Analysis of large new South African data set using two host specificity indices shows generalism in both adult and larval ticks of mammals

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Running title: Host specificity of South African ticks

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SUMMARY

Ticks and tick-borne pathogens can have considerable impacts on the health of livestock, wildlife, and people. Knowledge of tick host preferences is necessary for both tick and pathogen control. Ticks were historically considered as specialist parasites, but the range of sampled host species has been limited, infestation intensity has not been included in prior analyses, and phylogenetic distances between hosts have not been previously considered. We used a large data set of 35,604 individual collections and two host specificity indices to assess the specificity of 61 South African tick species, as well as distinctions between adult and juvenile ticks, for 95 mammalian hosts. When accounting for host phylogeny, most adult and juvenile ticks behaved as generalists, with juveniles being significantly more generalist than adults. When we included the intensity of tick infestation, ticks exhibited a wider diversity of specificity in all life stages. Our results show that ticks of mammals in South Africa tend to behave largely as generalists and that adult ticks are more host-specific. More generally, our analysis shows that the incorporation of life-stage differences, infestation intensity, and phylogenetic distances between hosts, as well as the use of more than one specificity index, can all contribute to a deeper understanding of host-parasite interactions.

Key words: Host-parasite interaction, ticks, host specificity, South Africa, Ixodidae.

INTRODUCTION

Ticks are obligate ectoparasites that feed on blood of a variety of host species, including birds, reptiles, amphibians and mammals (Klompen *et al.* 1996). They are vectors of many important pathogens, including protozoan, rickettsial, viral, bacterial and fungal organisms (Oliver, 1989; Sonenshine, 1991). Approximately 10% of the 867 currently recognised tick species are known to transmit infectious microorganisms (Jongejan and Uilenberg, 2004) that threaten not only livestock and wildlife, but also human health, causing diseases such as heartwater, Lyme disease, and babesiosis (Karesh *et al.* 2005). Ticks may also cause severe damage to their hosts, including injuries to skin and hides, wounds, abscesses, and bleeding (Muchenje *et al.* 2008; Moyo and Masika, 2009); and they secrete substances that can generate toxicosis and host paralysis (Stone *et al.* 1989).

Tick host preferences are an important component of their ecology (Hoogstraal and Aeschlimann, 1982; Uilenberg, 1995; Cumming, 1998; Jongejan and Uilenberg, 2004). A parasite´s host specificity is closely related to its ability to persist in a given environment and its potential to expand its range or colonise new areas (Poulin and Mouillot, 2003; Koh *et al.* 2004). A deep understanding of tick-host relationships is needed not only for comprehending the evolution and basic ecology of ticks, but also for the management and control of ticks and tick-borne pathogens, prediction of future changes in the epidemiology of tick-borne diseases, and proactive responses to relevant environmental drivers such as deforestation and climate change (Cumming and Van Vuuren, 2006).

Ticks were historically considered to be specialist parasites, exhibiting morphological adaptations to feed on particular hosts (Hoogstraal and Aeschlimann, 1982; Hoogstraal and Kim, 1985). For example, the soft tick *Argas* (*Microargas*) *transversus* feeds exclusively on the Galapagos giant tortoise (*Geochelone elephantopus*) (Hoogstraal *et al.* 1973). However, most ticks are able to feed on a greater variety of host species (Oliver, 1989; Cumming, 1998). Experimental studies have revealed that they can feed and reproduce successfully using a wide diversity of hosts (James and Oliver, 1990; Belan and Bull, 1995; Marques Lisbôa Lopes *et al.* 1998). In the wild, ticks are often collected from a limited number of species and may appear to be host specialists (Hoogstraal and Aeschlimann, 1982). Tick-host interactions are, however, influenced not only by the physiological and morphological characteristics of ticks and hosts (Sonenshine, 1993), but also by their habitat preferences (Klompen *et al.* 1996; Nava and Guglielmone, 2013). Ticks exhibiting preferences for certain micro- and macro-habitats, such as *Ixodes* species commonly found on bats (Chiroptera), may preferentially parasitize hosts living in similar habitats (Sonenshine, 1993; Klompen *et al.* 1996). Similarly, the nature of animal movements is such that ticks that are under-dispersed (clumped) in the environment will be more likely to be perceived as specialists, regardless of their true host preferences (Cumming, 2004).

For many tick-host combinations, there is still considerable uncertainty as to whether an absence of an observed tick–host interaction indicates that the interaction cannot occur or is simply a matter of it not having been observed (Klompen *et al.* 1996; Cumming, 1998, 2004; Petney *et al.* 2007). In addition, the most comprehensive previous analysis of tick-host specificity for African species (Cumming, 1998) did not distinguish between larval and adult ticks or consider phylogenetic differences between host species. Thus, a re-evaluation of the classification of ticks as more generalist or more specialist parasites in light of evolutionary and life stage differences is necessary. If ticks are more generalist than previously indicated, they may have an increased chance of transmitting the pathogens they carry to a wider diversity of host species, altering animal populations on a larger scale (Power and Mitchell, 2004), and threatening the survival of small host populations (Altizer *et al.* 2003). Also, since the transmission of some pathogenic agents can be associated with a particular tick life stage (e.g., tick-borne encephalitis virus, *Babesia* spp., and the Lyme disease agent *Borrelia burgdorferi* are preferentially transmitted by juvenile ticks) (Sonenshine, 1993; Ostfeld *et al.* 1995; Randolph and Storey, 1999), it is important to differentiate the host specificity of juvenile and adult ticks.

Host specificity was classically determined as the number of host species a parasite uses (Lymbery, 1989; Poulin and Mouillot, 2003; Poulin and Keeney, 2007). More recent host specificity indices, however, include ecological characteristics (e.g., prevalence or intensity of parasite infestation; Rohde, 1980, 1993, 2002); evolutionary history, (i.e., host taxonomic or phylogenetic distances; Caira *et al.* 2003; Poulin and Mouillot, 2003); or both (Poulin and Mouillot, 2005). These indices offer deeper insights into differences in host specificity and help to reduce the biases associated with inadequate sampling.

We used a large, newly assembled data set of unusually high quality to re-evaluate the specificity of South African ticks for mammalian hosts. We used this opportunity to both reassess existing knowledge of tick-host specificity in southern Africa and explore the utility of two state-of-the-art host specificity indices. Specifically, we asked (1) whether ticks are dominantly host specialists or host generalists; (2) whether differences in host specificity between juvenile and adult ticks occur; and (3) whether the two host specificity indices, which accounted for (i) host phylogeny and (ii) host phylogeny and tick infestation intensity respectively, would provide the same or different insights and conclusions about the nature of tick-host relationships.

MATERIALS AND METHODS

Data

The data were collected by Prof. Ivan Horak (IH) over a 36-year period. Each tick sampled was either pulled off from a dead (natural death, roadkill, hunted) or a living host (domestic species). The animals were not captured or restricted under any circumstances. Data were captured digitally from hand-written notebooks over a two-year period, under the direct supervision of IH; each row of data was individually re-checked post capture for errors. All ticks in the data set were individually identified by IH and post-identification taxonomic revisions and reclassifications were included in the database, ensuring that both nomenclature and identification were contemporary and consistent throughout the data set. Using ‘collection’ to refer to samples of one or more ticks of a given species taken from a single host, the final data set used in this analysis consisted of 35,604 collections of 61 tick species (from 9 genera of the family Ixodidae) obtained from 95 mammal host species (85 wild mammals and 10 domestic mammals) (Supplementary Material A) collected from 1976 to 2012 in all nine provinces of South Africa.

For each collection, the tick species, life stage (larva, nymph or adult), the number of individual ticks collected, the host species, the host health condition, the geographic location of the sample, and the date of collection were recorded. In some cases, the host species was not known but its genus or family was indicated. All of the hosts considered in this analysis were mammalian. They belonged to 11 orders of mammals: Carnivora (29 spp.), Cetartiodactyla (32 spp.), Rodentia (14 spp), Primates (3 spp.), Perissodactyla (6 spp.), Macroscelidea (4 spp.), Lagomorpha (3 spp.), Proboscidea (1 sp.), Hyracoidean (1 spp.), Eulipotyphla (1 spp.), and Soricomorpha (1 family, Soricidae).

Host specificity indices

We calculated two different state-of-the-art indices for the data set. The first of these, S_{TD} (Poulin and Mouillot, 2003), quantifies the specificity of each tick species that parasitized two or more mammal hosts. Low values indicate tick species that primarily infested closely related hosts, while high values reflect tick species that were found across divergent host species. A higher S_{TD} index indicates a more generalist parasite.

The S_{TD} index accounts for the number of host species used by the tick species, *S*, and for the divergence time between each pair of host species *i* and *j*, ω_{ij}, expressed in millions of years:

$$S_{\mathrm{TD}} = 2\frac{\sum\sum_{i<j}\omega_{ij}}{S(S-1)} \qquad (1)$$

The variance of the index S_{TD} ($VarS_{TD}$) was calculated for tick species feeding on a minimum of three host species (it is always zero with two species; Poulin and Mouillot 2003). The $VarS_{TD}$ index provides information about the distribution of hosts across the phylogenetic tree. The higher the $VarS_{TD}$, the more hosts are evenly distributed across the phylogenetic tree. The variance of the S_{TD} index was computed as follows:

$$VarS_{\mathrm{TD}} = \frac{\sum\sum_{i \neq j}(\omega_{ij} - \bar{\omega})^2}{S(S-1)} \quad (2)$$

where $\bar{\omega}$ was the average phylogenetic distance over all pairs of parasitized hosts.

