

Natural infestation of *Hydrochoerus hydrochaeris* by *Amblyomma dubitatum* ticks

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Abstract Natural infestation of *Amblyomma dubitatum* in relation to individual specific attributes of *Hydrochoerus hydrochaeris* such as sex, body mass and body condition was analyzed. The anatomical distribution of *A. dubitatum* on *H. hydrochaeris* was also evaluated. Prevalence of adults and nymphs were significantly higher than prevalence of larvae. Non-significant differences in the infestation levels were found among host sex. Multiple regression analysis did not show any statistically significant association among the level of infestation with ticks and body mass and body condition of the host. All parasitic tick stages were collected in all five anatomical areas of the host, but they exhibited significant differences in feeding site preference. Factors associated to the host which determine the high levels of infestation with *A. dubitatum* could be assigned to a combination of population-level properties of the host as abundance, ubiquity and aggregation, rather than individual specific attributes related to body condition, body mass or sex.

Keywords *Amblyomma dubitatum* · *Hydrochoerus hydrochaeris* ·
Host-parasite relationship

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Introduction

Macroparasites are subject to the external environment and the within-host environment (Hugot 2006). The interface host-parasite is governed by several factors which usually results in parasite burdens within host populations with a ubiquitous pattern of negative binomial distribution (Wilson et al. 1996; Shaw et al. 1998). Knowledge of the factors which may determine this distribution is necessary to understand the dynamics of the parasite-host interaction. In this sense, individual attributes of the hosts as body mass, body size, sex and physiological condition, are among the factors determining the heterogeneous distribution of parasites within their host populations (Pacala and Dobson 1988; Mooring et al. 1996; Hughes and Randolph 2001; Klein 2004; Krasnov et al. 2004, 2005; Krist et al. 2004; Poulin and George-Nascimento 2007; Brunner and Ostfeld 2008; Patterson et al. 2008).

Hard ticks (Acari: Ixodidae) are hematophagous ectoparasites of amphibians, reptiles, birds and mammals, including humans and domestic animals. These parasites affect the dynamics of host populations due to the transmission of pathogenic microorganisms or by effects attributable to the parasitism per se which reduce the overall fitness of the hosts. *Amblyomma dubitatum* is a hard tick species distributed in South America, in areas associated with wetlands and watercourses from Argentina, Brazil, Paraguay and Uruguay (Nava et al. 2010). Although *A. dubitatum* was recorded parasitizing several species of mammals and one bird species (Nava et al. 2010; Dantas-Torres et al. 2010; Debárbora et al. 2012, 2014), the principal host for all parasitic stages of this tick is *Hydrochoerus hydrochaeris* (Rodentia: Caviidae, Hydrochoerinae) (Nava et al. 2010).

Previous research on the ecology of *A. dubitatum* were principally focused on the life cycle under laboratory and field conditions, records of tick-host associations, seasonality and biogeographic distribution (Almeida et al. 2001; Chacón et al. 2004; Labruna et al. 2004 (all these author named *A. dubitatum* as *Amblyomma cooperi*); Nava et al. 2010; Dantas-Torres et al. 2010; Debárbora et al. 2012, 2014), but quantitative studies concerning natural infestation of *A. dubitatum* on its principal host are lacking, with the exception of Corriale et al. (2013). The prevalence of the natural infestation of *A. dubitatum* on *H. hydrochaeris* in Corrientes Province found by Corriale et al. (2013) was very high (close to 95 %) but the results of this work are difficult to interpret since tick stages found on hosts were not specified by these authors. Because the association *H. hydrochaeris*–*A. dubitatum* is an ubiquitous phenomenon along the distributional area of this tick, the analysis of the relationship between *A. dubitatum* and *H. hydrochaeris* can be used for ecological analyses of the patterns that characterize a strong relationship between hosts and parasites. Therefore, the aim of this work was to describe and analyse the levels of natural infestation of *A. dubitatum* in relation to individual specific attributes of its principal host, *H. hydrochaeris*, such as sex, body mass and body condition, under the hypothesis that individual correlates of the hosts determine parasite loads. The spatial distribution pattern of *A. dubitatum* on *H. hydrochaeris* was also evaluated in order to determine whether each parasitic stage prefer a certain area of the body of the hosts, and the overlap in body distribution of both immature and adults stages.

