷	<i>Caluromys philander</i> ⁵ , <i>Cerdocyon thous</i> ⁵ , <i>Didelphis marsupialis</i> ⁵ , <i>Dasypsecta azarae</i> ⁵ , <i>Hydrochoerus hydrochaeris</i> ⁵ , <i>Mazama gouazoubira</i> ⁴ , <i>Metachirus nudicaudatus</i> ⁴ , <i>Myrmecophaga tridactyla</i> ^{5,9} , <i>Nasua nasua</i> ⁵ , <i>Panthera onca</i> ⁵ , <i>Pecari tajacu</i> ⁵ , <i>Pteronura brasiliensis</i> ³ , <i>Tapirus terrestris</i> ⁵ , <i>Tayassu pecari</i> ⁵	AM ³ , MA ⁴ , MT ⁵ , PA ⁶ , RO ⁷ , RR ⁸ , TO ⁹	[32, 36, 42, 88–91]
<i>Amblyomma calcaratum</i>		<i>Myrmecophaga tridactyla</i> ⁷ , <i>Tamandua tetradactyla</i> ^{4,5,6}	MA ⁴ , MT ⁵ , PA ⁶ , RO ⁷	[36, 38, 42]
<i>Amblyomma coelebs</i>	<i>Equus caballus</i> ⁷	<i>Agouti paca</i> ⁷ , <i>Cuniculus paca</i> ⁶ , <i>Dasypsecta azarae</i> ⁵ , <i>Dasypsecta sp</i> ⁷ , <i>Didelphis albiventris</i> ⁵ , <i>Didelphis marsupialis</i> ^{3,5} , <i>Hydrochoerus hydrochaeris</i> ⁷ , <i>Metachirus myosuroides</i> ⁵ , <i>Nasua nasua</i> ⁵ , <i>Neacomys spinosus</i> ⁵ , <i>Panthera onca</i> ⁵ , <i>Sapajus macrocephalus</i> ³ , <i>Tayassu pecari</i> ⁶ , <i>Pecari tajacu</i> ⁷ , <i>Tapirus terrestris</i> ^{3,5,7}	AM ³ , MT ⁵ , PA ⁶ , RO ⁷	[30–32, 38, 42, 88]
<i>Amblyomma dissimile</i>		<i>Bradypus tridactylus</i> ³ , <i>Choloepus didactylus</i> ³ , <i>Coendou sp</i> ³ , <i>Dasypsecta leporina</i> ³	AM ³	[31, 36, 40]
<i>Amblyomma dubitatum</i>		<i>Hydrochoerus hydrochaeris</i> ^{1,5,7} , <i>Tamandua tetradactyla</i> ⁹	AC ¹ , MT ⁵ , RO ⁷ , TO ⁹	[30, 32, 39, 54]
<i>Amblyomma geayi</i>		<i>Alouatta nigerrima</i> ⁶ , <i>Artibeus lituratus</i> ³ , <i>Bradypus tridactylus</i> ^{3,6} , <i>Bradypus variegatus</i> ^{1,3,4,6,9} , <i>Caluromys lanatus</i> ³ , <i>Choloepus hoffmanni</i> ⁷ , <i>Choloepus didactylus</i> ^{3,7} , <i>Cyclopes didactylus</i> ³ , <i>Didelphis marsupialis</i> ⁶ , <i>Philander opossum</i> ³ , <i>Proechimys sp</i> ³ , <i>Oecomys sp</i> ⁶ , <i>Saguinus bicolor</i> ³ , <i>Tamandua tetradactyla</i> ³	AC ¹ , AM ³ , MA ⁴ , PA ⁶ , RO ⁷ , TO ⁹	[30, 31, 33, 36, 39, 40, 42, 92]
<i>Amblyomma goeldii</i>		<i>Tamandua tetradactyla</i> ^{3,6} , <i>Bradypus tridactylus</i> ³	AM ³ , PA ⁶	[31, 40, 42]
<i>Amblyomma humerale</i>		<i>Bradypus tridactylus</i> ³ , <i>Chrotopterus auritus</i> ³ , <i>Cyclopes didactylus</i> ⁷ , <i>Dasypus novemcinctus</i> ^{5,6} , <i>Didelphis marsupialis</i> ^{3,5,6} , <i>Hydrochoerus</i>	AC ¹ , AM ³ , MT ⁵ , PA ⁶ , RO ⁷	[30–33, 38–40, 42, 54, 88]