The second index, S_{TD}* (Poulin and Mouillot, 2005), differs from the first index by its inclusion of abundance data (i.e., the number of ticks of each species collected from each infested host and not just the presence or absence of each tick species such as in Supplementary Material B). Low values indicate that the tick species achieve a high intensity of infestation on a few closely related hosts, while high values reflect tick species that reach their highest intensity of infestation in distantly related host species. The higher the S_{TD}* index, the more generalist is the parasite. The S_{TD}* index weights the sum of the phylogenetic distances, ω_{ij}, by the intensity of infestation in host i (I_i) and host j (I_j):

$$S_{\mathrm{TD}} * = \frac{\sum\sum_{i<j} \omega_{ij} I_i I_j}{\sum\sum_{i<j} I_i I_j} \quad (3)$$

where I_i and I_j were calculated as the average number of individual ticks of a given species found on the infested individuals of the host species i and j, respectively (Margolis *et al.* 1982).

The variance of the index S_{TD}* ($VarS_{TD}$*) was calculated for tick species feeding on a minimum of three host species. The $VarS_{TD}$* provides information about the distribution of hosts across the phylogenetic tree and the distribution of infestation intensities. The higher the $VarS_{TD}*$, the more hosts are evenly distributed across the phylogenetic tree and across the distribution of infestation intensity. The variance of $S_{TD}*$ was computed as follows:

$$VarS_{\mathrm{TD}} *= \frac{\sum\sum_{i\neq j}\left[(\omega_{ij}I_iI_j)-(\overline{\omega_{ij}I_iI_j})\right]^2}{\sum\sum I_iI_j} \quad (4)$$

where $\overline{\omega_{ij}I_iI_j}$ was the average of the ω_{ij} x I_iI_j product.

Phylogenetic data

The majority of the divergence times between mammal species were obtained from the phylogenetic tree published by Bininda-Emonds *et al.* (2007). The species of interest were selected and separated from the rest of the tree using the package '*ape 3.1-1'* (Paradis *et al.* 2004) in the R software 3.1.2. (R Core Team, 2014), and the divergence times were visualized with the programme FigTree v1.4.2 (Supplementary Material C). Phylogenetic information for two domestic mammal species (*Felis silvestris catus* and *Bos indicus*) was derived from other sources (Driscoll *et al.* 2007; Hiendleder *et al.* 2008).

Analyses of indices

The indices and their variances were computed for three categories of ticks: all ticks (whatever their life stage), juveniles (larva and nymph), and adults. The values of the indices and their variances were tested for normality using Shapiro-Wilks tests and for skewness using D'Agostino skewness tests in the R package *'moments 0.14'*. We tested for differences between juvenile and adult indices using a Wilcoxon signed rank test (Siegel and Castellan Jr., 1998). All calculations and statistical tests were conducted in R 3.1.2. (R Core Team, 2014).

RESULTS

Collections vs. host species

The most-collected ticks came from 50 different host species (Fig. 1). Although the number of host species increased initially with sampling effort, the number of mammal species recorded for each individual tick species reached a plateau beyond about a thousand collections (Fig. 1).

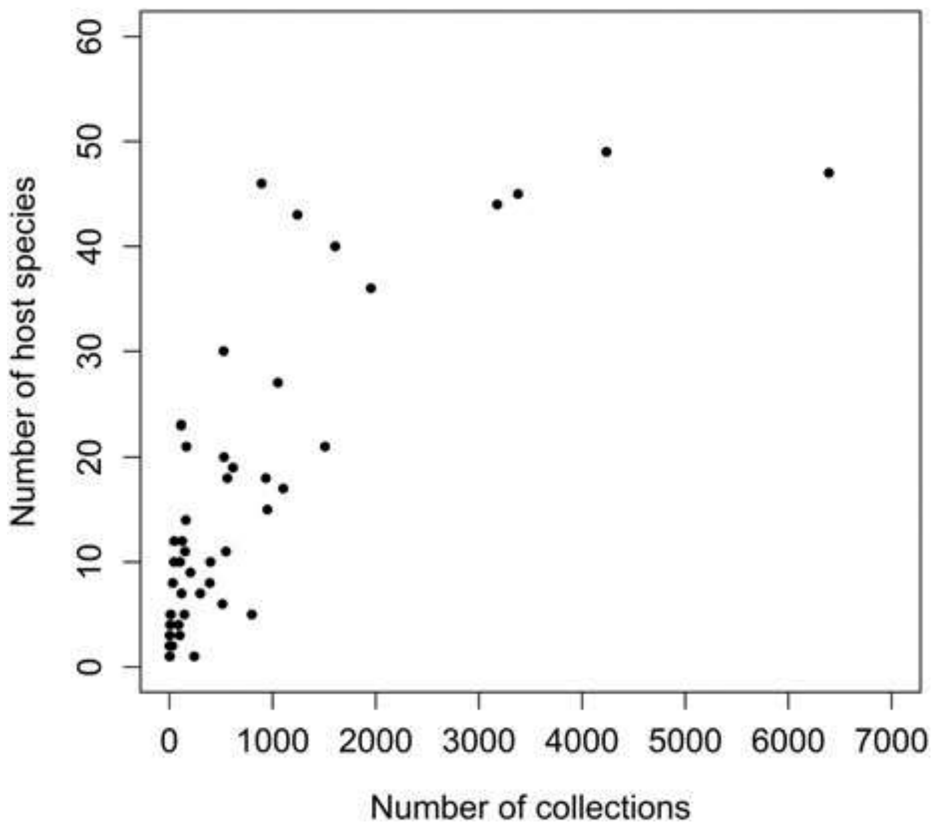

Figure 1. Number of mammalian host species (total n = 95 species) as a function of the number of collections (total n = 35,604 collections) for the 61 recorded tick species. Collections refer to samples of one or more ticks taken from a single host.

Host specificity indices

The S_{TD} and S_{TD}* indices were calculated for 54 of the 61 recorded tick species (7 species fed on <2 mammal host species and were not included) (Supplementary Material D).

The S_{TD} index had a mean value of 70.65 and a median of 71.85 for ticks of all life stages; a mean of 68.72 and a median of 71.41 for juvenile ticks; and a mean of 62.88 and a median of 63.40 for adult ticks. The lowest S_{TD} index values (most specialised ticks) for pooled life stages and juvenile ticks was found for *Amblyomma nuttalli* Dönitz, 1909 ($S_{TD} =$ 16.80 in both cases), a tick species that commonly parasitizes reptiles. It was collected from two carnivores, *Acinonyx jubatus* and *Panthera leo*. The lowest index value for adult ticks was found for *Dermacentor rhinocerinus* (Denny, 1843) ($S_{TD} =$ 14.70), which was collected from two rhinoceroces, *Ceratotherium simum* and *Diceros bicornis*. The highest S_{TD} index value (most generalist tick) for pooled life stages and juvenile ticks was found for *Amblyomma tholloni* Neumann, 1899 (all life stages: $S_{TD} =$ 97.70; juvenile ticks: $S_{TD} =$ 96.10). This tick species was found on three very different hosts when looking at all life stages: *Lepus saxatilis*, *Loxodonta africana* and *Panthera leo*, and on two of these host species (*Panthera leo* and *Lepus saxatilis*) when considering juvenile ticks. For adult ticks, the S_{TD} index was highest for *Ixodes bakeri* Arthur and Clifford, 1961 ($S_{TD} =$ 98.50), which was found on two small mammals: *Elephantulus myurus* and *Otomys sp.*. The distribution of the S_{TD} index was significantly negatively skewed globally ($z = -2.54$, $p = 0.01$; Fig.2a) and for juvenile ticks ($z = -2.52$, $p = 0.01$; Fig.2c), indicating that according to this index, the majority of these tick species behaved as generalists. For adult ticks however, the distribution of the S_{TD} index was not significantly skewed ($z = -0.9$, $p = 0.36$; Fig.2e), suggesting that they do not behave more as generalists than as specialists.

The S_{TD}* index had a mean value of 65.54 and a median of 70.61 for ticks of all life stages, a mean of 55.24 and a median of 51.99 for juvenile ticks, and a mean of 58.78 and a median of 63.40 for adult ticks. The lowest S_{TD}* index value (most specialist tick) was again found for *Amblyomma nuttalli* Dönitz, 1909 ($S_{TD}* =$ 16.8) for pooled life stages and

