

Original article

Ticks (Acari: Ixodidae, Argasidae) associated with wild birds in Argentina

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ABSTRACT

The aim of this study was to report tick infestations on wild birds from four Phytogeographic Provinces of Argentina. A total of 1085 birds was captured (124 species, 97 genera, 29 families and 13 orders), and ticks were collected from 265 birds (48 species, 40 genera and five orders). A total of 1469 ticks (1102 larvae, 363 nymphs and 4 females) belonging to 15 tick species (*Amblyomma calcaratum*, *Amblyomma dubitatum*, *Amblyomma nodosum*, *Amblyomma ovale*, *Amblyomma parvum*, *Amblyomma sculptum*, *Amblyomma tigrinum*, *Amblyomma triste*, *Haemaphysalis juxtakochi*, *Haemaphysalis leporispalustris*, *Ixodes auritulus* sensu lato, *Ixodes parvicinus*, *Ixodes silvanus*, *Ixodes* sp. cf. *I. affinis* and *Ornithodoros* sp. cf. *O. mimon*). Eighty-one new associations between bird species and stages of tick species are detected. The families Thamnophilidae, Turdidae, Thraupidae, Passerellidae, Furnariidae and Troglodytidae were the most prevalent. According to the Phytogeographic Provinces involved in this study, the prevalence of infection for each of them in birds was: (1) Chaco: 28.2% (11 tick species); (2) Yungas: 22.0% (8 tick species); (3) Espinal: 11.1% (2 tick species); and (4) Pampa: 3.9% (1 tick species). This study provided information on the diversity of tick species that parasitize wild birds, the variability of the specific tick-bird associations between the different Phytogeographic Provinces and the relevance of some families of birds as hosts of different tick species.

1. Introduction

In the world, more than half of the species of hard ticks (Acari: Ixodida: Ixodidae) as well as 30% of soft tick species (Acari: Ixodida: Argasidae) feed on birds in at least one of their parasitic stages (Camicas et al., 1998; Estrada-Peña et al., 2010; Guglielmone et al., 2014, 2021; Guglielmone and Nava, 2017). Particularly, in the Neotropical region it is known that Passeriformes families of birds play an important role as hosts for the ticks of the genera *Ixodes*, *Amblyomma* and *Haemaphysalis* (Guglielmone et al., 2021). This fact highlights the relevance of birds for the life cycle of ticks and the epidemiology of tick-borne pathogens.

The tick fauna of Argentina is composed of 57 species, 44 of them belong to the family Ixodidae (25 *Amblyomma*, 1 *Dermacentor*, 2 *Haemaphysalis*, 13 *Ixodes* and 3 *Rhipicephalus*) and 13 to the family Argasidae (5 *Argas*, 7 *Ornithodoros* and 1 *Otobius*) (Nava et al., 2017; Venzal et al.

2019; Guglielmone et al., 2021; Apanaskevich et al., 2022).

To date, 32 of the 57 tick species were found associated with birds in at least one parasitic stages (Nava et al., 2017; Guglielmone et al., 2021; Apanaskevich et al. 2022). Information on ticks reported on birds in Argentina has grown in recent decades (Ortiz et al., 2011; Cicuttin et al., 2013, 2022; Venzal et al., 2014; Flores et al., 2016, 2018, 2020; Saracho-Bottero et al., 2017, 2021; Lamattina et al., 2018a; Sebastian et al., 2020), however, the ecological works that analyze birds as hosts of ticks are still scarce (Beldomenico et al., 2003; Nava et al., 2006a, 2006b, 2009, 2011; Mastropaolo et al., 2011; Flores et al., 2014; Lamattina et al., 2018b; Cicuttin et al., 2019).

The study of the relationship between ticks and birds has ecological relevance since birds sustain totally or partially the life cycle of several tick species and can act as reservoirs of tick-borne pathogens, and also entails epidemiological implications because they facilitate the

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geographical dispersion of ticks and tick-borne human and animal pathogens (Scott et al., 2001; Dietrich et al., 2011). Therefore, the present study aims in analyzing the pattern of parasite-host association between ticks and wild birds in different ecological areas of Argentina.

2. Materials and methods

Ticks were collected from wild birds during twenty-three samplings at eighteen localities, which belong to four Phytogeographic Provinces: (a) Chaco (PPC); (b) Yungas (PPY); (c) Espinal (PPE) and; (c) Pampa (PPP) according to Oyarzabal et al. (2018) (Table 1 and Fig. 1).

Birds were captured by using sets of 8–12 mist nets (12 m long x 2.5 m wide, 36 mm mesh) kept open during morning and twilight hours in convenience samplings, with permissions of Argentinean authorities from the Administración de Parques Nacionales or Provincial authorities. The captured individuals were identified following Narosky and Yzurieta (2010) and classified according the checklist of Clements et al. (2019). Each bird was examined for ticks using fine-tipped tweezers and temporarily marked to detect recaptures. Afterwards, all birds were released at the same capture site and the collected unengorged ticks were stored in tube with ethanol (96%) until specific morphological identification in the laboratory. Engorged larvae or nymphs were stored alive, transferred to the laboratory and kept in an incubator at 25 °C and RH 85% for moult.

Morphological identification of *Amblyomma* nymphs and larvae was made following Martins et al. (2014), Joan (1930), Guglielmo et al.

(1990), Famadas et al. (1997), Estrada-Peña et al. (2005) and Barbieri et al. (2008, 2013). Nymphs of *Haemaphysalis* were identified following Nava et al. (2017) and larvae according to Cooley (1946), Kohls (1960) and Egizi et al. (2019). Regarding ticks belonging to the genus *Ixodes*, adults were identified following Nava et al. (2017), Saracho-Bottero et al. (2020, 2021), nymphs following Oliver et al. (1987), Venzal et al. (2005), Nava et al. (2017), Saracho-Bottero et al. (2021), and larvae according to Nuttall (1916), Keirans et al. (1985), Oliver et al. (1987) and Venzal et al. (2005). Larvae of the genus *Ornithodoros* were identified following Nava et al. (2017). The morphological determination of immature ticks was also performed by comparison with known laboratory-reared material deposited in the Tick Collection of Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Rafaela, Argentina. In addition, it was performed comparisons of DNA partial sequences in cases where morphological determination of engorged immature ticks was not feasible. DNA was extracted from individual specimens using the Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA). A 400-base pair fragment of the mitochondrial 16S rRNA gene was amplified using the primers and the polymerase chain reaction (PCR) conditions designed by Mangold et al. (1998). The sequences were edited using BioEdit Sequence Alignment Editor (Hall, 1999) and aligned with the program Clustal W (Larkin et al. 2007). Sequences were compared by using BLAST (National Center for Biotechnology Information, Bethesda, MD, USA).