Tick species	Domestic mammals	Wild mammals	States	References
		<i>hydrochaeris</i> ¹ , <i>Marmosa constantiae</i> ⁵ , <i>Marmosa</i> sp ³ , <i>Metachirus myosuroides</i> ⁵ , <i>Philander opossum</i> ³ , <i>Proechimys roberti</i> ⁵ , <i>Tamandua tetradactyla</i> ^{3,6}		
<i>Amblyomma incisum</i>		<i>Tapirus terrestris</i> ⁷	RO ⁷	[38, 93]
<i>Amblyomma latepunctatum</i>		<i>Tapirus terrestris</i> ^{3,6,7} , <i>Tayassu pecari</i> ³ , <i>Dasyprocta fuliginosa</i> ³ , <i>Didelphis marsupialis</i> ³	AM ³ , PA ⁶ , RO ⁷	[31, 38, 93]
<i>Amblyomma longirostre</i>		<i>Coendou</i> sp ³ , <i>Coendou prehensilis</i> ^{6,7} , <i>Coendou nycthemera</i> ⁶	AM ³ , PA ⁶ , RO ⁷	[30, 31, 33, 40, 42]
<i>Amblyomma naponense</i>		<i>Dasyprocta fuliginosa</i> ³ , <i>Galictis</i> sp ³ , <i>Hydrochoerus hydrochaeris</i> ¹ , <i>Mazama gouazoubira</i> ⁴ , <i>Myoprocta acouchy</i> ³ , <i>Tapirus terrestris</i> ⁷ , <i>Tayassu pecari</i> ^{3,4}	AC ¹ , AM ³ , MA ⁴ , RO ⁷	[31, 36, 38, 54]
<i>Amblyomma nodosum</i>		<i>Tamandua tetradactyla</i> ^{4,5,6,7,9} , <i>Bradypus variegatus</i> ⁹ , <i>Myrmecophaga tridactyla</i> ⁹	MA ⁴ , MT ⁵ , PA ⁶ , RO ⁷ , TO ⁹	[30, 32, 38–40, 42]
<i>Amblyomma oblongoguttatum</i>	<i>Canis familiaris</i> ^{4,6,9} , <i>Sus scrofa</i> ⁷	<i>Agouti paca</i> ⁷ , <i>Cuniculus paca</i> ⁹ , <i>Dasyprocta</i> sp ⁷ , <i>Myrmecophaga tridactyla</i> ⁹ , <i>Tayassu tacajú</i> ⁷ , <i>Tayassu pecari</i> ^{3,5,6,7} , <i>Dasyprocta fuliginosa</i> ³ , <i>Mazama americana</i> ³ , <i>Tapirus terrestris</i> ^{5,7} , <i>Panthera onca</i> ⁷	AM ³ , MA ⁴ , MT ⁵ , PA ⁶ , RO ⁷ , TO ⁹	[31, 32, 38, 39, 42, 91, 94, 95]
<i>Amblyomma ovale</i>	<i>Canis familiaris</i> ^{3,4,9} , <i>Sus scrofa</i> ⁷	<i>Panthera onca</i> ^{3,5,7,9} , <i>Tapirus terrestris</i> ³ , <i>Leopardus pardalis</i> ³ , <i>Proechimys quadruplicatus</i> ³ , <i>Proechimys</i> sp ³ , <i>Tapirus terrestris</i> ³ , <i>Pauxi tuberosa</i> ⁵ , <i>Puma concolor</i> ⁵ , <i>Procyon cancrivorus</i> ⁷ , <i>Tayassu tacajú</i> ⁷ , <i>Tayassu pecari</i> ⁷ , <i>Agouti paca</i> ⁷ , <i>Dasyprocta</i> sp ⁷ , <i>Eira barbara</i> ⁷ , <i>Nasua nasua</i> ⁷ , <i>Cerdocyon thous</i> ⁹	AM ³ , MA ⁴ , MT ⁵ , RO ⁷ , TO ⁹	[30–32, 38, 39, 42, 91, 94]
<i>Amblyomma paca</i>	<i>Canis familiaris</i> ⁷	<i>Hydrochoerus hydrochaeris</i> ¹ , <i>Cuniculus paca</i> ⁵ , <i>Tamandua tetradactyla</i> ⁶ , <i>Monodelphis glirina</i> ⁶ , <i>Didelphis marsupialis</i> ⁷	AC ¹ , MT ⁵ , PA ⁶ , RO ⁷	[38, 42, 54, 92]
<i>Amblyomma parkeri</i>		<i>Didelphis marsupialis</i> ⁵	MT ⁵	[32]
<i>Amblyomma romitii</i>		<i>Hydrochoerus hydrochaeris</i> ^{5,6,7}	MT ⁵ , PA ⁶ , RO ⁷	[32, 41, 96]
<i>Amblyomma rotundatum</i>		<i>Hydrochoerus hydrochaeris</i> ⁱ , <i>Xenodon merremii</i> ⁹	RO ⁷ , TO ⁹	[30–33, 36, 38, 39, 41, 42, 54]
<i>Amblyomma scalpturatum</i>	<i>Canis familiaris</i> ⁷ , <i>Sus scrofa</i> ⁷	<i>Agouti paca</i> ⁷ , <i>Dasyprocta fuliginosa</i> ³ , <i>Didelphis marsupialis</i> ⁵ , <i>Pecari tajacu</i> ^{5,7}	AM ³ , MT ⁵ , RO ⁷	[30–32, 38, 88]

