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

S. Nava* and A.A. Guglielmone
Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Rafaela and Consejo Nacional de Investigaciones Científicas y Técnicas, CC 22, CP 2300 Rafaela, Santa Fe, Argentina

Abstract

Host specificity of Neotropical hard ticks (Acari: Ixodidae) was analyzed by using the number of host 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.

Keywords: ticks, Ixodidae, host specificity, Neotropical region

(Accepted 3 July 2012; First published online 7 September 2012)

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,
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 ectoparasites of amphibians, reptiles, birds and mammals, and they are divided into Prostriata (genus Ixodes) and Meta-

Strict-total and less-specific categories might be the basis for comparing the number of collections, and they concluded that

Compluriscutula, Amblyomma, Anomalohimalaya, Bothriocroton, Compluriscutula, Corulaplatunur, Cosmiomma, Dermacentor, Haemaphysalis, Hyalomma, Margaropus, Nosomma, Rhipicentor, Rhipicephalus) are genera 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 moult of engorged larvae and nymphs, oviposition of engorged females, incubation of eggs and host-seeking of all parasitic stages. Some ticks have a two-host or 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 specialisation 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 “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 cospeciation) 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 STD*) 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 ontogenetic 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 laboratory 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 oryzomyine rodents), Voss & Jansa (2009) (for marsupials), Barquez et al. 2006 (for Felidae and Tayassuidae) and Francés & D’Elia (2006) and D’Elia 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
proportion values, the index STD* reaches its maximum value
records). The value of this index is inversely proportional to
product of the parasite prevalence (in this work, proportion of
tends towards its minimum value (1) when all hosts belong to
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
caution 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
important to sustain tick development and reproduction. The
index STD* 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
differ 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 STD* 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 STD* 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/zooology/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 STD* values. The statistical significance of the
differences in STD* 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 STD* 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 STD* (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 STD* 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 with a single species or with a single host
genus. The mean number of hosts differed significantly
(mean= 12.56; mean= 8; range= 349) and immatures (mean= 21.72;
mean= 15; range= 5-90). The frequency distribution of STD* 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 STD* were between 2.5 and 3.5. The average
values of STD* 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=0.0001) (fig. 3a).
 Conversely, there was no correlation of STD* with the number of records (fig. 3b). This absence of
covariation indicates that STD*, 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.,
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 STD*, however, appears to be largely
independent from sampling effort. Most tick species showed
values of STD* ranging between 2.5 and 3.5, with an average
close to 3 (table 1, fig. 2). These results show that, in general,
a raised 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 (STD* 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 STD* 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.