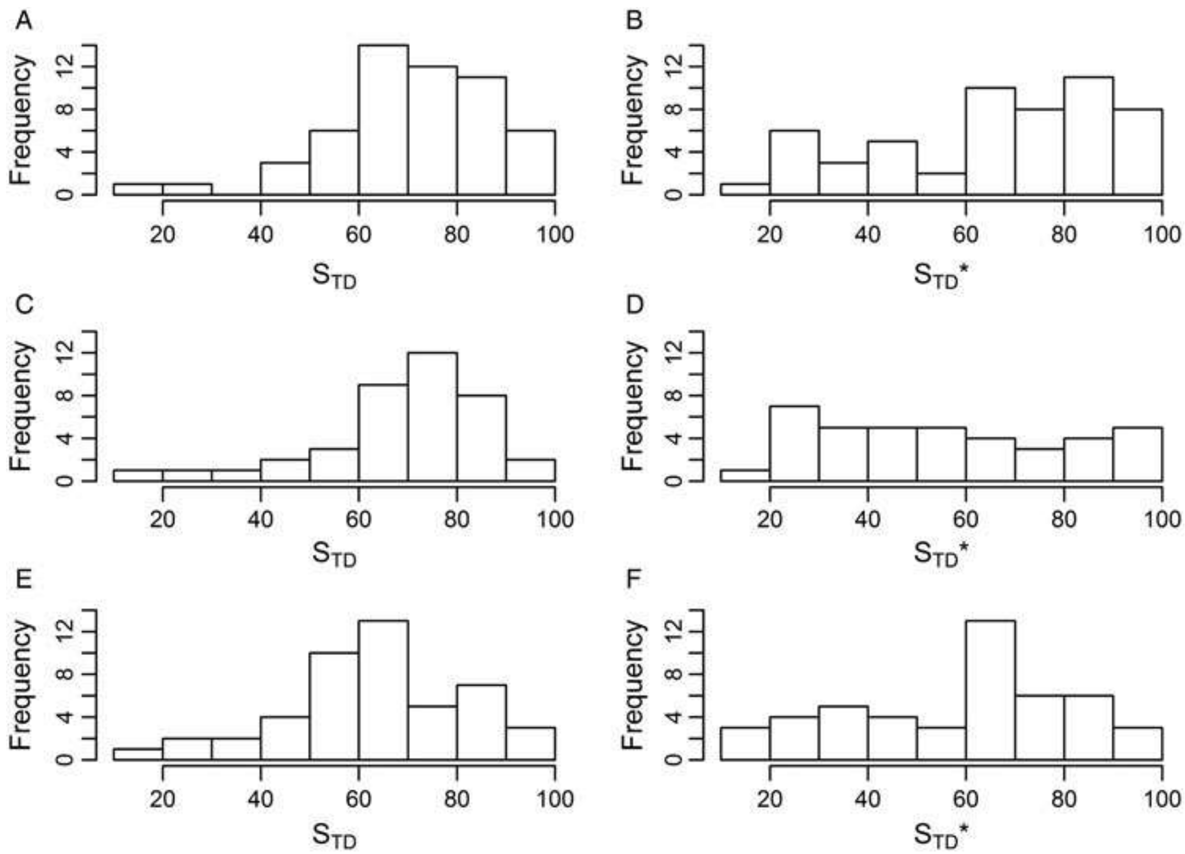

Figure 2. Distribution of the host specificity indices S_{TD} and S_{TD}* obtained for all ticks of all life stages (A, B), for juvenile ticks only (C, D), and for adult ticks only (E, F).

juvenile ticks. The lowest index values for adult ticks was again found for *Dermacentor rhinocerinus* (Denny, 1843) (S_{TD} = 14.70). The highest S_{TD}* index value (most generalist tick) for all life stages was found for *Amblyomma tholloni* Neumann, 1899 (S_{TD}* = 97.99), which was collected from *Lepus saxatilis*, *Loxodonta africana* and *Panthera leo*. For juvenile ticks, the S_{TD}* index was highest for *Rhipicephalus distinctus* Bedford, 1932 (S_{TD}* = 97.06), which was found on ten host species (*Caracal caracal*, *Elephantulus edwardii*, *Elephantulus myurus*, *Galerella pulverulenta*, *Lepus saxatilis*, *Pedetes capensis*, *Procavia capensis*, *Pronolagus rupestris*, *Rhabdomys pumilio* and *Saccostomus campestris*). For adult ticks, the S_{TD}* index was highest for *Ixodes bakeri* Arthur and Clifford, 1961 (S_{TD} =

98.74), which was found on *Elephantulus myurus* and *Otomys sp.*. The distribution of the S_{TD}* index was not significantly skewed (all: z = -1.46, p = 0.14; juveniles: z = 0.78, p = 0.43; adults: z = -0.76, p = 0.44; Fig. 2b, 2d, 2f), indicating that according to this index and across all life stages, ticks do not behave more as specialists than as generalists, and that all degrees of host specificity are observed (Fig. 2).

Variance of host specificity indices

The variances of each index were calculated for 42 tick species (all life stages), 36 species in their juvenile stage and 36 species in their adult stage. The $VarS_{TD}$ and $VarS_{TD}$* values exhibited a high frequency of small values, whether for all ticks, juveniles only, or adults

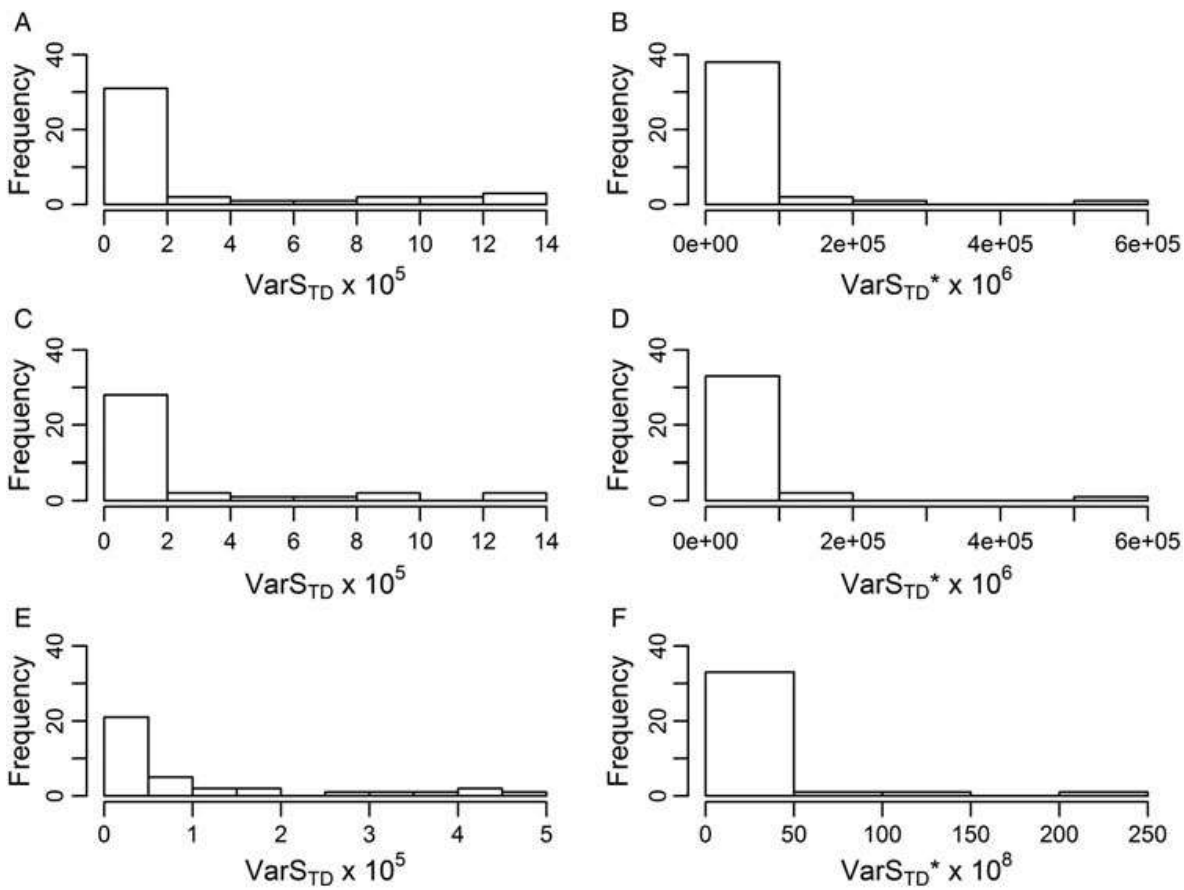

Figure 3. Distribution of $VarS_{TD}$ and $VarS_{TD}$* obtained for all ticks of all life stages (A, B), for juvenile ticks only (C,D), and for adult ticks (E,F).

only (Fig. 3). There was thus little taxonomic heterogeneity among groups of host species and little heterogeneity in the intensity of infestation among hosts (Fig. 3).

Comparison of host specificity indices for juvenile and adult ticks

S_{TD} and S_{TD}* values for adult ticks followed a normal distribution, but those for juvenile ticks did not. A non-parametric Wilcoxon signed rank test was thus used to compare the values of the two life-stages. Significant differences were found between them for S_{TD} (V = 486, p = 0.001), with juvenile ticks having higher S_{TD} values than adults (Fig. 4a). Conversely, the S_{TD}* values of adult and juvenile ticks were not significantly different (V = 294, p = 0.74) (Fig. 4b).

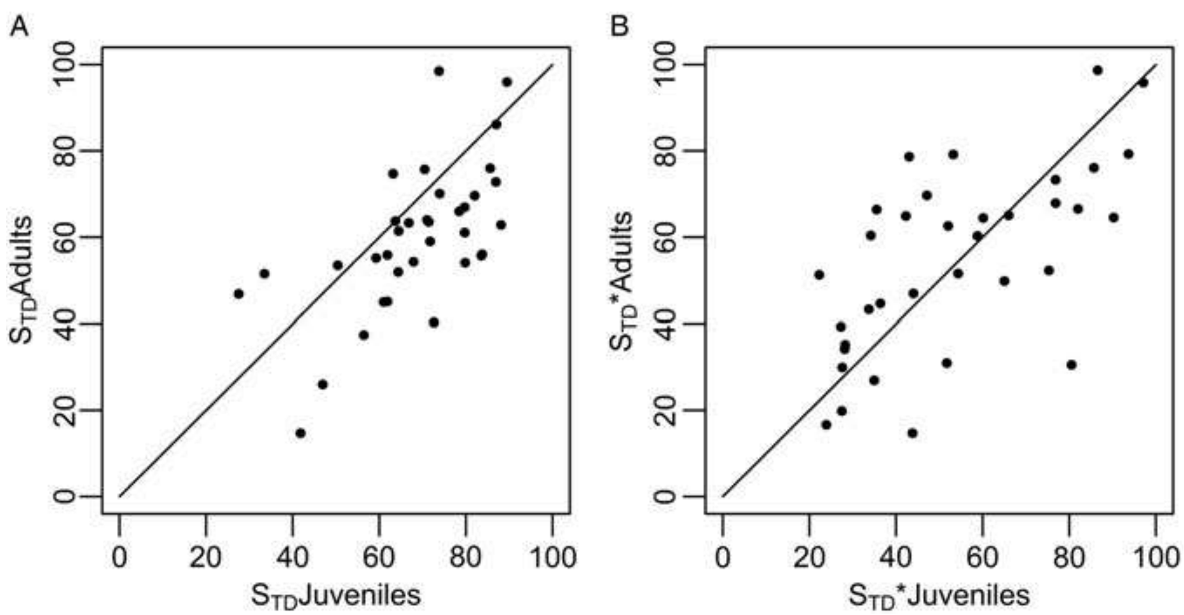

Figure 4. Relationship between the host specificity of juvenile and adult ticks, using the S_{TD} index (A) and the S_{TD}* index (B). The solid line represents the expected relationship if juveniles' and adults' values are similar.