Mean abundance, prevalence of infestation and the corresponding two-sided 95% Wilson confidence interval (CI) were calculated

Table 1

GPS data of locality and year surveys for tick-collections from birds in Phytogeographic Provinces and vegetation units as defined by Oyarzabal et al. (2018). ID. Identification data for each locality.

Phytogeographic Province	Physiognomic-floristic	Locality	ID	Coordinates	Year	Month
Chaco	Chaco Semiárido	Parque Provincial Fuerte Esperanza	A	-25.146669, -61.810572	2019	July
		Palma Sola	B	-23.983293, -64.279248	2014	May
	Chaco Subhúmedo	Parque Provincial Pampa del Indio	C	-26.276446, -59.969056	2017	May
		Chaco húmedo con bosques y cañadas	Parque Nacional Chaco	D	-26.8105139, -59.598222	2019
	Reserva Privada El Bagual		E	-26.304175, -58.816536	2015	July, October
			Cañada Ombú	F	-28.362758, -60.150532	2018 2021
	Chaco húmedo con bosques, pajonales y palmares de Caranday		Parque Nacional Pilcomayo	G	-25.140194, -58.176871	2016
		Pajonales y palmares de Yatay	Parque Nacional Mburucuyá	H	-28.0138889, -58.022222	2018
Espinal	Ñandubayzal y Selva de Montiel	Área Natural Protegida Don Sebastián	I	-30.3518611, -59.203139	2009	March
Pampa	Pampa Mesopotámica	Aurora del Palmar	J	-31.822812, -58.319226	2007	December
Yungas	Selva de Transición	Dique La Ciénaga	K	-24.434222, -65.248446	2008	May
		Selva Montana y Bosque de Aliso y Pino del cerro	Portal de piedra	L	-24.093762, -64.398111	2008
	San Francisco, Valle Grande		M	-23.621444, -64.946489	2014 2017	March March
			Sierra de Zapla	N	-24.241982, -65.117283	2008
	Valle Colorado, Valle Grande		O	-23.405510, -64.933751	2009 2017	November March
			Isla de Cañas	P	-22.903148, -64.663676	2019
	Cochuna		Q	-27.322643, -65.925682	2008	November
	Siambon	R	-26.768291, -65.468450	2017 2010	December May	

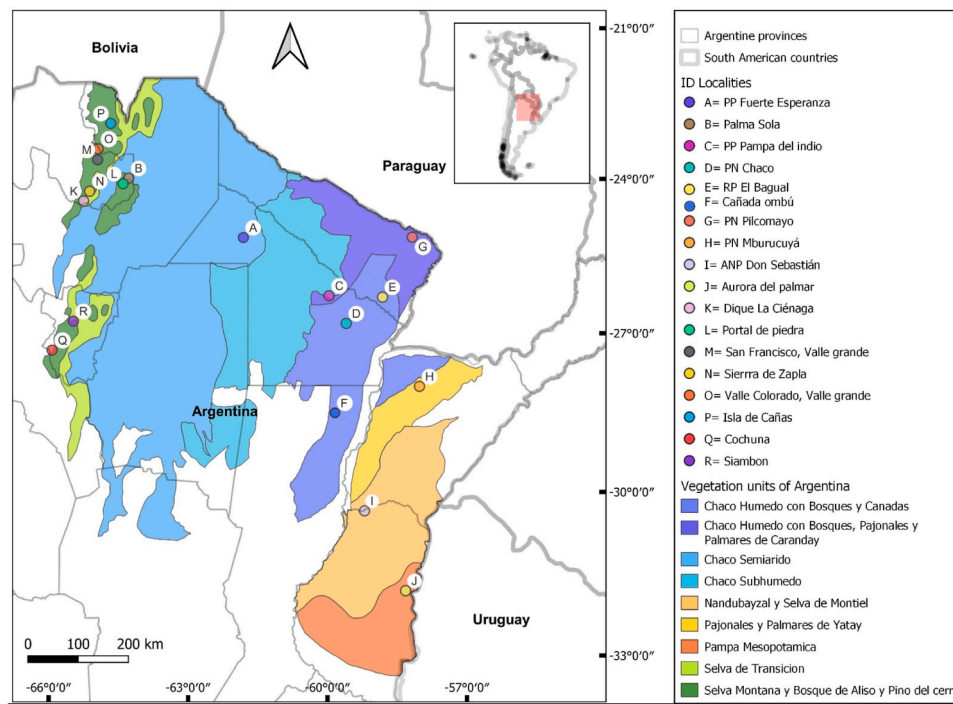


Fig. 1. Geographical coordinates for localities of tick-collections on birds in different Phytogeographic Provinces and vegetation units from Argentina as defined by Oyarzabal et al. (2018). ID Localities: Identification data for each locality in Table 1.

according to Bush et al. (1997). Statistical differences in prevalence values between Phytogeographic Provinces were tested by chi-square tests.

3. Results

A total of 1085 birds belonging to 124 species, 97 genera, 29 families and 13 orders (3 Accipitriformes, 17 Caprimulgiformes, 1 Cariamiformes, 3 Charadriiformes, 26 Columbiformes, 8 Coraciiformes, 2 Cuculiformes, 4 Gruiformes, 1003 Passeriformes, 2 Pelecaniformes, 11 Piciformes, 1 Psittaciformes and 5 Strigiformes) were captured. Ticks were collected on 265 birds belonging to 48 species, 40 genera and five orders: Accipitriformes (1 family, 1 species), Columbiformes (1 family, 1 species), Gruiformes (1 family, 2 species), Passeriformes (11 families, 43 species) and Piciformes (1 family, 1 species). A total of 1469 ticks (1102 larvae, 363 nymphs and 4 females) belonging to four genera were collected: (Argasidae: *Ornithodoros*; Ixodidae: *Amblyomma*, *Haemaphysalis* and *Ixodes*). Fifteen tick species were found: *Amblyomma calcaratum*, *Amblyomma dubitatum*, *Amblyomma nodosum*, *Amblyomma ovale*, *Amblyomma parvum*, *Amblyomma sculptum*, *Amblyomma tigrinum*, *Amblyomma triste*, *Haemaphysalis juxtakochi*, *Haemaphysalis*

leporispalustris, *Ixodes auritulus* sensu lato, *Ixodes parvicinus*, *Ixodes silvanus*, *Ixodes* sp. cf. *I. affinis* and *Ornithodoros* sp. cf. *O. mimon*. A total of 18 ticks could not be identified to the species level: *Amblyomma* (5 larvae), *Haemaphysalis* (3 larvae) and *Ixodes* (7 larvae and 3 nymphs). The partial 16S rDNA sequences of representative immatures specimens of *A. calcaratum*, *A. dubitatum*, *A. nodosum*, *A. parvum*, *A. sculptum*, *H. juxtakochi*, *H. leporispalustris*, *I. silvanus* and *Ixodes* sp. cf. *I. affinis* are presented in Table 2.