Tick species	Domestic mammals	Wild mammals	States	References
		<i>Tapirus terrestris</i> ^{5,7} , <i>Hydrochoerus hydrochaeris</i> ⁷		
<i>Amblyomma sculptum</i>	<i>Equus caballus</i> ^{4,7,9}	<i>Myrmecophaga tridactyla</i> ⁹	MA ⁴ , RO ⁷ , TO ⁹	[88]
<i>Amblyomma varium</i>		<i>Bradypus tridactylus</i> ³ , <i>Bradypus</i> <i>sp</i> ³ , <i>Bradypus variegatus</i> ⁷ <i>Choleopus didactylus</i> ^{3,7} , <i>Choleopus hoffmanni</i> ^{3,7} , <i>Choleopus sp</i> ⁷ <i>Dasyprocta</i> <i>aguti</i> ³ , <i>Tamandua tetradactyla</i> ³	AM ³ , PA ⁶ , RO ⁷	[30, 31, 33, 38, 40, 97]
<i>Dermacentor nitens</i>	<i>Bos taurus</i> ⁴ , <i>Canis</i> <i>familiaris</i> ^{4,7} , <i>Equus</i> <i>caballus</i> ^{4,7,8,9} <i>Capra</i> <i>hircus</i> ⁴ , <i>Ovis aires</i> ⁴	<i>Agouti paca</i> ⁷ , <i>Mazama</i> <i>gouazoubira</i> ⁹	MA ⁴ , RO ⁷ , RR ⁸ , TO ⁹	[36, 38, 39, 95, 98]
<i>Ixodes amarali</i>		<i>Hylaeamys megacephalus</i> ⁶ , <i>Monodelphis glirina</i> ⁶ , <i>Monodelphis touan</i> ⁶ ,	PA ⁶	[99]
<i>Ixodes bocatorensis</i>		<i>Bradypus tridactylus</i> ³ , <i>Cyclopes</i> <i>didactylus</i> ³ , <i>Dasyprocta</i> <i>leporina</i> ³ , <i>Tamandua</i> <i>tetradactyla</i> ³	AM ³	[16]
<i>Ixodes spinosus</i>		<i>Dasyprocta sp</i> ⁷ , <i>Myoprocta</i> <i>pratti</i> ¹	RO ⁷ , AC ¹	[13]
<i>Ixodes lasallei</i>		<i>Dasyprocta variegata</i> ⁷	RO ⁷	[16]
<i>Ixodes luciae</i>		<i>Didelphis marsupialis</i> ^{1,3,4,7} , <i>Marmosa murina</i> ⁶ , <i>Marmosa</i> <i>demerarae</i> ³ , <i>Monodelphis sp</i> ⁷ , <i>Oecomys sp.</i> ⁷ , <i>Oryzomys sp.</i> ⁷ , <i>Oligorysomys sp.</i> ⁷ , <i>Philander</i> <i>opossum</i> ⁶	AC ¹ , AM ³ , MA ⁴ , PA ⁶ , RO ⁷	[31, 36, 38, 100]
<i>Ixodes schulzei</i>		<i>Monodelphis touan</i> ⁶	PA ⁶	[92]
<i>Haemaphysalis juxtakochi</i>	<i>Canis familiaris</i> ^{4,7} ,	<i>Mazama americana</i> ^{3,9} , <i>Mazama p</i> ⁷ , <i>Dasyprocta</i> <i>azarae</i> ⁵ ; <i>Dasyprocta fuliginosa</i> ³ ,	AM ³ , MA ⁴ , MT ⁵ ; RO ⁷ , TO ⁹	[31, 36, 38, 39, 42]
<i>Rhipicephalus microplus</i>	<i>Bos taurus</i> ^{4,7,8,9} , <i>Canis</i> <i>familiaris</i> ^{4,7,9} , <i>Felis catus</i> ⁷ , <i>Equus caballus</i> ^{4,7,8,9} , <i>Capra hircus</i> ^{4,7} , <i>Ovis aires</i> ⁴	<i>Alouatta puruensis</i> ⁷ , <i>Mazama</i> <i>gouazoubira</i> ^{5,9} , <i>Mazama sp.</i> ⁷ , <i>Tapirus terrestris</i> ^{7,9} , <i>Tayassu sp</i> ⁷	MA ⁴ , MT ⁵ ; RO ⁷ , RR ⁸ ; TO ⁹	[32, 33, 36, 38, 39, 95, 98]
<i>Rhipicephalus sanguineus sensu lato</i>	<i>Canis familiaris</i> ^{1,3,4,7,9}	<i>Bradypus tridactylus</i> ³ , <i>Galictis</i> <i>cuja</i> ⁴ , <i>Saquinus bicolor</i> ³	AC ¹ , AM ³ , MA ⁴ , RO ⁷	[30–33, 36, 38, 39, 95, 98, 101]