DISCUSSION

Accounting for host phylogeny using the S_{TD} index (Poulin and Mouillot, 2003), we found that across all life stages, most ticks behaved as generalists; and that juvenile ticks tended to be more generalist than their adults. By contrast, when the intensity of tick infestation was accounted for using the S_{TD}* index (Poulin and Mouillot, 2005), tick species were not found to be more generalist than specialist and both adults and juveniles exhibited a wide range of specificity for mammal species.

The results of our analysis are broadly in support of the results obtained by Cumming (1998) for his pan-African analysis across all host taxonomic groups. Cumming (1998) included a number of more specialised species on reptiles and birds that were not included in this analysis; incorporation of these data into a comparable analysis would probably reduce the degree of host generalism that we found in our analysis, although the potential for some species to be found across classes (e.g., on both birds and reptiles) might have the converse effect.

Our finding that juvenile ticks tend to be more generalist than their adults is novel. This is also the first time that the evolutionary host-parasite relationship (Poulin and Mouillot, 2003) has been considered in assessing tick-host specificity in Africa. According to the S_{TD} index, ticks in South Africa can infest a variety of hosts with distant divergence times (i.e., high S_{TD} index values). This suggests that some tick species have made relatively long jumps across their hosts´ phylogenetic tree (Cumming, 2000). However, the low $VarS_{TD}$ values also showed that the host distribution was homogenous in the phylogenetic tree for most ticks, implying that the majority of tick species at any life stage tended to infest host species with similar divergence time distributions across the phylogenetic tree.

The S_{TD} index shows that juvenile ticks behave more as generalists than adult ticks. In general, juvenile ticks appear to be able to infest host species from different phylogenetic groups, becoming more host-specific as adults. Some tick species (e.g., *Rhipicephalus exophthalmos* Keirans and Walker, 1993; *Rhipicephalus capensis* Koch, 1844; *Hyalomma glabrum* Delpy, 1949; and *Dermacentor rhinocerinus* (Denny, 1843)) exhibited a large decrease in S_{TD} values from juvenile to adult stages, denoting an important change of strategy from generalist to specialist during their lifetime. This shift may be mediated by mouthpart morphology; juvenile ticks are unable to pierce the hide of most large mammals and must feed on thinner-skinned organisms. The need to find a mate may also impose greater specificity on adults. Experimental studies also suggest that juvenile ticks have low levels of specificity (Oliver, 1989; James and Oliver, 1990; Belan and Bull, 1995; Marques Lisbôa Lopes *et al.* 1998) and the juveniles of many species can be reared successfully on domestic rabbits. In South Africa, the larvae and nymph of ixodid tick species are typically found on small mammals, but these juvenile ticks have also been found on a large variety of domestic and wild animal species (Horak *et al.* 2000). These findings stress the need to consider the different life stages of the vectors in the study of tick-borne diseases. Considering only adult ticks may lead to an important under-estimation of pathogen transmission rates and/or of the range of hosts at risk. For example, *Rickettsia africae,* the causal agent of African tick bite fever, is transmitted by *Amblyomma* larvae and nymphs that infest a broader host range (including domestic and wild mammals, humans, as well as reptiles and birds) than *Amblyomma* adults (Cumming, 1998; Jensenius *et al.* 2003).

Using the S_{TD}* index (Poulin and Mouillot, 2005), different results were obtained for tick host specificity in South Africa. Adding infestation intensity to host phylogenetic distinctness lowered the values of the specificity index and led to a non-skewed distribution of specificity degrees. Contrary to what was found using the S_{TD} index, this index indicates that ticks were neither more generalists nor more specialists. This result differs from that of Nava and Guglielmone (2013) for neotropical ixodid ticks of wild and domestic hosts (mammals, birds, amphibians and reptiles), who found that juvenile ticks fed on a broader taxonomic range of hosts and exhibited higher $S_{TD}*$ values than adults. The difference between their study and ours may be attributable to differences in host species diversity and/or phenology and in the measure of host exploitation by the ticks (prevalence, i.e., presence-absence, *vs* infestation intensity).

As with the first index, $VarS_{TD}*$ values were low at any life stage, suggesting that the majority of tick species infested more intensively host species with similar phylogenetic distances. Poulin and Mouillot (2004) similarly found a negative correlation between parasites' average infection success and the taxonomic or phylogenetic distances among their hosts. These authors argued that a parasite may reach a higher abundance in congeneric hosts because of shared host features (e.g. immune system, behaviour, anatomy, biochemistry) to which it is pre-adapted, whilst colonizing distantly related hosts requires parasite physiological and morphological adaptations that may affect its ability to achieve a high abundance.

Together, our results suggest that ticks are generalist, but do not infest with the same intensity hosts that are phylogenetically too distant (as revealed by the S_{TD} and the $S_{TD}*$ indices, respectively). Although host phylogenetic distinctness denotes host switching over evolutionary time scales (Poulin and Mouillot, 2003; Poulin and Mouillot, 2004), considering infestation intensity emphasizes host use more strongly (Poulin and Mouillot, 2005).

Despite the more sophisticated conclusions about tick feeding preferences offered by the inclusion of both phylogeny and infestation intensity, incorporating these elements in the analyses requires data of good quality. It is difficult to accurately estimate the number of ticks on a host. For example, when studying heavily infested animals, special attention is given to a fixed area (i.e., ears, neck and head) (Sonenshine, 1993); orifices, such as the rectum and ear cavities, are hard to search effectively on a live animal. Ticks may also attach to their hosts only at particular times during their life cycle (Jongejan and Uilenberg, 2004); and microclimatic conditions may influence when either a juvenile or adult tick may be found on a particular host (Randolph and Storey, 1999).

We conclude that although ticks as a group appeared to follow a range of strategies from specialist to generalist, a majority of tick species behaved as generalist when feeding on mammals in South Africa and that for many tick species, generalism was higher during the juvenile stage. The separation of different life history stages and the inclusion of evolutionary and ecological data using two state-of-the-art indices provided new insights into tick-mammal interactions. Our results also demonstrate the value of comparing different host specificity indices, while indicating that further research is needed to determine their sensitivity to data type and quantity.

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REFERENCES

Altizer, S., Harvell, D. and Friedle, E. (2003). Rapid evolutionary dynamics and disease threats to biodiversity. *Trends in Ecology and Evolution* **18**, 589–596. doi:10.1016/j.tree.2003.08.013.

Belan, I. and Bull, C. M. (1995). Host-seeking behaviour by Australian ticks (Acari: Ixodidae) with differing host specificities. *Experimental & Applied Acarology* **19**, 221–232. doi: 10.1007/BF00130825.

Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L. and Purvis, A. (2007). The delayed rise of present-day mammals. *Nature* **446**, 507–512. doi: 10.1038/nature05634.

Caira, J. N., Jensen, K. and Holsinger, K. E. (2003). On a new index of host specificity. In *Taxonomy, ecology and evolution of metazoan parasites* (ed. Combes, C. and Jourdane, J.), pp 161–201. University of Perpignan Press, Perpignan, France.

Cumming, G. S. (1998). Host preference in African ticks (Acari: Ixodida): a quantitative data set. *Bulletin of Entomological Research* **88**, 379–406. doi: 10.1017/S0007485300042139.

Cumming, G. S. (2000). Host use does not clarify the evolutionary history of African ticks (Acari: Ixodoidea). *African Zoology* **35**, 43–50. doi: 10.1080/15627020.2000.11407190.

Cumming, G. S. (2004). On the relevance of abundance and spatial pattern for interpretations of host–parasite association data. *Bulletin of Entomological Research* **94**, 401–409. doi: 10.1079/BER2004319.

Cumming, G.S. and Van Vuuren, D. P. (2006). Will climate change affect ectoparasite species ranges?. *Global Ecology and Biogeography* **15**, 486–497. doi: 10.1111/j.1466-822x.2006.00241.x.

Driscoll, C. A., Menotti-Raymond, M., Roca, A. L., Hupe, K., Johnson, W. E., Geffen, E., Harley, E. H., Delibes, M., Pontier, D., Kitchener, A. C., Yamaguchi, N., O'Brien, S. J. and Macdonald, D. W. (2007). The Near Eastern origin of cat domestication. *Science* **317**, 519–523. doi: 10.1126/science.1139518.

