6 Taxonomy, host associations, life cycles and vectorial importance of ticks parasitizing small mammals

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1 Introductory remarks

Ticks transmit more kinds of pathogens than any other group of blood-feeding arthropods and, among arthropods, are second in importance only to mosquitoes in their public health impact worldwide (Hoogstraal 1985; Sonenshine et al. 2002; Goodman et al. 2005). In this chapter, small mammals are interpreted as being the smaller marsupials (Marsupialia) and bats (Chiroptera), most insectivores (Insectivora), most rodents (Rodentia), and all tree shrews (Scandentia), elephant shrews (Macroscelidea), and lagomorphs (Lagomorpha). Taxonomy, host-associations, life cycles and vectorial trends for ticks parasitizing these groups of mammals are considered from a worldwide perspective. Because of the widespread and abundant nature of small mammals and their associated ticks, these two groups of ecological partners have immense importance in many ecosytems (Durden and Keirans 1996). From a human perspective, these associations have most relevance with respect to tick-borne zoonotic pathogens that utilize small mammals as reservoir or amplifying hosts.

2 Tick taxonomy

The recently published and widely accepted taxonomic treatment of the world's ~825 species of ticks by Horak et al. (2002) is followed in this chapter. However, the state of tick taxonomy is currently in a state of partial flux as some researchers place more importance in molecular versus

morphological tick phylogenies and taxon recognitions (Barker and Murrell 2004; Horak et al. 2002). Future works should start to reach a concensus on interpretations from these two approaches (Beati and Keirans 2001; Klompen et al. 2000). Significantly, the classifications of both Horak et al. (2002) and Barker and Murrell (2004) treat some formerly recognized ixodid (hard tick) taxa as follows: 1) *Boophilus* as a junior synonym (or subgenus) of *Rhipicephalus*; 2) *Aponomma* as a junior synonym of *Amblyomma*; 3) *Bothriocroton* as a full genus (originally described as a subgenus) for Australasian members of the former *Aponomma*. Further, the bat-associated argasid (soft tick) genera *Antricola* and *Nothoaspis* are treated as junior synonyms of *Carios*.

3 Overview of small mammal-tick associations worldwide

Underlining the importance of small mammals as hosts of ticks, representatives of 13 of the 17 genera of ticks (76%) recognized by Horak et al. (2002) are known to be ectoparasites of small mammals in at least one active stage (larvae, nymphs and/or adults) of their life cycle. These include all 4 currently recognized argasid genera (*Argas, Carios, Ornithodoros* and *Otobius*) and 8 of the 12 currently recognized ixodid genera (*Amblyomma, Anomalohimalaya, Dermacentor, Haemaphysalis, Hyalomma, Ixodes, Rhipicentor* and *Rhipicephalus*). The true hosts of the rarely collected *Nuttalliella namaqua*, the sole representative of the third tick family, the Afrotropical Nuttalliellidae, are unknown but 1 specimen has been recovered from the skin of a rodent so the host repertoire of this tick may also include small mammals (Keirans et al. 1976). Therefore, the only 4 tick genera (all belonging to the family Ixodidae) recognized by Horak et al. (2002) without members that are known to feed on small mammals in any of their active stages are *Bothriocroton, Cosmiomma, Nosomma* and *Margaropus*. However, it is likely that immatures (or possibly even adults in the case of *Bothriocroton*) of some species within these genera also occasionally feed on small mammals; future research on the host associations for these ticks will provide more definitive data. With respect to host-tick associations, Klompen et al. (1996) advocated that ecological/habitat specificity is often more important than host specificity for several tick species – this seems to be especially true for many argasid species.

Smaller marsupials (opossums, etc.) are parasitized by immature and adult stages of several species of ixodids in Australiasia and the Americas, and sometimes also by certain argasids (e.g., *Ornithodoros hermsi, O. parkeri* and *O. turicata* in North America, and *O. macmillani* in Australia).