Details of tick infestations according to orders, families and species of birds are presented in Tables 3 and 4 (Supplementary Table S1 provides information about birds negative or positive to tick infestation). The most prevalent families, with at least 20 examined individuals, were Thamnophilidae (56.3%; CI_{95%}: 44.1 – 67.7) with 2 genera and 3 species, Turdidae (53.5%; CI_{95%}: 46.0 – 60.7) with 2 genera and 4 species, Thraupidae (28.6%; CI_{95%}: 22.2 – 36.0) with 7 genera and 9 species, Passerellidae (24.3%; CI_{95%}: 17.3 – 33.1) with 3 genera and 4 species), Furnariidae (22.8%; CI_{95%}: 16.1 – 31.3) with 10 genera and 10 species and Troglodytidae (22.2%; CI_{95%}: 11.7 – 38.1) with 1 genus and 1 species.

In the PPC11 tick species (4 genera), in the PPY 8 tick species (3 genera), in the PPE with 2 tick species (2 genera) and in the PPP 1 tick

Table 2
Information from the DNA sequences generated from ticks collected in the present study and search results of BLAST analyzes in public data.

Tick species	Stage	Host	Locality	Closest identity (%) in GenBank (accession number)	GenBank accession number
<i>Amblyomma calcaratum</i>	Nymph	<i>Xiphocolaptes major</i>	PP Pampa del Indio	KF179346 (96.30%)	ON382300
<i>Amblyomma dubitatum</i>	Larva	<i>Turdus amaurochalinus</i>	PN Mburucuyá	DQ858955 (99.01%)	ON382301
<i>Amblyomma nodosum</i>	Nymph	<i>Turdus rufiventris</i>	PN Mburucuyá	MW654243 (99.75%)	ON382302
<i>Amblyomma nodosum</i>	Nymph	<i>Taraba major</i>	PN Pilcomayo	MW654243 (99.50%)	ON382303
<i>Amblyomma parvum</i>	Larva	<i>Troglodytes aedon</i>	PP Fuerte Esperanza	EU306136 (99.75%)	ON382304
<i>Amblyomma sculptum</i>	Larva	<i>Cyanocorax cyanomelas</i>	RP El Bagual	KT820361 (98.30%)	ON382305
<i>Haemaphysalis juxtakochi</i>	Larva	<i>Cyanoloxia brissonii</i>	Portal de piedra	AY762324 (96.46%)	ON382306
<i>Haemaphysalis leporispalustris</i>	Larva	<i>Arremon flavirostris</i>	Portal de piedra	KU096986 (100%)	ON382307
<i>Ixodes</i> sp. cf. <i>I. affinis</i>	Nymph	<i>Campylorhynchus trochilirostris</i>	PN Mburucuyá	MN173296 (100%)	MT604111
<i>Ixodes</i> sp. cf. <i>I. affinis</i>	Nymph	<i>Turdus rufiventris</i>	PN Mburucuyá	MN173296 (100%)	MT604112
<i>Ixodes</i> sp. cf. <i>I. affinis</i>	Nymph	<i>Turdus rufiventris</i>	PN Mburucuyá	MN173296 (100%)	MT604113
<i>Ixodes</i> sp. cf. <i>I. affinis</i>	Larva	<i>Turdus rufiventris</i>	PN Mburucuyá	MN173296 (100%)	MT604114

Table 3

Number of orders, families, species and specimens of birds captured and infested by ticks in twenty-two surveys of different vegetation units from four Phytogeographic Provinces in Argentina as defined by Oyarzabal et al. (2018).

Phytogeographic Province	Locality	Month/Year	Birds No. infested orders/ No. captured orders	No. infested Families/ No. captured Families	No. infested species/ No. captured species	No. infested birds/ No. captured birds	Ticks Specie	Prevalence									
Chaco	PP Fuerte Esperanza	07/2019	3/3	8/11	16/27	54/85	<i>Amblyomma parvum</i>	0.60									
							<i>Amblyomma tigrinum</i>	0.25									
							<i>Ornithodoros</i> sp. cf. <i>O. mimon</i>	0.01									
	Palma Sola	05/2014	0/2	0/11	0/16	0/33											
										PP Pampa del Indio	05/2017	1/2	4/12	6/26	12/142	<i>Amblyomma calcaratum</i>	0.02
																<i>Amblyomma nodosum</i>	0.01
																<i>Amblyomma ovale</i>	0.01
							<i>Haemaphysalis juxtakochi</i>	0.04									
	PN Chaco	04/2019	1/4	5/12	5/21	6/51											
										RP El Bagual	07/2015	1/3	6/11	8/19	13/42	<i>Ixodes</i> sp. cf.	0.03
																<i>I. affinis</i>	
																<i>Amblyomma nodosum</i>	0.02
							<i>Amblyomma ovale</i>	0.10									
	RP El Bagual	07/2015	1/3	6/11	8/19	13/42											
																<i>Amblyomma nodosum</i>	0.02
																<i>Amblyomma ovale</i>	0.17
																<i>Haemaphysalis juxtakochi</i>	0.19
							<i>Ixodes</i> sp. cf.	0.19									
		10/2015	1/2	5/10	5/19	10/43											
																<i>I. affinis</i>	0.02
																<i>Amblyomma ovale</i>	0.14
															<i>Amblyomma sculptum</i>	0.09	
						<i>Haemaphysalis juxtakochi</i>	0.14										
	06/2018	3/5	6/8	8/10	29/46												
															<i>I. affinis</i>	0.02	
															<i>Amblyomma nodosum</i>	0.41	
															<i>Amblyomma ovale</i>	0.04	
						<i>Amblyomma sculptum</i>	0.02										
Cañada Ombú	06/2021	1/4	1/9	2/22	2/49												
															<i>Amblyomma triste</i>	0.02	
															<i>Haemaphysalis juxtakochi</i>	0.33	
															<i>Ixodes</i> sp.	0.02	
						<i>Amblyomma ovale</i>	0.04										
PN Pilcomayo	11/2016	1/5	4/10	8/22	11/43												
															<i>Haemaphysalis juxtakochi</i>	0.02	
															<i>Amblyomma calcaratum</i>	0.02	
															<i>Amblyomma nodosum</i>	0.05	
						<i>Amblyomma ovale</i>	0.05										
PN Mburucuyá	12/2018	1/4	7/13	11/26	34/73												
															<i>Amblyomma sculptum</i>	0.05	
															<i>Haemaphysalis juxtakochi</i>	0.14	
															<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.05	
						<i>Ornithodoros</i> sp. cf. <i>O. mimon</i>	0.04										
						<i>Amblyomma</i> sp.	0.04										
						<i>Amblyomma dubitatum</i>	0.21										
						<i>Amblyomma nodosum</i>	0.16										
						<i>Haemaphysalis juxtakochi</i>	0.18										
						<i>Ixodes</i> sp.	0.03										
						<i>Ixodes</i> sp. cf.	0.23										
						<i>I. affinis</i>											