Materials and methods

Monthly samples of *A. dubitatum* ticks parasitizing *H. hydrochaeris* were carried out from April 2010 to March 2012 in Estancia Rincón del Socorro (28°42'S 57°29'W), Corrientes

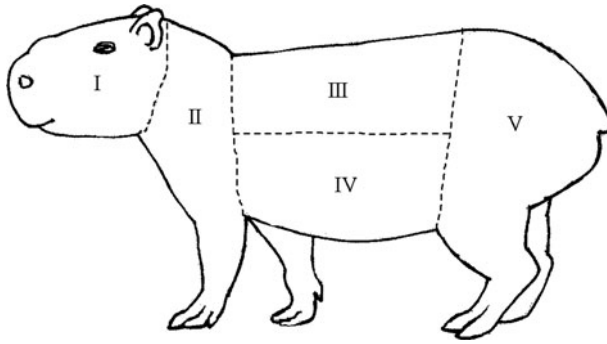


Fig. 1 Anatomical areas of *Hydrochoerus hydrochaeris*

Province, Argentina. The study area belongs to the macrosystem Esteros del Iberá. This ecosystem is characterized by the prevalence of swamps and marshlands that connect an extensive system of shallow lakes (Neiff and Poi de Neiff 2006). The mean annual rainfall is approximately 1,500 mm, and the summer rains are slightly more abundant than during the rest of the year (600–700 mm) (Neiff and Poi de Neiff 2006). At terrestrial habitats, vegetation is dominated by shrubland forests and temporarily flooded grasslands.

Specimens of *H. hydrochaeris* were captured by shot during a program to control overpopulation with permission of the Dirección de Recursos Naturales of the Corrientes Province. Larvae, nymphs and adults of *A. dubitatum* were determined following Joan (1930), Guglielmone and Viñabal (1994) and Martins et al. (2010). Counts of larvae and nymphs were made only considering engorged specimens. The body of each specimen of *H. hydrochaeris* was divided into 5 distinct parts (areas I–V), as it is detailed in Fig. 1, and the site of attachment of each tick collected was recorded.

Prevalence (number of hosts infested/number of hosts examined), mean (95 % bootstrap confidence intervals) and median (first and third quartiles) of the infestation were calculated for larvae, nymphs and adults of *A. dubitatum* ticks associated to *H. hydrochaeris*, and for adults and immature together. Because Shapiro–Wilk’s test (Zar 1999) showed significant departure from normality, the non parametric test of Kruskal–Wallis was used to compare the frequency distributions of ticks among the three stages. Prevalence were compared by using Fisher’s exact test. The same statistical procedures were applied to determine the statistical significance of the difference in the infestation level and prevalence between males and females of *H. hydrochaeris*. The level of aggregation of *A. dubitatum* ticks within *H. hydrochaeris* population was assessed by obtaining the index of discrepancy (D) (Poulin 1993, 2007) and the parameter k (Krebs 1999) were estimated by using Quantitative Parasitology 3.0 (Rózsa et al. 2000). In D , 0 constitutes null aggregation (all hosts with equal level of infestation) and 1 complete aggregation (all members of a parasite population on one individual host) (Poulin 1993, 2007). Parameter k can be used as an inverse index of aggregation, the larger the k , the less the aggregation (Krebs 1999).

The distribution of ticks among different anatomical areas of the host were compared applying assessed by an analysis of variance (ANOVA) followed by Dunn’s test for non-parametric multiple comparisons (Zar 1999). Additionally, the anatomical distribution of all parasitic stages of *A. dubitatum* was also analyzed by calculating the Levins’s measure of standardized niche breadth (B_s) and the Pianka’s measure of niche overlap (O_{XY}) as described in Krebs (1999). In these analyses, each anatomical area of *H. hydrochaeris* (see

Fig. 1) was considered as a resource state. The range of B_S is from 0 (minimum niche breadth) to 1 (an equal number of individual occurs in each resource state), and O_{XY} also ranges from 0 (no resources used in common) to 1 (complete overlap) (Krebs 1999).