¹Acre – AC.
²Amapá – AP.
³Amazonas – AM.
⁴Maranhão – MA.
⁵Mato Grosso – MT.
⁶Pará – PA.
⁷Rondônia – RO.
⁸Roraima – RR.
⁹Tocantins – TO.

Table 3.
Records of ticks in the Amazon biome, Brazil, according to tick species, hosts (domestic and wild animals), states, references.

rodents (e.g., Cricetidae) in the larvae and nymph stages, with adults feeding mostly on marsupials (e.g., *Didelphis* spp., *Monodelphis* spp.) [17, 83], and agoutis (e.g., *Dasyprocta*) [13, 16]. Most species were found parasitizing *Monodelphis glirina* (*I. amarali*, *I. schulzei*, *I. luciae*) and *Monodelphis touan* (*I. amarali*, *I. schulzei*), with some reports of *I. amarali* on the rodent *Hylaeamys megacephalus* [30, 38, 92, 99, 100]. Also on rodents the species *I. spinosus*, *I. lasallei* and *I. bocatorensis* have been recorded [30, 31, 38], although these previous records referred to them erroneously as *Ixodes fuscipes*, which according to more recent data, does not occur in the Amazon biome (**Figure 5** and **Table 3**) [13, 16].

In general, the greatest diversity of ticks was recorded on *T. tetradactyla* with 10 species, followed by the rodent *H. hydrochaeris* with nine species. These records indicate the importance of these hosts for maintaining local tick diversity, in addition to act as dispersers of these ectoparasites. Additional hosts have also been shown to be important in maintaining diversity of tick in the Amazon: *Tapirus terrestris*, *Tayassu pecari*, *Pecari tajacu*, *Agouti paca*, *Dasyprocta fuliginosa*, *Bradypus tridactylus*, *Bradypus variegatus*, *Panthera onca*, *Nasua nasua*, *Choleopus didactylus*, *Choleopus hoffmanni*, *Cyclopes didactylus*, *Dasyprocta azarae*, *Dasyprocta leporina*, *Philander opossum*, *M. glirina*, *M. touan*, *Mazama gouazoubira*, *Mazama americana* and *M. tridactyla* (**Table 3**), because they are parasitized by more than one species of ticks. There is also a record of *A. cajennense* s.s. on *Pteronura brasiliensis* a semi-aquatic animal [89].

Interestingly, three species of ticks commonly found on domestic animals have also been found parasitizing wild animals: *Rhipicephalus sanguineus* sensu lato, *R. microplus* and *D. nitens*. Although occasional, the encounter of these species of ticks on wild animals is possible, especially when wild animals coexist with domestic animals infested by ticks (e.g., pastures, corrals, houses). A total of 11 species of ticks have been recorded parasitizing domestic animals in Amazon (**Table 3**).