(continued on next page)

Table 3 (continued)

Phytogeographic Province	Locality	Month/Year	Birds No. infested orders/ No. captured orders	No. infested Families/ No. captured Families	No. infested species/ No. captured species	No. infested birds/ No. captured birds	Ticks Specie	Prevalence
TOTAL Chaco			5/9	14/22	37/81	171/607		
Espeñal	Don Sebastián	03/2009	1/4	1/9	2/11	2/18	<i>Amblyomma dubitatum</i>	0.06
							<i>Haemaphysalis juxtakochi</i>	0.06
Pampa	Aurora del Palmar	12/2007	1/4	1/12	2/22	2/51	<i>Amblyomma dubitatum</i>	0.04
Yungas	Dique La Ciénaga	05/2008	1/2	4/7	5/11	9/27	<i>Amblyomma tigrinum</i>	0.04
							<i>Haemaphysalis sp.</i>	0.07
							<i>Haemaphysalis leporispalustris</i>	0.19
							<i>Ixodes pararicinus</i>	0.04
							<i>Ixodes silvanus</i>	0.19
	Portal de piedra	05/2008	1/1	4/8	4/16	8/50	<i>Amblyomma ovale</i>	0.04
							<i>Haemaphysalis leporispalustris</i>	0.08
							<i>Ixodes sp.</i>	0.02
							<i>Ixodes pararicinus</i>	0.02
		03/2014	1/2	1/2	1/20	1/45	<i>Haemaphysalis juxtakochi</i>	0.02
	San Francisco Sierra de Zapla	03/2017	1/1	1/4	1/4	1/4	<i>Ixodes pararicinus</i>	0.25
		05/2008	1/4	4/9	5/10	6/17	<i>Haemaphysalis juxtakochi</i>	0.06
							<i>Haemaphysalis leporispalustris</i>	0.06
							<i>Ixodes pararicinus</i>	0.12
							<i>Ixodes silvanus</i>	0.12
		11/2009	1/7	2/16	3/29	3/68	<i>Amblyomma sp.</i>	0.01
							<i>Amblyomma sculptum</i>	0.01
							<i>Haemaphysalis leporispalustris</i>	0.01
	Valle Colorado	03/2017	1/1	6/8	7/11	8/19	<i>Ixodes sp.</i>	0.05
							<i>Ixodes pararicinus</i>	0.21
							<i>Ixodes silvanus</i>	0.32
	Isla de Cañas	09/2019	1/3	4/9	4/19	17/74	<i>Amblyomma sculptum</i>	0.18
							<i>Haemaphysalis leporispalustris</i>	0.05
							<i>Ixodes pararicinus</i>	0.04
	Cochuna	11/2008	1/2	2/8	3/12	19/42	<i>Haemaphysalis leporispalustris</i>	0.02
							<i>Ixodes pararicinus</i>	0.40
							<i>Ixodes silvanus</i>	0.17
		12/2017	1/2	3/9	6/14	15/38	<i>Ixodes sp.</i>	0.03
							<i>Ixodes auritulus s. l.</i>	0.21
							<i>Ixodes pararicinus</i>	0.16
							<i>Ixodes silvanus</i>	0.24
	Siambon	05/2010	1/2	1/9	1/10	3/25	<i>Haemaphysalis leporispalustris</i>	0.08
							<i>Ixodes pararicinus</i>	0.04
							<i>Ixodes silvanus</i>	0.08
TOTAL Yungas			1/7	9/19	19/71	90/409		

species were found parasitizing birds. The prevalence of infested birds in the PPC was 28.2% (CI_{95%}: 24.7 – 31.9), followed by the PPY 22.0% (CI_{95%}: 18.3 – 26.3), PPE 11.1% (CI_{95%}: 3.1 – 32.8) and PPP 3.9% (CI_{95%}: 1.1 – 13.2). There was a difference in overall tick prevalence between Phytogeographic Province ($X^2 = 19.3$, $df = 3$, $p < 0.01$). It should be noted that in the PPC and PPY the sampling effort was greater (eight locations each) than in PPE and PPP (Table 3). Prevalence differences between PPC and PPY were not significant ($X^2 = 4.9$, $df = 1$, $p = 0.027$). The mean abundance of tick species found on birds in PPC and PPY is showed in Fig. 2.

4. Discussion

The present study reports 15 tick species (8 *Amblyomma*, 2 *Haemaphysalis*, 4 *Ixodes* and 1 *Ornithodoros*) parasitizing birds in different Phytogeographic Provinces of Argentina. With these results, the number of tick species recorded on birds in Argentina amounts to 27 (Beldomenico et al., 2003; Nava et al., 2006a, 2006b, 2009, 2011, 2017; Mastropaolo et al., 2011; Ortiz et al., 2011; Flores et al., 2014, 2016, 2018, 2020; Venzal et al., 2014; Saracho-Bottero et al., 2017, 2021; Lamattina et al., 2018a, 2018b; Cicuttin et al., 2019, 2022; Sebastian et al., 2020; Guglielmone et al., 2021; this work). Most of the records correspond to larvae and nymphs, as expected. The only adult ticks that

Table 4
Species of ticks collected on wild bird species from seventeen localities from Argentina.

