Ticks as vectors: taxonomy, biology and ecology

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Summary
Ticks are prominent parasites and competent vectors of pathogens that affect both humans and animals. This review outlines and illustrates the main features of the morphology of ticks of the families Ixodidae and Argasidae, and summarises the basic components of their life cycles. It focuses mainly on development processes and mortality among tick populations so as to provide an overview of how they are regulated in nature and how pathogens can be transmitted under such a framework. The effects of the weather on these life cycles are reviewed. The author also examines how landscape structure and biotic factors, such as the presence and abundance of hosts, may shape the density of tick populations. The uncertainty inherent in dealing with the transmission of pathogens by ticks is highlighted; this results from the sometimes complex relationships among the vectors, the climate and the presence and density of host populations. The need to obtain reliable field estimations of such relationships before drawing conclusions about the effects of the isolated components of the system is stressed. A section is devoted to addressing the expected (and not yet totally understood) effects of trends in climate on the spread of ticks, and how these can be analysed and tracked.

Keywords
Biology – Climate – Ecology – Host composition – Landscape composition – Tick.

Introduction

Ticks are obligate parasites that transmit a multitude of pathogens to animals and humans. Interest in tick-transmitted pathogens has experienced an upsurge in the past few decades. Routine application of tools for the detection of fragments of foreign nucleic acid in ticks, together with a greater interest in the quantification of disease risks for humans, has led to a marked increase in the number of reports on the ecology and epidemiology of tick-borne diseases in humans and other animals. The discovery of formerly unknown mechanisms of pathogen transmission (such as the non-viraemic [co-feeding] transmission of the tick-borne encephalitis virus [1]) and the re-emergence of certain tick-borne diseases (such as the ongoing epidemic of Crimean-Congo haemorrhagic fever in Turkey [2]) have also created a wealth of research interest. A recent surge in interest in ticks and tick-borne pathogens has been inspired by claims about the impact of the observed trends in climate, and forecasted climate change, on the spatial distribution of ticks and associated pathogens (3, 4, 5, 6).

Most interest in the ecology of ticks is focused on species that have a role in the transmission of pathogens to humans. However, there is a growing body of research on species of ticks that can seriously affect animal health and production. Investigation of the invasive behaviour of some ticks, such as *Rhipicephalus microplus* in parts of Africa (7, 8), continues, as do efforts to develop a universal vaccine against ticks that affect livestock (9). The attempts to eradicate cattle-fever ticks (former genus *Boophilus*) in the southern United States are a classic example of coordinated action to eliminate a threat through chemical treatment and restriction of the movements of infested animals (10). Such efforts are necessary in large areas of Africa and South America, where multiple factors, such as the complex faunal tick composition and the lack of allocated resources, make any initiative aimed at controlling ticks in these regions difficult (11). The cattle-fever ticks, *R. annulatus*, *R. australis* and *R. microplus*, are serious threats to animal health and production economics in many countries of Central and South America, parts of Africa, and a large region of Australia, areas to which they have been introduced. The causes of tick introduction and spread include the uncontrolled movements of domestic or wild animals, small but sustained climate trends, and changes in the use of land resources that allow the increased abundance of tick hosts. After ticks have been introduced to a region, they can persist only if the climate is compatible with the requirements of the ticks and if sufficient hosts are available. When ticks are introduced into territories where there is no competition with other species of tick, they are likely to colonise the complete range of abiotic conditions that is compatible with their physiological plasticity (11).

This review provides an introductory text on the morphology and systematics of ticks, as currently acknowledged by most authors, and on the basics of their biology and ecology. The author reviews the life cycle of ticks, how it is affected by the weather, and how other biotic factors (including the presence and abundance of hosts) may shape the abundance of ticks at a site. The review finishes with an appraisal of the expected effects of the trends in climate on ticks, and how these could affect their fitness and the transmission of pathogens.

Systematics of ticks

There are about 900 different species of ticks, most of which belong to one of the two main large families, the Argasidae and the Ixodidae (12). The former are commonly known as 'soft ticks' and the latter as 'hard ticks'. Several lists of accepted generic and specific names of ticks have been published (13, 14, 15, 16, 17, 18). This paper adheres to the opinions of previous authors (12, 19) who have published a complete appraisal of the species of ticks, their hosts, and their distribution. As of May 2013, 707 species of hard tick had been accepted. A further study (20) published the complete list of names used for ticks, and their synonyms; this is an essential reference for those involved in the study of the systematics of ticks.