5. Hard ticks associate with humans

Spotted fevers caused by *R. rickettsii* and *Rickettsia parkeri* are currently the only confirmed tick-borne disease affecting humans in the country, and *A. sculptum*, *A. aureolatum*, *A. ovale* are the main vectors. The disease is severe and highly lethal when caused by the bacterium *R. rickettsii* (vectors *A. sculptum* and *A. aureolatum*) and moderate, non-lethal, when caused by *R. parkeri*, vectored mainly by *A. ovale* [10]. Only *A. sculptum* and *A. ovale* have been recorded in the Brazilian Amazon, the first in rare reports and the second frequently recorded and populations established in this biome. In fact, considering only the tick adult stage, *A. ovale* has been reported as the most common human-biting tick in the Amazon [38].

In the last century, papers about ticks on human beings have been published in the Brazilian Amazon, however these studies are fragmented and scarce. At least 14 species of hard ticks have already been found and documented parasitizing humans within the limits of the Brazilian Amazon. Of these, the vast majority (11 species) belong to the genus *Amblyomma*: *A. cajennense* s.s., *A. coelebs*, *A. dissimile*, *A. latepunctatum*, *A. naponense*, *A. oblongoguttatum*, *A. ovale*, *A. romitii*, *A. rotundatum*, *A. scalpturatum* and *A. sculptum*. The other three species belong to the genus *Rhipicephalus*, including *R. microplus* and *R. sanguineus* s.l., and the genus *Haemaphysalis* with only *H. juxtakochi*. The public health importance of human-tick associations in the Amazon biome is unclear and further research are needed to clarify the issue.

Nymphs of *H. juxtakochi* have been reported on humans in the states of Rondônia (municipality not precisely indicated) and Amazonas, in the municipality

of Santa Isabel do Rio Negro [31, 38]. *H. juxtakochi* has been found infected with the bacterium *Rickettsia rhipicephali* in the Amazon region, more precisely in the municipalities of Monte Negro and Confresa, states of Rondônia and Mato Grosso, respectively [42, 93]. Human parasitism by *R. microplus* was expected, since this species can parasitize humans when it comes into direct contact with domestic cattle, as reported by [38]. Therefore, its importance is much more economical, causing severe losses to livestock in the country than for public health.

Despite sporadic records of *R. sanguineus* s.l. on humans in Brazil, this association in the Brazilian Amazon requires confirmation. Records of approximately 4,020 *R. sanguineus* s.l. (larva, nymph, and adult), supposedly collected on humans, in the state of Pará by Serra-Freire et al. [103] do not corroborate the common findings in country. The bioecology of this endophilic and introduced tick is well studied. In other countries, *R. sanguineus* s.l. is vector of some zoonotic agents for humans (*Rickettsia conorii*, *Rickettsia massiliae* and *R. rickettsii*) [83]. Adults of *A. cajennense* s.s. have been reported on humans in the municipality of Monte Alegre (Pará state) [90]. Reports of *Amblyomma cajennense* sensu lato parasitizing humans published by Martins et al. [90] in the municipalities of Sinop and Tucuruí in the states of Mato Grosso and Pará, is possibly *A. cajennense* s.s. taking into account the area of occurrence of this species. This tick is aggressive to humans. In the Amazon biome the *R. bellii* bacterium was detected in this species in Mato Grosso state and *R. amblyommatis* in Mato Grosso, Maranhão and Rondônia state [32, 42, 53, 83, 88, 90, 91, 104, 105].

Nymphs and adult of *A. coelebs* were found on humans in Rondônia state [38]. An adult of this tick was found on human in Roraima state, municipality of Caroebe [106]. The nymph and adult stages of *A. coelebs* were also found on humans in Amazonas state, in the municipalities of Coari, Fonte Boa, Presidente Figueiredo and Santa Isabel do Rio Negro [31, 107]. There are reports of infection by *R. amblyommatis* in *A. coelebs* in the Amazon region in the states of Rondônia and Mato Grosso, respectively [32, 53, 88]. Adult of *A. dissimile* was recorded on humans in the Maicurú River/Amazon biome, located in Pará state [106]. Adults of the species *A. latepunctatum* have been reported on humans in Coari and Santa Isabel do Rio Negro, both municipalities located in the state of Amazonas [31].

Adults of the tick *A. naponense* (published as *Amblyomma mantiquirens*) were found on humans in the state of Pará (municipality not reported) [108]. Human parasitism also by adults was later reported on the Maicurú River, located in this same state [106]. However, nymphs have been found on humans in the states of Rondônia (municipality not specified precisely) and Amazonas, in the municipalities of Coari and Santa Isabel do Rio Negro [31, 38]. The bacteria *R. bellii* and *Rickettsia* sp. strain PA were identified in this species in the Amazon region of the municipalities of Santarém and Rurópolis, in the state of Pará [42]. *Rickettsia* sp. strain Tapirapé was found in this tick in the municipalities of Confresa and Rio Branco, in the states of Mato Grosso and Acre, respectively [42, 54].