Hiendleder, S., Lewalski, H. and Janke, A. (2008). Complete mitochondrial genomes of *Bos taurus* and *Bos indicus* provide new insights into intra-species variation, taxonomy and domestication. *Cytogenetic and Genome Research* **120**, 150–156. doi: 10.1159/000118756

Hoogstraal, H. and Aeschlimann, A. (1982). Tick-host specificity. *Bulletin de la Société Entomologique Suisse* **55**, 5–32.

Hoogstraal, H. and Kim, K. C. (1985). Tick and mammal coevolution, with emphasis on *Haemaphysalis.* In *Coevolution of Parasitic Arthropods and Mammals* (ed. Kim, K. C.), pp 505–568. Wiley & Sons, New York.

Hoogstraal, H., Clifford, C. M. and Keirans, J. E. (1973). *Argas (Microargas) transversus* (Ixodoidea: Argasidae) of Galapagos giant tortoises: description of the female and nymph. *Annals of the Entomological Society of America* **66**, 727–732. doi: http://dx.doi.org/10.1093/aesa/66.4.727.

Horak, I. G., Braack, L. E., Fourie, L. J. and Walker, J. B. (2000). Parasites of domestic and wild animals in South Africa. XXXVIII. Ixodid ticks collected from 23 wild carnivore species. *The Onderstepoort Journal of Veterinary Research* **67**, 239–250.

James, A. and Oliver, J. H. (1990). Feeding and host preference of immature *Ixodes dammini*, *I. scapularis*, and *I. pacificus* (Acari: Ixodidae). *Journal of Medical Entomology* **27**, 324–330. doi: 10.1093/jmedent/27.3.324 324-330.

Jensenius, M., Fournier, P., Kelly, P., Myrvang, B. and Raoult, D. (2003). African tick bite fever. *The Lancet Infectious Diseases* **3**, 557–564. doi: 10.1016/S1473-3099(03)00739-4.

Jongejan, F. and Uilenberg, G. (2004). The global importance of ticks. *Parasitology* **129**, S3–S14. doi: : 10.1017/S0031182004005967.

Karesh, W. B., Cook, R. A., Bennett, E. L. and Newcomb, J. (2005). Wildlife trade and global disease emergence. *Emerging Infectious Diseases* **11**, 1000–1002.

Klompen, J. S. H., Black, W. C., Keirans, J. E. and Oliver Jr., J. H. (1996). Evolution of ticks. *Annual Review of Entomology* **41**, 141–161. doi: 10.1146/annurev.en.41.010196.001041.

Koh, L. P., Dunn, R. R., Sodhi, N. S., Colwell, R. K., Proctor, H. C. and Smith, V. S. (2004). Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634. doi: 10.1126/science.1101101.

Lymbery, A. J. (1989). Host specificity, host range and host preference. *Parasitology Today* **5**, 298.

Margolis, L., Esch, G. W., Holmes, J. C., Kuris, A. M. and Schad, G. A. (1982). The use of ecological terms in parasitology (report of an ad hoc committee of the American society of parasitologists). *Journal of Parasitology* **68**, 131–133. doi: 10.2307/3281335.

Marques Lisbôa Lopes, C., Cerequeira Leite, R., Bahia Labruna, M., de Oliveira, P. R., Miranda Ferreira Borges, L., Batista Rodrigues, Z., Avila de Carvalho, H., Vianna de Freitas, C. M. and Vieira Junior, C. R. (1998). Host specificity of *Amblyomma cajennense* (Fabricius, 1787) (Acari: Ixodidae) with Comments on the drop-off rhythm. *Memorias Do Instituto Oswaldo Cruz* **93**, 347–351. doi: 10.1590/S0074-02761998000300014.

Moyo, B. and Masika, P. J. (2009). Tick control methods used by resource-limited farmers and the effect of ticks on cattle in rural areas of the Eastern Cape Province, South Africa. *Tropical Animal Health and Production* **41**, 517–523. doi: 10.1007/s11250-008-9216-4.

Muchenje, V., Dzama, K., Chimonyo, M., Raats, J. G. and Strydom, P. E. (2008). Tick susceptibility and its effects on growth performance and carcass characteristics of Nguni, Bonsmara, and Angus steers raised on natural pasture. *Animal* **2**, 298–304. doi: 10.1017/S1751731107001036.

Nava, S. and Guglielmone, A. A. (2013). A meta-analysis of host specificity in Neotropical hard ticks (Acari: Ixodidae). *Bulletin of Entomological Research* **103**, 216–224. doi: 10.1017/S0007485312000557.

Oliver, J. H. (1989). Biology and systematics of ticks (Acari: Ixodida). *Annual Review of Ecology and Systematics* **20**, 397–430.

Ostfeld, R. S., Cepeda, O. M., Hazler, K. R. and Miller, M. C. (1995). Ecology of Lyme disease: habitat associations of ticks (*Ixodes scapularis*) in a rural landscape. *Ecological Applications* **5**, 353–361. doi: 10.2307/1942027.

Paradis, E., Claude, J. and Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. doi: 10.1093/bioinformatics/btg412.

Petney, T. N., Kolonin, G. V. and Robbins, R. G. (2007). Southeast Asian ticks (Acari: Ixodida): a historical perspective. *Parasitology research* **101**, 201–205. doi: 10.1007/s00436-007-0687-4.

Poulin, R. and Mouillot, D. (2003). Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology* **126**, 473–480. doi: 10.1017/S0031182003002993.

Poulin, R. and Mouillot, D. (2004). The relationship between specialization and local abundance: the case of helminth parasites of birds. *Oecologia* **140**, 372–378. doi: 10.1007/s00442-004-1593-4.

Poulin, R. and Mouillot, D. (2005). Combining phylogenetic and ecological information into a new index of host specificity. *Journal of Parasitology* **91**, 511–514. doi: 10.1645/GE-398R.

Poulin, R. and Keeney, D. B. (2007). Host specificity under molecular and experimental scrutiny. *Trends in Parasitology* **24**, 24–28. doi: 10.1016/j.pt.2007.10.002.

Power, A. G. and Mitchell, C. E. (2004). Pathogen spillover in disease epidemics. *The American Naturalist* **164**, S79–S89. doi: 10.1086/424610.

R Development Core Team (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Randolph, S. E. and Storey, K. (1999). Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *Journal of Medical Entomology* **36**, 741–748. doi: http://dx.doi.org/10.1093/jmedent/36.6.741

Rohde, K. (1980). Host specificity indices of parasites and their application. *Experientia* **36**, 1369–1371. doi: 10.1007/BF01960103.

Rohde, K. (1993). Ecology of Marine Parasites. CAB International, Wallingford, U.K.

Rohde, K. (2002). Ecology and biogeography of marine parasites. *Advances in Marine Biology* **43**, 1–86. doi: 10.1016/S0065-2881(02)43002-7.

Siegel, S. and Castellan Jr., N. J. (1998). The case of one sample, two measures or paired replicates. In *Nonparametric statistic for the behavioral sciences* (ed. Siegel, S. and Castellan Jr., N. J.), pp 87–95. McGraw Hill, New York.

Sonenshine, D. E. (1991). Introduction. In *Biology of ticks*, pp 3–12. Oxford University Press, New York.

Sonenshine, D. E. (1993). Tick-borne and tick-caused diseases. In *Biology of ticks*, pp 107–330. Oxford University Press, New York.

Stone, B. F., Binnington, K. C., Gauci, M. and Aylward, J. H. (1989). Tick/host interactions for *Ixodes holocyclus*: Role, effects, biosynthesis and nature of its toxic and allergenic oral secretions. *Experimental and Applied Acarology* **7**, 59–69. doi: 10.1007/BF01200453.

Uilenberg, G. (1995). International collaborative research: significance of tick-borne hemoparasitic diseases to world animal health. *Veterinary Parasitology* **57**, 19–41. doi: 10.1016/0304-4017(94)03107-8.

Supplementary Material

Supplementary Material A. Mammal host species, their scientific names, common names and type of animal (wild or domestic). The term "domestic" refers to animal species that are dependent on or associated with humans to survive. The term "wild" refers to animal species that do not depend on humans and live in their natural environments. When the host species was not known, its genus or family was indicated.

Scientific name	**Common name**	**Mammalian family**	**Type**
Acinonyx jubatus	Cheetah	Felidae	wild
Aepyceros melampus	Impala	Bovidae	wild
Aethomys chrysophilus	Red rock rat	Muridae	wild
Aethomys namaquensis	Namaqua rock rat	Muridae	wild
Alcelaphus buselaphus	Hartebeest	Bovidae	wild
Antidorcas marsupialis	Springbok	Bovidae	wild
Atelerix frontalis	Southern African hedgehog	Erinaceidae	wild
Bos indicus	Zebu	Bovidae	domestic
Bos sp.	Bovine	Bovidae	domestic
Bos taurus	Cattle	Bovidae	domestic
Canis lupus familiaris	Domestic dog	Canidae	domestic
Canis mesomelas	Black-backed jackal	Canidae	wild
Capra hircus	Goat	Bovidae	domestic
Caracal caracal	Caracal	Felidae	wild
Cephalophus natalensis	Red forest duiker	Bovidae	wild
Ceratotherium simum	White rhinoceros	Rhinocerotidae	wild
Chlorocebus aethiops	Vervet monkey	Cercopithecidae	wild
Civettictis civetta	African civet	Viverridae	wild
Connochaetes gnou	Black wildebeest	Bovidae	wild

