Ticks associated with wild mammals in Ghana

Y. Ntiamoa-Baidu[1]*, C. Carr-Saunders[2], B.E. Matthews[2], P.M. Preston[2] and A.R. Walker[3]

[1]Zoology Department, University of Ghana, Legon, Accra, Ghana: [2]Institute for Immunology and Infection Research, School of Biological Sciences, University of Edinburgh, King's Buildings, West Mains Road, Edinburgh, EH9 3JT, UK: [3]Department of Tropical Animal Health, Royal (Dick) School of Veterinary Studies, University of Edinburgh, Roslin, EH25 9RG, UK

Abstract

The host ranges of a collection of 21 tick species found on wild mammals in the savanna, forests and coastal zone of Ghana suggested that most species were adapted to feeding mainly on host species within a single mammalian order, i.e. on artiodactyls (bovids/suids), carnivores, rodents or pholidotes (pangolins). Only a few species were dispersed evenly across a range of orders. Seven out of ten of the most common ticks on forest mammals were significantly associated with a particular host species or a group of closely related host species, which could be viewed as their major host or hosts, but they were also recorded much less frequently on a wide range of host species. Two other species were confined to their major hosts. Only one species appeared to be widely dispersed on forest mammals and to lack a particular major host. The majority of tick species therefore occurred on hosts with very distinctive biological, behavioural and ecological characteristics. The study provided no evidence to support the view that host specificity is an artefact of sampling. Finding that the tick species on Ghanaian wild mammals occurred on particular hosts, as well as in distinct habitats, indicated that tick–host associations are important for tick survival and confirmed the importance of climate and vegetation in tick distribution.

Introduction

Historically, ticks have been viewed as organisms exhibiting a range of feeding associations with their vertebrate hosts. The concept of a range of specificity in tick–host feeding associations, as first applied to argasid and ixodid tick species, was based on global reports of the natural tick–host feeding associations exhibited by adult ticks and immature stages (Hoogstraal & Aeschlimann, 1982). These authors defined 'host specificity' as an association between a tick species and a vertebrate species, or a clearly related group of vertebrates, which was critical for reproduction and

continued survival of the tick species. At least 700 of 800 species of ticks were considered to exhibit a 'strict total' or less limited degree of specificity during all stages of their life cycles; very few were thought to be catholic in their tastes – feeding on a wide range of unrelated vertebrates (Hoogstraal, 1978; Hoogstraal & Aeschlimann, 1982). These authors considered host specificity to be one of several important biological factors contributing to limiting ecological and geographical distributions and population densities of most tick species. Other important factors – tick–host selection, distribution, tick questing behaviour and host foraging patterns, life cycle extensions (diapause) and seasonal dynamics – were considered to relate to the fact that most ticks spend considerable periods of time as free-living organisms. These ideas and the concept of co-evolution of ticks with their hosts were accompanied by a tendency to associate the geographical distributions of ticks both with any hosts for which they appeared to have a high specificity and with the

*Current address: World Wide Fund for Nature, Avenue du Mont-Blanc, 1196 CH Gland, Switzerland
Fax: 0041 22 364 4238
E-mail: YNtiamoa@wwfint.org

environmental determinants required by free-living ticks (Hoogstraal & Aeschlimann, 1982). Sonenshine (1993) later defined ticks as being either specialist species adapted to feed on a particular host taxon (species, genus, family or order) or as generalists feeding opportunistically on any vertebrate animal encountered.

In marked contrast, Klompen *et al*. (1996) suggested that tick–host-association patterns might be explained by restrictions imposed by biogeographical and ecological specificity rather than by host specificity. These authors viewed the evolution of ticks as an adaptation to a particular habitat type and not to a particular host taxon. In their scheme, the distribution of a tick species is determined by environmental conditions and within its habitat, a tick species will feed on any species of host it encounters. They found a positive correlation between the number of records and the number of host species or families of ticks of the genus *Ixodes* and between the number of records and the number of host species of the argasid sub-genus *Carios*. These findings were taken as evidence to support the hypothesis that ticks are not host specific and raised the possibility that the distinction between 'strict total' and less specific categories of specificity postulated by Hoogstraal & Aeschlimann (1982) was largely due to differences between rarely and frequently collected species. According to this scheme (Klompen *et al*., 1996), the concept of 'host specificity' is an artefact of incomplete sampling and the number of hosts infested by a tick species will be found therefore to increase with sampling effort.

The concept of host specificity was subsequently analysed using a very large set of data on African ticks (43,615 records) compiled from literature sources (Cumming, 1998). The author concluded that, while many ticks are relatively catholic in host preferences, there are some which specialize as suggested by Hoogstraal & Aeschlimann (1982) and that tick species range from specialists to generalists with some ticks exhibiting intermediate degrees of specificity. Cumming (1998) argued that there are several well-sampled tick species that are found only on hosts of a particular type and not on other well sampled, potential hosts living in the same environment and rejected the suggestion by Klompen *et al*. (1996) that the perception of host specificity in these instances is an artefact.

Unfortunately, at the time that Cumming's database was compiled only very sparse data were available for Ghana. Neither the records of ticks on domestic animals reported by Walker & Koney (1999) nor those on wild mammals reported by Ntiamoa-Baidu *et al*. (2004) had been published. In addition, the list of ticks from Ghana that was included may not have been entirely valid because, as described by Ntiamoa-Baidu *et al*. (2004), it included early reports of ticks whose specific identities are no longer clear and a number of tick species that have recently undergone major taxonomic revisions (Pegram *et al*., 1987a,b,c; Pegram & Walker, 1988; Walker *et al*., 1988; Camicas *et al*., 1998).

The tick collection from Ghanaian wild mammals described by Ntiamoa-Baidu *et al*. (2004) comprises 1863 records of adult ticks of 21 species, whose identities have been checked against current taxonomic understanding. The adult ticks were collected during the period 1971–1978 from 1258 hosts representing 28 species, 13 families and six orders of wild mammals. These animals were not caught specifically for this study but were examined for ticks either at bushmeat market centres in four different areas of Ghana or in the Mole National Park, where they had been captured for other purposes. The fact that the wild hosts described here were not infested by the ticks commonly found on domestic stock in Ghana (Walker & Koney, 1999) indicated that the ticks were derived from localized tick–host associations, that had not been disturbed by the introduction of exotic tick species by domestic stock or by the adaptation of the indigenous ticks of mammals to hosts of unnaturally wide distributions, such as cattle.

The collection therefore provided suitable data with which to assess tick–host interactions and to look for statistical evidence of host specificity, while adding to our knowledge of the biology of Ghanaian ticks. Differences in the nature of the tick–host associations were very clear-cut and the data could be used for regression analyses to examine the question of whether ticks are specific for one host or not, as described by Klompen *et al*. (1996), and in the chi-square goodness-of-fit test to analyse the patterns of dispersion of the ticks on their hosts. It was hoped that this approach would help to explain why some authors claim that ticks exhibit a high degree of host specificity (Hoogstraal & Aeschlimann, 1982; Sonenshine, 1993; Cumming, 1998) while others claim they are not host specific (Klompen *et al*., 1996).

Materials and methods

The climate and ecological zones of Ghana, the tick collection sites (bushmeat market centres and Mole National Park), the methods used to sample hosts for ticks, identification of ticks and hosts, and the creation and searching of the Microsoft Access database of the information relating to the ticks have been described previously (Ntiamoa-Baidu *et al*., 2004). The information relating to adult ticks, their hosts and distribution in different vegetation zones examined in this paper was described in tables 2–6 in Ntiamoa-Baidu *et al*. (2004). Throughout the present text, as in the previous paper, the number of records refers to the number of individual animals on which a given tick species was found and not to the number of ticks collected from individual animals.

Mammalian hosts and assessment of their relative abundance in different vegetation zones

The wild mammals on which ticks were recorded are listed in appendix 1. Their scientific names and taxonomic designations are as described by Kingdon (2001) and the taxonomic authorities for their scientific names were obtained from Wilson & Reeder (1993). The relative abundance of the different mammal species in the three different vegetation zones of Ghana (savanna, forests, coastal zone) was expressed as the number of mammals of a given species examined at a particular collection point calculated as a percentage of the total number of individuals of that species examined at all collection points.

Host ranges of ixodid ticks

The host ranges of the 21 species of ticks belonging to the family Ixodidae collected from Ghanaian wild mammals, that had been revealed by querying the database, are given in appendix 2. For each tick species, the appendix lists the authority name according to Horak *et al*. (2002), the number

of records of each tick species found in the collection, the number of each species of mammals (listed by common name) infested by each tick species and the order and family to which each mammalian species belongs.