The two families of ticks not only have different life cycles but also have numerous morphological and physiological features that clearly delimit these two large taxa. Figure 1 compares the external morphology of hard and soft ticks. Hard ticks of all life stages possess a sclerotised scutum and an apically located gnathosoma. They feed for prolonged periods (several days to weeks) and ingest more than 100 times their body mass in blood. Soft ticks do not possess a scutum, their prognathous mouthparts are located anterioventrally and they have a leathery integument that can rapidly expand, allowing nymphs and adults to engorge up to ten times their body mass within a few hours, sometimes within minutes. Numerous physiological processes also differ between the two families, including the way they digest blood (21). Hard ticks secrete the excess of water derived from a blood meal back into the host via their salivary glands, while soft ticks use their coxal organs, a specialised ultrafiltration organ on coxae I.

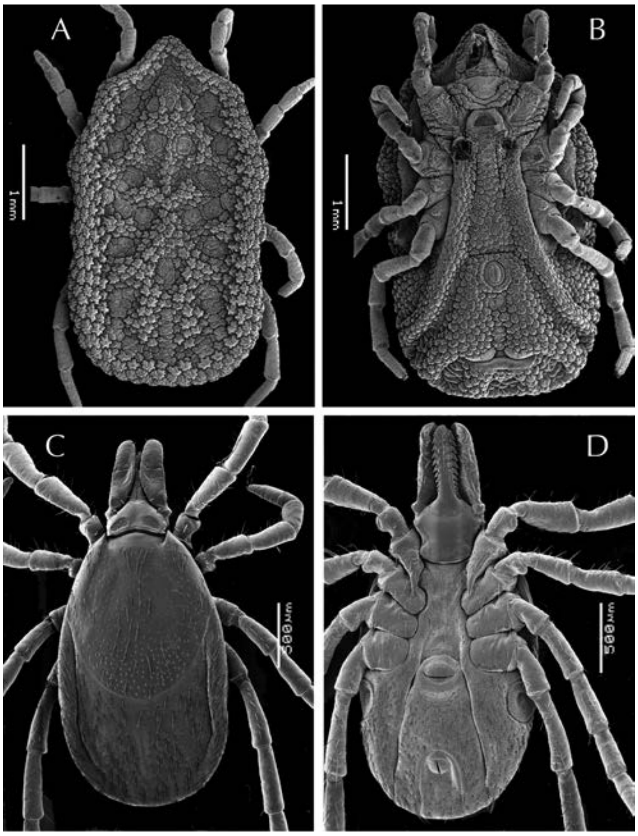

Fig. 1
The general morphology of ticks of the families Argasidae and Ixodidae
Plates A and B show the dorsal and ventral views, respectively, of a female *Ornithodoros puertoricensis*, an argasid (soft) tick. Plates C and D show the main morphological features of a female *Ixodes ricinus*, a representative of the family Ixodidae

A third family, Nuttalliellidae, with only one species, *Nuttalliella namaqua*, exhibits features associated with both hard and soft ticks. Classification with regard to its relationship to the other tick families on the basis of morphology and biology therefore remains problematic. Analysis of the 18S ribosomal ribonucleic acid from *N. namaqua* has indicated that it is basal to the other tick families, suggesting that it is the closest extant relative to the last common ancestral tick lineage (22). There is controversy about the evolutionary origin of ticks. This is outside the scope of this paper, but the interested reader may consult previous studies (23, 24). Most molecular clock estimates agree that ticks originated in the Carboniferous period (23). However, there is less consensus about when divergence occurred: some propose that separate families of hard and soft ticks emerged in the Middle Permian, but others propose that this occurred in the Early Permian, which coincided with the origin and diversification of therapsids (24).

