

THE ROLE OF HOSTS AND ENVIRONMENT IN THE NATURAL DISSEMINATION OF TICKS

STUDIES ON A SWISS POPULATION
OF *IXODES RICINUS* L., 1758¹

by

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The ticks (*Ixodoidea*) are important vectors of pathogenic agents affecting man and animals. Among the diseases they transmit are tick-borne encephalitis, rickettsiosis, relapsing fever, tularemia, babesiosis, theileriosis and filariasis. In addition, as a direct effect of their bite, these ectoparasites can also cause anemia and allergic reactions. Tick saliva, injected during the course of the blood meal, also contains toxins responsible for the notorious tick paralysis. Thus, each year these arthropods account for considerable losses of livestock and play a not inconsiderable role in human medicine. Numerous authors have reported on the development of infectious agents within the organs of the tick. These papers also touch upon the varied means of transmission to the vertebrate host, be it via the salivary glands, the coxal glands or by transovarian transmission.

The economic importance of ticks obviously raises the problem of their survival and dissemination in the wild; of note there is the problem of circulation of infectious agents among healthy and diseased hosts, and also that of establishment and maintenance of the natural focus of infection in favourable biotopes. The important concept of "natural foci" was put forward by PAVLOVSKY 1963, and to be elucidated in any given case requires detailed findings on the biology of many important parasitic species, on their parasitic specificity during each of their developmental stages, on their ecological needs and on their behaviour in the environment. Before turning to *Ixodes ricinus*, the most prevalent tick of Switzerland (AESCHLIMANN 1972) and vector, in this country, of tick-borne encephalitis (KRESCH et al. 1969, RADDA et al. 1974,

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SPIESS et al. 1969, WANDELER et al. 1972, 1973, WYLER et al. 1973), of a variety of babesias: *B. bovis* and *B. divergens* (MORISOD et al. 1972, BROSSARD and AESCHLIMANN 1975, AESCHLIMANN et al. 1975, BROSSARD 1976) and perhaps also *Coxiella burnetti*, we wish to outline briefly some aspects of the biology of the *Ixodoidea* which are relevant to our theme.

Biology of the *Ixodoidea*

Life cycles. In order to characterize the life cycles of the 2 families, *Ixodidae* and *Argasidae*, we shall employ the terminology proposed by MOREL 1969. Let us recall that the developmental cycle of ticks comprises the following 4 stages: egg, larva, nymph(s) and adult. The cycles are mono-, di- and triphasic in the *Ixodidae* and polyphasic in the *Argasidae*. Parasitic specificity. Monotropic ticks are ones which, during each stage, feed on the same group of hosts; it may refer to specificity down to the level of species (for example, *I. lividus* and *Riparia riparia*), or to order (ticks of the Chiropterans). One type of monotropic specificity is exemplified by those ticks which complete their development on hosts which are found in the same ecological niche (*I. trianguliceps* on Rodents and Insectivores).

Ditropic ticks parasitize one group of hosts in the immature stages and another group in the adult stage. The best examples are those bovine ticks which as larvae and nymphs parasitize small animals, rodents in particular. No ticks are known to be truly tritropic, that is to say choosing at each instar a different host or group of hosts². When the immature stages show no particular host preference (accepting equally well reptiles, birds or mammals) and when the adults prefer mammals of large size, such ticks are called telotropic. Ecological needs. Ticks can also be roughly categorized according to 2 major behavioural patterns: endophily (cryptic) and exophily. During the course of their lives ticks must cope with many hazardous conditions, particularly during the free-living phases. The gravid female, the embryo, the larva and nymph undergoing moulting all hide away in anfractuosités of the terrain, under a carpet of dead leaves, in the soil, etc. To our knowledge, all recorded species of ticks practice endophily at some time or other to escape from adverse fluctuations of the external environment. Certain species are, moreover, endophilic throughout their lives, living constantly under cover, for example in the burrows of small mammals (*I. trianguliceps*), in the nests of birds (*I. lividus*), in human habitations (*Ornithodoros moubata*), etc. With many other species, however, the fasting stages leave their hiding places to climb the surrounding vegetation and lie in

² We point out, however, that in Switzerland *I. ricinus* shows a certain tendency to tritropy.

wait for a passing host. During this time, the parasites are exophilic. These species are generally better able to withstand the rigors of harsh external conditions. It must indeed be an interesting aspect of their physiology which allows them to pass at various stages from endophily to exophily.