Body condition and body mass index (weigh/total length) of the specimens of *H. hydrochaeris* examined for ticks were recorded. Body condition score was estimated following in Eberhardt et al. (2013). Briefly, this parameter is obtained by palpating the fat and muscle cover over the thoracic vertebrae and pelvic bones, and each area was scored on a scale between 1 and 5. Multiple-regression analysis was done with number of ticks as the dependent variable, and body condition (thoracic and pelvic) and body mass index as the independent variables. Data were log-transformed to satisfy normality criteria and stabilize the variances.

Results

A total of 72 specimens of *H. hydrochaeris* were examined for ticks. With the exception of one male and one nymph of *Amblyomma triste*, was the only tick species collected from these hosts was *A. dubitatum*. Quantitative data (mean abundance, median, prevalence, D and k) of the infestation of all parasitic stages of *A. dubitatum* on *H. hydrochaeris* are presented in Table 1. Values of percentage of prevalence and mean for the three parasitic stages were higher than 68 and 44, respectively. When all stages were analyzed together, prevalence was 100 %, the mean higher than 200, median 162 and the levels of aggregation were relatively low (D : 0.46; k : 1.34). Prevalence of adults and nymphs were significantly higher than prevalence of larvae (Fisher's exact test, $P < 0.05$), and significant differences were found among the three stages when tick distributions on hosts were compared (Kruskal–Wallis, $P < 0.05$). Discordance between values of mean and median was observed, indicating skewed distributions (Table 1).

Non-significant differences were found among host sex when prevalence and tick distributions on *H. hydrochaeris* were compared for adults, nymphs and larvae, nor when immature and adults were grouped [prevalence: Fisher's exact test, $P = 0.58$ (larvae), 0.48 (nymphs), 1.0 (adults, immature + adults); tick distribution: Kruskal–Wallis, $P = 0.84$ (larvae), 0.39 (nymphs), 0.57 (adults), 0.81 (immature + adults)]. The values of body mass, body condition and number of *A. dubitatum* ticks for each specimen of *H. hydrochaeris* examined (in this analysis, $n = 54$) are showed in Table 2. Multiple regression analysis did not show any statistically significant association among the level of infestation with ticks and body mass and body condition (thoracic and pelvic) of *H. hydrochaeris*.

The results of the analysis about anatomical distribution of *A. dubitatum* on *H. hydrochaeris* are showed in Table 3. Although all parasitic stages were collected in the five

Table 1 Percentage of prevalence, mean (with 95 % confidence limits), median [first and third quartiles (1Q–3Q)], index of discrepancy (D) and k parameter for the infestation of all parasitic stages of *Amblyomma dubitatum* on *Hydrochoerus hydrochaeris*

Tick stage	Prevalence (%)	Mean (CL 95 %)	Median (1Q–3Q)	D	K
Larvae	68.1	110.2 (66.2–205.1)	19.5 (0–96.5)	0.78	0.19
Nymphs	86.1	44.53 (31.2–65.6)	8 (3–62)	0.70	0.37
Adults	91.7	75.26 (57.1–96.4)	44.5 (8.5–113.5)	0.57	0.58
All stages together	100	226.6 (182.7–322.2)	162 (100.5–269)	0.46	1.34

Table 2 Values of body mass index, body condition (BC) and number of *Amblyomma dubitatum* ticks for each specimen of *Hydrochoerus hydrochaeris* examined