Connochaetes taurinus	Blue wildebeest	Bovidae	wild
Crocuta crocuta	Spotted hyena	Hyaenidae	wild
Cynictis penicillata	Yellow mongoose	Herpestidae	wild
Damaliscus lunatus	Common tsessebe	Bovidae	wild
Damaliscus pygargus	Bontebok	Bovidae	wild
Diceros bicornis	Black rhinoceros	Rhinocerotidae	wild
Elephantulus brachyrhynchus	Short-snouted elephant shrew	Macroscelididae	wild
Elephantulus edwardii	Cape elephant shrew	Macroscelididae	wild
Elephantulus myurus	Eastern rock elephant shrew	Macroscelididae	wild
Equus asinus	Donkey	Equidae	domestic
Equus burchelli	Plains zebra	Equidae	wild
Equus caballus	Horse	Equidae	domestic
Equus zebra	Mountain zebra	Equidae	wild
Felis silvestris catus	Domestic cat	Felidae	domestic
Felis nigripes	Black-footed cat	Felidae	wild
Felis silvestris cafra	Southern African wild cat	Felidae	wild
Galerella pulverulenta	Cape gray mongoose	Herpistidae	wild
Galerella sanguinea	Slender mongoose	Herpistidae	wild
Genetta genetta	Common genet	Viverridae	wild
Genetta sp.	Genets	Viverridae	wild
Genetta tigrina	Cape genet	Viverridae	wild
Giraffa camelopardalis	Giraffe	Giraffidae	wild
Hippotragus equinus	Roan antelope	Bovidae	wild
Hippotragus niger	Sable antelope	Bovidae	wild
Hystrix africaeaustralis	Cape porcupine	Hystricidae	wild
Ichneumia albicauda	White-tailed mongoose	Herpestidae	wild
Ictonyx striatus	Striped polecat	Mustelidae	wild
Lemniscomys rosalia	Single-striped grass mouse	Muridae	wild

Leptailurus serval	Serval	Felidae	wild
Lepus capensis	Cape hare	Leporidae	wild
Lepus saxatilis	Scrub hare	Leporidae	wild
Loxodonta africana	African bush elephant	Elephantidae	wild
Lycaon pictus	Wild dog	Canidae	wild
Macroscelides proboscideus	Round-eared elephant shrew	Macroscelididae	wild
Mastomys coucha	Southern multimammate mouse	Muridae	wild
Mastomys natalensis	Natal multimammate mouse	Muridae	wild
Mellivora capensis	Honey badger	Mustelidae	wild
Mungos mungo	Banded mongoose	Herpestidae	wild
Neotragus moschatus	Suni	Bovidae	wild
Oreotragus oreotragus	Klipspringer	Bovidae	wild
Oryx gazella	Gemsbok	Bovidae	wild
Otocyon megalotis	Bat-eared fox	Canidae	wild
Otolemur crassicaudatus	Brown greater galago	Galagidae	wild
Otomys occidentalis	Western Vlei Rat	Muridae	wild
Otomys sp.	Vlei rat	Muridae	wild
Ovis aries	Sheep	Bovidae	domestic
Panthera leo	Lion	Felidae	wild
Panthera pardus	Leopard	Felidae	wild
Papio hamadryas	Hamadryas baboon	Cercopithecidae	wild
Parahyaena brunnea	Brown hyaena	Hyaenidae	wild
Pedetes capensis	South African springhare	Pedetidae	wild
Pelea capreolus	Grey rhebok	Bovidae	wild
Phacochoerus africanus	Warthog	Suidae	wild
Potamochoerus larvatus	Bushpig	Suidae	wild
Praomys sp.	Mouse	Muridae	wild
Procavia capensis	Rock hyrax	Procaviidae	wild

Pronolagus rupestris	Smith's red rock hare	Leporidae	wild
Proteles cristatus	Aardwolf	Hyaenidae	wild
Raphicerus campestris	Steenbok	Bovidae	wild
Raphicerus melanotis	Cape grysbok	Bovidae	wild
Rattus rattus	Black rat	Muridae	domestic
Redunca arundinum	Southern reedbuck	Bovidae	wild
Redunca fulvorufula	Mountain reedbuck	Bovidae	wild
Rhabdomys pumilio	Four-striped grass mouse	Muridae	wild
Rhynchogale melleri	Meller's mongoose	Herpestidae	wild
Saccostomus campestris	South African pouched mouse	Nesomyidae	wild
Soricidae	Shrew	Soricidae	wild
Suricata suricatta	Meerkat	Herpestidae	wild
Sylvicapra grimmia	Common duiker	Bovidae	wild
Syncerus caffer	African buffalo	Bovidae	wild
Tatera leucogaster	Bushveld gerbil	Muridae	wild
Taurotragus oryx	Common eland	Bovidae	wild
Tragelaphus angasii	Nyala	Bovidae	wild
Tragelaphus scriptus	Bushbuck	Bovidae	wild
Tragelaphus strepsiceros	Greater kudu	Bovidae	wild
Vulpes chama	Cape fox	Canidae	wild

Supplementary Material B. Tick species distribution among mammal host species: **+** and **-** refers to the presence or absence of a tick species on a determined mammal host species respectively.

Mammal host species	**Tick species***																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Acinonyx jubatus	+	+	+	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Aepyceros melampus	+	+	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Aethomys chrysophilus	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Aethomys namaquensis	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alcelaphus buselaphus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Antidorcas marsupialis	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	+	-	+	+	-
Atelerix frontalis	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bos indicus	+	+	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	+	+	-	-	-	+	-	-	-	+	-	-	-	-
Bos sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Bos taurus	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Canis lupus familiaris	+	+	-	-	-	-	+	-	-	+	-	-	-	+	+	+	-	-	+	-	-	-	+	+	-	-	+	+	+	-	-
Canis mesomelas	+	+	-	-	-	-	-	-	-	+	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+
Capra hircus	+	+	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	+	+	+	-	-	-	-	-	-	+	-	+	-	-

Caracal caracal	+	+	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	-
Cephalophus natalensis	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ceratotherium simum	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Chlorocebus aethiops	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Civettictis civetta	+	+	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Connochaetes gnou	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	+	+	-
Connochaetes taurinus	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Crocuta crocuta	+	+	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Cynictis penicillata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Damaliscus lunatus	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Damaliscus pygargus	-	+	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-
Diceros bicornis	+	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Elephantulus brachyrhynchus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Elephantulus edwardii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Elephantulus myurus	-	+	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	+	+	-	-	+	-	-	-	-	-	-	+	-	+
Equus asinus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Equus burchelli	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Equus caballus	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	+	-
Equus zebra	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	+	-

Felis catus	+	+	-	-	-	-	-	+	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	+	-	+	+	-	-	-	+
Felis nigripes	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Felis silvestris	+	+	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-
Galerella pulverulenta	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Galerella sanguinea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Genetta genetta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Genetta sp.	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Genetta tigrina	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Giraffa camelopardalis	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Hippotragus equinus	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Hippotragus niger	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hystrix africaeaustralis	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ichneumia albicauda	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Ictonyx striatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemniscomys rosalia	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptailurus serval	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepus capensis	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-
Lepus saxatilis	+	+	-	+	-	-	-	-	-	+	+	-	-	+	+	-	+	+	+	-	-	-	-	-	-	-	+	-	+	+	-
Loxodonta africana	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Lycaon pictus	+	+	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Macroscelides proboscideus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mastomys coucha	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mastomys natalensis	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mellivora capensis	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Mungos mungo	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neotragus moschatus	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oreotragus oreotragus	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oryx gazella	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-
Otocyon megalotis	-	+	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Otolemur crassicaudatus	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Otomys occidentalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Otomys sp.	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-
Ovis aries	+	+	-	-	-	-	-	-	-	+	-	-	-	+	+	+	+	+	+	-	-	-	-	-	-	-	+	-	+	+	-
Panthera leo	+	+	+	+	-	-	-	-	-	+	-	-	-	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Panthera pardus	+	+	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+
Papio hamadryas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parahyaena brunnea	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Pedetes capensis	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-

Pelea capreolus	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-
Phacochoerus africanus	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Potamochoerus larvatus	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Praomys sp.	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Procavia capensis	-	+	-	-	-	-	-	-	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	+	-
Pronolagus rupestris	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	+	+	-
Proteles cristatus	-	+	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Raphicerus campestris	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Raphicerus melanotis	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Rattus rattus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Redunca arundinum	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Redunca fulvorufula	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	+	-
Rhabdomys pumilio	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-
Rhynchogale melleri	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saccostomus campestris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Soricidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Suricata suricatta	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sylvicapra grimmia	+	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Syncerus caffer	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-

Tatera leucogaster	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Taurotragus oryx	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	+	+	-	-	-	-	-	-	-	+	-	+	+	-
Tragelaphus angasii	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Tragelaphus scriptus	+	-	-	-	-	-	+	-	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tragelaphus strepsiceros	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-	+	+	-	-	-
Vulpes chama	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Mammal host species	**Tick species**																													
	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
Acinonyx jubatus	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	+	+	-
Aepyceros melampus	+	-	-	+	-	+	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	+	+	-
Aethomys chrysophilus	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-
Aethomys namaquensis	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Alcelaphus buselaphus	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Antidorcas marsupialis	-	-	-	-	-	+	-	+	+	-	+	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-
Atelerix frontalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bos indicus	+	-	-	+	-	+	+	+	+	+	+	-	+	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Bos sp.	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Bos taurus	+	-	-	+	-	+	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Canis lupus familiaris	+	-	+	+	-	+	-	-	+	+	-	-	-	+	-	+	-	-	+	-	+	+	+	-	-	+	+	+	-	-
Canis mesomelas	+	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Capra hircus	+	-	+	+	-	+	-	+	-	+	+	-	+	-	-	+	-	-	-	-	-	-	+	-	-	-	-	+	-	-
Caracal caracal	-	+	+	+	+	+	-	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Cephalophus natalensis	+	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-
Ceratotherium simum	+	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Chlorocebus aethiops	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Civettictis civetta	+	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Connochaetes gnou	-	-	-	+	-	+	-	-	+	+	+	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Connochaetes taurinus	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Crocuta crocuta	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Cynictis penicillata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Damaliscus lunatus	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Damaliscus pygargus	+	-	+	+	-	+	-	-	+	+	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Diceros bicornis	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-
Elephantulus brachyrhynchus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-