Approaches to assessing host specificity of ticks

The host ranges of the ticks were assessed for evidence of host specificity as follows. First, the overall tick–host associations recorded in the three different vegetation zones were assessed to see if any tick species was closely associated with a particular host species or a group of related host species within a family or order. The chi-square (χ^2) goodness-of-fit test was used to determine if any tick had a significant affinity for any particular type or types of mammalian species. Second, the patterns of dispersion of the ten most common ticks on the forest mammals were analysed. The χ^2 goodness-of-fit test was used to determine if any species of tick exhibited a significant association with any mammal species or group of closely related species. If a significant association was found, this was interpreted as identifying a mammal or a group of related mammals for which the tick exhibited host specificity. Third, regression analyses were used to test the hypothesis that tick species are not associated with any one particular host species.

Assessment of the overall tick–host associations recorded in the savanna, forests and coastal zone

The number of records of the tick species on different mammals in the three vegetation zones (appendix 2) could not be used as a direct measure of the extent to which different mammals were infested by different ticks because the sizes of the different groups of mammals examined varied markedly. The extent to which the 18 mammal species, that occurred at least five times in collections from the three zones (savanna, forests and coastal), were infested by the 18 tick species found on them was therefore calculated as follows. The proportion of each individual mammal species infested with a given tick species was expressed as a percentage of the total number of that mammal species examined for ticks in all three zones, using data from tables 2–6 in Ntaimoa-Baidu *et al*. (2004). For example, eight out of the ten Togo hares were infested with *Rhipicephalus sulcatus* Neumann giving a percentage infestation of 80%; 412 out of 439 bushbucks were infested with *Haemaphysalis parmata* Neumann giving a percentage infestation of 94%. Of the mammal species that were examined less than five times, the cheetah, jackal, lion, leopard, marsh mongoose and white-tailed mongoose were grouped together as carnivores and the two green monkeys and one spot-nose monkey were grouped as primates. The different sample sizes reflected the frequency with which hunters brought different mammals to bushmeat markets.

The different patterns of dispersion of the tick species on different types of hosts were analysed with the χ^2 goodness-of-fit test to determine if the ticks were randomly distributed or if any tick had any significant affinity for any particular type or types of mammalian species (Fowler & Cohen, 1996). The mammals examined in the savanna were grouped into bovids, suids, lagomorphs, primates, carnivores or rodents. The mammals examined in the forests and coastal zone were grouped into artiodactyls (bovids, suids), carnivores, rodents or pholidotes. The tick records used for these analyses were

derived directly from the data in tables 2–6 in Ntiamoa-Baidu *et al*. (2004); they are not shown here. The number of individuals of the different mammalian species examined for ticks was not uniform; for example, there were 439 bush-bucks, 136 black duikers, 39 civets. Calculating the expected frequency values of a tick species on the different host species compensated for this discrepancy. For each tick species, the number of individuals of a given host species examined for that tick was first expressed as a proportion of the total host sample size, i.e. by dividing the number of individuals of the given host species by the total number of hosts examined for that tick. The expected frequency value of a tick species on a given host species was then derived by multiplying the proportion of the total hosts represented by that host species by the total number of records of the tick species on all its hosts.

The following formula was used to calculate χ^2: Σ((observed frequency of a tick on a particular mammal or group of mammals $-$ expected frequency of a tick on a particular mammal or group of mammals)^2/expected frequency of a tick on a particular mammal or group of mammals). The degrees of freedom were n-1; a test was valid only if none of the expected frequencies were <1 and no more than 20% of frequencies were <5. $P<0.005$ was taken to indicate a significant difference between the observed and expected frequency of a tick species on a particular mammal or group of mammals and to infer that ticks were not distributed randomly but exhibited significant associations with their host(s).

Assessment of the patterns of dispersion of tick species on forest mammals

The patterns of dispersion of the ten most common tick species on forest mammals, which had been examined at Sunyani, Kumasi and Swedru, were visualized by plotting the level of infestation of a mammal species by a particular tick species. The level of infestation was calculated by expressing the proportion of each of the nine mammal species infested with a given tick species as a percentage of the total number of that mammal species examined for ticks in the forests. The records of the tick species on different mammal species used for this calculation were derived from tables 2–6 in Ntiamoa-Baidu *et al*. (2004) and are tabulated below. These records were then used to analyse the different patterns of dispersion of tick species on different mammals by employing the χ^2 goodness-of-fit test, described above, to assess the probability that the ticks were not distributed randomly and that the patterns of dispersion had not arisen by chance. If any species of tick exhibited a significant association with any mammal species or group of closely related species, this was interpreted as identifying a mammal or a group of mammals for which the tick exhibited host specificity. If the tick species had been recorded significantly more often on a particular host(s) than any other host(s) such that $P<0.005$, the former host(s) were viewed as the major host(s) for the tick species in question. The test was used to assess the significance of the different distributions of tick species recorded: on ungulates (bush-bucks, four species of duikers, royal antelopes) and non-ungulate mammals (grasscutters, civets, pangolins); on the three genera of ungulates (*Tragelaphus, Cephalophus, Neotra-gus*); on the six different species of ungulates (bushbucks, four species of duikers, royal antelopes); on the three

different species of non-ungulates (civets, grasscutters and pangolins).

Testing the hypothesis that tick species are not associated with particular host species

The hypothesis that ticks are not associated with a particular host species was tested by analysing the relationship between the number of records of a tick species and the number of host species on which it occurred in two ways. In the first instance, the relationship between tick species and their hosts was tested for the total 21 tick species on the 27 host species, using data tabulated below and linear regression as employed by Klompen et al. (1996). A significant, positive regression was taken to indicate that the number of host species infested by a given tick species was linked to the number of records of that tick species, i.e. that the tick did not exhibit any strong natural association with a particular host species. Conversely, a lack of significance between the number of records of a given tick species and the number of host species would have meant that the tick species exhibited a significant natural association with that host species. In the second instance, host specificity was tested for ticks that had been collected 20 times or more, using data tabulated below. For each tick species, the host species that had proportionally the highest level of infestation, i.e. the highest percentage of infested hosts, was listed against this tick. This host could be regarded as the one for which the tick had the most specificity, i.e. the major host. The proportion of the named host species found infested with each tick species was obtained by dividing the percentage infestation of the host by 100. The ticks were arranged in descending order of this proportion. The hypothesis that host specificity exists led to the prediction that there would be a negative correlation between the proportion of the major host infested and the total numbers of host species infested by each tick species. The proportion data were arcsine transformed for analysis using Pearson's correlation coefficient.

Results

Distribution of the Ghanaian wild mammals examined for ticks

The 28 mammals described in this paper are listed in appendix 1. Their relative abundance at the five collection sites in the three different vegetation zones (table 1) shows a definite separation of species. Some occurred only in the savanna zone (large bovids, warthogs). Some occurred in both savanna and forest zones (two species only – Togo hare, red river hog). A few species were confined to the forest zone (red-flanked duiker, pangolin, civet, ground squirrel). The remaining species occurred in both forest and coastal zones. A single species, the giant pouched rat, was found in all zones.

Host ranges of all tick species recorded on mammals in this collection

The host ranges of the 21 tick species belonging to the family Ixodidae found on wild mammals are shown in appendix 2. For each tick species, the appendix shows the total number of records on all mammal species and the number of records on each individual mammal species. These data were used, as described below, to assess and analyse the extent to which the ticks in the collection exhibited host specificity.

Table 1. Relative abundance of the mammal species from which adult ticks were collected in different vegetation zones in Ghana.

Mammals	Total number examined	Vegetation zones and collection sites				
		Savanna	Semi-deciduous forest			Coastal
		Mole	Sunyani	Kumasi	Swedru	Kantamanto
Kongoni	22	100	0	0	0	0
Kob	7	100	0	0	0	0
Waterbuck	6	100	0	0	0	0
Warthog	12	100	0	0	0	0
Red river hog	6	33	17	0	33	17
Togo hare	10	90	10	0	0	0
Bushbuck	439	<1	76	22	<1	1
Royal antelope	70	0	26	43	14	17
Black duiker	136	0	16	73	6	5
Maxwell's duiker	237	0	37	36	9	17
Bay duiker	33	0	91	0	3	6
Red-flanked duiker	16	0	81	19	0	0
Ground squirrel	5	0	0	100	0	0
Grasscutter	140	0	0	63	36	1
Giant pouched rat	25	4	24	20	4	48
Brush-tailed porcupine	20	0	90	0	5	5
Civet	39	0	62	38	0	0
Pangolin	26	0	12	88	0	0

The relative abundance of the mammal species was expressed as the number of mammals of a given species examined at a particular collection point calculated as a percentage of the total number of individuals of that species examined at all collection points.
Distribution of animals examined less than five times in the collections from: Mole: side-striped jackal, leopard, marsh mongoose, white-tailed mongoose, green monkey, crested porcupine; Kumasi: cheetah, lion (in zoo); Kantamanto: spot-nose monkey.

Table 2. Occurrence of adults of different tick species on mammals examined in the savanna, forests and coastal zone of Ghana.