Nevertheless, there are few host-specific ticks of smaller marsupials, particularly for species that parasitize this host group as adult ticks. Rather, and especially in North America, opossums are often parasitized by immature and adult ticks that belong to species with wide host ranges. In eastern North America, these include all active stages of at least three tick species (*Amblyomma americanum, Dermacentor variabilis* and *Ixodes scapularis*) that are important vectors of zoonotic pathogens.

Tick species with adult stages that parasitize small mammals (small marsupials, insectivores, rodents, lagomorphs and elephant shrews) in different zoogeographical regions are as follows:

- AFROTROPICAL REGION
    - On insectivores
        - Argasidae: *Argas brumpti, A. echinops, A. foleyi.*
        - Ixodidae: *Haemaphysalis elongata, H. erinacei, H. simplex, H. simplicima, H. subelongata, H. theileraе, H. tiptoni, Ixodes alluaudi, I. bedfordi, I. dawsi, I. lunatus.*
    - On rodents
        - Argasidae: *Argas brumpti, A. eboris, A. foleyi, A. zumpti, Ornithodoros arenicolous, O. erraticus, O. graingeri, O. grenieri, O. sonrai.*
        - Ixodidae: *Haemaphysalis anoplos, H. calcarata, H. houyi, H. nesomys, H. tauffliebi, Ixodes albignaci, I. bedfordi, I. elongatus, I. minutae, I. myotomys, I. nesomys, I. randrianasoloi, I. rhabdomysae, I. transvaalensis, Rhipicephalis simpsoni.*
    - On lagomorphs
        - Ixodidae: *Rhipicephalus arnoldi, R. deltoideus.*
    - On elephant shrews
        - Ixodidae: *Ixodes nchisiensis, I. rasus* group, *I. vanidicus, Rhipicephalus oculatus, R. pravus.*
- AUSTRALASIAN REGION
    - On marsupials
        - Argasidae: *Ornithodoros macmillani*
        - Ixodidae: *Ixodes antechini, I. fecialis.*
- NEARCTIC REGION
    - On marsupials
        - Ixodidae: *Amblyomma americanum, Dermacentor variabilis, Ixodes scapularis.*
    - On insectivores

        - Ixodidae: *Ixodes eastoni, I. soricis.*
    - On rodents
        - Argasidae: *Carios talaje, Ornithodoros eremicus, O. hermsi, O. nicollei, O. parkeri, O. turicata, Otobius sparnus*? (adults of *Otobius* spp. do not typically feed but *O. sparnus* was recently transferred from *Ornithodoros* – Horak et al., 2002).
        - Ixodidae: *Ixodes angustus, I. eadsi, I. eastoni, I. hearlei, I. jellisoni, I. marmotae, I. marxi, I. minor, I. muris, I. peromysci, I. sculptus, I. spinipalpis, I. woodi.*
    - On lagomorphs
        - Argasidae: *Ornithodoros hermsi, O. parkeri, O. turicata.*
        - Ixodidae: *Amblyomma inornatum, Dermacentor parumapertus, Haemaphysalis leporispalustris, Ixodes dentatus, I. ochotonae, I. spinipalpis.*
- NEOTROPICAL REGION
    - On marsupials
        - Argasidae: *Carios chironectes, C. marmosae.*
        - Ixodidae: *Ixodes loricatus, I. luciae.*
    - On rodents
        - Argasidae: *Carios aragaoi, C. casebeeri, C. chironectes, C. daviesi, C. echimys, C. puertoricensis, C. rudis, C. talaje, C. tuttlei, Ornithodoros rostratus.*
        - Ixodidae: *Amblyomma pacae, Ixodes andinus, I. capromydis, I. dampfi, I. galapagoensis, I. guatemalensis, I. jonesae, I. lasallei, I. nectomys, I. nuttalli, I. sigelos, I. sinaloa, I. tamaulipas, I. tancitarius, I. tecpanensis, I. tiptoni, I. tropicalis, I. uruguayensis.*
    - On lagomorphs
        - Ixodidae: *Amblyomma inornatum, Haemaphysalis leporispalustris, Ixodes dicei, I. pomerantzi.*
- ORIENTAL REGION
    - On insectivores
        - Ixodidae: *Ixodes granulatus.*
    - On tree shrews
        - Ixodidae: *Ixodes granulatus, I. malayensis.*
    - On rodents