From the microbiotope where a gorged, mated female has laid, the dissemination of her descendants is going to be subjected to certain biological imperatives as we shall explain in the following pages with reference to a particular example: *Ixodes ricinus*. The species is triphasic, telotropic and endoexophilic. As we aim in this paper for an overall synthesis of several years work, we shall not endeavour to outline all the methods used. Our goal is to unfold the fundamental features of the biology of *I. ricinus* in Switzerland so as to be able in the end to compare this species with other *Ixodoidea*. The reader will find complementary studies in a series of papers published in *Acarologia* (1973–1976).

Ixodes ricinus

Biotopes. We have studied the ecology and behaviour of this species in a forest on a plain in the Swiss Plateau (Staatswald, 430 meters altitude; MERMOD et al. 1973, 1974, 1975, GRAF 1974, 1975, AESCHLIMANN 1976). This biotope is very favourable to the maintenance of *Ixodes ricinus*. It is a deciduous forest (dominant trees being alder mixed with some ash), possessing damp soil covered with a thick layer of humus and with a rich undergrowth (shrubs, ferns, nettles, bramble, horse-tails, yellow iris, graminaceae in some areas)³. The ground litter and the nature of the upper layer of the soil provides the necessary hiding places for the endophilic stages to complete their development, and a considerable undergrowth to support the exophilic ones. These will remain, moreover, protected from the very large climatic variations in the shelter of the large trees (sylvo-exophily). The passage from endo- to exophily is thus facilitated. It seems that a hardwood forest at low altitude in a moderate continental climate provides the ideal biotope for *I. ricinus*. In this confined milieu, the life-cycle of this species is able to proceed with the maximum chance for success. It is important to emphasize, however, that forest and undergrowth are not the only biotopes possible for *I. ricinus*. One can find this species equally well in the hedgerows, thickets, scrub and forest-gallery. But the absence of adequate ground-cover does represent an important limiting factor for the distribution of this tick. It is not found in grazed, open pasture, permanent marshland or peat-bog. It is found only rarely in intensively cultivated fields. Carried by a domestic

³ The analysis of vegetation charts can be used to study the distribution of *I. ricinus* in any given region (GILOT et al. 1975a, b).

animal, it sometimes finds its way to an urban garden. Abiotic factors: climate and microclimate. Ambient RH undoubtedly plays a significant role in the activity and survival of a population of *I. ricinus*. In the laboratory, rearing this species is successful at room temperature (20°C) and at RH approaching saturation. In the forest studied, the annual temperature varied from -12°C to +25°C. The exophile stages are rarely noted on vegetation when the temperature drops to 10°C, and are completely absent below 4°C. This is not to say that ticks have completely disappeared during this time of year, but only that they are inactive and remain hidden in the shelter of the soil. We have, indeed, found living ticks 17 to 22 cm within the soil in December and January⁴. Similar findings have been published by DANIEL et al. 1972. At the same time, there is a reduction of activity of exophiles at high temperature. The elevated temperature is often accompanied by a lower RH, forcing exophilic ticks to retire within their hiding places in the ground litter and soil. Thus, one finds with progression of the seasons, 2 peaks of activity in the *I. ricinus* population in a favourable biotope: the first in the spring, the second, more modest one, in autumn, and 2 troughs when activity is more or less reduced or absent, namely the summer and winter (ČERNÝ et al. 1965, MERMOD et al. 1973, GILOT et al. 1975a, b).

The influence of humidity on tick survival has been confirmed by many authors. It seems as if this is the most significant factor determining the survival time of these creatures. Long dry periods definitely eliminate a large number of *I. ricinus*. Also, the species is absent in exposed areas and numbers progressively diminish as the altitude increases. Above 1200 m the relative dryness of the air and rigors of the long winter serve to interrupt progression of the life cycle. *I. ricinus* is not able to establish itself in these regions, and the few specimens found at high altitude (AESCHLIMANN 1972), should be regarded as a temporary installation during the less harsh summer months following the occasional importation by a host. In flat country, during unfavourable conditions, exophilic stages can always escape by regaining shelter closer to the ground. It thus appears that the existence of a biotope possessing characteristic microclimatic conditions (constant RH approaching saturation, temperature fluctuations which remain for only short durations at extreme values) are necessary for the survival of *I. ricinus*.