Hosts \ Tick species	Rhipicephalus sulcatus (23)	R. cuspidatus (9)	Amblyomma variegatum (15)	Haemaphysalis aciculifer (5)	R. lunulatus (11)	R. senegalensis (50)	R. simpsoni (118)	Ixodes oldi (12)	I. cumulatimpunctatus (60)	I. muniensis (279)	Hae. leachi (45)	I. rasus (3)	A. compressum (30)	Hae. houyi (3)	R. ziemanni (178)	Hae. parmata (799)	I. moreli (135)	I. aulacodi (85)
Savanna																		
Kongoni [22]	36*	0	27	5	18	0	0	0	0	0	0	0	0	0	0	0	0	0
Kob [7]	0	0	14	45	29	29	14	0	0	0	0	0	0	0	0	0	0	0
Waterbuck [6]	0	50	7	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0
Warthog [12]	16	50	16	0	0	33	33	0	0	0	0	0	0	0	0	0	0	0
Red river hog [6]	0	0	0	0	16	0	0	0	17	0	0	0	0	0	16	0	0	0
Togo hare [10]	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primates [3]	66	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0
Carnivores [6]	50	0	50	0	0	17	17	0	0	0	0	0	0	0	0	17	0	0
Forests and coastal zone																		
Bushbuck [439]	0	0	0.5	0	0.5	0.5	1	0	5	39	0	0	0.5	0	31	94	13	2
Royal antelope [70]	0	0	0	0	0	11	9	0	0	6	0	0	0	0	7	63	1	7
Black duiker [136]	0	0	0	0	0	4	4	0	7	21	1	0	2	0	4	82	26	5
Maxwell's duiker [237]	0	0	0	0	0	10	2	0	1	16	1	0	0	0	6	71	10	6
Bay duiker [33]	0	0	0	0	0	3	0	0	45	70	3	0	0	0	18	70	24	0
Red-flanked duiker [16]	0	0	0	0	0	0	6	0	0	25	0	0	0	0	13	81	19	0
Ground squirrel [5]	0	0	0	33	0	0	0	0	0	0	0	0	0	60	0	0	0	0
Grasscutter [140]	0	0	0	0	0	1	58	0	1	3	2	1	0	0	1	12	2	33
Giant pouched rat [25]	0	0	0	0	0	4	32	0	20	0	0	0	0	0	0	16	0	20
Brush-tailed porcupine [20]	0	0	0	0	0	5	5	0	0	0	0	5	0	0	0	5	0	0
Civet [39]	0	0	0	0	0	0	3	31	13	10	97	3	0	0	13	8	5	3
Pangolin [26]	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	4	0	0

* Proportion of each individual mammal species infested with a given tick species expressed as a percentage, calculated from data in tables 2–6 (Ntiamoa-Baidu et al., 2004).
[ ] total number of individuals of that species examined; ( ) total number of records for that tick species.

Assessment of the overall tick–host associations observed in the savanna, forests and coastal zone

The different proportions of the mammal species infested by the different tick species (table 2), expressed as percentage infestation, showed very clearly that some tick species were found only on the mammals examined in the savanna zone. Other ticks were only found on the mammals examined in the forests and the coastal zone. Only two ticks, *Rhipicephalus simpsoni* Nuttall and *Rhipicephalus senegalensis* Koch, occurred in all three vegetation zones.

Within the different vegetation zones, some mammalian species were much more frequently infested with certain tick species than others indicating strong associations between these mammals and their ticks. In contrast, some mammals were only infrequently infested or not infested at all with certain tick species indicating the absence of any strong association between tick and mammal. Some tick species showed marked associations with particular mammals belonging to certain families or orders, such that some ticks were associated with artiodactyls (bovids and/or suids), some with rodents, two species with a carnivore and one species with pholidotes (pangolins). While the majority of ticks were associated with a species or a group of closely related species, that might be termed their major host or hosts, the majority of ticks were associated less frequently with a much wider range of hosts as well. Of ticks recorded more than once, only two species, *Haemaphysalis houyi* Nuttall & Warburton and *Ixodes oldi* Nuttall, were recorded from a single host species. The three specimens of *Ixodes rasus* Neumann were found on a grasscutter, a brush-tailed porcupine and a civet. Of the 16 species of tick recorded more than five times, five were markedly associated with a number of mammal species within an order, five with a number of mammal species within a family and three with one host species only. Only three tick species out of 16 were evenly dispersed across more than one order of mammals.

Members of the order Artiodactyla (i.e. both suids and bovids) were the most frequently infested hosts of *Amblyomma variegatum* Koch, *Rhipicephalus lunulatus* Neumann and *Rhipicephalus ziemanni* Neumann. A quarter of the kongonis were infested with *A. variegatum*, a third of the kobs and the waterbucks were infested with *R. lunulatus* and a third of the bushbucks with *R. ziemanni*. Two tick species showed a marked association with the order Rodentia in that grasscutters and giant pouched rats were the most frequently infested hosts of both *Ixodes aulacodi* Arthur and *R. simpsoni*.

The hosts most frequently infested by *Haemaphysalis aciculifer* Warburton, *Hae. parmata*, *Ixodes moreli* Arthur and *Ixodes muniensis* Arthur & Burrow were all members of the family Bovidae. Almost half of the kobs were infested with *Hae. aciculifer*, almost all of the bushbucks with *Hae. parmata*, a quarter of the black duikers with *I. moreli* and nearly three quarters of the bay duikers with *I. muniensis*. *Rhipicephalus cuspidatus* Neumann was found solely on members of the family Suidae.

Three tick species showed a marked association with one particular host species. Most specimens of *Amblyomma compressum* (Macalister) were found on pangolins (order Pholidota) and, with the exception of one specimen of *Hae. parmata*, *A. compressum* was the only tick species found on pangolins. All but one of the civets were infested with *Haemaphysalis leachi* (Audouin). All 12 records of *Ixodes oldi*

(one of the only two species in the collection that were found on only one host species) came from civets. A third of all civets examined were infested with this tick species.

Three tick species were more evenly recorded across a variety of mammalian orders. *Ixodes cumulatimpunctatus* Schulze was recorded on small bovids, suids, rodents and civets. *Rhipicephalus senegalensis* was recorded on large and small bovids, suids, primates, carnivores and rodents. *Rhipicephalus sulcatus* was recorded on bovids, primates, carnivores including a marsh mongoose, and the Togo hare. While this tick did not appear to have a particular association with the hare, it was the only species found on the hare with 80% being infested.

Only isolated examples of some host species, i.e. cheetah, jackal, lion (in the zoo), leopard, spot-nose monkey, green monkey, marsh mongoose, white-tailed mongoose and crested porcupine were examined. The records from these single specimens are represented in table 2 as belonging to a group of six carnivores or a group of three primates. Only very few specimens of a limited number of tick species were collected from them – *A. variegatum*, *R. senegalensis*, *R. simpsoni* and *R. sulcatus*. The crested porcupine was infested with single specimen of *R. sulcatus* (appendix 2). Three tick species were collected only once – *Rhipicephalus* (*Boophilus*) *geigyi* (Aeschlimann & Morel) from a kongoni, *Hyalomma truncatum* Koch from a warthog and *Ixodes loveridgei* Arthur from a civet (appendix 2).

The χ^2 goodness-of-fit test was used to analyse the different patterns of dispersion of the ticks recorded on mammals examined in the savannah or in the forests and the coastal zone combined to see if any tick had a significant affinity for any particular type of mammalian species. The different patterns of dispersion of *R. sulcatus*, *R. cuspidatus*, *A. variegatum*, *Hae. aciculifer*, *R. lunalatus*, *R. senegalensis* and *R. simpsoni* on mammals in the savannah were tested by grouping the host species into bovids, suids, lagomorphs, primates, carnivores or rodents. However, the number of records of each tick species and the number of hosts examined were insufficient to carry out any analyses as in all tests >20% of the expected frequency values were <5. The different patterns of dispersion of *R. senegalensis*, *R. simpsoni*, *I. cumulatimpunctatus*, *I. muniensis*, *Hae. leachi*, *A. compressum*, *R. ziemanni*, *Hae. parmata*, *I. moreli* and *I. aulacodi* on mammals examined in the forests and the coastal zone were tested by grouping the host species into artiodactyls, rodents, carnivores or pangolins. In this case, with the exception of the tests on *Hae. parmata* and *I. muniensis*, the number of records of each tick species and the number of hosts examined were again insufficient to carry out the analyses as >20% of the expected frequency values were <5. The tests carried out with *Hae. parmata* and *I. muniensis* both showed that there were significantly more records of these tick species on artiodactyls and fewer on rodents, carnivores and pangolins than would be expected if the ticks were randomly distributed (for *Hae. parmata*, $\chi^2 = 156.60$; for *I. muniensis*, $\chi^2 = 56.87$; for both tick species, $n = 4$; $P < 0.005$).