Elephantulus edwardii	-	+	-	-	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elephantulus myurus	-	+	-	-	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Equus asinus	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Equus burchelli	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Equus caballus	-	-	+	+	-	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Equus zebra	-	+	-	-	-	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Felis catus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	+	-
Felis nigripes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Felis silvestris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Galerella pulverulenta	-	+	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Galerella sanguinea	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Genetta genetta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Genetta sp.	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Genetta tigrina	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Giraffa camelopardalis	+	-	-	+	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-
Hippotragus equinus	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Hippotragus niger	-	-	-	+	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hystrix africaeaustralis	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-

Ichneumia albicauda	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Ictonyx striatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemniscomys rosalia	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-
Leptailurus serval	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-
Lepus capensis	-	-	-	+	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	+	-	-
Lepus saxatilis	+	+	-	+	+	+	+	+	+	+	+	+	-	-	+	-	+	-	+	+	-	-	+	-	-	+	+	+	+	-
Loxodonta africana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lycaon pictus	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	+	-
Macroscelides proboscideus	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mastomys coucha	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Mastomys natalensis	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Mellivora capensis	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-
Mungos mungo	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Neotragus moschatus	+	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-
Oreotragus oreotragus	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oryx gazella	-	-	+	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Otocyon megalotis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-

Otolemur crassicaudatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Otomys occidentalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Otomys sp.	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Ovis aries	+	-	+	+	-	+	-	+	+	+	+	-	+	-	-	-	-	+	+	+	-	-	+	-	-	-	-	+	-	-
Panthera leo	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	+	-
Panthera pardus	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	+	+
Papio hamadryas	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parahyaena brunnea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Pedetes capensis	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-
Pelea capreolus	-	-	-	+	-	+	-	+	-	+	+	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-
Phacochoerus africanus	+	-	-	+	-	+	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
Potamochoerus larvatus	+	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	+
Praomys sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Procavia capensis	-	+	-	-	+	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pronolagus rupestris	-	+	-	-	+	+	-	-	+	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-
Proteles cristatus	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Raphicerus campestris	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Raphicerus melanotis	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-

Rattus rattus	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Redunca arundinum	+	-	-	+	-	+	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Redunca fulvorufula	-	-	-	-	-	+	-	+	-	-	+	-	+	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
Rhabdomys pumilio	-	-	+	+	+	-	-	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Rhynchogale melleri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-
Saccostomus campestris	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Soricidae	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Suricata suricatta	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sylvicapra grimmia	+	-	-	+	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syncerus caffer	+	-	-	+	-	+	-	-	+	+	-	-	-	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-
Tatera leucogaster	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Taurotragus oryx	+	-	+	+	-	+	-	+	+	+	+	-	+	-	-	+	-	-	-	-	-	-	+	-	-	-	+	+	+	-
Tragelaphus angasii	+	-	-	+	-	+	-	-	-	-	-	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-
Tragelaphus scriptus	+	-	+	+	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-
Tragelaphus strepsiceros	+	-	-	+	-	+	-	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-
Vulpes chama	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-

*Key to the tick species

1 *Amblyomma hebraeum Koch, 1844*

2 *Amblyomma marmoreum Koch, 1844*

3 *Amblyomma nuttalli Dönitz, 1909*

4 *Amblyomma tholloni Neumann, 1899*

5 *Cosmiomma hippopotamensis _Denny, 1843*

6 *Dermacentor rhinocerinus _Denny, 1843*

7 *Haemaphysalis aciculifer Warburton, 1913*

8 *Haemaphysalis colesbergensis Apanaskevich and Horak, 2008*

9 *Haemaphysalis cooleyi Bedford, 1929*

10 *Haemaphysalis elliptica _Koch, 1844*

11 *Haemaphysalis hoodi Warburton and Nuttall, 1909*

12 *Haemaphysalis hyracophila Hoogstraal, Walker and Neitz, 1971*

13 *Haemaphysalis parmata Neumann, 1905*

14 *Haemaphysalis silacea Robinson, 1912*

15 *Haemaphysalis spinulosa Neumann, 1906*

16 *Haemaphysalis zumpti Hoogstraal and El Kammah, 1974*

17 *Hyalomma glabrum Delpy, 1949*

18 *Hyalomma rufipes Koch, 1844*

19 *Hyalomma truncatum Koch, 1844*

20 *Ixodes alluaudi Neumann, 1913*

21 *Ixodes aulacodi Arthur, 1956*

22 *Ixodes bakeri Arthur and Clifford, 1961*

23 *Ixodes cavipalpus Nuttall and Warburton, 1908*

24 *Ixodes corwini Keirans, Clifford and Walker, 1982*

25 *Ixodes drakensbergensis Clifford, Theiler and Baker, 1975*

26 *Ixodes neitzi Clifford, Walker and Keirans, 1977*

27 *Ixodes pilosus Koch, 1844*

28 *Ixodes rhabdomysae Arthur, 1959*

29 *Ixodes rubicundus Neumann, 1904*

30 *Margaropus winthemi Karsch, 1879*

31 *Rhipicentor nuttalli Cooper and Robinson, 1908*

32 *Rhipicephalus appendiculatus Neumann, 1901*

33 *Rhipicephalus arnoldi Theiler and Zumpt, 1949*

34 *Rhipicephalus capensis Koch, 1844*

35 *Rhipicephalus decoloratus Koch, 1844 _Boophilus*

36 *Rhipicephalus distinctus Bedford, 1932*

37 *Rhipicephalus evertsi evertsi Neumann, 1897*

38 *Rhipicephalus evertsi mimeticus Dönitz, 1910*

39 *Rhipicephalus exophthalmos Keirans and Walker, 1993*

40 *Rhipicephalus follis Dönitz, 1910*

41 *Rhipicephalus gertrudae Feldman-Muhsam, 1960*

42 *Rhipicephalus glabroscutatum Du Toit, 1941*

43 *Rhipicephalus kochi Dönitz, 1905*

44 *Rhipicephalus lounsburyi Walker, 1990*

45 *Rhipicephalus lunulatus Neumann, 1907*

46 *Rhipicephalus maculatus Neumann, 1901*

47 *Rhipicephalus microplus _Canestrini, 1888 _Boophilus*

48 *Rhipicephalus muehlensi Zumpt, 1943*

49 *Rhipicephalus neumanni Walker, 1990*

50 *Rhipicephalus nitens Neumann, 1904*

51 *Rhipicephalus oculatus Neumann, 1901*

52 *Rhipicephalus sanguineus _Latreille, 1806*

53 *Rhipicephalus simpsoni Nuttall, 1910*

54 *Rhipicephalus simus Koch, 1844*

55 *Rhipicephalus sulcatus Neumann, 1908*

56 *Rhipicephalus theileri Bedford and Hewitt, 1925*

57 *Rhipicephalus tricuspis Dönitz, 1906*

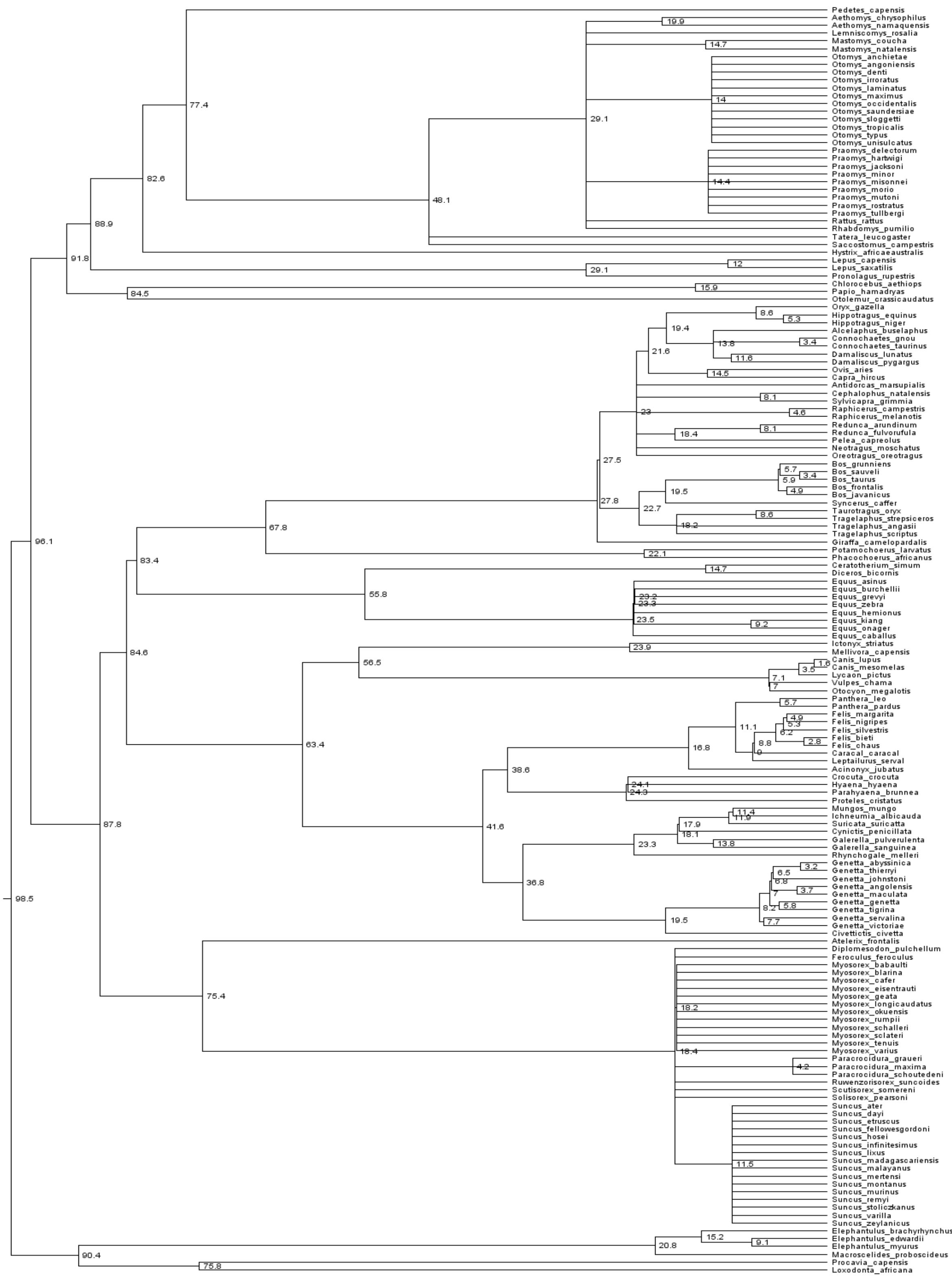
58 *Rhipicephalus turanicus Pomerantzev, 1940*