<table>
<thead>
<tr>
<th>Tick species</th>
<th>No. of hosts species</th>
<th>No. of records</th>
<th>$S_{TD}^*$</th>
<th>$S_{TD}^*$ excluding domestic hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ADULTS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Amblyomma albopictum</em></td>
<td>6</td>
<td>23</td>
<td>1.80</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma argentinae</em></td>
<td>8</td>
<td>61</td>
<td>3.81</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma aureolatum</em></td>
<td>20</td>
<td>152</td>
<td>2.68</td>
<td>2.69</td>
</tr>
<tr>
<td><em>Amblyomma auricularium</em></td>
<td>24</td>
<td>60</td>
<td>3.77</td>
<td>3.80</td>
</tr>
<tr>
<td><em>Amblyomma cajennense</em></td>
<td>44</td>
<td>219</td>
<td>2.60</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma calcaratum</em></td>
<td>8</td>
<td>44</td>
<td>2.61</td>
<td>2.27</td>
</tr>
<tr>
<td><em>Amblyomma coelebs</em></td>
<td>49</td>
<td>231</td>
<td>3.48</td>
<td>3.41</td>
</tr>
<tr>
<td><em>Amblyomma dubitatum</em></td>
<td>5</td>
<td>76</td>
<td>2.99</td>
<td>2.97</td>
</tr>
<tr>
<td><em>Amblyomma fuscin</em></td>
<td>6</td>
<td>16</td>
<td>4.58</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma gigui</em></td>
<td>6</td>
<td>37</td>
<td>3.40</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma hemerale</em></td>
<td>3</td>
<td>98</td>
<td>1.7</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma incisum</em></td>
<td>3</td>
<td>92</td>
<td>1.82</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma longirostre</em></td>
<td>14</td>
<td>70</td>
<td>1.99</td>
<td>1.93</td>
</tr>
<tr>
<td><em>Amblyomma naponense</em></td>
<td>8</td>
<td>33</td>
<td>2.47</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma neumanni</em></td>
<td>12</td>
<td>150</td>
<td>3.58</td>
<td>3.57</td>
</tr>
<tr>
<td><em>Amblyomma nulosum</em></td>
<td>3</td>
<td>31</td>
<td>2.31</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma oblongoguttatum</em></td>
<td>19</td>
<td>43</td>
<td>3.59</td>
<td>3.72</td>
</tr>
<tr>
<td><em>Amblyomma ovale</em></td>
<td>33</td>
<td>152</td>
<td>3.40</td>
<td>3.29</td>
</tr>
<tr>
<td><em>Amblyomma paca</em></td>
<td>6</td>
<td>40</td>
<td>2.76</td>
<td>2.75</td>
</tr>
<tr>
<td><em>Amblyomma parkeri</em></td>
<td>3</td>
<td>19</td>
<td>1.67</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma parvilarum</em></td>
<td>3</td>
<td>19</td>
<td>2.20</td>
<td>2</td>
</tr>
<tr>
<td><em>Amblyomma parvum</em></td>
<td>33</td>
<td>330</td>
<td>3.64</td>
<td>3.65</td>
</tr>
<tr>
<td><em>Amblyomma pecarium</em></td>
<td>3</td>
<td>19</td>
<td>1.41</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma pseudoconcolor</em></td>
<td>12</td>
<td>35</td>
<td>2.54</td>
<td>2.43</td>
</tr>
<tr>
<td><em>Amblyomma pseudoparvum</em></td>
<td>8</td>
<td>38</td>
<td>2.88</td>
<td>2.74</td>
</tr>
<tr>
<td><em>Amblyomma quadriracum</em></td>
<td>3</td>
<td>17</td>
<td>2.53</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma rotundatum</em></td>
<td>38</td>
<td>123</td>
<td>3.53</td>
<td>3.51</td>
</tr>
<tr>
<td><em>Amblyomma sabaneae</em></td>
<td>4</td>
<td>30</td>
<td>1.13</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma sculpuratum</em></td>
<td>4</td>
<td>63</td>
<td>1.40</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma tigrinum</em></td>
<td>15</td>
<td>117</td>
<td>2.50</td>
<td>2.69</td>
</tr>
<tr>
<td><em>Amblyomma triste</em></td>
<td>15</td>
<td>45</td>
<td>3.65</td>
<td>3.62</td>
</tr>
<tr>
<td><em>Amblyomma varium</em></td>
<td>4</td>
<td>62</td>
<td>1.73</td>
<td>NA</td>
</tr>
<tr>
<td><em>Dermacentor nitens</em></td>
<td>11</td>
<td>117</td>
<td>2.31</td>
<td>**</td>
</tr>
<tr>
<td><em>Haemaphysalis juxtakochi</em></td>
<td>15</td>
<td>57</td>
<td>2.87</td>
<td>2.42</td>
</tr>
<tr>
<td><em>Haemaphysalis leporispalustris</em></td>
<td>4</td>
<td>29</td>
<td>1.84</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes auritulus</em></td>
<td>23</td>
<td>25</td>