Assessment of the patterns of dispersion of tick species on forest mammals

The patterns of dispersion of the ten most common tick species (*A. compressum*, *Hae. leachi*, *Hae. parmata*, *I. aulacodi*, *I. cumulatimpunctatus*, *I. moreli*, *I. muniensis*, *I. oldi*, *R. simpsoni* and *R. ziemanni*) on the nine species of mammals examined
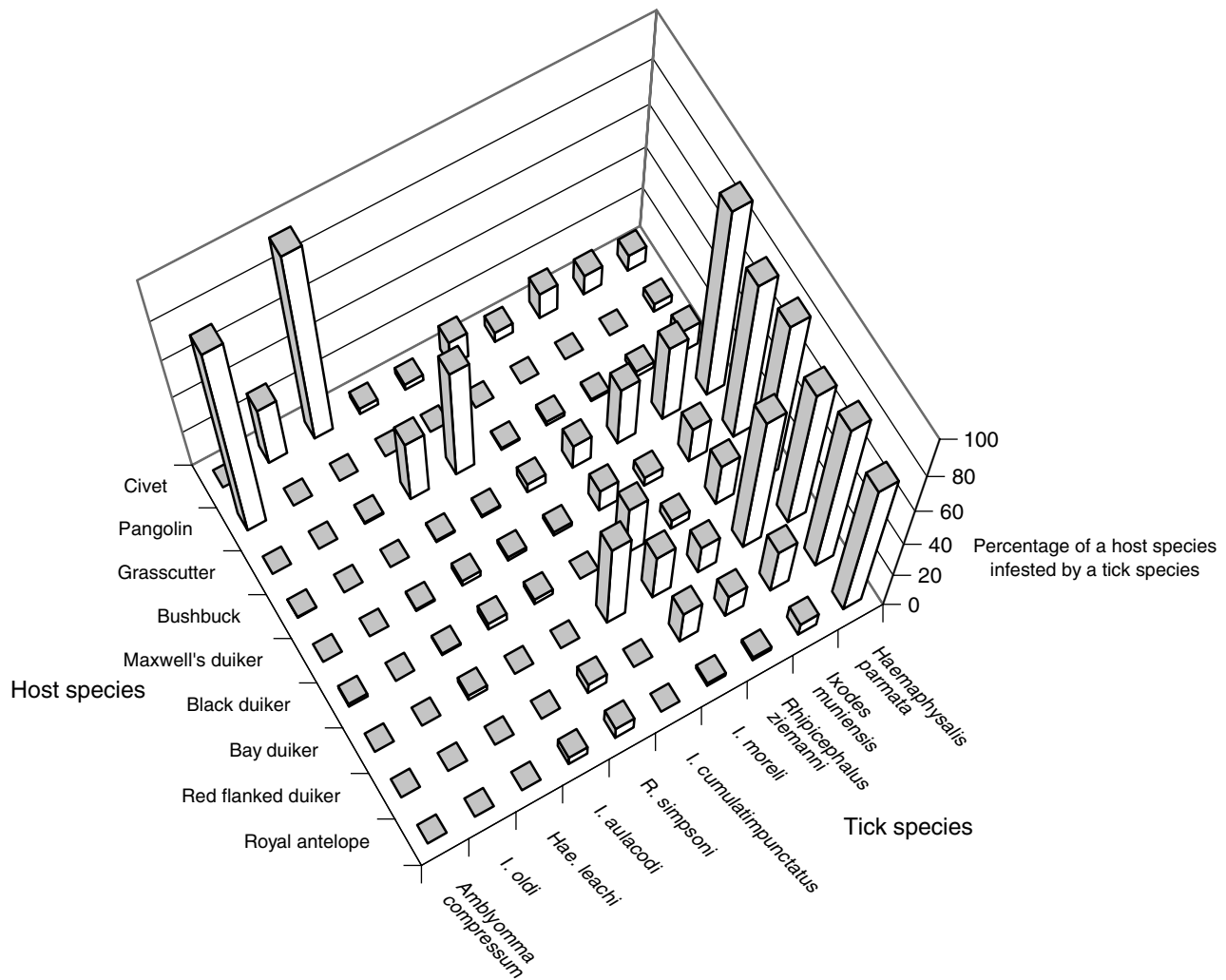
Fig. 1. Patterns of dispersion of the ten most common tick species on the nine most common species of mammals examined more than 15 times in the semi-deciduous forest zones at Sunyani, Kumasi and Swedru. The level of infestation was calculated by expressing the proportion of each of the nine mammal species infested with a given tick species as a percentage of the total number of that mammal species examined for ticks in the forests. Data derived from table 3.

more than 15 times at Sunyani, Kumasi and Swedru were analysed in depth. The marked differences in levels of infestation of the different host species by a given tick species (fig. 1), calculated from data in table 3, indicated that the ticks were not randomly dispersed on their hosts, but exhibited strong associations with particular host species. These varied levels of infestation of different hosts by a tick species suggested that some hosts served as major hosts for certain ticks. Ungulates appeared to be the major hosts of *Hae. parmata*, *I. moreli*, *I. muniensis, R. ziemanni* and possibly *I. cumulatimpunctatus*. Grasscutters appeared to be the major host for *I. aulacodi* and *R. simpsoni*, civets for *Hae. leachi* and *I. oldi*, and pangolins for *A. compressum*. These patterns also showed a marked absence of some tick species from certain host species.

The data shown in table 3 were used in the χ^2 goodness-of-fit test to analyse the probability that the ticks were not distributed randomly and that the distinct patterns of dispersion of nine of the tick species on the nine host

species had not arisen by chance. As shown in table 4, in most cases the probability that ticks were randomly distributed was < 0.005, indicating that the patterns of dispersion had not, for the most part, arisen by chance. The results of the tests indicated that eight of the tick species exhibited significant natural associations with a particular mammalian species or group of related mammalian species. There were insufficient records of *I. oldi* to analyse its distribution in any of the tests.

The significance of the absence or presence of each of the tick species on the different groups of host species was tested first by comparing the combined number of records of each tick species on all ungulate hosts (bushbucks, four species of duikers, royal antelopes) with the combined number of records of each tick species on all non-ungulate hosts (grasscutters, civets, pangolins). The probability that the high level of infestation of ungulates by *Hae. parmata*, *I. moreli*, *I. muniensis* and *R. ziemanni* and the low level of infestation of non-ungulates by these four tick species

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Table 3. Occurrence of tick species on different host species of forest mammals in Ghana.

Hosts / Tick species	*Amblyomma compressum*	*Haemaphysalis parmata*	*Ixodes muniensis*	*Rhipicephalus ziemanni*	*I. moreli*	*I. cumulatimpunctatus*	*R. simpsoni*	*I. aulacodi*	*Hae leachi*	*I. oldi*
Pangolin (*Manis tricuspis*) (26)	26	1	0	0	0	0	0	0	0	0
Bushbuck (*Tragelaphus scriptus*) (433)	2	411	173	136	58	20	6	6	0	0
Maxwell's duiker (*Cephalophus maxwelli*) (196)	0	161	38	10	23	3	3	6	2	0
Black duiker (*Cephalophus niger*) (129)	2	109	29	6	36	0	4	5	1	0
Bay duiker (*Cephalophus dorsalis*) (31)	0	23	23	5	8	15	0	0	1	0
Red-flanked duiker (*Cephalophus rufilatus*) (16)	0	13	4	2	3	0	1	0	0	0
Royal antelope (*Neotragus pygmaeus*) (58)	0	43	4	5	1	0	4	3	0	0
Grasscutter (*Thyronomys swinderianus*) (139)	0	17	4	1	3	1	81	46	2	0
Civet (*Civettictis civetta*) (39)	0	3	4	5	2	5	1	1	38	12
Total number of records of each tick	30	781	279	170	134	44	100	67	44	12

The occurrence of a tick species expressed as the number of records of that tick species on a host species.
( ) total number of that host species examined. Data derived from tables 2–6 (Ntiamoa-Baidu *et al.*, 2004).

had occurred by chance was < 0.005. The probability that the high levels of infestation of non-ungulates by *A. compressum*, *Hae. leachi*, *I. aulacodi* and *R. simpsoni* and the low levels of infestation of ungulates by these four tick species had occurred by chance was also < 0.005. *Ixodes cumulatimpunctatus* was not significantly associated with either ungulates or non-ungulates ($P = 0.75$–0.50). Thus the differences in patterns of dispersion of eight of the nine tick species on the two different types of mammals were statistically significant. It was concluded that the presence or

Table 4. Probability that tick species were distributed randomly on different forest mammals, as assessed by the χ^2 goodness-of-fit test using the data shown in table 3.