Hosts. If abiotic factors are fundamental in determining the survival of *I. ricinus* in any given region, the presence of suitable hosts in the same area is obviously of equal importance. *I. ricinus* is eclectic vis-à-vis the available hosts, which at least in part may explain its wide distribution. Immature stages feed primarily on small or medium-sized vertebrates: lizards, birds

⁴ Gorged females seem to resist low temperature (-20°C) in the laboratory but only for short periods of time. This observation, however, requires further experimental confirmation.

which frequent the ground, rodents, insectivores, carnivores, sometimes domestic and wild Artiodactyles as well as man. The adults prefer large animals, above all, deer, cattle, dogs, etc. Actually, a statistical study now in progress leads us to believe that, at least in Switzerland, each developmental stage shows a preference for different hosts. Thus, in the Staatswald forest, larvae feed mostly on rodents⁵, insectivores and birds; the nymphs are rarely found on rodents but instead are found on birds (AESCHLIMANN et al. in preparation), squirrels, badgers and foxes. The adults are found above all on roe-deer, dogs and perhaps the occasional wild boar⁶. From these observations arises the conclusion that *I. ricinus* practices a sort of "tritropism" which has not been demonstrated before.

Life-cycle and dissemination of *I. ricinus*. Let us now recall that the cycle of *I. ricinus* is triphasic, i.e. 3 hosts must be found for complete development to be completed. This task is aided somewhat by the fact that *I. ricinus* exhibits only feeble parasitic specificity. Since the tick experiences free and parasitic phases in alternation, it has, theoretically, 2 means of ensuring its dissemination on the ground — that of its own horizontal movement, and that of transport by the host. Copulation and nutrition. In a previous work (AESCHLIMANN and GRANDJEAN 1973a, b) we showed that the final phase of engorgement is triggered only after copulation. In the majority of Ixodids (*Metastricata*) meeting of the sexes takes place on the host after a brief feed by the males. The situation with the *Prostriata* (genus *Ixodes*) is unique in that the males of some species do not feed and that copulation, although at times occurring on the host, may also frequently take place off the host before the female has fed. In effect, a tally has shown that more than 2/3 of the females captured in the wild are already fertilized (GRAF 1974, 1978a, b, c). Thus the rule that a preliminary copulation is necessary for feeding to be accomplished is equally valid for *I. ricinus*. As not all the males meet the females on the host, in these cases it is during the free phase that the sexes will find each other. One of us (GRAF 1975) has demonstrated that this is facilitated by a sex pheromone produced by females to attract the males. Indeed, it is not a rare occurrence to catch in the wild couples in copula by the "flag method" (AESCHLIMANN 1972).

Exophile adults lie in wait for passing hosts on the upper strata of the undergrowth. This waiting period may last for several weeks during favourable weather. However, the ticks may always resort to the lower strata during unfavourable conditions. Individuals who have failed to find a host by autumn are capable of passing the winter in their hiding places to return again in the spring. This remarkable ability to fast increases their chances of

⁵ ČERNÝ 1961 also stressed that rodents are the primary hosts for larvae.

⁶ Cattle have no access to the studied forest.

eventually meeting with a host and makes up for their relative lack of mobility. It is a remarkable finding that ticks tend to move hardly at all in the horizontal sense, and so do not actively seek their hosts. This phenomenon was particularly well examined in *Dermacentor reticulatus* by IMMLER 1973 who found that ticks marked in the autumn could be found again the following spring on the same plants. *I. ricinus* seems to exhibit the same behaviour. Horizontal movement is negligible (ČERNÝ 1961 confirms this view) and only vertical displacement is practised. It follows that foci of infestation will vary in severity in relation to absolute population size. Displacement to new biotopes is favoured by the lengthy sojourn on the host: 4 to 14 days. We can now discuss the epidemiological importance of this phenomenon.

