A meta-analysis of host specificity in Neotropical hard ticks (Acari: Ixodidae)

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Abstract

Host specificity of Neotropical hard ticks (Acari: Ixodidae) was analyzed by using the number of hosts species for each tick species and the index of host specificity S_{TD}*, which integrates phylogenetic and ecological information. The analyses were based on 4172 records of hard ticks collected from wild and domestic tetrapods. Most tick species included in this study were associated with three to 20 host species. No tick species has been associated either with a single species or with a single genus of host. It was found that the number of host species is sensitive to sampling effort, but not the S_{TD}*. The most frequent values of S_{TD}* were between 2.5 and 3.5, which shows that the host species more frequently used by Neotropical hard tick species belong to different families or different orders. Immature stages tend to use a broader taxonomic range of hosts than adults, and the interpretation of both measures of host specificity used in this study led to the conclusion that the impact of non-endemic hosts does not alter the patterns of host specificity in Neotropical hard ticks. The index S_{TD}* showed that a high proportion of tick species has phylogenetically unrelated species as principal hosts. The conclusion reached in this work indicates that strict host specificity is not common among Neotropical hard ticks and suggests that the influence of tick ecology and evolution of habitat specificity, tick generation time, phenology, time spent off the host and the type of life-cycle could be more important than hosts species.

Introduction

One of the most important properties characterizing a parasite taxon is its host specificity. It is indicative of intrinsic biological characteristics of both host and parasite and an emergent property of their ecological and evolutionary relationship (Dick & Patterson, 2007). Host specificity can be defined as the extent to which a parasite taxon is restricted in the number of host species used at a given stage in the life cycle (Poulin, 2007). Thus, highly host-specific parasites have one host species, and specificity declines as the number of suitable

host species increases (Poulin, 2007). The parasite-host association has been focused from two perspectives, the host centred view (the focus of coevolution is the host species) and the parasite-centred view (the resources for parasites are attributes of the host species, not the host species themselves) (Brooks & McLennan, 1993; Fenton & Pedersen, 2005; Brooks & Hoberg, 2007). The biological significance of these two visions lies in the frequency of host-switch events, which determines the host range and potential distribution of a parasite species. Host switching results in low host specificity because a parasite colonizes host lineages related or unrelated to its original host (Poulin, 2007). A parasite interacts with its host (physiology, immunity, ecology, phylogeny, size) but also with the environment. The external environment in which parasite and host interact can affect the strength and the evolution of the host-parasite interaction (Krasnov *et al.*, 2008,

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2010; Wolinska & King, 2009). Therefore, the degree of host specificity of a parasite and its variation in time and space not only are functions of intrinsic properties of host and parasite but also depends on external environmental conditions.

Hard ticks (Acari: Ixodidae) are haematophagous ecto-parasites of amphibians, reptiles, birds and mammals, and they are divided into Prostriata (genus *Ixodes*) and Meta-striata (genera *Amblyomma, Anomalohimalaya, Bothriocroton, Compluriscutula†, Cornupalpatum†, Cosmiomma, Dermacentor, Haemaphysalis, Hyalomma, Margaropus, Nosomma, Rhipicentor, Rhipicephalus*) (genera are listed according to Guglielmone *et al.*, 2010). The life cycle of hard ticks encompasses parasitic and non-parasitic phases. In the former, larvae, nymphs and adults feed or mate on the host (members of Prostriata and a few species of *Amblyomma* and *Bothriocroton* have adults with ability to mate off host). However, hard ticks spend most of their life cycle off host, exposed to environmental conditions. In three-host cycle species, the non-parasitic phase includes important biological processes, such as moulting of engorged larvae and nymphs, oviposition of engorged females, incu-bation of eggs and host-seeking of all parasitic stages. Some ticks have a two-host or a one-host life cycle (i.e. species of the genera *Rhipicephalus, Hyalomma, Dermacentor* and *Margaropus*), where larvae or both nymphs and larvae moult on the host, respectively. Overall, it is evident that the life cycle of hard ticks is strongly influenced by both host and environmental factors.