Tick species	Ungulates and non-ungulates $n = 2$	*Tragelaphus* sp., *Cephalophus* spp. and *Neotragus* sp. $n = 3$	Bushbucks, four species of duikers and royal antelopes $n = 6$
Haemaphysalis parmata	$\chi^2 = 136$ $P < 0.005$*	$\chi^2 = 4.73$ $P = 0.1$–0.05	$\chi^2 = 4.13$ $P = 0.5$–0.25
Ixodes moreli	$\chi^2 = 20.7$ $P < 0.005$	$\chi^2 = 11.2$ $P < 0.005$	$\chi^2 = 26.2$ $P < 0.005$
I. muniensis	$\chi^2 = 47.6$ $P < 0.005$	$\chi^2 = 26.0$ $P < 0.005$	$\chi^2 = 53.1$ $P < 0.005$
Rhipicephalus ziemanni	$\chi^2 = 26.5$ $P < 0.005$	$\chi^2 = 71.3$ $P < 0.005$	$\chi^2 = 73.1$ $P < 0.005$
I. cumulatimpunctatus	$\chi^2 = 0.855$ $P = 0.75$–0.50	Not tested	Not tested

	Ungulates and non-ungulates $n = 2$	Civets, grasscutters and pangolins $n = 3$	Civets and pangolins** Civets and grasscutters*** $n = 2$
Amblyomma compressum	$\chi^2 = 88.2$ $P < 0.005$	$> 20\%$ expected frequency values < 5	**$\chi^2 = 39.0$ $P < 0.005$
Hae. leachi	$\chi^2 = 147$ $P < 0.005$	$\chi^2 = 150$ $P < 0.005$	***$\chi^2 = 132$ $P < 0.005$
I. aulacodi	$\chi^2 = 110$ $P < 0.005$	$\chi^2 = 16.2$ $P < 0.005$	***$\chi^2 = 10.8$ $P < 0.005$
R. simpsoni	$\chi^2 = 251$ $P < 0.005$	$\chi^2 = 35.5$ $P < 0.005$	***$\chi^2 = 20.5$ $P < 0.005$

* $P < 0.005$ was taken to indicate a significance difference between the observed and expected frequency of a tick species on a mammal species or a group of species and to infer that the ticks were not distributed randomly but exhibited significant associations with their host(s).

absence of these ticks on the two different types of mammals reflected significant natural associations or a significant lack of such associations, respectively.

Assessing the patterns of dispersion of *Hae. parmata*, *I. moreli*, *I. muniensis* and *R. ziemanni* on the three genera of ungulates (*Tragelaphus*, *Cephalophus*, *Neotragus*) showed that *Hae. parmata* was evenly dispersed on all genera ($P = 0.1$–0.05). The other tick species were not randomly distributed on these ungulates. The observed levels of infestation of royal antelopes (genus *Neotragus*) by *I. moreli* were significantly lower than expected and this tick species appeared more closely associated with duikers (genus *Cephalophus*) than expected ($P < 0.005$). Both *I. muniensis* and *R. ziemanni* were significantly associated with bushbucks (genus *Tragelaphus*), but *I. muniensis* occurred on fewer royal antelopes (*Neotragus*) than expected and *R. ziemanni* occurred on fewer duikers (*Cephalophus*) than expected ($P < 0.005$ for both ticks).

The patterns of dispersion of *Hae. parmata*, *I. moreli*, *I. muniensis* and *R. ziemanni* on ungulates were then assessed by comparing the levels of infestation of each of these four tick species on the six different species of ungulates. *Haemaphysalis parmata* was evenly dispersed on all six species of host ($P = 0.25$–0.5). *Ixodes moreli* occurred on significantly more black duikers and fewer royal antelopes than would be expected ($P < 0.005$). *Ixodes muniensis* occurred on significantly more bushbucks and bay duikers and on fewer Maxwell's duikers and royal antelopes than would be expected ($P < 0.005$). *Rhipicephalus ziemanni* showed a significant association with bushbucks but occurred on significantly fewer Maxwell's duikers and bay duikers than expected ($P < 0.005$). Thus three out of four species of ticks on ungulates could be shown to express significant associations with particular ungulate species.

The patterns of dispersion of each of the four ticks (*A. compressum*, *Hae. leachi*, *I. aulacodi*, *R. simpsoni*) shown to be significantly associated with non-ungulate mammals were each tested separately to assess the significance of their distributions on the three species (civets, grasscutters, pangolins). The probability that the high levels of infestation of pangolins by *A. compressum* and the tick's absence from both grasscutters and civets could not be assessed as $> 20\%$ of the expected frequency values were < 5. The probability that the high levels of infestation of civets by *Hae. leachi*, the very low infestations of grasscutters by this species and its absence from pangolins had occurred by chance was < 0.005. This result indicated that this tick was positively and significantly associated with civets and that its absence from grasscutters and pangolins was unlikely to have occurred by chance. The probability that the high levels of infestation of grasscutters by *I. aulacodi* and *R. simpsoni*, the low levels of infestation of civets by these two tick species and their absence from pangolins had occurred by chance was < 0.005. This result indicated that both ticks were positively and significantly associated with grasscutters and that their absences from civets and pangolins were unlikely to have occurred by chance.

Testing the patterns of dispersion of *A. compressum* on civets and pangolins showed this tick to be significantly associated with pangolins ($P < 0.005$). The significance of the different patterns of *A. compressum* on pangolins and grasscutters could not be tested as $> 20\%$ of the expected frequency values were < 5 due to many more grasscutters being examined than pangolins. However, the complete absence of *A. compressum* from the sample of 139 grasscutters

suggests that this was not due to chance. Testing the patterns of dispersion of *Hae. leachi*, *I. aulacodi* and *R. simpsoni* just on civets and grasscutters confirmed that *Hae. leachi* was significantly associated with civets and that *I. aulacodi* and *R. simpsoni* were significantly associated with grasscutters ($P < 0.005$ for all ticks).

Taken together, these tests confirmed that eight of the nine forest tick species manifested either significant positive or negative associations with ungulates or non-ungulates and were not randomly dispersed on their hosts. Furthermore, the eight tick species expressed significant host preferences for representatives of different orders of mammals, while being significantly absent from other orders. *Ixodes cumulatimpunctatus* was exceptional in being evenly dispersed over a range of hosts belonging to different orders. At least two of the four species found most commonly on ungulates, *I. muniensis* and *R. ziemanni*, were significantly associated with a single host, the bushbuck. In addition *I. muniensis* occurred on significantly fewer royal antelopes and *R. ziemanni* on significantly fewer duikers than expected. *Ixodes moreli* appeared to be more significantly associated with duikers and less closely associated with royal antelopes than expected. *Haemaphysalis parmata* was significantly associated with small bovids but evenly dispersed on the six species examined here. Four of the tick species on non-ungulates were significantly associated with a single host species: *Hae. leachi* with civets; *I. aulacodi* and *R. simpsoni* with the grasscutters. *Amblyomma compressum* was significantly associated with pangolins as opposed to civets. Although its distribution on pangolins and grasscutters could not be compared, it seems unlikely that *A. compressum's* absence from grasscutters was due to chance. The existence of significant natural associations between ticks and their host species revealed the existence of a major host or hosts for many tick species confirming that the majority of ticks were host specific, although most were recorded much less frequently on a wide range of other host species. The significant absences of ticks from certain mammal species lends further support to the concept of host specificity.

Tests of the hypothesis that tick species are not associated with particular host species

The first regression analysis plotted the total number of host species for that particular species of tick against the number of times that positive records for that tick were made from these hosts, as in Klompen *et al.* (1996), using the data for all 21 species given in table 5. The hypothesis that host specificity exists leads to the prediction that there will be a poor correlation between the number of host species infested (column 2) and the number of tick records (column 3). However, the regression was positive ($R^2 = 0.32$) and although not strongly positive it was significant ($P = 0.006$). The relationship would have been stronger but for the outlying 799 records of *Hae. parmata*. The results indicated that the number of different host species infested was linked to the number of records of a tick species; or conversely, that tick species did not associate with a single host species in particular and that the hypothesis was not supported.

The data shown in table 6, for the 11 tick species that had been collected 20 times or more, were analysed for tick–host associations. The ticks were arranged in descending

Table 5. Data for statistical analysis of degree of host specificity exhibited by the 21 tick species recorded on wild mammals in Ghana.