Host specimen	Number of ticks	BC (Thoracic)	BC (Pelvic)	Body mass index
1	342	4	4	0.4
2	43	4	4	0.47
3	106	4	4	0.4
4	172	3	3	0.48
5	390	4	4	0.53
6	115	4	4	0.53
7	298	3	4	0.77
8	232	3	4	0.72
9	128	3	4	0.53
10	115	3	3	0.26
11	222	3	4	0.43
12	336	3	2	0.49
13	117	3	3	0.41
14	259	3	2.5	0.46
15	98	3	3	0.47
16	32	3.5	3.5	0.35
17	224	4	4	0.47
18	68	3	3	0.4
19	388	3	3	0.46
20	315	3	3	0.4
21	140	3	3	0.42
22	205	3	3	0.44
23	367	3.5	3.5	0.43
24	351	3.5	3.5	0.47
25	57	3.5	3.5	0.48
26	282	2	2	0.48
27	44	3.5	3.5	0.48
28	55	3	3	0.51
29	167	2.5	2	0.48
30	103	3	3.5	0.48
31	1,914	3.5	3.5	0.43
32	686	3	3	0.45
33	77	2.5	2.5	0.36
34	135	3.5	3.5	0.35
35	197	1	1	0.29
36	104	2.5	3	0.42
37	573	2	2	0.42
38	1,212	2.5	2.5	0.47
39	589	2.5	3	0.4
40	279	3	2.5	0.46
41	280	3	3	0.38
42	242	3.5	3.5	0.45

Table 2 continued

Host specimen	Number of ticks	BC (Thoracic)	BC (Pelvic)	Body mass index
43	126	2.5	2.5	0.38
44	127	3	3	0.5
45	104	2.5	3	0.46
46	12	3.5	3	0.48
47	81	3	3	0.42
48	8	3.5	3.5	0.47
49	179	3.5	3.5	0.46
50	251	2.5	2.5	0.36
51	69	3.5	3.5	0.33
52	127	2.5	2.5	0.48
53	151	2.5	3	0.55
54	235	3	3	0.49

Table 3 Mean number (with 95 % confidence limits) of *Amblyomma dubitatum* ticks collected on different anatomical areas of *Hydrochoerus hydrochaeris*

Tick stage	Anatomical areas				
	I	II	III	IV	V
Larvae	2.2 (0.9–4.6) ^a	5.8 (3.1–11.1) ^a	23.6 (11.6–56.7) ^b	6.6 (3.9–11.7) ^a	18.2 (11.4–32.7) ^b
Nymphs	0.7 (0.3–1.3) ^a	2.4 (1.5–4.2) ^b	2.1 (1.3–4.2) ^b	19.8 (13.3–30.4) ^c	4.8 (3.2–7.3) ^b
Adults	12.9 (9.6–17.1) ^b	11.8 (9.3–15.3) ^b	2.7 (1.6–4.9) ^a	14.3 (10.3–19.9) ^b	1.6 (1.1–2.3) ^a

Kruskal–Wallis followed by Dunn’s test. Numbers not sharing superscripts are significantly different

See Fig. 1 for the reference number of the five anatomical areas

anatomical areas, they exhibited significant differences in the feeding site preference (in all cases Kruskal–Wallis, $P < 0.0001$). The analysis of niche breadth showed that nymphs (B_S : 0.22) have a higher site selection than larvae (B_S : 0.41) and adults (B_S : 0.56), and the interstadial niche overlap between adults and nymphs (O_{XY} : 0.70) was higher than the niche overlap between larvae and nymphs (O_{XY} : 0.43) and between larvae and adults (O_{XY} : 0.40). Larvae were principally found in areas III and V, nymphs in area IV and adults in areas I, II and IV (see Fig. 1; Table 3).

Discussion

When adult and immature ticks were grouped together, the analysis of the parasitism of *A. dubitatum* in a natural population of *H. hydrochaeris* showed high prevalence and abundance. However, the values of prevalence and median differed among larvae, nymphs and adults (Table 1), indicating that infestation parameters are properties of a tick stage, as suggested by Krasnov et al. (2007). Although parasite burdens are usually aggregated, their degree is not homogenous in all host-parasite associations (Shaw et al. 1998). Aggregation was lower for adults and nymphs of *A. dubitatum* than for larvae (see Table 1). The spatial

distribution of host-seeking parasites may be a dominant factor determining the subsequent distribution of parasites on hosts (Devevey and Brisson 2012). Randolph and Steele (1985) and Daniels and Fish (1990) (for *Ixodes ricinus* and *Ixodes scapularis*, respectively) have demonstrated that the distribution of larvae in the environment is more aggregated than in nymphs and adults. If the same fact occurs in the case of *A. dubitatum*, the differences in the degree of aggregation among tick stages reported in this study could be assigned to a differential rate of contact between *H. hydrochoeris* and each stage of *A. dubitatum*, which probably is higher for adults and nymphs than for larvae.