Egg-laying, behaviour and nutrition of the larvae. The gorged female detaches from the host and falls to the ground⁷. It seeks a hiding-place in the immediate vicinity, lays eggs and dies. As the larvae hatching from these eggs remain largely confined to the area chosen by the female, they comprise "nests", horizontal movement from which being negligible. Unpublished observations show that a limited displacement of larvae from the egg-laying site is possible, for example, if the prevailing microclimatic conditions become unfavourable (lower degree of humidity). The larvae then actively seek more sheltered microbiotopes. The distances covered have not been established for *I. ricinus* but very likely they are modest. It is by sojourning near a "nest" of larvae that passing hosts become infested and consequently disperse the larvae which remain attached to the host for 3 to 6 days. The actual distance displaced will depend on the "wanderlust" of the given host. Once again, here intervenes the rhythm of "drop-off" which in larvae tends to predominate during the day⁸, a time when rodents are inactive in their nests. Undoubtedly the gorged larvae find this microhabitat favourable for moulting. As rodents only rarely serve as hosts for nymphs, one must consider that the latter leave the burrows of the rodents by grappling on to their fur without actually attaching. Being exophiles, they then take up their usual stalking positions on the surrounding vegetation. Thus the nymphs are aided in their dispersal from the strictly localized nests of larvae by the intervention of the larval hosts, and from a very spotty distribution the immature stages become more evenly distributed. However, as rodents rarely stray far from their territories, it is only over relatively modest areas that nymphs will be

⁷ The problem of "drop-off" rhythm in *I. ricinus* as in other species has not yet been fully elucidated.

⁸ Recent experiments by GRAF et al., (in preparation) show that all gorged stages of *I. ricinus* tend to detach (from white mice and guinea pigs) during the daytime (principally 12.00 to 14.00 h). We are still ignorant as to the detachment rhythm of ticks fed on birds.

scattered. It is only by the intervention of more adventurous hosts that these parasites are eventually transported elsewhere.

Behaviour and nutrition of nymphs and adults. The exophile nymphs, now more evenly distributed in their biotopes await the passing of their hosts. We have already mentioned that the *Muridae* and Insectivores serve only infrequently as hosts for the nymphs of *I. ricinus*. The list of possible hosts for the nymphs is nevertheless impressive as it comprises, besides birds and several reptiles, carnivores such as the fox, various *Mustelidae*, squirrels, various Artiodactyls (boar, deer, chamois) and domesticated animals (cattle, sheep, goats, dogs; AESCHLIMANN 1972). Certain of these animals live in the same territories as the rodents parasitized by larvae thus assuring a more homogenous distribution of nymphs in the biotope under consideration. Other animals (foxes, hares, roe-deer) have a wider range enabling further dispersal of nymphs which become ready to detach after a feed of 3 to 7 days. These hosts may be reinfested on their next return. Finally, certain animals, such as the wild boar are only "passers-by" so their role as dispersal vectors is evident. The same phenomenon applies to the adults but with a less varied series of hosts and for a feeding duration which may last for 6 to 14 days.

CONCLUSIONS

I. ricinus is a most interesting example in the study of tick dissemination as a function of environment and available hosts because of its triphasy and telotropism (tritropism?). Of special significance to the epidemiologist is the relative (at times even extreme) location of the foci of diseases transmitted by this vector. We know that among the favourable biotopes where *I. ricinus* is numerous, in some areas the ticks are infectious and in others not. The explanation for this may be found in the tick's behaviour in the wild and in the phenomenon of transovarial transmission. For a biotope to be conducive to the maintenance of *I. ricinus*, it must have abundant ground litter and a developed undergrowth. The forest, a hedgerow, a thicket all present such a favourable milieu. These phytosociological imperatives are responsible for the punctate nature of the *I. ricinus* population in Switzerland as well as in other European countries. The survival of this species depends also on a near saturated environment which it can experience in the vegetation cover described above. The mean annual temperature cycle influences both the seasonal activity and abundance of the population.

The survival of *I. ricinus* is also aided by the remarkable fasting ability of all stages of this species. In addition, the fact that free-living stages move principally in the vertical sense gives them access to ground-level protection when adverse meteorological conditions prevail. Thus endo-exophily is an advantageous adaptation for the survival of ticks. The larvae of *I. ricinus*

are less exophile than the nymphs which in turn are less so than the adults. Thus larvae principally occupy the inferior, the nymphs a median and the still more resistant adults the highest level of the undergrowth. It is not a rare occurrence to find females lurking on shrubs more than a metre off the ground. Perhaps this would also serve to explain the relative "tritropism" of the species and why it does not show strict parasitic specificity. This hypothesis clearly demands closer study.