Locality	Birds Order	Family	Specie	No. infested/ No. captured	Ticks Specie	Mean abundance				
						Larvae	Nymphs	Females		
PP Fuerte Esperanza	Columbiformes	Columbidae	<i>Columbina picui</i>	1/2	<i>Amblyomma parvum</i>	0.50 ^a				
		Passeriformes	Furnariidae	<i>Coryphistera alaudina</i>	2/2	<i>Amblyomma parvum</i>	6.50 ^a			
					2/2	<i>Amblyomma tigrinum</i>	2.00	1.00		
				<i>Furnarius rufus</i>	2/3	<i>Amblyomma parvum</i>	4.67 ^a			
					2/3	<i>Amblyomma tigrinum</i>	2.67	0.33		
				<i>Lepidocolaptes angustirostris</i>	1/3	<i>Ornithodoros</i> sp. cf. <i>O. mimon</i>	1.33			
				<i>Pseudoseisura lophotes</i>	1/1	<i>Amblyomma parvum</i>	14.00 ^a			
			Thamnophilidae	<i>Taraba major</i>	2/2	<i>Amblyomma parvum</i>	48.50 ^a			
				<i>Thamnophilus caerulescens</i>	5/6	<i>Amblyomma parvum</i>	1.83 ^a			
			Thraupidae	<i>Coryphospingus cucullatus</i>	21/23	<i>Amblyomma parvum</i>	3.74 ^a			
					12/23	<i>Amblyomma tigrinum</i>	3.00	0.26		
				<i>Microspingus melanoleucus</i>	5/12	<i>Amblyomma parvum</i>	1.83 ^a			
				<i>Saltator aurantirostris</i>	6/6	<i>Amblyomma parvum</i>	18.83 ^a	0.17		
					4/6	<i>Amblyomma tigrinum</i>	2.17	0.33		
				<i>Saltatricula multicolor</i>	1/1	<i>Amblyomma parvum</i>	10.00			
				<i>Sporophila caerulescens</i>	1/1	<i>Amblyomma parvum</i>	7.00 ^a			
			Troglodytidae	<i>Troglodytes aedon</i>	1/1	<i>Amblyomma parvum</i>	7.00 ^a			
			Turdidae	<i>Turdus amaurochalinus</i>	1/1	<i>Amblyomma parvum</i>	4.00			
			Tyrannidae	<i>Stigmatura budytoidea</i>	1/5	<i>Amblyomma parvum</i>	0.40 ^a			
		Piciformes	Picidae	<i>Colaptes melanochloros</i>	1/1	<i>Amblyomma parvum</i>	4.00 ^a			
				1/1	<i>Amblyomma tigrinum</i>	1.00 ^a				
PP Pampa del Indio	Passeriformes	Furnariidae	<i>Xiphocolaptes major</i>	1/1	<i>Amblyomma calcaratum</i>		1.00 ^a			
		Thamnophilidae	<i>Taraba major</i>	1/5	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.20 ^a				
			<i>Thamnophilus caerulescens</i>	2/13	<i>Amblyomma calcaratum</i>		0.15			
		Thraupidae	<i>Saltator similis</i>	1/8	<i>Amblyomma nodosum</i>		0.13			
				2/8	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.13 ^a	0.13 ^a			
		Turdidae	<i>Turdus amaurochalinus</i>	3/6	<i>Haemaphysalis juxtakochi</i>	0.83 ^a				
				1/6	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.17				
				<i>Turdus rufiventris</i>	1/3	<i>Amblyomma ovale</i>	0.33	0.33		
					2/3	<i>Haemaphysalis juxtakochi</i>	1.00	0.33		
					2/3	<i>Amblyomma ovale</i>	2.67 ^a	0.67 ^a		
PN Chaco	Passeriformes	Furnariidae	<i>Syndactyla rufosuperciliata</i>	2/3	<i>Amblyomma ovale</i>	0.33 ^a	0.67 ^a			
		Parulidae	<i>Myiothlypis leucoblephara</i>	1/9	<i>Amblyomma ovale</i>	0.11 ^a				
		Passerellidae	<i>Arremon flavirostris</i>	1/3	<i>Amblyomma ovale</i>	0.33				
		Thamnophilidae	<i>Taraba major</i>	1/1	<i>Amblyomma ovale</i>	1.00				
		Turdidae	<i>Turdus amaurochalinus</i>	1/7	<i>Amblyomma nodosum</i>		0.14			
RP El Bagual	Accipitriformes	Accipitridae	<i>Rupornis magnirostris</i>	1/1	<i>Amblyomma sculptum</i>		1.00			
		Gruiformes	Rallidae	<i>Aramides cajaneus</i>	1/1	<i>Haemaphysalis juxtakochi</i>	50.00 ^a	2.00 ^a		
			<i>Mustelirallus albicollis</i>	1/3	<i>Amblyomma triste</i>		0.33 ^a			
	Passeriformes		Cardinalidae	<i>Cyanoloxia brissonii</i>	1/1	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	2.00 ^a			
			Corvidae	<i>Cyanocorax chrysops</i>	1/3	<i>Haemaphysalis juxtakochi</i>	0.33			
				<i>Cyanocorax cyanomelas</i>	2/9	<i>Amblyomma ovale</i>	0.11 ^a	0.11 ^a		
					1/9	<i>Amblyomma sculptum</i>	1.56 ^a			
				Furnariidae	<i>Dendrocolaptes platyrostris</i>	1/2	<i>Ixodes</i> sp. cf. <i>I. affinis</i>		0.50 ^a	
				Passerellidae	<i>Arremon flavirostris</i>	3/14	<i>Amblyomma ovale</i>	0.14	0.07	
						1/14	<i>Amblyomma sculptum</i>		0.07 ^a	
						2/14	<i>Haemaphysalis juxtakochi</i>	0.14		
						2/14	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.21		
				Thamnophilidae	<i>Taraba major</i>	16/27	<i>Amblyomma ovale</i>	2.85	0.59	
					1/27	<i>Amblyomma nodosum</i>		0.04		
					13/27	<i>Haemaphysalis juxtakochi</i>	1.70 ^a	0.33 ^a		
					1/27	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.04			
					1/27	<i>Ixodes</i> sp.	0.18			
				<i>Thamnophilus caerulescens</i>	1/3	<i>Haemaphysalis juxtakochi</i>	0.33 ^a			
			Thraupidae	<i>Saltator similis</i>	1/4	<i>Amblyomma sculptum</i>		0.25 ^a		
			<i>Tachyphonus rufus</i>	1/1	<i>Amblyomma ovale</i>		1.00 ^a			
			1/1	<i>Haemaphysalis juxtakochi</i>		1.00				
	Troglodytidae	<i>Troglodytes aedon</i>	2/5	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.20	0.20				
	Turdidae	<i>Turdus amaurochalinus</i>	2/4	<i>Amblyomma ovale</i>		0.50				
			3/4	<i>Haemaphysalis juxtakochi</i>	0.75	2.75 ^a				
			3/4	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	1.75					
		<i>Turdus rufiventris</i>	3/6	<i>Amblyomma ovale</i>		1.00				
			4/6	<i>Amblyomma sculptum</i>		0.67 ^a				
			5/6	<i>Haemaphysalis juxtakochi</i>	0.67	1.50				
			4/6	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	1.83	0.17				
	Tyrannidae	<i>Hemitriccus margaritaceiventer</i>	1/4	<i>Amblyomma nodosum</i>		0.25				
Cañada Ombú	Passeriformes	Thamnophilidae	<i>Taraba major</i>	1/2	<i>Amblyomma ovale</i>		0.50			
		Turdidae	<i>Turdus amaurochalinus</i>	1/4	<i>Amblyomma ovale</i>		0.50			
				1/4	<i>Haemaphysalis juxtakochi</i>	0.75	0.25			
PN Pilcomayo	Passeriformes	Furnariidae	<i>Dendrocolaptes platyrostris</i>	1/1		2.00 ^a				

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Table 4 (continued)

