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Ticks and disease: susceptible hosts, reservoir hosts, and vectors

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Introduction

Ticks (both Ixodidae—hard ticks, and Argasidae—soft ticks) play an important role as vectors of diseases. They transmit pathogenic agents to wild or domestic animals and to humans (e.g. viruses, rickettsiae, borreliae, tularemia, piroplasmida, filariae). Since Smith and Kilbourn's historical discovery in 1893 that an arthropod can transmit a pathogen (transmission of *Babesia bigemina* by *Boophilus annulatus*), the list of micro-organisms transmitted by ticks has become so long that inexperienced people may wonder if it is not exhaustive. However, the 800 tick species described world-wide (Fig. 8.1; Hoogstraal and Aeschlimann 1982) have not revealed all their secrets in this field. Surprises are always possible.

The epidemiologist must understand how these transmissible micro-organisms circulate in nature, in wild or domestic cycles. Among other things, determining the durable endemicity of a disease in a region (i.e. 'natural focus' of disease) is essential. Several biological factors are involved and are linked together to form an epidemiological chain.

Tick life cycles

The biology of ticks has been studied in detail by many authors. The basic life cycle schema (Fig. 8.2) is the same for every species. A hexapod larva hatches from the egg and develops into an octopod nymph before it moults into an adult, male or female. Each developmental step depends on a blood meal, followed in the immature stages by moulting. Adult female ticks must also take a blood meal, during which copulation generally occurs. If the female does not obtain a blood meal, vitellogenesis and consequently egg-laying are not possible, although exceptions are observed.