Tick species	Total number of host species infested by each tick species	Total number of records of each tick species
Amblyomma compressum	3	30
A. variegatum	8	15
Haemaphysalis aciculifer	3	5
Hae. houyi	1	3
Hae. leachi	5	45
Hae. parmata	12	799
Hyalomma truncatum	1	1
Ixodes aulacodi	7	85
I. cumulatimpunctatus	8	60
I. loveridgei	1	1
I. moreli	8	135
I. muniensis	8	279
I. oldi	1	12
I. rasus	3	3
Rhipicephalus (Boophilus) geigyi	1	1
R. cuspidatus	2	9
R. lunulatus	5	11
R. senegalensis	12	50
R. simpsoni	13	118
R. sulcatus	7	23
R. ziemanni	9	178

The data, derived from appendix 2, were used for the regression analysis between the total number of host species infested by adults of a given tick species and the total number of records of each tick species in the collection.

order of the proportion of the major host found infested. As all 26 pangolins were found infested with *A. compressum*, it occupied top place with apparent high host specificity. The total number of host species and families of all the

ticks ranged from three to 13 and two to seven respectively (columns 6, 7). If host specificity exists (in terms of single host species association), it would be predicted that there will be a negative correlation between the proportion of records from the major host (column 5) and the total number of host species infested by each tick species (column 6). As the data in table 6 show, it is clear that this relationship was not strong (the correlation coefficient was -0.36) and was not significant ($P = 0.14$) and this analysis provided no evidence to support the prediction that the ticks exhibited a strong association with individual host species.

The two analyses supported both the proposition that tick species were not usually significantly associated with any one particular host species and the prediction that the more individual specimens of a tick species that are recorded the greater will be the number of individual host species infested by that species.

Comparison of results of analysing data with regression analyses and the χ^2 goodness-of-fit test

Although the regression analyses failed to show that any of the ticks were significantly associated with any one particular host species, the χ^2 goodness-of-fit test showed that the majority of ticks were significantly associated with a single host species or a group of related host species. The reason that the regression analyses gave a misleading understanding of the significance of tick–host associations appeared to be because the regression analyses, unlike the χ^2 goodness-of-fit test, did not allow for ticks being unevenly dispersed on their different host species. Seven out of ten forest ticks were both significantly concentrated on a particular host species or on members of a particular family, and dispersed over a number of host species. Two other species (*A. compressum* and *I. oldi*) were confined to their major hosts.

Table 6. Data for statistical analysis of the degree of host specialism exhibited by 11 ticks collected more than 20 times from wild mammals in Ghana.

Tick species	Major host	Number of records on major host	Total number of individual hosts	Proportion of records on major host	Total number of host species infested	Total number of host families
Amblyomma compressum	Pangolin	26	26	1.00	3	2
Haemaphysalis leachi	Civet	38	39	0.97	5	3
Hae. parmata	Bushbuck	412	439	0.94	12	7
Rhipicephalus sulcatus	Togo hare	8	10	0.80	7	6
Ixodes muniensis	Bay duiker	23	33	0.70	8	3
R. simpsoni	Grasscutter	81	140	0.58	13	7
I. cumulatimpunctatus	Bay duiker	15	33	0.45	8	4
R. senegalensis	Warthog	4	12	0.33	12	7
I. aulacodi	Grasscutter	46	140	0.33	7	4
R. ziemanni	Bushbuck	137	439	0.31	9	4
I. moreli	Black duiker	36	136	0.26	8	3

The data were used to investigate the prediction that the ticks exhibited a strong association with one particular host species; i.e. that there will be a negative correlation between the proportion of records of a tick species on its major host (column 5) and the total number of host species infested by each tick species (column 6).
Major host: the host species that was most frequently infested with a particular tick species. The major hosts of the 11 ticks collected more than 20 times were identified from data in table 2.
Proportion of records on major host: the proportion of a major host species found infested with a given tick species was obtained by dividing the number of records on the major host (derived from appendix 2) by the total number of individuals of that host species from which ticks were collected (derived from table 2).

Only one species, *I. cumulatimpunctatus*, appeared to be widely dispersed and to lack a particular major host.

Discussion

The data set obtained by analysing the tick species of Ghanaian wild mammals described by Ntiamoa-Baidu *et al*. (2004) provided an opportunity to examine the conflicting views on host specificity in relation to ticks. As far as is known, this is the first time that data obtained from a well-documented tick collection, comprising a range of genera from a well-defined geographical region and whose identities have been checked in accordance with recent taxonomic revisions, have been used in the current debate on tick–host associations. As reported previously (Ntiamoa-Baidu *et al*., 2004) some ticks occurred in savanna feeding mainly on large bovids and/or suids; others occurred in forests feeding mainly on small bovids, large rodents or small carnivores. The overall observations reported here showed that a few tick species were exclusively or almost exclusively associated with only one mammalian species. The majority of tick species tended to be associated with a group of closely related species, that could be considered to be their major hosts, as well as being associated less frequently with a much wider range of host species. For the 16 tick species that occurred more than once, five associations were at the level of host order, five at the level of host family and three at the level of host species. Analysis of the tick–host combinations of the most common forest ticks demonstrated statistically significant associations between tick species and host species confirming that tick species have a major host(s). These findings supported the views on host specificity propounded by Hoogstraal & Aeschlimann (1982), Sonenshine (1993) and Cumming (1998) but not the claim that ticks are not at all host specific and that host specificity is an artefact of incomplete sampling of hosts (Klompen *et al*., 1996).

As indicated by Ntiamoa-Baidu *et al*. (2004), many of the associations between tick species and host taxa found in the collection were the same as those described in the neighbouring country of Ivory Coast (Aeschlimann, 1967) and in other regions of Africa by Hoogstraal & Aeschlimann (1982). In Ghana, as elsewhere in Africa, the adults of some ticks were almost exclusively associated with one host species: *A. compressum* with pangolins; *I. oldi* and *Hae. leachi* with small carnivores. The infrequent specimens of *Hae. houyi* and *Hae. aciculifer* occurred on ground squirrels and bovids respectively. Other tick species were strongly associated with members of one order, e.g. *A. variegatum*, *Hae. parmata, I. muniensis, I. moreli, R. cuspidatus, R. lunulatus* and *R. ziemanni* were mainly found on artiodactyls – either suids and/or bovids. The predominant distribution of *I. aulacodi* and *R. simpsoni* on rodents reflected their distribution on grasscutters as reported by Campbell *et al*. (1978) and Ntiamoa-Baidu (1980) for large samples of this rodent in Ghana and on brush-tailed porcupines as described by Aeschlimann (1967) in the Ivory Coast. A very few tick species, namely *I. cumulatimpunctatus, R. senegalensis* and *R. sulcatus*, had a wide range of host species. Finding the three specimens of *I. rasus* on three different host species reflects the wide distribution recorded for this tick in the Ivory Coast (Aeschlimann, 1967). Our general observations therefore supported the view (Hoogstraal & Aeschlimann, 1982) that most ticks display some varying degree of host specificity,

i.e. that most ticks are found most frequently associated with certain host species but are also found on other hosts, although less frequently.

The varied proportions of tick species feeding on certain host taxa supported the proposition that ticks exhibit a range of specificity in their feeding associations with host species (Sonenshine, 1993; Cumming, 1998). According to their schemes, most of the Ghanaian tick species might be viewed as specialists because they were associated with only one host species (*Hae. houyi*, *I. oldi*) or a restricted number of related host species within a family or order. Only three tick species, *R. senegalensis*, *R. sulcatus* and *I. cumulatimpunctatus*, might be considered relatively non-specific feeders as these species were spread more evenly across their different host species than other tick species. At this level of analysis, therefore, our results closely agreed with and supported the propositions of those that claimed that ticks display host specificity.

Analysis of the patterns of dispersion of the ten most common forest ticks on their hosts by the χ^2 goodness-of-fit test confirmed that tick species were associated significantly with particular host species. Four species, *Hae. parmata*, *I. muniensis*, *R. ziemanni* and *I. moreli*, were strongly and significantly associated with a number of species belonging to the family Bovidae. Four species were almost exclusively and significantly associated with one host species belonging to a particular order: *A. compressum* with pangolins (order Pholidota), *Hae. leachi* with civets (order Carnivora) and *I. aulacodi* and *R. simpsoni* with grasscutters (order Rodentia). It was concluded that these forest tick species associated naturally with certain host species that might be viewed as their major host or hosts because they occurred most frequently on these host species. In some cases, their major host was a single host species representing a particular order and in other cases the major hosts comprised groups of related species, e.g. members of the family Bovidae. With the exception of certain small mammal species, the animals marketed in the Ghanaian bushmeat markets generally represent the mammalian fauna of Ghana. It is probable therefore that the associations observed between the different tick species and the particular mammals examined in this survey represent those that exist in the ticks' natural habitats.

Regression analysis of the relations between the numbers of records for each of the 21 tick species recorded on mammals and the numbers of host species on which they had been found indicated that the ticks were not specific for these particular host species. These results agreed with the overall observations that very few ticks were found exclusively on a single host species. However, the conflicting results of the χ^2 goodness-of-fit test suggested that previous claims that ticks are not host specific (Klompen *et al*., 1996) arose from a failure to consider the possibility that ticks are not evenly dispersed on their range of hosts and that they may associate with groups of related species. It was concluded that regression analyses were not ideal tests for assessing host specificity because they make no provision for circumstances where ticks are both widely dispersed over a number of host species and numerically concentrated on particular host taxa. The nature of the tick collection analysed by Klompen *et al*. (1996) is unknown. However, it seems possible that further analysis would have shown that the ticks in question associated naturally with groups of related hosts, unless they were among those unusual ticks

that appear to be genuine generalists, feeding opportunistically on any available vertebrate (Sonenshine, 1993).