Two contrasting hypotheses have been developed about host specificity in ticks. The first assumes that host specialis-ation was instrumental in the evolution of ticks and of their morphological characters (Hoogstraal, 1978; Hoogstraal & Aeschlimann, 1982; Hoogstraal & Kim, 1985) and is based on the idea of coevolution between ticks and terrestrial tetrapods. These authors state that phenotypic variations in mouthparts and coxae are the result of adaptation to a particular group of hosts, which lead to a high host specificity. Furthermore, Hoogstraal & Aeschlimann (1982) presented a classification system with six categories characterized by decreasing levels of host-specificity, namely: (i) strict-total, (ii) moderate-total, (iii) strict-stage-stage, (iv) strict/moderate-stage-stage, (v) moderate-stage-stage and (vi) nonparticular. Klompen *et al.* (1996) raised an alternative hypothesis that stresses the importance of ecological specificity. According to this opinion, adaptation to a particular habitat is more relevant for tick evolution than adaptation to a particular host. Klompen *et al.* (1996) found a strong positive correlation between the total number of collections and the number of hosts, through an analysis using data from ixodid (*Ixodes*) and argasid (*Carios*) collections, and they concluded that "much of the distinction between strict-total and less-specific categories might be the difference between rarely and frequently collected species". Additionally, Klompen *et al.* (1996) criticized the lack of differentiation between the processes of adaptation and speciation in the Hoogstraal's studies. Klompen *et al.* (1996) stated that "although the presence of host adaptations may lead to host specificity, observed host specificity is not necessarily an indicator of host adaptation. Host specificity may also arise because of no opportunity to transfer to alternative hosts (which secondarily may result in cospecia-tion) or as a secondary effect of adaptation to off-host habitat". In the same way, Balashov (2004) rejected the idea of coevolution as a key factor in the evolution of ticks affirming that "phylogenetic parallelism between ticks and their hosts is absent or limited to short evolutionary periods". After the

analysis of a large data set of African ticks, Cumming (1998) reached a conclusion that can be interpreted as intermediate between the two aforementioned hypotheses. This author suggested that both host specificity and ecological specificity could be important and that it depends on each particular tick species. However, in a subsequent analysis on limiting factors for species ranges of African ticks, Cumming (2002) concluded that the distribution of ticks over a wide spatial scale is mainly determined by direct climatic effects, while hosts only generate heterogeneity in tick distribution at a smaller geographical scale.

In a broad sense, the host specificity of a parasite is quantified as the number of hosts species, or host range. The number of host species in itself is not informative because it implies that a parasite uses each host species equally. However, the utilization of a spectrum of host species by a given parasite is typically uneven. In fact, from an ecological perspective, some host species are used more intensively than others; and, from a phylogenetic perspective, some host species used by a parasite can be phylogenetically more closely related than others (Poulin *et al.*, 2006; Poulin, 2007). Therefore, an attempt at evaluating the importance of host specificity must take into account all these aspects. In this work, a meta-analysis of host specificity in Neotropical hard ticks was performed. The number of hosts for each tick species and the index of host specificity (index S_{TD}^*) proposed by Poulin & Mouillot (2005), which integrates phylogenetic and ecological information, were applied to the analysis. In addition, the two values were generated separately for adult and immature stages in order to investigate possible onto-genetic changes in host specificity, and the role of domestic animals in determining host specificity was also analyzed.

Materials and methods

The data set used in this study was obtained from a list of host records for all species of Neotropical ticks compiled from the literature (scientific papers, book sections and selected meeting proceedings) by one of us (AAG). The list is available under request. A record is defined as the finding of a tick species, on a determined host, and at a given locality, regardless of the number of host sampled and of ticks collected on a particular host. Findings on the same species of host and at the same locality, but on different dates, are each considered separate records. Only references that include tick stage, locality and scientific name of the host were considered, and tick species with less than 15 records were not included in the analysis. Records of immature stages made before the description of larva and nymph of the corresponding tick species became available were excluded. Exceptions were made for those references where the taxonomic determination method was explained (e.g. immature ticks identified to species after rearing the ticks to the adult stage in the lab-oratory or by using molecular tools). Records from humans, from hosts kept in captivity (laboratories, zoos, etc.) and from imported animals were not considered. When necessary, scientific names of mammal hosts have been updated following Wilson & Reeder (2005), Weksler *et al.* (2006) (for oryzomyne rodents), Voss & Jansa (2009) (for marsupials), Barquez *et al.* 2006 (for Felidae and Tayassuidae) and Francés & D'Elía (2006) and D'Elía *et al.* (2008) for some synonymized sigmodontine rodents. Scientific names of birds were taken from Clements (2007), and the nomenclature of amphibians and reptiles was the same chosen in Guglielmone & Nava

(2010). *Rhipicephalus* (*Boophilus*) *microplus* and the *Rhipicephalus sanguineus* species group were not considered in this work because they have a wide world distribution, and both taxa were recently introduced in the Neotropical region (approximately 400 years ago); therefore, an accurate analysis of their host-association should include records of other biogeographic regions. The list of host species recorded for each tick species is shown in the supplementary appendix 1.