Adults of the species *A. oblongoguttatum* were recorded parasitizing humans in the state of Pará, in the Maicurú River and in the municipality of Uruará [106, 108, 109]. Human parasitism by nymphs and adults of this tick was recorded in the state of Rondônia (municipality not specified with precision) [38]. However, the nymphal stage of this species was later recorded on humans in the municipality of Monte Negro in the same state [106]. Human parasitism by adult of this tick was also recorded in the municipality of Caroebe, state of Roraima [106]. Nymphs and adults of this species have been recorded parasitizing humans in three municipalities (Coari, Manacapuru and Santa Isabel do Rio Negro), all located in the state of Amazonas [31, 106, 107]. On the other hand, the life cycle of this tick has already been studied under laboratory conditions [110]. The bacteria *R. bellii* and

R. amblyommatis were detected in this species in the Amazon in the municipalities of Governador Jorge Teixeira and Pimenta Bueno, in the state of Rondônia [53, 105].

Adults of the tick *A. ovale* have been reported to parasitize humans in several areas of the state of Rondônia [38]. As previously reported in this chapter, adults of *A. ovale* parasitize mainly domestic and wild carnivores, while immature (larva and nymph) parasitize rodents of the families Cricetidae and Echimyidae, with sporadic reports on wild birds [17, 75, 83]. This preference for such host groups was observed in the laboratory [111]. This tick is a vector of the protozoan *Hepatozoon canis* and the bacterium *R. parkeri*, agents of importance in veterinary and human medicine, respectively [83]. In the Amazon region, the bacterium *R. bellii* was identified in this species in the municipalities of Governador Jorge Teixeira and Monte Negro, in the state of Rondônia; and in the municipality of Cururupu, in the state of Maranhão [53, 91].

The adult stage of the species *A. romitii* (published as *Amblyomma tasquei*) was found parasitizing humans in the north of the state of Pará (municipality not reported) [108]. In this same state, the larval and adult stages of this tick were found on humans in the municipality of Rurópolis [96, 112]. The life cycle of this tick was studied under laboratory conditions [113].

Parasitism by adults of *A. rotundatum* was recorded in the municipality of Belém in the state of Pará on a human who worked in frequent contact with reptiles in the Zoobotanical Park of the Museu Paraense Emílio Goeldi [114].

Adults of the *A. scalpturatum* have been reported to parasitize humans in the state of Pará (municipality not reported) [108], and in the Maicurú River located in this state [93, 106]. Human parasitism by the nymphal and adult stages of this species has been reported in the states of Mato Grosso (municipality of Jauru) and Rondônia (municipality not precisely indicated), however in this latter state it was not specified whether these adult ticks were fixed or walking on humans [38, 93]. The nymphal stage was also collected from a human who was probably infested with this tick in the municipality of Porto Velho in the state of Rondônia [115]. The nymph and adult stages of this species were also found parasitizing humans in the state of Amazonas, in the municipalities of Coari, Fonte Boa, Jutai, Presidente Figueiredo and Santa Isabel Rio Negro [31, 107]. In the Amazon biome, two species of rickettsiae (*R. bellii* and *R. amblyommatis*) were detected in *A. scalpturatum*, in the municipalities of Governador Jorge Teixeira and Sinop, states of Rondônia and Mato Grosso, respectively [53, 88].

Human parasitism by adults of *A. sculptum* was recorded in the municipality of Jauru in the state of Mato Grosso [90]. The Jauru territory comprises 90% of the Amazon biome and 10% of the Cerrado biome, so this human record in this region is in accordance with the transition area of the occurrence of this species in sympatry with *A. cajennense* s. s. [90]. The bioecology of this native tick has been extensively studied due to its aggressive parasitism towards domestic animals and humans in the Brazilian territory. In the geographical area in which this species occurs, it completes an annual generation, with larvae occurring mostly during autumn, nymphs during winter, and adults during spring and summer, with larval behavioral diapause being the main regulating factor of its life cycle [116, 117]. Besides being considered a pest for domestic animals (dogs, cattle and horses), the species can transmit to humans the Brazilian Spotted Fever caused by the bacterium *R. rickettsii*, being this the most important zoonotic disease transmitted by ticks within the limits of the National territory. Additionally, *A. sculptum* has also been identified with the bacterium *R. amblyommatis* in the municipality of Pium, state of Tocantins [118].