<td>3.55</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes boliviensis</em></td>
<td>10</td>
<td>19</td>
<td>3.50</td>
<td>3.29</td>
</tr>
<tr>
<td><em>Ixodes loericatus</em></td>
<td>10</td>
<td>82</td>
<td>1.84</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes luciae</em></td>
<td>8</td>
<td>60</td>
<td>1.85</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes paranicus</em></td>
<td>4</td>
<td>28</td>
<td>3.28</td>
<td>2</td>
</tr>
<tr>
<td><strong>IMMATURE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Amblyomma aureolatum</em></td>
<td>20</td>
<td>75</td>
<td>2.79</td>
<td>2.57</td>
</tr>
<tr>
<td><em>Amblyomma cajennense</em></td>
<td>47</td>
<td>178</td>
<td>4.06</td>
<td>4.03</td>
</tr>
<tr>
<td><em>Amblyomma coelebs</em></td>
<td>12.9</td>
<td>16</td>
<td>4.39</td>
<td>4.44</td>
</tr>
<tr>
<td><em>Amblyomma dissinale</em></td>
<td>24</td>
<td>50</td>
<td>3.87</td>
<td>3.83</td>
</tr>
<tr>
<td><em>Amblyomma dubitatum</em></td>
<td>12</td>
<td>41</td>
<td>2.56</td>
<td>2.54</td>
</tr>
<tr>
<td><em>Amblyomma longirostre</em></td>
<td>90</td>
<td>140</td>
<td>3.30</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma neumanni</em></td>
<td>12</td>
<td>77</td>
<td>3.61</td>
<td>3.57</td>
</tr>
<tr>
<td><em>Amblyomma nulosum</em></td>
<td>19</td>
<td>19</td>
<td>3.42</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma ovale</em></td>
<td>18</td>
<td>30</td>
<td>3.87</td>
<td>3.74</td>
</tr>
<tr>
<td><em>Amblyomma parvum</em></td>
<td>11</td>
<td>22</td>
<td>3.04</td>
<td>3.12</td>
</tr>
<tr>
<td><em>Amblyomma rotundatum</em></td>
<td>13</td>
<td>24</td>
<td>3.34</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma tigrinum</em></td>
<td>45</td>
<td>161</td>
<td>3.86</td>
<td>NA</td>
</tr>
<tr>
<td><em>Amblyomma triste</em></td>
<td>15</td>
<td>31</td>
<td>2.94</td>
<td>NA</td>
</tr>
<tr>
<td><em>Dermacentor nitens</em></td>
<td>5</td>
<td>59</td>
<td>2.73</td>
<td>***</td>
</tr>
<tr>
<td><em>Haemaphysalis juxtakochi</em></td>
<td>15</td>
<td>25</td>
<td>4.21</td>
<td>NA</td>
</tr>
<tr>
<td><em>Haemaphysalis leporispalustris</em></td>
<td>10</td>
<td>23</td>
<td>3.67</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes auritulus</em></td>
<td>42</td>
<td>53</td>
<td>3.26</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes longiscutatus</em></td>
<td>8</td>
<td>19</td>
<td>2.31</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes loericatus</em></td>
<td>15</td>
<td>35</td>
<td>3.02</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes luciae</em></td>
<td>20</td>
<td>42</td>
<td>3.05</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes paranicus</em></td>
<td>13</td>
<td>17</td>
<td>3.99</td>
<td>NA</td>
</tr>
<tr>
<td><em>Ixodes sigelos</em></td>
<td>12</td>
<td>28</td>
<td>2.02</td>
<td>NA</td>
</tr>
</tbody>
</table>

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.
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 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; Heberg & 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 koriatus 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 (Pardinas 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...
Strict host specificity is not common among hard ticks. Nevertheless, the evidence presented in this work shows that species, through the measurement of biological parameters, is interesting to evaluate the levels of fitness achieved by a given 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 Klopsch 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

We are very grateful to Lorenza Beati, Robert Poulin and Marcelo B. Labruna for their valuable comments on an earlier version of the manuscript. We thank the financial support of Instituto Nacional de Técnologia Agropecuaria, Asociación Cooperadora of EEA-INTA Rafaela and Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina.

Supplementary material

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

References


Host specificity in Neotropical hard ticks