The specificity index S_{TD}^* proposed by Poulin & Mouillot (2005) was calculated for each hard tick species. This index measures the average taxonomic distinctness of all host species used by a parasite, weighted by the prevalence of the parasite in the different hosts (Poulin & Mouillot, 2005). Because of the lack of data on prevalence in most tick-host associations cited in the literature, we calculated instead, for each tick species, the proportion of records corresponding to each host species. It is obvious that the proportion of records is less informative than prevalence because it increases the risk of biases associated with differential sampling efforts. Another caveat to keep in mind is that presence of a representative of a given tick species on a given host does not mean this host is competent to sustain tick development and reproduction. The index S_{TD}^* places hosts within the Linnean taxonomic hierarchy (phylum, class, order, family, genera, species). Taxonomic distinctness between two host species represents the mean number of steps up the taxonomic hierarchy that must be taken to reach a taxon common to both (for example: when two host species are congeners, one step species-to-genus is necessary to reach a common node; if two host species belong to different genera but are included in the same family, two steps species-to-genus and genus-to-family are necessary) (Poulin & Mouillot, 2005). This value is weighted by the product of the parasite prevalence (in this work, proportion of records). The value of this index is inversely proportional to specificity. A high index value means that the host species more frequently used by a parasite are not closely related (Poulin & Mouillot, 2005). In absence of differences in the proportion values, the index S_{TD}^* reaches its maximum value (5) when all host species belong to different classes, whereas it tends towards its minimum value (1) when all hosts belong to a same genus. Index S_{TD}^* was calculated with a computer program developed by Poulin & Mouillot (2005) using Borland C++ Builder 6.0 (available online at http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv2). The classifications used to place each host species within the correct classes, orders and families were Wilson & Reeder (2005) for class Mammalia, Clements (2007) for class Aves and Guglielmone & Nava (2010) for classes Reptilia and Amphibia.

A Pearson's correlation analysis was performed to assess the extent of co-variation between number of records of each tick species and number of host species and between number of records and S_{TD}^* values. The statistical significance of the differences in S_{TD}^* values between the samples which included domestic hosts and samples which excluded them was determined through a Student's *t*-test. The significance of the differences in number of host species between adult and immature stages was tested with a Mann-Whitney *U* test, while the significance of the differences in S_{TD}^* values between adult and immature stages was evaluated with a Student's *t*-test.

Results

A total of 4172 records of hard ticks (species of the genera *Amblyomma*, *Dermacentor*, *Haemaphysalis*, and *Ixodes*) collected from wild and domestic tetrapods were obtained. The data included 41 tick species for adult specimens (3007 records) and 22 for immature stages (1165 records) (table 1). Of the 4172 records, 1012 (24.2%) were from domestic mammals (cattle, goat, sheep, pig, horse, donkey, mule, dog, cat) and corresponded to adults of 22 tick species and immature stages of nine tick species. Number of host species, number of records and values of S_{TD}^* (calculated with and without domestic hosts) for each tick species are shown in table 1. In the cases where domestic hosts were excluded from the analysis, the difference in the values of S_{TD}^* for each species was not significant (see table 1) when the sample was analyzed as a whole ($P = 0.28$, Student's *t*-test).

The distribution of number of host species was skewed for adults (fig. 1a), for immature ticks (fig. 1b) and also when immature and adults were grouped (fig. 1c). The figures clearly show that most tick species in this study parasitize between three and 20 different host species. No tick species has been associated either with a single species or with a single host genus. The mean number of hosts differed significantly ($P = 0.002$, Mann-Whitney *U* test) between adults (mean = 12.56; median = 8; range = 3–49) and immatures (mean = 21.72; median = 15; range = 5–90). The frequency distribution of S_{TD}^* values are shown in fig. 2a for adults, in fig. 2b for immatures, and in fig. 2c for adults and immatures together. The most frequent values of S_{TD}^* were between 2.5 and 3.5. The average values of S_{TD}^* for adults and immatures were 2.78 (median = 2.71; range = 1.13–4.58) and 3.32 (median = 3.31; range = 2.02–4.39), respectively ($P = 0.001$, Student's *t*-test). A significant positive correlation between number of host species and number of records was found ($r = 0.64$; $P \leq 0.0001$) (fig. 3a). Conversely, there was no correlation of S_{TD}^* ($r = 0.19$; $P = 0.12$) with the number of records (fig. 3b). This absence of covariation indicates that S_{TD}^*, unlike the number of host species, is far less sensitive to sampling effort.