There is a trend of seasonal behavior for some species of *Amblyomma* in the Amazon biome, with immatures predominating in the dry period (June to October),

and adults in the rainy period (October to March) [119]. Similar to the pattern observed for *A. sculptum* in areas outside the Amazon biome [116].

6. Soft ticks in the Brazilian Amazon

Taxonomy of Argasidae is currently questionable and relies on five schemes that divide the family in up to ten genera [120]. Achieving a consensus between soft tick taxonomists depends now chiefly on the molecular characterization of early collected type specimens for some genera. For instance, elucidating the status of pivotal taxa such as *Alectorobius* is mandatory if we are to understand the systematics of the Argasidae, particularly in the American Continent. Considering a practical approach, in this chapter we adopt but not necessarily endorse the classification of soft ticks into five genera, namely: *Antricola*, *Argas*, *Nothoaspis*, *Ornithodoros*, and *Otobius* [121].

The fauna of argasid ticks in Brazil is currently composed by 24 species [15]. Ticks of this family parasitize terrestrial vertebrates including amphibians in this country [25, 26]. With the exception of larvae from an undetermined *Ornithodoros* sp. collected on *Potus flavus* (Procionidae) [84], reports of soft ticks parasitizing mammals in the Brazilian Amazon are few and almost restricted to larvae collected on bats. Adults and nymphs have been collected either inside bat-inhabited caves or over massive rock formations where bats shelter (**Table 4**).

The first record of a soft tick in the Brazilian Amazon was published by North American entomologists Robert A. Cooley and Glen M. Kohls back in 1941. They received a tick collected inside a bat-inhabited three hole at Marajó Island (Pará state) and identified it as female of *Ornithodoros hasei* (mentioned as *Ornithodoros dunni*) [126]. Nowadays, we know that *O. hasei* is a wide spread species in Brazil and that three-roosting bats *Artibeus planirostris* and *Noctilio* spp. could act as main hosts [87, 130–132]. With the exception of recent collection of larvae on *A. planirostris* [87], knowledge on the distribution of *O. hasei* along the Brazilian Amazon is still poorly vague.

Tadarida laticaudata were the first bats reported to be parasitized by soft ticks in the Brazilian Amazon [133]. This report referred to *Ornithodoros setosus*, which was recently reclassified as *Nothoaspis setosus* [124]. In 1972, the bats *Noctilio labialis* and *T. laticaudata* were reported to be parasitized by *Ornithodoros stageri* in the Brazilian Amazon [129], which was recently confirmed [11]. A report in the Brazilian Amazon is a remarkable fact for *O. stageri*, since it also has distribution in Southern United States and Mexico [126, 134].

Bat inhabited caves constitute excellent niches to find argasid ticks. In particular, special, large colonies of insectivorous bats dwelling inside small chambers create high temperature conditions (28–40°C) where hundreds of *Antricola*, *Nothoaspis* and *Ornithodoros* ticks might occur [135]. Between 2004 to 2010 collections of ticks performed in hot caves from Porto Velho (Rondônia) fostered the description of two novel species (e.g., *Nothoaspis amazoniensis* and *Ornithodoros rondoniensis*) [122, 123]; the redescription of larvae and description of postlarval stages of *Ornithodoros marinkellei* [127], and the expansion of geographical distribution of *Antricola delacruzi* and *Antricola guglielmonei* into Brazilian Amazon [122]. At least for two species, *O. marinkellei* and *O. rondoniensis*, further collections performed in caves from Pará state underpinned a larger distribution along the Amazon ecosystems [128].

Most amazing feature of soft ticks inhabiting hot caves, is that adaptation to this particular milieu seems to have modified their morphology and biology drastically. For instance, evidence showing that adults of *Antricola* ticks lack the capacity to