The Ixodidae or hard ticks are long feeders. Each blood meal,

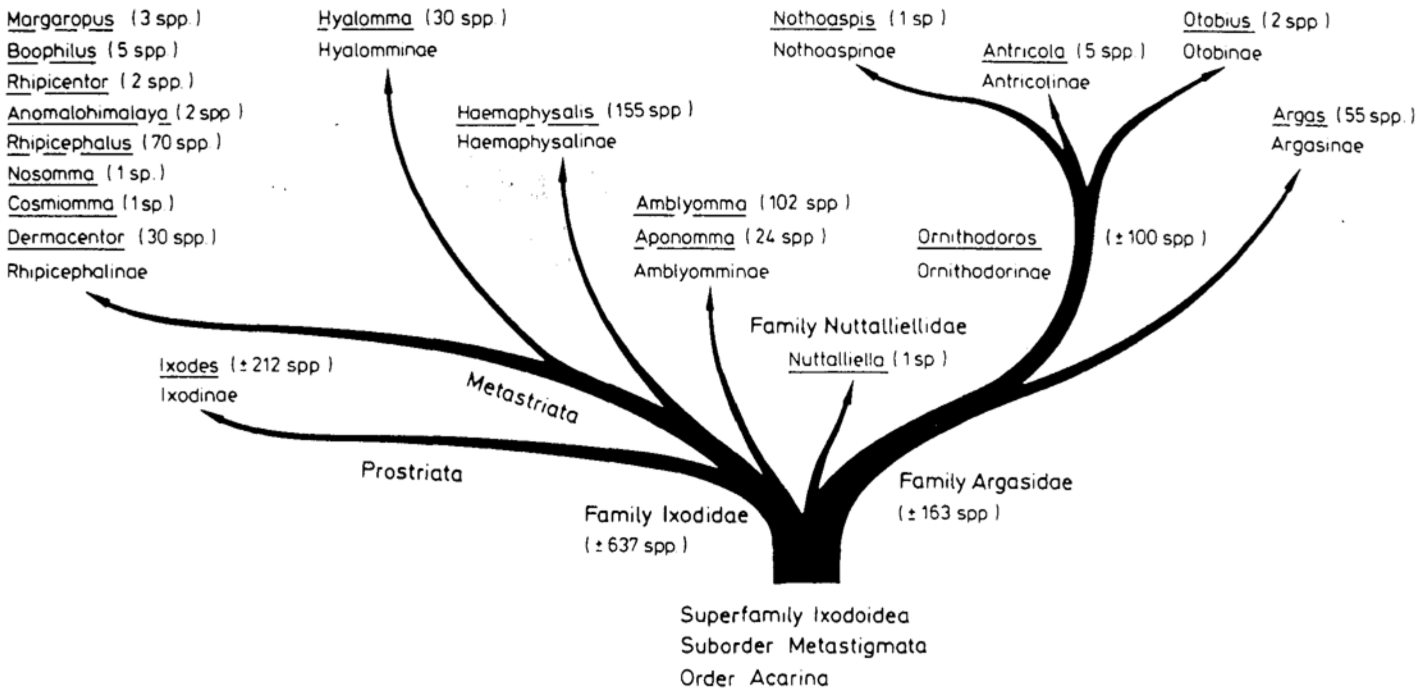

Fig. 8.1. Phylogeny and systematics of ticks (Ixodoidea), from Hoogstraal and Aeschlimann (1982). About 800 tick species are described world-wide.

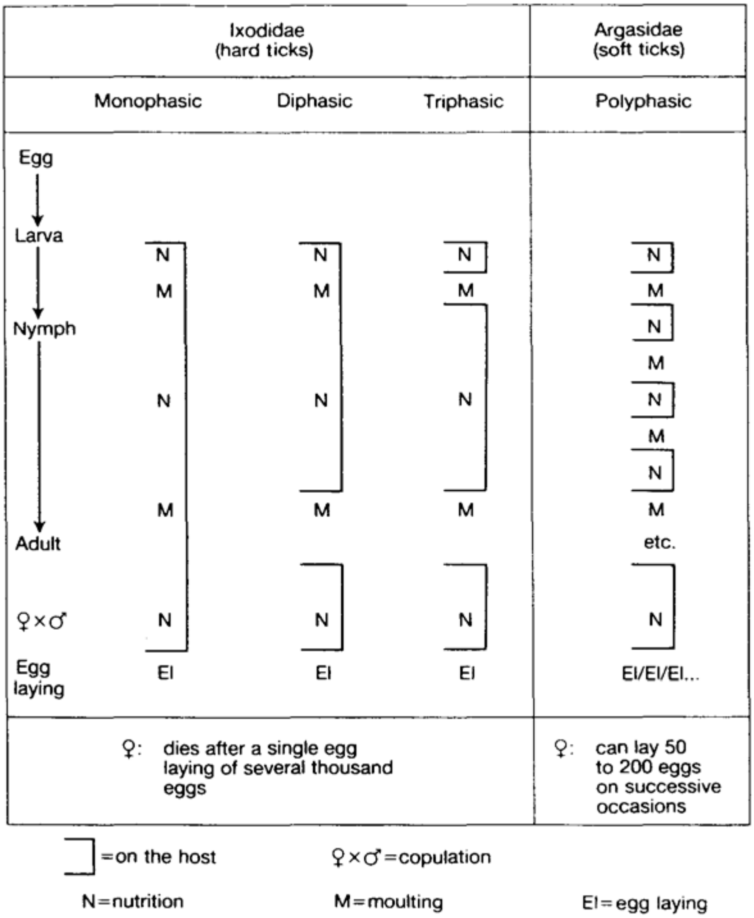

Fig. 8.2. Life cycle of ticks, both Ixodidae and Argasidae. The biology of the family Nuttalliellidae, with only one genus and one species, is still unknown.

depending on the developmental stage, is 4 to 7 days long. The life cycle can be tri-, di-, or monophasic. Females always die after laying one clutch of eggs. Copulation occurs during feeding in the Metastriata. The Ixodinae is an exception. Ticks of the genus *Ixodes* copulate before the blood meal, very often off the host while ticks are free living (Graf 1978).

Triphasic ticks leave the host after each blood meal. Moulting and egg-laying occur while ticks are free living. Such ticks therefore spend a long time away from the hosts and depend on favourable external conditions for survival. They can fast for a long period, from several months for the larvae and nymphs, to more than 1 year for adult hard ticks. Such ticks must search for a new host three times. Many tick species await the host on the vegetation, in a characteristic 'waiting-attitude'. The tarsi of the first pair of legs carry a sensory zone, containing the Haller's organ, which is composed of many receptors (mecano-, thermo-, hygro-, and chemoreceptors) (Thonney 1987).

Diphasic ticks leave their first host as engorged nymphs, i.e. after two blood meals separated by a moult on the same host. Adults have to find a new host. Monophasic ticks attach to a host as larvae and do not leave it before being fully engorged as adults. They feed three times and moult twice on the same host.