        - Ixodidae: *Haemaphysalis atherurus, H. bandicota, H. bartelsi, H. kadarsani, H. kutchensis, H. kyasanurensis, H. sciuri, H. verticalis, Ixodes audyi, I. granulatus, I. himalayensis, I. kuntzi, I. petauristae, I. radfordi, I. werneri, Rhipicephalus ramachandrai.*
    - On lagomorphs
        - Ixodidae: *Haemaphysalis kutchensis.*
- PALAEARCTIC REGION
    - On insectivores
        - Argasidae: *Argas brumpti, Ornithodoros arenicolous, O. marocanus, O. tartakovskyi, O. tholozani.*
        - Ixodidae: *Anomalohimalaya lama, Ixodes hexagonus.*
    - On rodents
        - Argasidae: *Argas brumpti, A. bureschi, A. delanoi, Ornithodoros alactagalis, O. arenicolous, O. erraticus, O. normandi, O. tartakovskyi, O. tholozani.*
        - Ixodidae: *Anomalohimalaya cricetuli, A. lama, A. lotozskyi, Haemaphysalis verticalis, Ixodes angustus, I. apronophorus, I. crenulatus, I. laguri, I. nipponensis, I. occultus, I. pomerantzevi, I. redikorzevi, I. triangulicеps, Rhipicephalus fulvus.*
    - On lagomorphs
        - Ixodidae: *Anomalohimalaya lama, Haemaphysalis hispanica, H. pentalagi, Ixodes festai, I. hyatti, I. sachalinensis, I. shahi, Rhipicephalus leporis, R. pumilio.*

Although some insectivores (especially aquatic species) are infrequently parasitized by ticks, there is a wide variety of ixodids and a few argasids that parasitize insectivores (shrews, hedgehogs, tenrecs, moles, etc.) in various parts of the world. Perhaps the most diverse group of insectivore-associated ticks is the array of species of *Haemaphysalis* that parasitize various tenrecs (family Tenrecidae) in Madagascar with many of these tick species exhibiting relatively specialized morphologies (Hoogstraal and Kim 1985). Most adult-stage ixodids that parasitize insectivores belong to the genera *Haemaphysalis* or *Ixodes* whereas insectivore-associated argasids belong to the genera *Argas* or *Ornithodoros*. Some insectivore-

associated ticks also sometimes parasitize other mammals; one example is the hedgehog-associated western Palaearctic species *Ixodes hexagonus*, immature stages of which also feed on rodents and adults on carnivores, etc.

Tree shrews are parasitized by immature stages of various species of *Amblyomma, Dermacentor, Haemaphysalis* and *Ixodes* in their native southeast Asia (Audy et al. 1960; Durden, unpublished) and also by most or all active stages (including adults) of at least two species of *Ixodes*. The latter group includes one species (*I. malayensis*) that may be host specific to tree shrews, and another (*I. granulatus*) that also parasitizes rodents and, occasionally, some other mammals in the Oriental zoogeographical region.