Species	State	Locality	Milieu of collection/Host	Reference
<i>Antricola delacruzii</i>	Rondônia	Porto Velho	Bat inhabited cave/ <i>Pteronotus</i> spp.	[122]
<i>Antricola guglielmonei</i>	Rondônia	Porto Velho	Bat inhabited cave/ <i>Pteronotus</i> spp	[122]
<i>Nothoaspis amazoniensis</i>	Rondônia	Porto Velho	Bat inhabited cave/ <i>Pteronotus parnellii</i>	[123]
<i>Nothoaspis setosus</i>	Rondônia	Monte Negro	Rock formation/ <i>Molossus molossus</i>	[124]
<i>Ornithodoros cavernicolous</i>	Rondônia	Monte Negro	Bat inhabited caves/Unknown	[125]
<i>Ornithodoros hasei</i>	Amapá	unknown	Mistnetted bat <i>Artibeus planirostris</i>	[87]
	Pará	Marajó Island	Bat-inhabited three hole/Unknown	[126]
<i>Ornithodoros kohlsi</i>	Rondônia	Monte Negro	Mistnetted bat <i>Molossops mattogrossensis</i>	[30]
<i>Ornithodoros marinkellei</i>	Rondônia	Porto Velho	Bat inhabited cave/ <i>Pteronotus</i> spp	[127]
	Pará	Carajás, Paraupebas, Canaã dos Carajás	Bat inhabited caves/Unknown	[128]
<i>Ornithodoros peropteryx</i>	Rondônia	Monte Negro	Bat inhabited cave/Unknown	[125]
<i>Ornithodoros rondoniensis</i>	Rondônia	Porto Velho	Bat inhabited cave/Unknown	[122]
	Pará	Carajás, Paraupebas, Canaã dos Carajás	Bat inhabited caves/Unknown	[128]
<i>Ornithodoros stageri</i>	Rondônia	Unknown	Unknown/ <i>Noctilio albiventris</i> , <i>Nyctinomops laticaudatus</i>	[129] [11]

Table 4.
Soft ticks and their respective hosts occurring in the Brazilian Amazon.

digest blood has been gained after transcriptomic analyses of their saliva [136]. In fact, scoop-like short mouth parts suggest that adults of *Antricola* do not suck blood [137]. Moreover, adults of *Antricola*, *O. marinkellei* and *O. rondoniensis* possess huge spiracular plates [122, 127, 137], perhaps necessary to thrive in such hot and extremely humid environments.

Except for larvae of *Ornithodoros kohlsi* collected on the bat *Molossops mattogrossensis* [30], prospections performed by our group between 2016 and 2019 focused mainly in the search for soft ticks inside natural cavities over massive rock formations. During these expeditions, *Ornithodoros cavernicolous* and *Ornithodoros peropteryx* were collected for the first time in caves from Monte Negro (Rondônia), extending their distribution of both species to the Brazilian Amazon [125]. Furthermore, analyses performed on large larvae isolated from *Molossus molossus* bats clarified that *O. setosus* was incorrectly classified in its original description. Indeed, *O. setosus* matches morphologically and molecularly within the genus *Nothoaspis* therefore the statement of *N. setosus* n. comb. was proposed [124]. It is important to note that our last collections performed at Monte Negro included several morphotypes of *Ornithodoros* pending formal description. Consequently, the fauna of soft ticks occurring in the Brazilian Amazon is likely to increase soon.

7. Conclusion

Ticks parasitize a wide variety of vertebrates around the world such as amphibians, reptiles, mammals and birds, including humans. Although there are a variety of studies of parasitism by ticks on animals and humans in the different ecoregions of Brazil, in the Amazon biome they are scarce and fragmented. Because of this, it is possible to infer that the diversity of ticks in the Brazilian Amazon is underestimated. In the Amazon, amphibians and reptiles were important hosts for *A. rotundatum*, *A. dissimile* and *A. humerale*, hard ticks common in these hosts in other regions of the country. Birds and mammals, on the other hand, proved important for the maintenance and dispersion of over 30 species of hard ticks in the Amazon, but there are still many gaps between hosts and their ticks in this region. Interestingly, immature *A. humerale* appears to be frequent on wild birds in this biome. No soft ticks have been reported parasitizing amphibians, reptiles, birds and/or non-flying mammals (except for a single record of *Ornithodoros* sp. on *P. flavus*), possibly due to scarcity of more studies in this biome. Some studies show that bats seem to have an important role spreading soft tick populations along Amazonian caves and that the diversity described for this group is still very poor. Two vector species of spotted fevers were found in the Amazon biomes parasitizing humans (*A. sculptum* and *A. ovale*). However, to date, there are no reports of BSF in humans in the region. Finally, it is of paramount importance that researchers (acarologists and epidemiologists) direct their attention to the Amazon biome, in order to fill the numerous existing gaps in the diversity of ticks in Brazil and prevent possible outbreaks of diseases transmitted by these ectoparasites to animals and humans.

Conflict of interest

No conflict of interest declared.

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