Discussion

This is the first attempt to describe general patterns of host specificity in Neotropical hard ticks through a quantitative approach. Although sometimes limited by incomplete data or lack of samples, in this study we generated a large database. We found a positive correlation between number of host species and number of records, which is in agreement with the findings reported by other authors for ticks (Klompen *et al.*, 1996) and for other parasites (Poulin, 1992; Walther *et al.*, 1995; Guégan & Kennedy, 1996; Walther & Morand, 1998). Therefore, the number of host species used by a particular tick species cannot be used as indicator of host specificity, because it can be an artefact caused by different sampling efforts. The index S_{TD}^*, however, appears to be largely independent from sampling effort. Most tick species showed values of S_{TD}^* ranging between 2.5 and 3.5, with an average close to 3 (table 1, fig. 2). These results show that, in general, an elevated proportion of tick species feeds on hosts that belong to different families or different orders. Naturally, some tick species are characterized by higher host specificity (S_{TD}^* values between 1.13 and 2) (see table 1). However, none of them parasitize a single host species. When the analyses of number of hosts species and S_{TD}^* in adult and immature specimens were performed separately, both measures were significantly higher for immatures than for adults, which suggests that immature stages tend to use a broader taxonomic range of hosts than adults. Two hypotheses can be stated for

Table 1. Number of host species and values of the specificity index $S_{TD}*$ proposed by Poulin & Mouillot (2005) (calculated with and without domestic hosts) for the species of Neotropical hard ticks included in this study.

Tick species	No. of hosts species	No. of records	$S_{TD}*$	$S_{TD}*$ excluding domestic hosts
ADULTS				
Amblyomma albopictum	6	23	1.80	NA
Amblyomma argentinae	8	61	3.81	NA
Amblyomma aureolatum	20	152	3.04	3.31
Amblyomma auricularium	24	60	2.68	2.69
*Amblyomma cajennense**	44	219	3.77	3.80
Amblyomma calcaratum	8	44	2.60	NA
Amblyomma coelebs	8	45	2.61	2.27
Amblyomma dissimile	49	231	3.48	3.41
Amblyomma dubitatum	5	76	2.99	2.97
Amblyomma fuscum	6	16	4.58	NA
Amblyomma geayi	6	37	3.40	NA
Amblyomma humerale	3	98	1.7	NA
Amblyomma incisum	3	92	1.82	NA
Amblyomma longirostre	14	70	1.99	1.93
Amblyomma naponense	8	33	2.47	NA
Amblyomma neumanni	12	150	3.58	3.57
Amblyomma nodosum	3	31	2.31	NA
Amblyomma oblongoguttatum	19	43	3.59	3.72
Amblyomma ovale	33	152	3.40	3.29
Amblyomma pacae	6	40	2.76	2.75
Amblyomma parkeri	3	19	1.67	NA
Amblyomma parvitarsum	3	19	2.20	2
Amblyomma parvum	33	330	3.64	3.65
Amblyomma pecarium	3	19	1.41	NA
Amblyomma pseudoconcolor	12	35	2.54	2.43
Amblyomma pseudoparvum	8	38	2.88	2.74
Amblyomma quadricavum	3	17	2.53	NA
Amblyomma rotundatum	38	123	3.53	3.51
Amblyomma sabanerae	4	30	1.13	NA
Amblyomma scalpturatum	4	63	1.40	NA
Amblyomma tigrinum	15	117	2.50	2.69
Amblyomma triste	15	45	3.65	3.62
Amblyomma varium	4	62	1.73	NA
Dermacentor nitens	11	117	2.31	**
Haemaphysalis juxtakochi	15	57	2.87	2.42
Haemaphysalis leporispalustris	4	29	1.84	NA
Ixodes auritulus	23	25	3.55	NA
Ixodes boliviensis	10	19	3.50	3.29
Ixodes loricatus	10	82	1.84	NA
Ixodes luciae	8	60	1.85	NA
Ixodes pararicinus	4	28	3.28	2
IMMATURE				
Amblyomma aureolatum	20	75	2.79	2.57
*Amblyomma cajennense**	47	178	4.06	4.03
Amblyomma coelebs	12	16	4.39	4.44
Amblyomma dissimile	24	50	3.87	3.83
Amblyomma dubitatum	12	41	2.56	2.54
Amblyomma longirostre	90	140	3.30	NA
Amblyomma neumanni	12	77	3.61	3.57
Amblyomma nodosum	19	19	3.42	NA
Amblyomma ovale	18	30	3.87	3.74
Amblyomma parvum	11	22	3.04	3.12
Amblyomma rotundatum	13	24	3.34	NA
Amblyomma tigrinum	45	161	3.86	NA
Amblyomma triste	15	31	2.94	NA
Dermacentor nitens	5	59	2.73	***
Haemaphysalis juxtakochi	15	25	4.21	NA
Haemaphysalis leporispalustris	10	23	3.67	NA
Ixodes auritulus	42	53	3.26	NA
Ixodes longiscutatus	8	19	2.31	NA
Ixodes loricatus	15	35	3.02	NA
Ixodes luciae	20	42	3.05	NA
Ixodes pararicinus	13	17	3.99	NA
Ixodes sigelos	12	28	2.02	NA