Bats are parasitized by many species of argasid ticks in different parts of the world. However, bat-associated ticks are not included in the above list because, in many cases, only (or mainly) immature stages of argasids are typically collected from bats with adults being rare or unknown for some species. The reason for this is because larval argasids typically attach to their hosts for extended periods (days) whereas nymphs and adults feed rapidly (minutes or hours) and are typically only found on the host when they are feeding. The importance of bats as hosts for members of the argasid genus *Carios* is underlined by calculations of the number of bat-associated species in each of the four argasid genera recognized by Horak et al. (2002). For example, 2 of 57 (4%) recognized species of *Argas* feed on bats, whereas 61 of 87 (70%) species of *Carios*, 4 of 38 (11%) *Ornithodoros*, and 0 of 3 (0%) of *Otobius* are known to parasitize bats. Moreover, as highlighted by Klompen et al. (1996), the host-specificity of several argasids is low so that, for example, many species of bat-associated *Carios* spp. may feed on 2 or more (sometimes several) different bat species. A few species even feed on bats in addition to other non-mammalian vertebrates; an example is the nearctic *Carios concanensis* which readily feeds on both bats and birds. In addition to argasids, a few species of prostriate ixodids (members of the genus *Ixodes*) also parasitize bats. Examples include *I. vespertilionis* mainly in the Palaearctic region, and *I. kopsteini, I. paradoxus* and *I. simplex* mainly in the Oriental region. Because bats are volant mammals, some species have large geographical ranges that are often mirrored by several of their ectoparasite species, including ticks.

Perhaps related to their taxonomic and zoogeographical diversity, rodents are parasitized by the widest variety of ticks, with immature and adult stages of many tick species being dependent on rodents for their survival. In fact, members of all 13 of the tick genera known to parasitize small mammals, have been found on rodents. This includes some highly specialized or geographically restricted ticks, such as the 3 members of the

Himalayan (Palaearctic) ixodid genus *Anomalohimalaya*. Typically, immature stages of ixodids are recorded as ectoparasites of rodents especially in temperate regions. However, adults of many ixodid species, especially some members of the genus *Ixodes*, also parasitize rodents, especially in tropical and subtropical regions. Moreover, a few abundant species of rodent-associated ixodids in the northern hemisphere are vectors of important zoonotic pathogens. Rodents are also important hosts of certain argasids, especially members of the genus *Ornithodoros*; following the tick list of Horak et al. (2002), 5 of 57 (9%) species of *Argas* are known to parasitize rodents, compared to 8 of 87 (9%) species of *Carios*, 16 of 38 (42%) *Ornithodoros* and 1 of 3 (33%) *Otobius.* Some species of rodent-associated *Ornithodoros* in both the Old and New worlds are vectors of zoonotic relapsing fever spirochetes.

Lagomorphs are parasitized by host specific (or nearly host specific) ixodid species in each of the major zoogeographical regions where they occur as part of the native mammal fauna. In addition to larvae and nymphs, adult stages of many of these ixodids are typical lagomorph ectoparasites. Lagomorph-associated ixodids mostly belong to the genera *Haemaphysalis* and *Ixodes* especially in the northern hemisphere, but adults of at least 4 species of *Rhipicephalus* and 1 species of *Anomalohimalaya* parasitize lagomorphs in the Old World, as well as at least 1 species of *Amblyomma* in the New World, and 1 species of *Dermacentor* in North America. Also in North America, at least 4 species of argasids frequently parasitize lagomorphs, including 3 species of *Ornithodoros* and immature stages of *Otobius lagophilus* (adults of this tick do not feed). Other opportunistically feeding species of burrow-dwelling *Ornithodoros* in the Afrotropical, Neotropical and Palaearctic regions will also feed on lagomorphs (Hoogstraal 1985).

Elephant shrews are known to be parasitized by a fairly wide variety of ixodid species in their native sub-Saharan Africa including some species with medical and veterinary importance (Fourie et al. 1995). Most of these ticks are represented by larval and nymphal stages but adults of a few tick species also parasitize elephant shrews.

4 Life cycles of ticks parasitizing small mammals

Argasid and ixodid ticks have very different life cycle strategies (Oliver 1989; Sonenshine et al. 2002) both of which are well adapted for exploiting small mammals as hosts. Argasid ticks have 6-legged larvae that typically feed and attach (once) to the host for an extended period (3-10 days).