The ticks' own mobility serves, above all, to place them in a suitable position on the vegetation when conditions are favourable. The role of temperature here is primordial. *I. ricinus* males, in search of mates and in response to a sex pheromone secreted by females, possibly move somewhat more in the horizontal plane than do the latter. The general lack, however, of horizontal displacement of ticks favours a mosaic distribution, and in consequence, the establishment of natural foci of infection. A gorged, infected female will give rise to, at a specific locality in the biotope, a number of larvae, of which a proportion will themselves be infected as a result of transovarian transmission. Obviously not all the hatched larvae will survive. Only those which find a host will be able to continue their development. In the case of *I. ricinus*, the first host will in general be a rodent which, keeping to a somewhat confined territory, will disseminate ticks only over a fairly localized range. In order for a tick to be carried farther afield, thus giving an opportunity for a new focus to be created, it must wait for an encounter with a more nomadic host. In this regard, some birds undoubtedly play an important role for the immature stages as large mammals do for the adult.

Thus, ticks are able to pass over adverse biotopes and reach adequate ones by travelling on their hosts; this process is aided by the relatively long duration of attachment.

The detailed study of host behaviour, of the ecological needs of the tick vector and of transovarial transmission are all indispensable in understanding how a natural focus of infection operates.

It was by the diversity and mobility of its hosts, its triphasy, its endo-exophily and the presence of many suitable vegetation areas that *I. ricinus* was able to spread itself throughout all of Switzerland. But its static behaviour in the field favours not only the localized nature but also the permanence of a natural focus of infection. In this country, the most frequent model of a biocenosis, consisting of the forest undergrowth, the ticks which shelter there and the hosts which roam, represent a closed system in which ticks are able to live out their existence without difficulty. An infectious agent present in ticks of such a biocenosis will be able to survive for long periods without the intervention of a susceptible vertebrate because

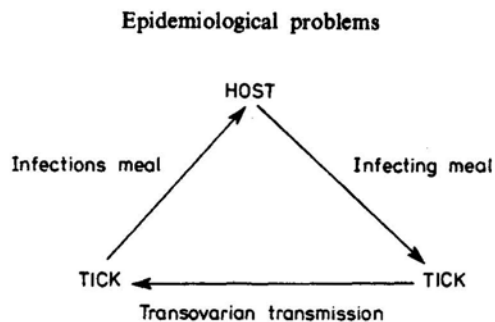
of the expedience of transovarian transmission. By such means an infectious agent can be carried through many generations thus making the tick not only a vector but also a reservoir of the agent. Also, in a given region, many foci have been established for a long time. But new foci created by the transport of infected ticks are not easy to discover by virtue of their strict localization. In a region full of ticks, but free from pathogenic agents, the introduction of diseased or preimmune animals (see BROSSARD and AESCHLIMANN 1975, on piroplasmosis) from which "clean" ticks can become infected always raises the possibility that a new focus of infection will be created. It is thus of paramount importance that veterinary services carefully monitor the state of domestic animals at the time of importation and transhumance.

Needless to say, it is tempting to extrapolate our knowledge of the *I. ricinus* system to that of other ticks, but that would be fraught with danger as we still lack sufficient knowledge on the biology, ecological needs and behaviour of other *Ixodoidea*, with the possible exception of those which are of medical and veterinary importance. In the case of the genus *Boophilus*, of which the 5 known species are monophasic (and thus by extension, monotropic), transovarian transmission is the only means possible for maintaining pathogenic agents in the biocenosis. Today, all *Boophilus* are primarily ticks of livestock, and so it is in the pasture where the ectoparasite completes its life-cycle. In this case the foci will be less punctate.

A completely different picture is painted by the Argasid tick, *O. moubata* and the agent responsible for human relapsing fever, *Borrelia duttoni*. In Africa, *O. moubata* lives in human habitations feeding during the night principally on human blood and on that of fowl. It takes refuge in order to digest its meals, moult, or lay eggs in the dirt floor, between planks etc. The duration of the nocturnal feed being short, and also because the tick feeds at a time when its hosts are inactive, transport between habitations is problematic⁹. *O. moubata* is without doubt one of the ticks most resistant to starvation (remaining alive in the laboratory for up to 5 years without a meal). It is also able to pass on from generation to generation the agent, *Borrelia*, by transovarian transmission. Thus the dual role of vector and reservoir is also united in this species in order that the natural focus (represented by an "infected" hut) can endure for many years.

The above examples show that one cannot generalize in epidemiology. There are many adaptations in the *Ixodoidea*, differing even among distinct geographical populations of the same species. The study of such a chain:

⁹ GEIGY 1955 says that man himself, by virtue of certain customs, transports *O. moubata* from one dwelling to another.



is one of the most intriguing activities of the epidemiologist.

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