NA, not applicable.
* Recent studies suggested that *Amblyomma cajennense* is a species complex (Labruna *et al.*, 2011; Mastropaolo *et al.*, 2011).
** Because 89% of the records of adults of *D. nitens* were made on domestic animals, the analysis excluding domestic animals is unjustified.
*** Because 87% of the records of immature stages of *D. nitens* were made on domestic animals, the analysis excluding domestic animals is unjustified.
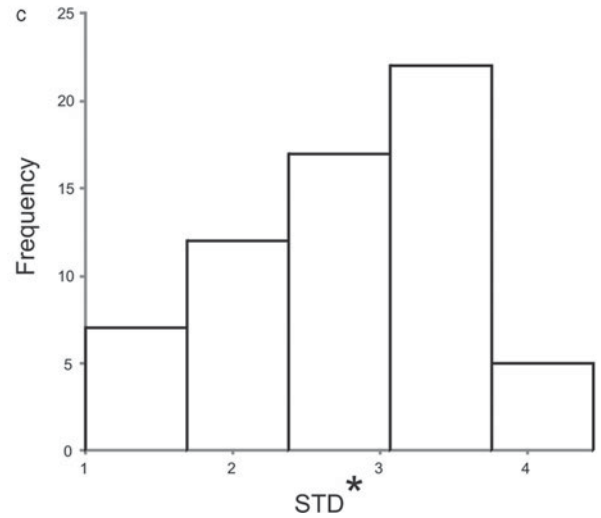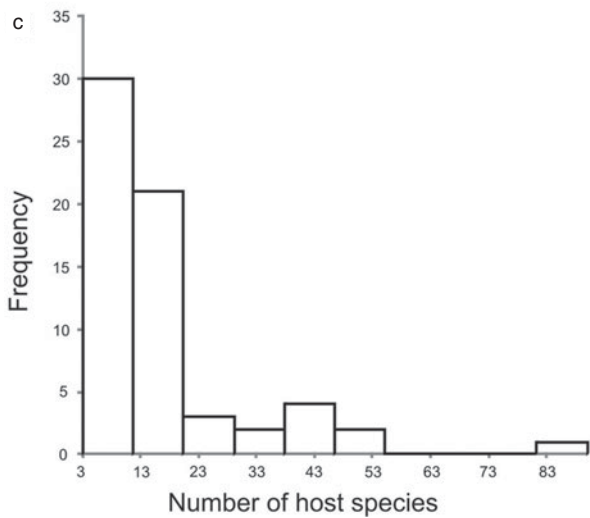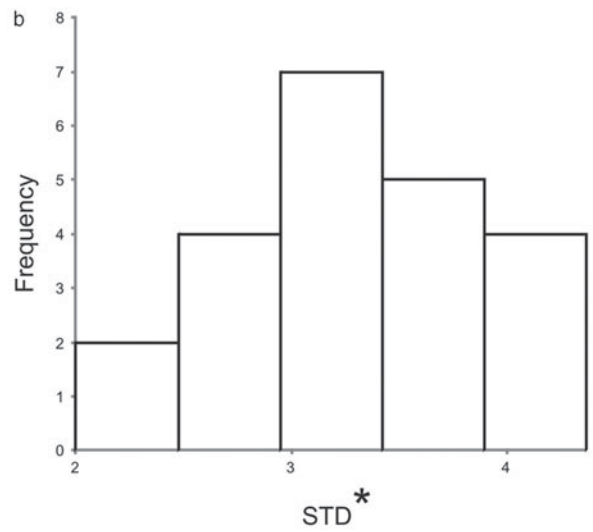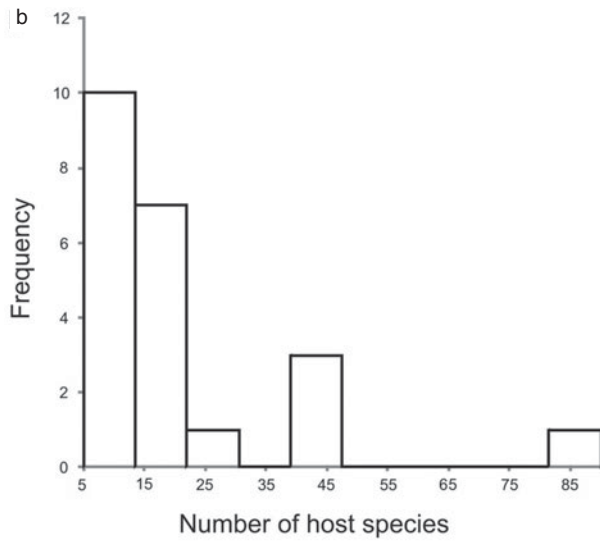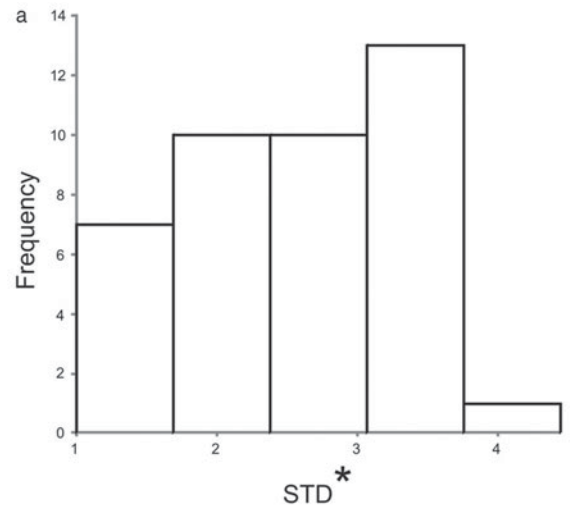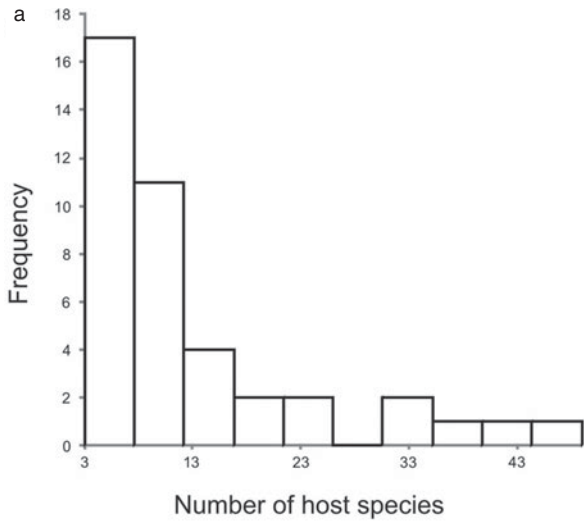
Fig. 1. Frequency distribution of number of host species among species of Neotropical hard ticks: (a) adults, (b) immature and (c) adults and immature grouped together.