After moulting, the first 8-legged nymphal stage of argasids then feeds relatively rapidly (~30 minutes to a few hours) on a host. Additional nymphal stages (2-8 depending on the species), each separated by a moult and feeding rapidly on the host, typically follow with the exact number of nymphal stages usually being dictated by the species and sex of the tick (females may have 1 more nymphal instar than conspecific males). Nymphal argasid instars typically feed once before moulting to the next stage but occasionally they feed twice especially if the first blood meal was small (Oliver 1989). Final instar argasid nymphs molt into adults but the morphological difference between nymphs and adults is subtle, with nymphs lacking a genital aperture. Similarly, male and female argasids are morphologically similar with the appearance of the genital aperture being the easiest method of distinguishing the 2 sexes. Like nymphs, adult argasids feed relatively rapidly on the host but they take multiple blood meals during their lifespans and females typically have multiple gonotrophic cycles and lay several separate, small egg batches each consisting of ~100 eggs. There are exceptions to this generalized argasid life cycle. For example, adults of at least 2 of the 3 species of *Otobius* and some species of bat-associated *Carios* spp. (those formerly assigned to *Antricola*) do not feed as adults. Further, larvae and first-instar nymphs of a small number of argasids do not feed before moulting to the next stage (Oliver 1989), and larvae of 1 bird-parasitizing species, *Argas cucumerinus*, are known to feed rapidly (in 7-25 minutes).

Because larval argasids typically attach to their hosts for extended periods, dispersal to new locations and host sites is typically achieved during this life stage. Also, the multiple feeding strategies of most argasid nymphs and adults often necessitates that these stages sequester themselves in host nests or burrows where the host is readily available for frequent blood meals. As Klompen et al. (1996) have discussed, this means that host nests and burrows, rather than specific hosts, become the focus of many argasid species and habitat rather than host specificity may develop. Different vertebrate species may share the same burrow or nest system and the argasid ticks residing in that burrow may feed on all of its vertebrate inhabitants and visitors. For example, in North America, rodent burrows occupied by *O. hermsi*, *O. parkeri* or *O. turicata*, may also be occupied at various times by snakes, lizards, tortoises, burrowing owls, shrews, lagomorphs and small carnivores, all of which may be fed on by these ticks. If the ticks in these burrow systems are infected with relapsing fever spirochetes, then these burrows also become foci for zoonotic pathogen transmission.

Ixodid ticks parasitizing small mammals almost invariably follow a 3-host (multi-host) life cycle with each of the active feeding stages (larva, nymph and adult) feeding on a different host individual. One- and 2-host

ticks (which remain on the same host individual after at least 1 of the 2 moults) appear to be rare on small mammals although larvae of 1-host ticks, such as *Rhipicephalus* (*Boophilus)* spp., are occasionally recovered from small mammals. Many species of 3-host ixodid ticks feed on a variety of progressively larger hosts as these ticks moult into larger stages (larva→nymph→adult), especially in temperate regions. This means that a large number of small mammal species in any given region may be parasitized by immature stages of one or more ixodid species such as members of the genera *Amblyomma*, *Dermacentor*, *Haemaphysalis*, *Hyalomma, Ixodes* and/or *Rhipicephalus.* In fact, immature stages of some of the most important vector ticks in the northern hemisphere feed on several small mammal species in this way. Examples of these ticks include *Ixodes scapularis*, *I. pacificus* and *Dermacentor variabilis* in North America, and *I. ricinus* and *I. persulcatus* in Eurasia. However, there are many species of ixodids in which the adult stages parasitize small mammals, especially in subtropical and tropical regions and a large number of these ticks appear to be host-specific (or nearly so) to various mammals.

Unlike argasids, each active feeding stage of ixodid ticks feeds just once and each stage attaches to a host for an extended period (2-12 days) which aids in the dispersal of all active stages of these ticks. After each stage has engorged with blood, it detaches from the host, drops to the ground (leaf litter, etc.), moults to the next stage and, after a certain period, then searches (quests) for another host. Adult ixodids mate either on or off the host; members of the genus *Ixodes* can do either, but members of all other ixodid genera must mate on the host after the female has attached and started to feed (Oliver 1989). Adults of several species of small mammal-associated *Ixodes* not only mate off the host but also do so in the host nest. Because males of some of these *Ixodes* spp. rarely (or never) feed on the host, males of these “nidicolous” tick species are typically found only in the host nest or burrow.