The Argasidae or soft ticks are short feeders (from minutes to 1 hour). The life-cycle is polyphasic with many (three to seven) nymphal instars. Females may feed several times and lay eggs after each blood meal, dying after laying five to seven clutches of eggs. Generally, copulation occurs after the blood meal. Soft ticks can also fast for a very long time. Under laboratory conditions, some *Ornithodoros* have survived for up to 5 years without a blood meal.

Host specificity

Some ticks can be highly host specific. Others show a very low degree of host specialization (Hoogstraal and Aeschlimann 1982).

Argasidae are 'monotropic', as they feed in each developmental stage on blood of the same groups of vertebrates (e.g. small rodents, bats, ground birds, and tortoises). Thus 'monotropy' means, depending on the tick species, that they are highly specific, feeding, on one single species of host, one family or order of hosts.

Monophasic Ixodidae all belong to the genus *Boophilus*, of which only five species exist in the world. As mentioned above, these ticks spend their whole life as true ectoparasites, leaving the host as engorged females only for egg-laying and death. They are obligately monotropic.

The great majority of hard ticks are 'ditropic'. The immature ticks (larvae and nymphs) feed on small vertebrates (i.e. rodents) and adults on vertebrates of greater size (e.g. wild ungulates, cattle, dogs, and so on).

Among triphasic ticks, truly 'tritropic' species are rare. *Ixodes ricinus*, the well-known sheep tick (commonly found in Europe), shows a tendency towards tritropy in Switzerland (Fig. 8.3). Larvae are mainly found on rodents and shrews, nymphs on birds, and adult females on big mammals (males do not feed at all in the *Ixodes*). It would be better to term such a tick–host relationship 'telotropic', i.e. without any specificity. However, triphasic ticks can also be monotropic (like the *Argasidae*) depending on their relations with certain groups of hosts living in a certain habitat.