Fig. 2. Frequency distribution of S_{TD}* values among species of Neotropical hard ticks: (a) adults, (b) immature and (c) adults and immature grouped together.
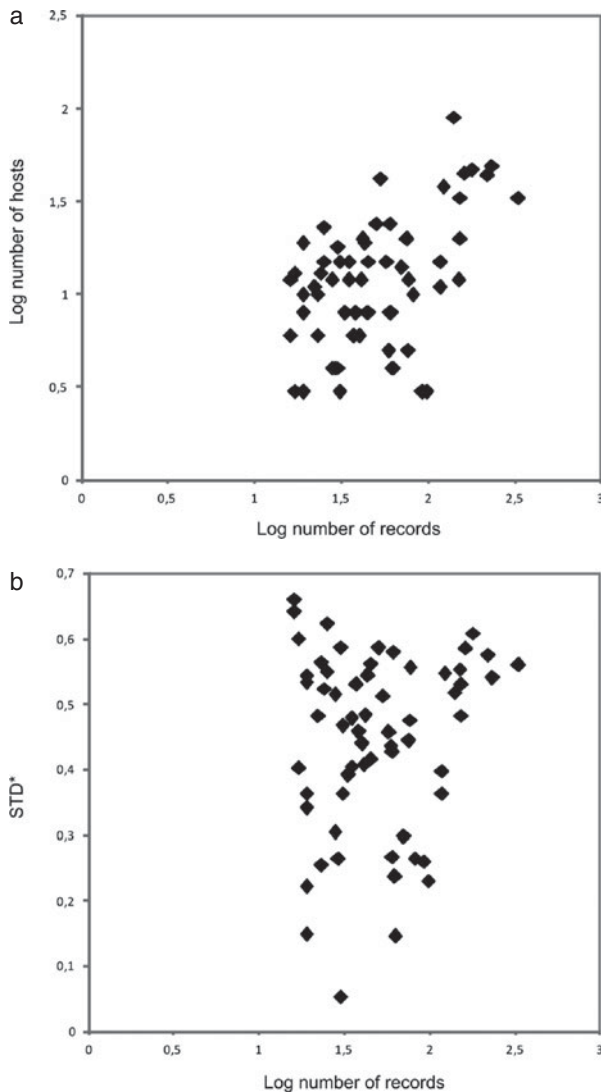
Fig. 3. Relationship between the number of records of each tick species included in this study and the number of (a) host species and (b) S_{TD}^* value per tick species (Pearson's correlation analysis).