Morphologically, ixodid larvae have 6-legs, nymphs and adults have 8-legs, and males have the hardened dorsal plate (scutum) virtually covering the entire dorsal surface. This “entire scutum” of male ixodids prevents significant enlargement (engorgement) of their bodies and adult male ixodids therefore take small blood meals (or none at all) whereas larvae, nymphs and females all engorge significantly. After mating and engorgement, female ixodids detach from the host and, over several days, lay one large egg mass (~1,000-10,000 eggs) before dying.

5 Ticks and small mammals as vectors and reservoirs of zoonotic pathogens

It could be argued that a wide variety of vertebrate pathogens (especially certain viruses, bacteria and protozoa) have evolved strategies to utilize the close associations between certain ticks and their small mammals hosts in order to perpetuate and amplify themselves and the infections they cause (Sonenshine et al. 2002, Goodman et al. 2005) (Table 1). For example, intimate associations between *Ixodes* ticks and small mammals in North America, Europe and central Asia promote the maintenance and spread of the Lyme disease. Similarly, in Eurasia, intimate associations between *Ixodes ricinus, I. persulcatus* and tick-borne encephalitis (TBE) virus promote the maintenance of this zoonotic disease.

Table 1. Important zoonotic tick-borne diseases for which small mammals are reservoir hosts

Disease	Agent	Main vector(s)	Distrubution
Tick-borne encephalitis	*Flavivirus*	*Ixodes ricinus, I. persulcatus*	Eurasia
Louping ill	*Flavivirus*	*I. ricinus*	United Kingdom
Kyasanur forest disease	*Flavivirus*	*Haemaphysalis spinigera*	Indian subcontinent
Powassan encephalitis	*Flavivirus*	Various ticks	N. America
Colorado tick fever	*Colitvirus*	*Dermacentor andersoni*	N. America
Crimean-Congo hemorrhagic fever	*Nairovirus*	*Hyalomma* spp.	Africa, Asia, Europe
Tick-borne relapsing fever	*Borrelia* spp.	*Ornithodoros* spp.	Old and New Worlds
Lyme disease	*Borrelia* spp	*Ixodes* spp.	N. Hemisphere
Rocky Mountain spotted fever	*Rickettsia rickettsii*	*D. andersoni, D. variabilis*	N. America
Tick typhus	*Rickettsia* spp.	Various ticks	Almost worldwide
Human granulocytic anaplasmosis	*Anaplasma phagocytophilum*	*Ixodes* spp.	N. Hemisphere
Human monocytic ehrlichiosis	*Ehrlichia chaffeensis*	*Amblyomma americanum*, other ticks in Eurasia	N. Hemisphere
Tularemia	*Francisella tularensis*	Various ticks	Almost worldwide
Human babesiosis	*Babesia* spp.	Ixodes spp.	N. Hemisphere

With respect to argasids, various species of *Borrelia* spirochetes are transmitted by characteristic species of *Ornithodoros* (often exhibiting tick specificity). Rodent burrows occupied by these *Ornithodoros* spp. ticks act as foci for tick-borne relapsing fever spirochetes and persons camping, hiking or resting near these burrows can be infected via relatively rapid infectious soft tick bites (Hoogtraal 1985). These and other zoonotic diseases with pathogens that exploit small mammal-tick associations in various parts of the world are listed in Table 1. Some other tick-borne infections of small mammals, such as certain members of the protozoan genus *Babesia*, are confined to particular mammals where the pathology to their hosts ranges from inapparent to severe. Clearly, intimate associations between small mammals and ticks not only have major ecological implications but also significant epidemiological consequences on a worldwide basis.

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