Sex differences in exposures and susceptibility to parasites contribute to sex-based differences in the intensity and prevalence of parasites. Some works showed that the levels of infestation are often higher in males than in females (Moore and Wilson 2002; Klein 2004; Krasnov et al. 2005; Rosá et al. 2006). The causes for such sex biases have been related to sexual size dimorphism, behavioural differences (e.g., physiological stress due to aggression in the breeding season, dispersal) and immunosuppressive effects associated to the levels of steroid hormones (Hughes and Randolph 2001; Moore and Wilson 2002; Klein 2004; Krasnov et al. 2005; Rosá et al. 2006). Sex-biased infestation rates were described for some species of hard ticks (Mooring et al. 1996; Hughes and Randolph 2001; Perkins et al. 2003; Aléssio et al. 2012; Lutermaun et al. 2012), but the findings of this study are in disagreement with those works. Differences in the levels of infestation with *A. dubitatum* were not found between males and females of *H. hydrochaeris*, in coincidence with Corriale et al. (2013). The analysis of the association *A. dubitatum*–*H. hydrochaeris* showed that sex is not good predictor of tick burdens, in correspondence with the conclusions reached by Brunner and Ostfeld (2008) and Beldoménico et al. (2005) after analyses of the parasitism of *I. scapularis* and *Ixodes loricatus* on small-mammal hosts, respectively. Thus, it can be concluded that sex-biased infestation rates is not an ubiquitous phenomenon in the case of hard ticks.

One of the objectives of this work was to test whether parameters such as body condition or body mass of the hosts have association with larger parasite loads. Hosts in poor condition would have higher susceptibility because they have fewer resources for defense (Jokela et al. 2000; Krist et al. 2004). Besides body condition, host body size may also influence the parasite burdens (Krasnov et al. 2004; Poulin and George-Nascimento 2007; Brunner and Ostfeld 2008; Patterson et al. 2008). In this study, host body condition and host body mass were not found to correlate with the number of *A. dubitatum* ticks, which is in coincidence with Corriale et al. (2013). In spite of previous assumptions, the empirical evidence (Krasnov et al. 2004; Krist et al. 2004; Patterson et al. 2008; Eberhardt et al. 2013; this work) shows that poor condition or body size of the host and intensity of the infestation with macroparasites are not always directly related.

The analysis of anatomical distribution showed that nymphs of *A. dubitatum* were more segregated spatially on the host body than larvae and adults, but a high value of niche overlap (0.70) was found between adults and nymphs, indicating that these stages are characterized by a similar microhabitat usage. According with the results of this work, larvae of *A. dubitatum* prefer to attach on areas III and V, nymphs on area IV and adults on areas I, II and IV, although it is important to keep in mind that the three stages were found in the five sites. The niche breadth of larvae and nymphs of *A. dubitatum* were narrower than that of adults, in coincidence with the results obtained by Kiffner et al. (2011) in a study on *I. ricinus* associated to the deer *Capreolus capreolus*. The preference for some body parts for the extraction of a resource (in this case, blood), intra- and interspecific competition, host behavioural defences and skin thickness of the host, are among the most important factors influencing the anatomical distribution of a parasite on its host (Kiffner

et al. 2011; Pilosof et al. 2012). In order to complement this analysis, experimental studies are needed to determine with certainty which are the factors with influence on spatial segregation of larvae and nymphs of *A. dubitatum* on *H. hydrochaeris*.

The association of *A. dubitatum* with *H. hydrochaeris* was characterized by high values of prevalence and abundance and a lack of relationship among individual attributes of the host (sex and corporal condition) and parasite loads. Furthermore, the differences in the degree of aggregation are probably related to the spatial distribution of host-seeking ticks in the environment and not to the inter-individual differences within host population. A large number of specimens of *H. hydrochaeris* are present in the area where this investigation was carried out. Therefore, the factors associated to the host which determine the high levels of infestation with *A. dubitatum* in *H. hydrochaeris* populations could be assigned to a combination of population-level properties as abundance, ubiquity and aggregation, rather than individual specific attributes related to body condition, body mass or sex.

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