these results. One of them is related to a physiological involvement, where larvae and nymphs may have greater adaptive plasticity than adults to feed on different host species. The other hypothesis is based on the number of host species available. If adult stages generally feed on hosts with larger body size (a fairly well-established trend), the number of host species available for those instars should be lower, given that there are relatively more small-bodied than large-bodied host species in most environments.

Approximately 24% of the records were from domestic mammals, but the variation in S_{TD}^* was statistically insignificant when domestic hosts were excluded from the analysis (see table 1). The capacity of some domestic mammals to totally or partially sustain the life cycle of endemic tick species is well known, as in the cases, for instance, of *Amblyomma tigrinum*, *Amblyomma aureolatum*, *Amblyomma parvum*, *Amblyomma neumanni* and *Amblyomma triste* (Guglielmone

et al., 2000; Pinter *et al.*, 2004; Nava *et al.*, 2008, 2009, 2011). Although this fact highlights the ability of some tick species for rapid adaptation to recently introduced host species, the impact of non-endemic hosts on the ecology of native ticks does not alter the patterns of host specificity.

The application of index S_{TD}^* to quantify host specificity in Neotropical hard ticks shows that a high proportion of ticks feed on phylogenetically distant host species. Similarities must be sought in other host characteristics, such as morphology, physiology or habitat usage, which appear to be more relevant. It has been established for other parasite taxa (e.g. helminthes of fishes, fleas of small mammals) that ecological similarity among host species is more important than host phylogeny (Poulin, 2005; Krasnov *et al.*, 2007) and that external environmental factors may play a key role in the evolution of host-parasite associations (Krasnov *et al.*, 2010). These conclusions are in agreement with the concept of ecological fitting, a process where organisms form a novel association with other species or use novel resources by ecological readjustment unrelated to previous evolutionary history, as a result of the suites of traits that they carry at the time they encounter the novel condition (Janzen, 1985; Agosta & Klemens, 2008). Ecological fitting is applicable to parasites when these can exploit a specific type of resource that is distributed across different host species (Brooks *et al.*, 2006a,b). In these cases, the main requirement for the parasite is the resource itself, not the way that resource is packaged (the host species) (Brooks *et al.*, 2006b). Support for ecological fitting in systems that involve parasites and hosts emerges from ecological and macroevolutionary evidence (Kethley & Johnston, 1975; Hoberg & Brooks, 2008; Kelly *et al.*, 2009; Agosta *et al.*, 2010). Following this concept, the association of a tick species with its hosts may be primarily determined by the environment occupied by an assemblage of suitable hosts, regardless of host phylogenetic relatedness. Host associations of larvae and nymphs of *Ixodes loricatus* and *Ixodes luciae* clearly illustrate ecological fitting. Small rodents (Cricetidae: Sigmodontinae) and marsupials (Didelphidae) are the principal hosts for immature stages of these two ticks (Guglielmone & Nava, 2011). Sigmodontine rodents and didelphids occupy the same ecological niche, but they are not phylogenetically related and have different evolutionary histories. The diversification of marsupials of the family Didelphidae in South America probably occurred between the Oligocene and Miocene (Steiner *et al.*, 2005), while sigmodontines appeared on the continent only in the Pliocene (Pardiñas *et al.*, 2010). This example, which could be applied to other tick species in this study, highlights the key role played by host ecological similarities in shaping host-parasite relationships in ticks. Also, our conclusions reject the hypothesis that coevolution was relevant in determining present tick-host associations, stressing the significance of host switching events during tick evolutionary history.

The widespread use of laboratory animals in experimental studies on life cycles or reproductive barriers is another issue that reinforces the idea of ticks as parasites with low host specificity. Hosts, such as rabbits (*Oryctolagus cuniculus*), guinea pigs (*Cavia porcellus*), chickens (*Gallus gallus*), rats (*Rattus norvegicus*), mice (*Mus musculus*), dogs (*Canis familiaris*), domestic pigs (*Sus scrofa*), horses (*Equus caballus*), among others, were successfully utilized to feed a wide spectrum of ticks under laboratory conditions. Some examples of this type of study in Neotropical hard ticks include the life cycle of *Amblyomma auricularium*, *Amblyomma incisum*, *A. triste*, *A. tigrinum*, *A. aureolatum*, *A. parvum*, *A. neumanni*, *Amblyomma*

brasiliense, *Amblyomma pseudoconcolor*, *Haemaphysalis leporispalustris* and *I. loricatus* (Guglielmone *et al.*, 1991; Aguirre *et al.*, 1999; Labruna *et al.*, 2000, 2002, 2003; Schumaker *et al.*, 2000; Chacon *et al.*, 2004; Pinter *et al.*, 2004; Sanches *et al.*, 2008; Szabó *et al.*, 2009; Faccini *et al.*, 2010; Olegário *et al.*, 2011). Cross-mating trials to elucidate reproductive barriers between *Amblyomma pseudoparvum* and *A. parvum*, and among the members of the *Amblyomma cajennense* species complex, were carried out using rabbits as hosts (Guglielmone & Mangold, 1993; Labruna *et al.*, 2011; Mastropaolo *et al.*, 2011). These examples show the physiological plasticity exhibited by ticks to feed successfully when they are exposed to a novel host not related to the natural hosts.

The results of this investigation provide evidence that supports the hypothesis of Klompen *et al.* (1996) that ticks are habitat- rather than host-specialists. When one considers that hard ticks spend most of their life cycle off host, this conclusion is not unexpected. However, and regardless of habitat specificity, other variables, such as size, parasite generation time, phenology, time spent off host and the type of life-cycle (three-, two- or one-host), should be considered for future studies, as they are factors which can influence tick host associations.

By using two measures of host specificity, we describe a general pattern based on a restricted data set pertaining to specific region of the world (Neotropical region). We do not pretend that our conclusions will be applicable everywhere else. Local adaptations or the size of the geographical range of a parasite species may cause intraspecific variations in host specificity across its distribution (Kaltz & Shykoff, 1998; Jackson & Tinsley, 2005; Krasnov *et al.*, 2005, 2011; Morgan *et al.*, 2005; Gandon *et al.*, 2008), and these variables should also be included in future analyses. Similarly, it would be interesting to evaluate the levels of fitness achieved by a particular tick species after feeding on different hosts species, through the measurement of biological parameters. Nevertheless, the evidence presented in this work shows that strict host specificity is not common among hard ticks.

Acknowledgements

Supplementary material

The online appendix can be viewed at http://journals.cambridge.org/ber.

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