Additional evidence that host specificity is not an artefact of incomplete sampling was provided by the different tick species–host species combinations described by Ntiamoa-Baidu *et al*. (2004). The majority (65/121) of these combinations was the same as those recorded for these tick species in other regions of Africa (Hoogstraal & Aeschlimann, 1982). The 56 new combinations mostly agreed with previous reports regarding the host types predominantly infested by the tick species in question, or involved tick species that were rare or infrequent in the collection or tick and/or host species about which there was little or no knowledge. Taken together, the results failed to show a marked increase in the host species infested by these ticks or to provide supporting evidence for claims (Klompen *et al*., 1996) that increased sampling would lead to tick species being found to infest significantly increased numbers of host species or families.

Experimental evidence of differences in host specificity was provided by observations on *I. aulacodi* and *R. simpsoni*, both species being naturally associated with the grasscutter. In the laboratory, while all stages of *R. simpsoni* fed successfully on a range of animals, such as guinea-pigs and rabbits, adult female *I. aulacodi* failed to feed on any of the laboratory animals tried (Ntiamoa-Baidu, 1987a,b).

The data and analyses reported here showed that as a general characteristic while certain ticks displayed a high degree of specificity for a single host species representing a particular mammalian order, others were strongly associated with groups of related host species within a family or order. In this way ticks were recorded on ungulates, carnivores, rodents or pholidotes. The infrequent occurrence of many of these species on an extensive range of hosts may have been due to the numerous confounding factors for such data. Such factors could include the tendency for carnivores to be infested with ticks transferred from their last prey, or for ticks found feeding which subsequently fail to engorge or to lay fertile eggs due to the effects of host resistance or incompatible blood (Sonenshine, 1993). Current knowledge indicates that ticks have a life pattern that produces apparently conflicting evolutionary selection pressures. When off their hosts, they may die from desiccation and/or starvation (Sonenshine, 1993) or be killed by predators and microbial pathogens (Sonenshine, 1993). Adaptation to a non-specialized feeding capability whereby a relatively wide range of suitable hosts will be attached to and can be fed on readily would reduce the time exposed to these factors and hence mortality. Whilst on the host, the main mortality and reduced fitness will be by host grooming (Hart, 2000) and host immunity to infestation (Walker & Fletcher, 1987; Sonenshine, 1993). Such mortality could be avoided by adaptation to a specialist feeding capability that enables the evolution of specific mechanisms such as the secretion of immunosuppressive saliva to overcome host immunity (Ribeiro *et al*., 1985).

The overall information provided by this tick collection leads us to speculate that a resolution to these apparently conflicting selection pressures may be through adaptations to habitats that include several specific hosts or more rarely one specific, but readily encountered, host. These habitats would thus be defined by a combination of characteristic temperature, humidity and physical structures on which the questing ticks can behave to reduce exposure to mortality factors, and by a range of hosts all of which would provide

adequate feeding. By feeding on a number of related hosts within a family or order, a tick species would be able to adapt to the behaviour and physiology of a number of host species and so maximize the number of potential hosts in an environment. By consistently feeding on related species, a tick species would presumably adapt to physiological differences in the blood meals taken from different host types (herbivores, carnivores or rodents) and develop mechanisms to avoid its hosts' anti-tick defences. Thus the conflict between maintaining a non-specialized feeding pattern and adaptation to a specialist feeding capacity would be resolved by feeding on a number of related host species. Adapting to a number of related animals should allow ticks to continue to feed and develop successfully should a particular host species disappear from a particular habitat and to take advantage of the immigration of new and related hosts into their habitats. Under particular circumstances, such feeding patterns could be envisaged as developing into a one-to-one relationship, where a tick species may become adapted to a single host species or a host species may only be infested by one tick species. It appears that for most of the species discussed here, the perceived advantages of pathogen specialization (adaptation to a single host species) are outweighed by the advantages of a host range that comprises more than one host species, as noted for the internal pathogens of mammals (Woolhouse *et al*., 2001). In this context, the very different hosts and host range sizes recorded for members within a tick genus, e.g. *Hae. houyi, Hae. leachi*, *Hae. parmata*; *I. oldi*, *I. moreli, I. cumulatimpunctatus*; *R. cuspidatus*, *R. simpsoni*, *R. sulcatus*, may be due to the finely balanced evolutionary advantages and disadvantages of adaptation to a single species of host versus adaptation to more than one species of host.

The different patterns of tick–habitat associations, described by Ntiamoa-Baidu *et al*. (2004) and the patterns of tick–host associations observed in the forest ticks provided supporting evidence that such a combination of adaptations to habitats and hosts has occurred and that the nature and extent of adaptations varies among tick species. Just as the tick species described here are unevenly dispersed among their forest hosts, so are their different hosts distributed unevenly in the forests in specialized ecological niches (Kingdon, 2001) which furnish the special microclimates and microhabitats required by different tick species (Arthur, 1962; Aeschlimann, 1967). *Haemaphysalis parmata*, *I. moreli*, *I. muniensis* and *R. ziemanni* occurred most frequently on the bushbucks, forest duikers and royal antelopes that inhabit different types of vegetation within the forests (Kingdon, 2001). The immature stages as well as the adults of *Hae. parmata* and *I. muniensis* infest bovids; the hosts of the immature stages of *R. ziemanni* and *I. moreli* are unknown. There is little information about these species but it is assumed that their free-living stages are adapted to microhabitats in the dense undergrowth and shady areas of the forest where they can shelter under vegetation, enjoy a saturated humidity and have ready access to their hosts (Aeschlimann, 1967). Grasscutters were the most frequently infested hosts of *I. aulacodi* and *R. simpsoni* but the adults of both tick species occurred on other rodents, such as giant pouched rats and brush-tailed porcupines, that frequent the areas of dense grasses and reed beds inhabited by grasscutters (Aeschlimann, 1967). All stages of both ticks feed on the grasscutter (Camicas *et al*., 1998); the nymphs of *R. simpsoni* have also been recorded on brush-tailed

porcupines (Aeschlimann, 1967). A few tick species appeared to be associated with one host species predominantly (*A. compressum*, *Hae. leachi, I. oldi*). Pangolins have particular refuges where the immature stages of *A. compressum* live; such cohabitation of host and tick supports the mono-specific, three-host life style of this tick species (Arthur, 1962). The life cycles of *Hae. leachi* and *I. oldi* are not well known, but the immature stages of *Hae. leachi* infest rodents (Aeschlimann, 1967). The fact that adult *Hae. leachi* are found almost exclusively on civets, as well as being the predominant tick on these animals, may be explained by the civets' being in close physical contact with the habitats of the rodent prey species that carry the immature stages of *Hae. leachi*. Given the opportunities for infesting groups of related mammals and the existence of sheltered microhabitats in the different vegetation zones, it is not surprising that the majority of ticks are not confined to just one species of mammal. The different patterns of tick–host associations described here appear to have resulted from tick species adapting to specific climates and habitats as well as to particular host taxa so that each tick species' physiology, behaviour and distribution now link it to a particular host or group of hosts within a specific habitat, as postulated by Hoogstraal & Aeschlimann (1982).

Host distribution may not be an overall constraint to tick distribution in that ticks may not always occur throughout the range of their mammalian hosts due to the limited distribution of suitable microhabitats for free-living stages, as discussed by Cumming (1999). However, the observations reported here clearly indicated that the distribution of some tick species depends on the occurrence of mammalian species with very particular environmental and vegetation requirements (Kingdon, 2001). As well as helping to clarify the discrepancies relating to tick–host specificity, our studies have shown how tick–host associations as well as climate and vegetation may influence the survival and distribution of the ticks of wild mammals. Such knowledge should aid attempts to predict the occurrence of tick species associated with hosts that have very particular environmental needs, when used in conjunction with information provided by the African Mammals Databank (Boitani *et al.*, 1999) and remotely sensed environmental factors (Randolph, 2000).

Acknowledgements

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Appendix 1

The 28 wild mammal species on which adult ticks were recorded in Ghana. Taxonomic designations of the mammals as described by Kingdon (2001); taxonomic authorities for scientific names from Wilson & Reeder (1993).