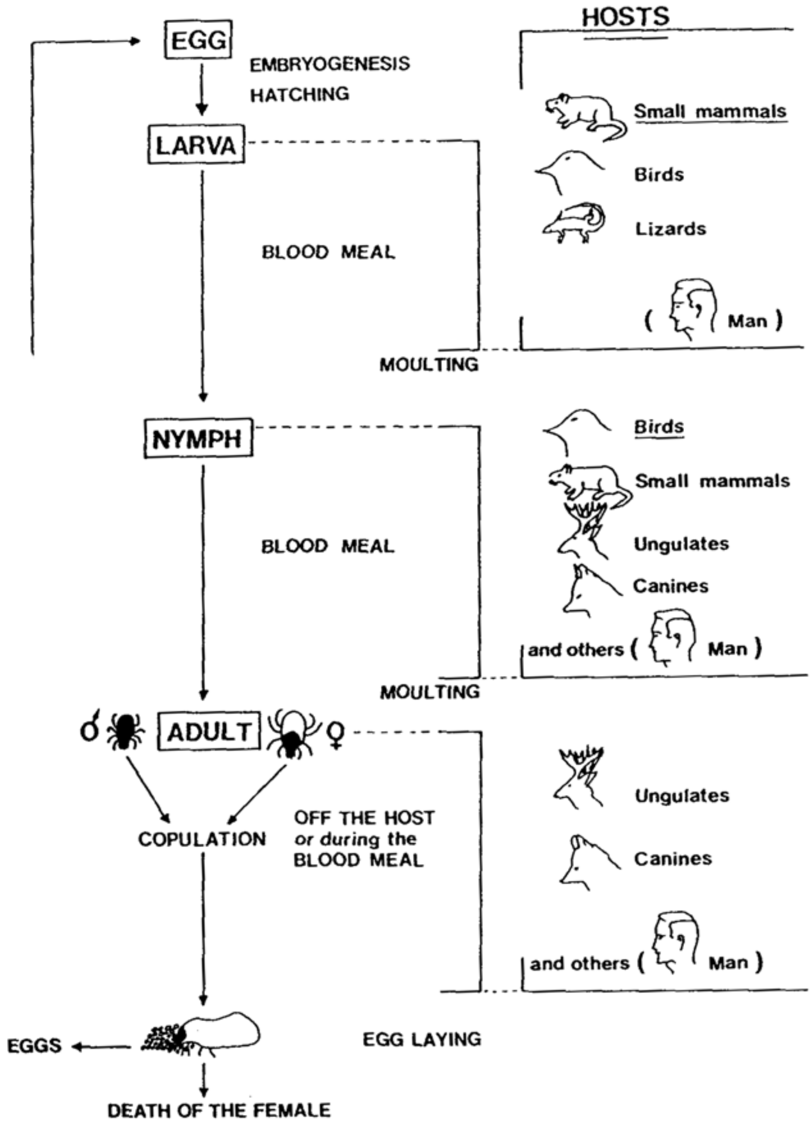

Fig. 8.3. Life cycle of a triphasic, telotropic, and exophilic tick, *Ixodes ricinus*. Humans can be the host for every developmental stage of this species.

Modes of transmission

Ticks transmit their pathogens through various organs, both in Ixodidae and Argasidae (Fig. 8.4). The salivarial route is the most common, and the micro-organisms are directly injected into the host, as with a syringe. Stercoral transmission (via the faeces) is rare. Only resistant pathogens (*Coxiella burnetti*, the Q-fever rickettsia) can survive out of the vectors in the rather dry excrement of ticks. Susceptible hosts may then be infected by inhalation of dust containing the tiny bacteria.

To osmoregulate, soft ticks produce, at the end of the blood meal, a clear fluid, called coxal fluid (excreted from the coxal glands). Spirochete-like microorganisms may be present in this fluid, and they can actively penetrate the skin of the host as they move by means of their own flagellae. This is known as coxal transmission.

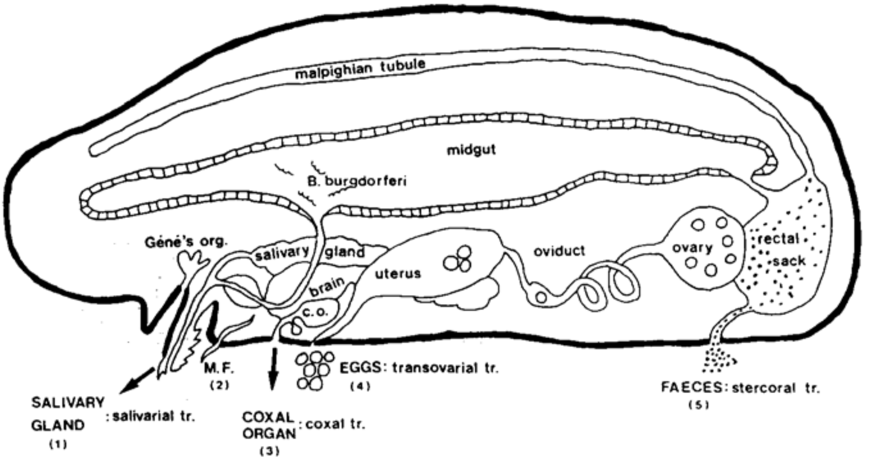

Fig. 8.4. Modes of pathogens transmissions (tr.) by ticks (see text) as illustrated in a schematic sagittal section of a hard and a soft tick: (*1*) viruses, bacteriae, protozoans, and toxins are transmitted with the saliva; (*2*) microfilariae (M.F.) are transmitted by effraction; *(3)* coxal transmission occurs in many *Borrelia* spirochetes (only by ticks in the Argasidae group; Ixodidae have no coxal organs); (*4*) transovarial transmission occurs in almost all pathogens, with the exception of *Theileria sp.* and microfilariae; and (*5*) transmission can occur via the faeces (*Rickettsia conorii*). Finally, *Borrelia burgdorferi*, the Lyme disease spirochete, multiplies in the midgut. This spirochete could be transmitted by regurgitation of the gut contents during the blood meal of *Ixodes* ticks, but the hypothesis still needs confirmation.

The Lyme disease spirochete, *Borrelia burgdorferi*, multiplies and survives mainly in the midgut of the tick, and is thus probably regurgitated into a host during the blood meal. However, this hypothesis of transmission by regurgitation has not been definitely demonstrated.

Infective microfilariae leave the tick by breaking the soft tegument at the rostrum basis and escape from this vector, penetrating actively into the host through the tiny wound during a tick bite. This is transmission by effraction.