Locality	Birds Order	Family	Specie	No. infested/ No. captured	Ticks Specie	Mean abundance						
						Larvae	Nymphs	Females				
PN Mburucuyá	Passeriformes	Furnariidae	<i>Furnarius rufus</i>	1/4	<i>Ornithodoros</i> sp. cf. <i>O. mimon</i>							
				2/4	<i>Haemaphysalis juxtakochi</i>	0.25 ^a						
				1/4	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.50 ^a						
				1/4	<i>Amblyomma nodosum</i>	0.50						
				1/4	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.25 ^a						
				1/1	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	1.00 ^a						
				1/2	<i>Amblyomma ovale</i>	0.50 ^a						
				1/2	<i>Amblyomma sculptum</i>	1.50 ^a						
				1/2	<i>Haemaphysalis juxtakochi</i>	1.00 ^a						
				1/2	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	2.00 ^a						
				1/2	<i>Ornithodoros</i> sp. cf. <i>O. mimon</i>	1.00 ^a						
				1/1	<i>Amblyomma calcaratum</i>	1.00 ^a						
				1/1	<i>Amblyomma sculptum</i>	1.00 ^a						
				1/4	<i>Amblyomma ovale</i>	0.25						
				1/4	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.25						
		1/1	<i>Amblyomma nodosum</i>	1.00 ^a								
		Parulidae	<i>Campylorhamphus trochilirostris</i>	1/1	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	2.00	5.00					
				1/1	<i>Amblyomma nodosum</i>		1.00 ^a					
				1/3	<i>Amblyomma dubitatum</i>	0.33 ^a						
				1/3	<i>Amblyomma nodosum</i>		0.33					
				1/3	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.33						
				1/11	<i>Amblyomma</i> sp.	0.09						
				2/11	<i>Amblyomma dubitatum</i>	0.09 ^a	0.18 ^a					
				3/11	<i>Amblyomma nodosum</i>		0.27 ^a					
				1/11	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.09						
				1/10	<i>Amblyomma nodosum</i>		0.09					
				2/10	<i>Haemaphysalis juxtakochi</i>	0.20	0.09 ^a					
				1/10	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.10						
				1/2	<i>Amblyomma dubitatum</i>	0.50 ^a						
				1/2	<i>Amblyomma nodosum</i>		1.00					
				1/2	<i>Ixodes</i> sp.		0.50					
		2/2	<i>Ixodes</i> sp. cf. <i>I. affinis</i>		1.00							
		1/2	<i>Ixodes</i> sp.	0.50								
		1/2	<i>Ixodes</i> sp. cf. <i>I. affinis</i>		0.50							
		1/1	<i>Ixodes</i> sp. cf. <i>I. affinis</i>		1.00							
		5/8	<i>Amblyomma dubitatum</i>	1.25 ^a	0.25 ^a							
		1/8	<i>Amblyomma nodosum</i>		0.13							
		4/8	<i>Haemaphysalis juxtakochi</i>	1.13	1.00							
		3/8	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	0.25	0.25							
		2/7	<i>Amblyomma</i> sp.	0.43								
		6/7	<i>Amblyomma dubitatum</i>	19.57	1.28 ^a							
		2/7	<i>Amblyomma nodosum</i>		0.71							
		7/7	<i>Haemaphysalis juxtakochi</i>	8.00	1.86							
		6/7	<i>Ixodes</i> sp. cf. <i>I. affinis</i>	1.29	1.28							
		1/2	<i>Amblyomma nodosum</i>		1.00 ^a							
ANP Don Sebastián	Passeriformes	Turdidae	<i>Turdus amaurochalinus</i>	1/1	<i>Haemaphysalis juxtakochi</i>	28.00						
				1/2	<i>Amblyomma dubitatum</i>	2.50						
				1/5	<i>Amblyomma dubitatum</i>		0.20					
Aurora del Palmar	Passeriformes	Turdidae	<i>Turdus amaurochalinus</i>	1/10	<i>Amblyomma dubitatum</i>		0.20					
				1/5	<i>Amblyomma dubitatum</i>		0.20					
Dique La Cienaga	Passeriformes	Furnariidae	<i>Syndactyla rufosuperciliata</i>	1/2	<i>Haemaphysalis leporispalustris</i>	0.50 ^a						
				2/2	<i>Ixodes silvanus</i>	1.00						
				1/4	<i>Ixodes silvanus</i>	0.25						
				1/5	<i>Amblyomma tigrinum</i>		0.20 ^a					
				2/5	<i>Haemaphysalis</i> sp.	0.60						
				2/5	<i>Haemaphysalis leporispalustris</i>	1.00						
				1/1	<i>Ixodes parvicinus</i>		1.00					
				1/1	<i>Ixodes silvanus</i>	2.00						
				1/1	<i>Haemaphysalis leporispalustris</i>	3.00 ^a						
				1/2	<i>Ixodes silvanus</i>	1.50						
				1/2	<i>Haemaphysalis leporispalustris</i>	2.00						
				Portal de piedra	Passeriformes	Cardinalidae	<i>Cyanoloxia brissonii</i>	1/3	<i>Haemaphysalis juxtakochi</i>	0.33 ^a		
								1/2	<i>Ixodes parvicinus</i>		0.50	
						Furnariidae	<i>Syndactyla rufosuperciliata</i>	3/11	<i>Haemaphysalis leporispalustris</i>	1.09		
								1/3	<i>Saltator aurantirostris</i>	0.33 ^a		

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Table 4 (continued)

Locality	Birds Order	Family	Specie	No. infested/ No. captured	Ticks Specie	Mean abundance		
						Larvae	Nymphs	Females
San Francisco Sierra de Zapla	Passeriformes	Turdidae	<i>Turdus rufiventris</i>	2/6	<i>Haemaphysalis leporispalustris</i>	4.33	0.17	7.00
				1/6	<i>Amblyomma ovale</i>			
				1/1	<i>Ixodes</i> sp.			
				1/1	<i>Ixodes pararicinus</i>			
				1/1	<i>Ixodes silvanus</i>			
				1/6	<i>Amblyomma</i> sp.			
				1/5	<i>Ixodes pararicinus</i>			
				1/6	<i>Haemaphysalis leporispalustris</i>			
				1/4	<i>Haemaphysalis juxtakochi</i>			
				1/5	<i>Amblyomma sculptum</i>			
Valle Colorado	Passeriformes	Turdidae	<i>Turdus rufiventris</i>	1/11	<i>Haemaphysalis leporispalustris</i>	0.18	0.09	1.00
				1/11	<i>Ixodes pararicinus</i>			
				1/3	<i>Ixodes silvanus</i>			
				1/1	<i>Ixodes pararicinus</i>			
				1/1	<i>Ixodes silvanus</i>			
				1/1	<i>Ixodes silvanus</i>			
				1/1	<i>Ixodes silvanus</i>			
				1/1	<i>Ixodes pararicinus</i>			
				1/1	<i>Ixodes</i> sp.			
				1/2	<i>Ixodes pararicinus</i>			
Isla de Cañas	Passeriformes	Turdidae	<i>Turdus rufiventris</i>	2/2	<i>Ixodes silvanus</i>	3.50	1.00	4.50
				1/1	<i>Ixodes pararicinus</i>			
				1/1	<i>Ixodes pararicinus</i>			
				1/5	<i>Ixodes silvanus</i>			
				1/5	<i>Amblyomma sculptum</i>			
				1/6	<i>Amblyomma sculptum</i>			
				1/6	<i>Ixodes pararicinus</i>			
				11/28	<i>Amblyomma scuptum</i>			
				4/28	<i>Haemaphysalis leporispalustris</i>			
				2/28	<i>Ixodes pararicinus</i>			
Cochuna	Passeriformes	Furnariidae	<i>Syndactyla rufosuperciliata</i>	2/5	<i>Ixodes silvanus</i>	0.04	0.04	0.80
				1/4	<i>Ixodes silvanus</i>			
				1/3	<i>Ixodes pararicinus</i>			
				1/3	<i>Ixodes silvanus</i>			
				1/1	<i>Ixodes auritulus</i>			
				1/1	<i>Ixodes silvanus</i>			
				1/2	<i>Ixodes auritulus</i>			
				1/15	<i>Ixodes auritulus</i>			
				8/15	<i>Ixodes pararicinus</i>			
				4/15	<i>Ixodes silvanus</i>			
Siambón	Passeriformes	Turdidae	<i>Turdus rufiventris</i>	2/15	<i>Ixodes</i> sp.	0.07	0.07	0.93
				1/20	<i>Haemaphysalis leporispalustris</i>			
				4/20	<i>Ixodes auritulus</i>			
				14/20	<i>Ixodes pararicinus</i>			
				7/20	<i>Ixodes silvanus</i>			
				2/10	<i>Haemaphysalis leporispalustris</i>			
				1/10	<i>Ixodes pararicinus</i>			
				2/10	<i>Ixodes silvanus</i>			