ORDER PRIMATES
Family Cercopithecidae
   Green monkey (*Chlorocebus aethiops* subsp. (Linnaeus)); spot-nose monkey (*Cercopithecus c. petaurista* (Schreber))

ORDER PHOLIDOTA
Family Manidae
   Tree pangolin (*Manis tricuspis* Rafinesque)

ORDER ARTIODACTYLA
Family Bovidae
   Kongoni or hartebeest (*Alcephalus buselaphus* (Pallas)); bay duiker (*Cephalophus dorsalis* Gray); black duiker (*Cephalophus niger* Gray); Maxwell's or grey duiker (*Cephalophus maxwelli* (H. Smith)); red-flanked duiker (*Cephalophus rufilatus* Gray); royal antelope (*Neotragus pygmaeus* (Linnaeus)); kob (*Kobus kob* (Erxleben)); waterbuck (*Kobus ellipsiprymnus* (Ogilby)); bushbuck (*Tragelaphus scriptus* (Pallas))
Family Suidae
   Common warthog (*Phacochoerus africanus* (Gmelin)); red river hog (*Potamochoerus porcus* (Linnaeus))

ORDER LAGOMORPHA
Family Leporidae
   Togo hare (*Lepus victoriae* Thomas (syn. *L. saxatilis* F. Cuvier; syn. *L. crawshayi* de Winton))

ORDER RODENTIA
Family Hystricidae
   African brush-tailed porcupine (*Atherurus africanus africanus* Gray); crested porcupine (*Hystrix cristata* Linnaeus)

Family Muridae
   Giant pouched rat (*Cricetomys gambianus* Waterhouse)
Family Sciuridae
   Striped ground squirrel (*Xerus erythropus* (Desmarest))
Family Thryonomyidae
   Grasscutter or savannah cane rat (*Thyronomys swinderianus* Temminck)

ORDER CARNIVORA
Family Canidae
   Side-striped jackal (possibly *Canis adustus* Sundevall)
Family Felidae
   Cheetah (*Acinonyx jubatus* (Schreber)); leopard (*Panthera pardus pardus* (Linnaeus)); lion (*Panthera leo* (Linnaeus)) (in zoo)
Family Herpestidae
   Marsh mongoose (*Atilax paludinosus* (G. [Baron] Cuvier)); white-tailed mongoose (*Ichneumia albicauda* (G. [Baron] Cuvier))
Family Viverridae
   African civet (*Civettictis civetta* (Schreber); palm civet (*Nandinia binotata* (Gray))

Appendix 2

The host ranges of 21 species of ticks (family Ixodidae) collected from wild mammals in Ghana. For each tick species, the data shows: the authority name according to Horak *et al.* (2002); the number of records of each tick species found in the collection, i.e. the number of individual animals from which a tick species was collected (not the number of ticks collected from individual animals); the number of each species of mammals (common name) infested by each tick species; the order and family to which each mammalian species belongs.

1. *Amblyomma compressum* (Macalister) 30 records as *A. cuneatum*. Order Pholidota, Family Manidae: pangolin 26; Order Artiodactyla, Family Bovidae: bushbuck 2, black duiker 2.
2. *Amblyomma variegatum* (Fabricius) 15 records. Order Artiodactyla, Family Bovidae: kongoni 6, kob 1, water-buck 1, bushbuck 2; Family Suidae: warthog 2. Order Carnivora, Family Canidae: jackal 1; Family Felidae: cheetah 1, lion 1.
3. *Haemaphysalis aciculifer* Warburton 5 records. Order Artiodactyla, Family Bovidae: kongoni 1, kob 3. Order Rodentia, Family Sciuridae: ground squirrel 1.
4. *Haemaphysalis houyi* Nuttall & Warburton 3 records. Order Rodentia: Family Sciuridae: ground squirrel 3.
5. *Haemaphysalis parmata* Neumann 799 records. Order Artiodactyla, Family Bovidae: bushbuck 412, royal antelope 44, Maxwell's duiker 169, bay duiker 23, black duiker 111, red-flanked duiker 13. Order Rodentia, Family Muridae: giant pouched rat 4; Family Thyronomyidae: grasscutter 17; Family Hystricidae: brush-tailed porcupine 1. Order Carnivora, Family Viverridae: civet 3; Family Herpestidae: white-tailed mongoose 1. Order Pholidota, Family Manidae: pangolin 1.
6. *Haemaphysalis leachi* group: sub-group *leachi* 45 records. *Haemaphysalis leachi* (Audouin) Neumann (syn. *H. leachii*; *H. leachi leachi*). Order Artiodactyla, Family Bovidae: bay duiker 1, black duiker 1, Maxwell's

duiker 2. Order Rodentia, Family Thyronomyidae: grasscutter 2. Order Carnivora, Family Viverridae: civet 39.

7. *Hyalomma truncatum* Koch 1 record. Order Artiodactyla, Family Suidae: warthog 1.

8. *Ixodes aulacodi* Arthur 85 records. Order Artiodactyla, Family Bovidae: bushbuck 7, royal antelope 5, Maxwell's duiker 14, black duiker 7. Order Rodentia, Family Muridae: giant pouched rat 5; Family Thyronomyidae: grasscutter 46. Order Carnivora, Family Viverridae: civet 1.

9. *Ixodes cumulatimpunctatus* Schulze 60 records. Order Artiodactyla, Family Bovidae: bushbuck 20, Maxwell's duiker 3, bay duiker 15, black duiker 10; Family Suidae: red river hog 1. Order Rodentia, Family Muridae: giant pouched rat 5; Family Thyronomyidae: grasscutter 1. Order Carnivora: Family Viverridae: civet 5.

10. *Ixodes loveridgei* Arthur 1 record. Order Rodentia, Family Muridae: giant pouched rat 1.

11. *Ixodes moreli* Arthur 135 records. Order Artiodactyla, Family Bovidae: bushbuck 59, Maxwell's duiker 23, bay duiker 8, black duiker 36, red-flanked duiker 3, royal antelope 1. Order Rodentia, Family Thyronomyidae: grasscutter 3. Order Carnivora, Family Viverridae: civet 2.

12. *Ixodes muniensis* Arthur & Burrow 279 records. Order Artiodactyla, Family Bovidae: bushbuck 173, royal antelope 4, Maxwell's duiker 38, bay duiker 23, black duiker 29, red-flanked duiker 4. Order Rodentia, Family Thyronomyidae: grasscutter 4. Order Carnivora, Family Viverridae: civet 4.

13. *Ixodes oldi* Nuttall 12 records. Order Carnivora, Family Viverridae: civet 12.

14. *Ixodes rasus* Neumann 3 records. Order Rodentia, Family Thyronomyidae: grasscutter 1; Family Hystricidae: brush-tailed porcupine 1. Order Carnivora, Family Viverridae: civet 1.

15. *Rhipicephalus* (*Boophilus) geigyi* Aeschlimann & Morel 1 record. Order Artiodactyla, Family Bovidae: kongoni 1.

16. *Rhipicephalus cuspidatus* Neumann 9 records. Order Artiodactyla, Family Suidae: warthog 6, red river hog 3.

17. *Rhipicephalus lunulatus* Neumann 11 records as *R. tricuspis*. Order Artiodactyla, Family Bovidae: kongoni 4, kob 2, waterbuck 2, bushbuck 2; Family Suidae: red river hog 1.

18. *Rhipicephalus senegalensis* Koch 50 records. Order Artiodactyla, Family Bovidae: kob 2, bushbuck 2, royal antelope 8, black duiker 5, Maxwell's duiker 23, bay duiker 1; Family Suidae: warthog 4. Order Rodentia, Family Muridae: giant pouched rat 1; Family Thyronomyidae: grasscutter 1; Family Hystricidae: brush-tailed porcupine 1. Order Carnivora, Family Felidae: leopard 1. Order Primates, Family Cercopithecidae: monkey 1.

19. *Rhipicephalus simpsoni* Nuttall 118 records. Order Artiodactyla, Family Bovidae: kob 1, bushbuck 6, royal antelope 6, Maxwell's duiker 4, black duiker 5, red-flanked duiker 1; Family Suidae: red river hog 2. Order Rodentia, Family Muridae: giant pouched rat 8; Family Thyronomyidae: grasscutter 81; Family Hystricidae: brush-tailed porcupine 1, crested porcupine 1. Order Carnivora, Family Felidae: leopard 1; Family Viverridae: civet 1.

20. *Rhipicephalus sulcatus* Neumann 23 records. Order Artiodactyla, Family Bovidae: kongoni 8; Family Suidae: warthog 2. Order Lagomorpha, Family Leporidae: Togo hare 8. Order Carnivora, Family Felidae: leopard 1; Family Canidae: jackal 1; Family Herpestidae: marsh mongoose 1. Order Primates, Family Cercopithecidae: monkey 2.

21. *Rhipicephalus ziemanni* Neumann 178 records. Order Artiodactyla, Family Bovidae: bushbuck 137, royal antelope 5, Maxwell's duiker 15, bay duiker 6, black duiker 6, red-flanked duiker 2; Family Suidae: red river hog 1. Order Rodentia, Family Thyronomyidae: grasscutter 1. Order Carnivora, Family Viverridae: civet 5.