Most of the micro-organisms that ticks harbour may penetrate into the developing ovocytes of the ovarian tissue. The freshly hatched larvae are already infected and can transmit pathogens during their first blood meal. This mode of transmission, from one generation to another, is called transovarial transmission. This interesting phenomenon is observed only in ticks and is in general absent in insects of medical importance (Fig. 8.4). importance (Fig. 8.4).

A larva that is infected during its first blood meal can transmit the pathogens to the nymph (which becomes infectious) and then to the adult, which also becomes infectious. This is called transtadial transmission (Fig. 8.4).

Epidemiological considerations

As we can see from this summary of the basic biology of ticks, many factors can affect the circulation of tick-vectored micro-organisms in the nature. These factors are linked together to form an epidemiological chain. We must also take into account the following.

First is the behaviour of free stages of ticks. Exophilic ticks do not move in nature. They wait on the vegetation until a host arrives (with exceptions in the genus *Hyalomma*). Other ticks are cryptophilic (ticks living in rodents' burrows or in birds' nests); they bite when hosts are 'at home' and leave it, engorged, 'at home' again. In other words, ticks are very faithful to their original habitat, even if it is a microhabitat.

Note that the possibility for ticks to support a fasting period of months, waiting for passing hosts, in exactly the same place (on the same grass or in the same burrow) enhances this very strong and faithful attachment to a microhabitat. Thus, the natural focus of a tick disease may be of a very small area.

Second, of course, the presence in the habitat of suitable hosts is essential to the development of the different life stages (tri-, di-, mono-, and polyphasy). This confronts ticks with the problem of the choice of hosts, and therefore with their parasitic specificity (mono-, di-, tri-, and telotropy) (see also Chapter 4 by Combes, this volume). But again, many hosts are also very faithful to their own territory and do not move about that much. Ticks and hosts must live together in syntopy in the same habitat, and therefore need comparable ecological conditions.

Third, to become infected, ticks must bite infected hosts at a favourable moment (i.e. when the blood parasitaemia in the vertebrate is high; Cheng, Chapter 2, this volume). They can also bite 'reservoir' hosts, which show some parasitaemia without being affected by the pathogens. Such hosts function in nature as permanent infectious sources for ticks.

Lastly, transtadial transmission allows ticks to be infectious during their entire lives following a primary infection from an infected vertebrate. Furthermore, transovarial transmission allows ticks to stay infectious for many generations after a single infection. Thus a natural focus of a tick disease may be active for long periods.

Summary

Tick species vary in the number of hosts fed upon during the life cycle, the specificity they have for certain host taxa, and the mode of transmission, among other life history details. What, then, is the definition of a 'natural focus' of a tick disease in an endemic region? It is the smallest possible intersection of a habitat (or microhabitat) in which the whole cycle of a parasitosis may be achieved in the wild, including the reservoir hosts, nutritional hosts, ticks and transmissible pathogens. Humans or domestic animals may reveal such a focus, when entering one. They become sick, and one observes the acquired disease clinically or serologically.

Such a natural focus may 'export' infected ticks with hosts. If such ticks are infected and leave the hosts out of a natural focus, they can begin new foci. I call such emigrations a 'pulsation' from an original focus. Young rodents, birds, or migrating large mammals may play an important role in originating new foci of diseases and then creating new endemic regions.

The possibility that ticks transmit their pathogens through the eggs, over many generations (transovarial transmission), means that ticks act not only as vectors but also as reservoirs of the pathogens they transmit.

References

Graf, J. F. (1978). Copulation, nutrition et ponte chez *Ixodes ricinus* L. (Ixodoidea: Ixodidae) -2ème partie. *Bulletin de la Societé Entomologique Suisse*, **51**, 241–53.

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

Smith, T. and Kilbourne, F. L. (1893). Investigation into the nature, causation and prevention of Texas or Southern cattle fever. *Bulletin of the Bureau of Animal Industry*, United States Department of Agriculture, **1**, 301 pp.

Thonney, F. (1987). Etude morphologique et structurale des récepteurs sensoriels du tarse I de la tique *Ixodes ricinus* L. Thèse, Faculté des Sciences, Université de Neuchâtel, 135 pp.