^a New association between host species-stage of parasite species.

were observed attached to birds correspond to *I. auritulus* s. l. and *I. silvanus*. *Haemaphysalis juxtakochi*, was present in three of four Phytogeographic Provinces. In contrast, *Ixodes* species associated with birds appear to have a more limited distribution because they were restricted to humid areas of the PPC and the PPY. *Amblyomma* was the genus with the higher number of species, and members of this genus were present in all Phytogeographic Provinces. Some *Amblyomma* species as *A. ovale* were found in different Phytogeographic Provinces but others such as *A. dubitatum* and *A. parvum* presented a more restricted distribution.

Birds belonging to the family Turdidae are regarded as the most important avian hosts for Neotropical ixodid ticks (Guglielmine et al., 2021). However, there are other families of birds in particular sites of the Neotropical region that may be equal or more important than

Turdidae in the maintenance of ticks, such as Thraupidae, Thamnophilidae and Furnariidae (Ogrzewalska et al., 2009, 2011; Lugarini et al., 2015; Luz et al., 2017; Martínez-Sánchez et al., 2020). In this study, Thamnophilidae and Turdidae were the bird families more infested by tick in terms of prevalence. Birds from the family Thamnophilidae were parasitized in 7 of the 8 localities where they were captured (mainly in PPC), while birds of the Turdidae were infested in 17 of the 18 localities (belonging to all the Phytogeographic Provinces included). Of the 15 tick species found in this study, 7 were on Thamnophilidae birds and 11 on Turdidae birds.

The PPC showed the highest number of bird species (31 species of five orders) and tick species. One Argasidae species, all *Amblyomma* species, one of the two *Haemaphysalis* species and one of the four *Ixodes* species were found in this Phytogeographic Province the largest number

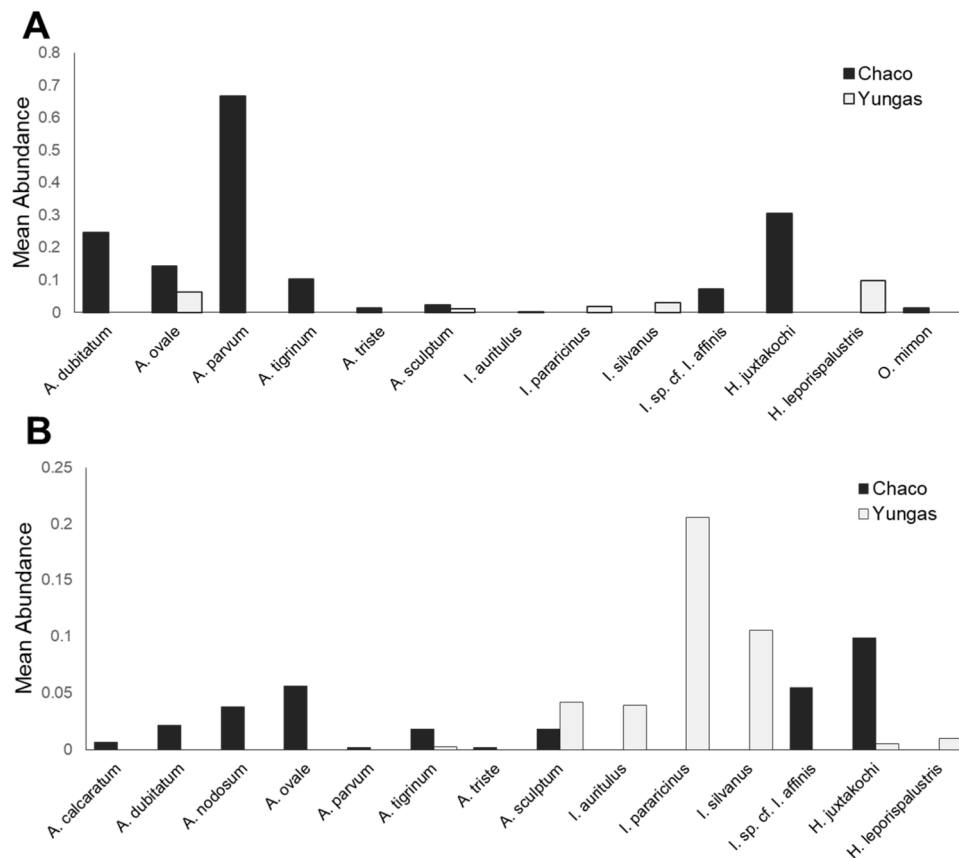


Fig. 2. Mean abundance of larvae (A) and nymphs (B) of ticks species collected on birds in the Chaco (black) and Yungas (grey) Phytogeographic Provinces of Argentina. *A.* = *Amblyomma*, *I.* = *Ixodes*, *H.* = *Haemaphysalis*.

of *Haemaphysalis* and *Ixodes* species associated to birds were reported for the PPY, where two species of *Haemaphysalis* and three of *Ixodes* were found. Only three of the eight species of *Amblyomma* found in this study were detected in the PPY.