59 *Rhipicephalus warburtoni Walker and Horak, 2000*

60 *Rhipicephalus zambeziensis Walker, Norval and Corwin, 1981*

61 *Rhipicephalus zumpti Santos Dias, 1950*

Supplementary Material C. Phylogenetic tree of the 95 mammal host species extracted from Bininda-Emonds *et al.* (2007). The branch lengths are expressed in millions of years.



Supplementary Material D. The 61 tick species considered in this study, their scientific names, and indices (S_{TD} and S_{TD}*) values for ticks whatever their life stage (*all*), juveniles (*juv*) and adults (*ad*). A higher S_{TD} or S_{TD}* index indicates a more generalist parasite. *NA* means 'Not applicable' for tick species that fed on <2 mammal host species.

Tick species scientific name	**S_{TD} all**	**S_{TD} juv**	**S_{TD} ad**	**S_{TD}* all**	**S_{TD}* juv**	**S_{TD}* ad**
Amblyomma hebraeum Koch, 1844	70.99	70.99	63.96	63.63	64.98	49.84
Amblyomma marmoreum Koch, 1844	72.14	72.14	NA	61.81	61.81	NA
Amblyomma nuttalli Dönitz, 1909	16.8	16.8	NA	16.8	16.8	NA
Amblyomma tholloni Neumann, 1899	97.7	96.1	NA	97.99	96.1	NA
Cosmiomma hippopotamensis Denny, 1843	NA	NA	NA	NA	NA	NA
Dermacentor rhinocerinus (Denny, 1843)	71.66	41.77	14.7	47.30	43.75	14.7
Haemaphysalis aciculifer Warburton, 1913	65.11	71.73	58.99	62.24	47.07	69.69
Haemaphysalis colesbergensis Apanaskevich and Horak, 2008	87.8	NA	87.8	87.80	NA	87.8
Haemaphysalis cooleyi Bedford, 1929	NA	NA	NA	NA	NA	NA
Haemaphysalis elliptica (Koch, 1844)	76.42	78.42	65.97	60.07	80.53	30.59
Haemaphysalis hoodi Warburton and Nuttall, 1909	NA	NA	NA	NA	NA	NA
Haemaphysalis hyracophila Hoogstraal, Walker and Neitz, 1971	95.8	95.8	NA	97.45	94.85	NA
Haemaphysalis parmata Neumann, 1905	46.9	46.9	26	31.85	34.93	27.00
Haemaphysalis silacea Robinson, 1912	61.83	61.83	45.09	24.05	23.88	16.68
Haemaphysalis spinulosa Neumann, 1906	53.46	50.35	53.46	47.37	43.99	46.93
Haemaphysalis zumpti Hoogstraal and El Kammah, 1974	51.49	33.43	51.49	38.65	27.25	39.35
Hyalomma glabrum Delpy, 1949	81.42	83.73	56.05	80.39	35.49	66.41
Hyalomma rufipes Koch, 1844	63.68	60.95	44.97	72.76	22.21	51.26
Hyalomma truncatum Koch, 1844	72.04	88.08	62.83	75.46	34.17	60.39
Ixodes alluaudi Neumann, 1913	96.1	NA	NA	96.1	NA	NA
Ixodes aulacodi Arthur, 1956	NA	NA	NA	NA	NA	NA

Ixodes bakeri Arthur and Clifford, 1961	86.13	73.77	98.5	90.08	86.53	98.74
Ixodes cavipalpus Nuttall and Warburton, 1908	84.6	NA	84.6	84.6	NA	84.6
Ixodes corwini Keirans, Clifford and Walker, 1982	63.4	NA	63.4	63.22	NA	63.22
Ixodes drakensbergensis Clifford, Theiler and Baker, 1975	NA	NA	NA	NA	NA	NA
Ixodes neitzi Clifford, Walker and Keirans, 1977	NA	NA	NA	NA	NA	NA
Ixodes pilosus Koch, 1844	65.25	64.42	61.44	73.41	54.32	51.56
Ixodes rhabdomysae Arthur, 1959	84.6	NA	84.6	84.6	NA	84.6
Ixodes rubicundus Neumann, 1904	80.12	85.59	76.01	84.02	76.83	67.89
Margaropus winthemi Karsch, 1879	79.81	79.81	54.1	75.77	76.81	73.32
Rhipicentor nuttalli Cooper and Robinson, 1908	67.25	NA	67.25	85.97	NA	70.22
Rhipicephalus appendiculatus Neumann, 1901	67.65	66.78	63.33	49.32	42.23	64.89
Rhipicephalus arnoldi Theiler and Zumpt, 1950	88.71	87	86.13	93.62	93.66	79.28
Rhipicephalus capensis Koch, 1844	72.33	83.55	55.73	72.09	60.10	64.45
Rhipicephalus decoloratus Koch, 1844 Boophilus	66.64	67.87	54.3	55.81	51.99	62.62
Rhipicephalus distinctus Bedford, 1932	90.42	89.48	96.03	97.15	97.06	95.83
Rhipicephalus evertsi evertsi Neumann, 1897	64.49	64.33	51.90	60.91	58.76	60.26
Rhipicephalus evertsi mimeticus Dönitz, 1910	96.1	NA	NA	96.1	NA	NA
Rhipicephalus exophthalmos Keirans and Walker, 1993	58.99	72.6	40.3	71.96	28.23	35.21
Rhipicephalus follis Dönitz, 1910	80.39	81.97	69.64	73.02	90.23	64.55
Rhipicephalus gertrudae Feldman-Muhsam, 1960	78.06	71.41	63.52	86.67	53.19	79.18
Rhipicephalus glabroscutatus Du Toit, 1941	61.84	61.84	55.87	28.83	28.10	34.19
Rhipicephalus kochi Dönitz, 1905	55.15	59.25	55.15	41.29	51.70	30.98
Rhipicephalus lounsburyi Walker, 1990	49.11	NA	37.37	27.53	NA	24.50
Rhipicephalus lunulatus Neumann, 1907	84.6	NA	84.6	84.6	NA	84.6
Rhipicephalus maculatus Neumann, 1901	68.25	63.17	74.69	62.16	43.02	78.68
Rhipicephalus microplus (Canestrini, 1888) Boophilus	46.82	27.5	46.82	29.93	27.57	29.96
Rhipicephalus muehlensi Zumpt, 1943	56.41	56.41	37.47	26.67	27.43	19.84
Rhipicephalus neumanni Walker, 1990	22.26	NA	22.26	22.25	NA	22.25

Rhipicephalus nitens Neumann, 1904	63.7	63.7	63.7	33.99	33.68	43.29
Rhipicephalus oculatus Neumann, 1901	74.18	79.68	66.98	43.75	36.37	44.64
Rhipicephalus sanguineus (Latreille, 1806)	NA	NA	NA	NA	NA	NA
Rhipicephalus simpsoni Nuttall, 1910	77.53	NA	84.6	77.53	NA	84.6
Rhipicephalus simus Koch, 1844	77.86	73.90	70.09	62.41	75.27	52.28
Rhipicephalus sulcatus Neumann, 1908	63.4	NA	63.4	63.4	NA	63.4
Rhipicephalus theileri Bedford and Hewitt, 1925	56.5	NA	NA	56.5	NA	NA
Rhipicephalus tricuspis Dönitz, 1906	96.1	NA	96.1	96.1	NA	96.1
Rhipicephalus turanicus Pomerantzev, 1940	66.67	79.68	61.04	69.27	65.99	65.07
Rhipicephalus warburtoni Walker and Horak, 2000	81.46	86.90	72.79	88.01	85.67	76.11
Rhipicephalus zambeziensis Walker, Norval and Corwin, 1981	72.30	70.43	75.72	80.29	81.99	66.53
Rhipicephalus zumpti Santos Dias, 1950	84.6	NA	84.6	84.6	NA	84.60