Although the relevance of birds as hosts for immature stages of *A. nodosum* and *A. calcaratum* well documented (see Guglielmone et al. 2021), the findings of this work constitute the first records of immature stages of both species on birds in Argentina. *Amblyomma dubitatum* is established in Argentina, Brazil, Paraguay and Uruguay (Nava et al., 2017), but the relevance of birds as hosts of immature stages has only been documented in Argentina by Flores et al. (2014) in the same Phytogeographic Province. These are the first findings of immature stages of this tick on birds in the PPE and PPP, showing that this parasite-host association is more frequent than previously recognized.

Amblyomma ovale and *A. parvum* are distributed from Argentina to USA and Mexico, respectively (Guglielmone et al., 2021). The main hosts for immature stages of these species are small and medium rodents, however there also records of larvae and nymphs of both species on birds (Guglielmone et al., 2021). Particularly in the case of *A. parvum*, the high value of prevalence (60.0%) of immature stages on birds recorded in this study was not previously documented.

The values of prevalence in the *A. parvum* infestations on birds reported in previous studies (Nava et al., 2006a; Luz et al., 2012; Lugarini et al., 2015) were much lower than the value obtained in this work, highlighting that the role of birds as hosts for larvae and nymphs of this tick is more important than previously assumed. This high level of infestation could be attributed to the fact that the sample was made in a season where immature stages of *A. parvum* reach their peak of abundance and in a locality belonging to a macro-region that is a highly favorable habitat for this tick (see Nava et al. 2008a, 2008b, 2016).

Amblyomma sculptum has been found in Argentina, Brazil, Bolivia

and Paraguay (Nava et al., 2017). The results of this study represent the first findings of *A. sculptum* on birds in Argentina. Adults, nymphs and larvae of this tick show low host specificity, and they are principally associated with large mammals of different orders, although both adults and immature were previously recorded on bird species of different orders from Neotropical other countries (Guglielmone et al., 2021). Therefore, the results of the current work where *A. sculptum* larvae and nymphs were found on birds, although novel for Argentina, are not unexpected.

Amblyomma tigrinum and *A. triste* are members of *Amblyomma maculatum* group (Estrada-Peña et al., 2005; Lado et al., 2018). The role of birds as hosts for *A. tigrinum* immature is recognized (Nava et al., 2006; Flores et al., 2014), and the results of this work confirm the importance of avian hosts for the development of the immature stages of this species. The main hosts for *A. triste* immature are small rodents (Cricetidae), and the results of this work suggest that birds are occasional hosts for the immature stages as previously stated by Guglielmone et al. (2021).

Haemaphysalis juxtakochi and *H. leporispalustris* are found from Argentina to USA and Mexico, respectively (Guglielmone et al., 2021). Usual hosts for immature of *H. juxtakochi* are mammals, but the relevance of birds is well documented (Guglielmone et al., 2021). All parasitic stages of *H. leporispalustris* are usually found on Lagomorpha, but birds are also frequently recorded as hosts for immature stages (Guglielmone et al., 2021). In Argentina, this report together with to Beldomenico et al. (2003) and Flores et al. (2014) are the only records of this species on birds, and all of them were made in the PPY.

Ixodes auritulus s. l. is widely distributed in the Afrotropical, Australasian, Nearctic and Neotropical Zoogeographic Regions and probably represents a complex of species (González-Acuña et al., 2005; Guglielmone et al., 2021; Apanaskevich et al. 2022). This tick species is specific of birds, with a few records from rodents (Guglielmone et al.,

2021). In this work, all stages of *I. auritulus* s. l. were found on birds and added new associations to the extensive list of records of this tick species of birds.

Ixodes pararicinus and *I. silvanus* have been found only in the Yungas Phytogeographic Province of Argentina (Guglielmone et al., 2021; Saracho-Bottero et al., 2021). The role of birds as hosts of larvae and nymphs of *I. pararicinus* is recognized (Flores et al., 2014; Saracho-Bottero et al., 2017), while birds are hosts of all parasitic stages of *I. silvanus* (Saracho-Bottero et al., 2021).

Ixodes sp. cf. *I. affinis* represent a species complex with populations distributed from Argentina to Canada, with records of immature stages on birds (Scott et al., 2012; Flores et al., 2020; Saracho-Bottero et al., 2020; Guglielmone et al., 2021). This paper reaffirms the importance of avian host for *Ixodes* sp. cf. *I. affinis*.

Ornithodoros sp. cf. *O. mimon* is distributed in Argentina, Brazil, Bolivia and Uruguay and most of the records of larvae were made on bats, but there also are findings on opossums (Didelphidae), rodents (Cricetidae), and birds (Nava et al., 2017). The findings of *Ornithodoros* sp. cf. *O. mimon* performed in this work represent the first records on this tick on birds in Argentina and add another two species of Woodcreepers that place nests inside hollow (*Dendrocolaptes platyrostris* and *Xiphocolaptes major*).

Birds are relevant hosts for the immature stages of some tick species, and they could have a role in transporting ticks infected with pathogens for animals and humans (Olsén et al., 1995; Björnsdóttir et al., 2001; Elfving et al., 2010). Eleven of the fifteen tick species collected in this study have been found feeding on domestic animals or humans (7 *Amblyomma*, 2 *Haemaphysalis*, 1 *Ixodes* and 1 *Ornithodoros*) and most of them have antecedents of infection with different microorganisms belonging to the genera *Rickettsia*, *Ehrlichia*, *Coxiella*, *Hepatozoon* or *Borrelia* (Nava et al., 2017; Guglielmone et al., 2021). Therefore, some of these bird species could participate in the enzootic cycles of the microorganisms transmitted by these tick species.

The results of the current study corroborate that wild birds are relevant hosts for a considerable number of Neotropical hard ticks, principally for their immature stages. Furthermore, it could be observed that the associations tick-bird are variable among the different vegetation units, although the parasitized birds belong, in general terms, to the same families (i.e. *Thamnophilidae*, *Turdidae*, *Thraupidae*, *Passerellidae*, *Furnariidae* and *Troglodytidae*) showing their relevance in the life cycles of this parasites.

CRedit authorship contribution statement

Fernando S. Flores: Conceptualization, Investigation, Formal analysis, Resources, Writing – original draft, Writing – review & editing. **Maria N. Saracho-Bottero:** Investigation, Writing – review & editing. **Evelina L. Tarragona:** Investigation, Resources, Formal analysis, Writing – original draft, Writing – review & editing. **Patrick S. Sebastian:** Investigation, Resources, Writing – original draft, Writing – review & editing. **Griselda N. Copa:** Investigation, Writing – review & editing. **Leonor Guardia:** Investigation, Writing – review & editing. **Atilio J. Mangold:** Funding acquisition, Resources, Writing – original draft, Writing – review & editing. **José M. Venzal:** Investigation, Writing – original draft, Writing – review & editing. **Santiago Nava:** Conceptualization, Investigation, Formal analysis, Funding acquisition, Resources, Writing – original draft, Writing – review & editing.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ttbdis.2023.102135.

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