The taxonomic situation of the Ixodidae has been studied in depth, and there is almost complete agreement on the systematic position of the families and genera. The family Ixodidae is now considered to include the genera *Ixodes*, *Haemaphysalis*, *Amblyomma*, *Rhipicephalus*, *Dermacentor*, *Hyalomma*, *Anomalohimalaya*, *Bothriocroton*, *Cosmiomma*, *Margaropus*, *Nosomma* and *Rhipicentor* (plus the fossil representatives *Compluriscutula* and *Cornupalpatum*). The situation is different for the family Argasidae, which includes around 190 species. Competing taxonomies for Argasidae have very different genus-level groupings; the opinion of the eastern school of taxonomists (25, 26, 27) is sometimes radically different from that of the western school (28, 29). A third group of researchers has developed a different approach to the systematics of the family, rearranging some genera and proposing new subgenera, in conflict with previous proposals (13, 30). A cladistic analysis (23) proposed a radically different view of the whole family. A further molecular taxonomic study (18) did not solve the main problems in the existing classifications because of the poor representation of different alleged natural groups; the classification was further reviewed later (31).

The genus- and species-level taxonomy of the family Argasidae is therefore much more uncertain than that of the Ixodidae. There are two factors related to such uncertainty. First, there is a lack of adequate guidelines based on stable morphological features that would allow reliable determination. Second, Argasidae have high biodiversity, which has been generally ignored. Extreme morphological variability has been observed in several groups of species, and seems to have been underestimated during the compilation of taxonomic keys. As discussed in the most recent study on the topic (31), the genus-level classification of the family Argasidae is obviously much less settled than that of the Ixodidae. Indeed, most species of Argasidae can be assigned to more than one genus: there is currently no agreement on generic placement for 133 of the 193 argasid species. It will be difficult to reach consensus about the genera of Argasidae without additional morphological and molecular studies of the type species of putatively monophyletic groups; these will be essential to an understanding of argasid phylogeny and evolutionary history.

A complete textbook on the determination of every stage of all the species of tick does not exist. It is necessary to compile information from published (re)descriptions of species. It has been customary to classify and report only the adult stages of ticks, probably because they are easier to find and to collect on their hosts, or because they are easier to classify than the immature stages. It must be stressed, however, that to understand actual tick–host relationships, and the epidemiological chain of events of any tick-transmitted pathogen, it is necessary to classify both the adults and the immature stages, or only a partial view of such relationships will be captured. Current advances in molecular biology are not yet sufficiently reliable to provide an unambiguous classification of ticks without the use of keys based on morphological details. Researchers should be aware that the systematics of ticks is an active field, and new opinions and reassessments are being produced every few years. The use of old keys for the classification of ticks might produce unreliable determinations.

Basic biology and ecology of ticks

All ticks are obligate temporary parasites of vertebrate animals and are characterised by a complex developmental cycle. All have three development stages (other than the eggs), namely larva, nymph, and adult (male and female). However, how these stages develop and how such development rates shape the duration of the life cycle in ticks is dependent upon the family of the tick. Ixodid and argasid ticks have different life cycles: the former feed for several days, while the latter feed only for minutes, and commonly at night time, while animals are resting in their burrows. Ticks that are restricted to the shelters of their hosts are said to exhibit 'endophilous' behaviour, because these ticks live in close proximity to a suitable source of blood, and their development is not influenced by the weather outside the burrow. All argasid ticks and some ixodid ticks show endophilous behaviours (32). Fed stages of the species that have evolved this survival strategy drop from the host inside the nest or burrow. This increases their chance of survival, because they moult in the shelter under a protected environment. The opposite type of behaviour, termed 'exophilous', involves the ticks waiting for a suitable host outside the burrow, exposed to the weather. Weather variables regulate the behaviour of such ticks while they are actively questing for a host. A complete section below is devoted to explaining how ticks find a host.

Figure 2 shows a diagram of the typical life cycle of an ixodid tick. The ixodid life cycle typically includes the larva (which hatches from the egg), the nymph and the adult. Ixodid ticks feed once in each active stage and ingest massive amounts of blood. Ticks may use different groups of hosts for each active stage. The immature stages (larvae and nymphs) usually feed upon small hosts, such as rodents and/or birds, while adults commonly feed upon large animals, including carnivores and ungulates. However, this is not a rule for every species of tick. Some species are highly specific for a particular type of host. The absence of such key host(s) in a particular area may prevent the occurrence of the ticks that specifically feed on them.

Once on the host, ticks actively search for a favourable place for feeding. They then probe the skin and insert their mouthparts. The first step in feeding is the secretion of a substance that solidifies in contact with the skin of the

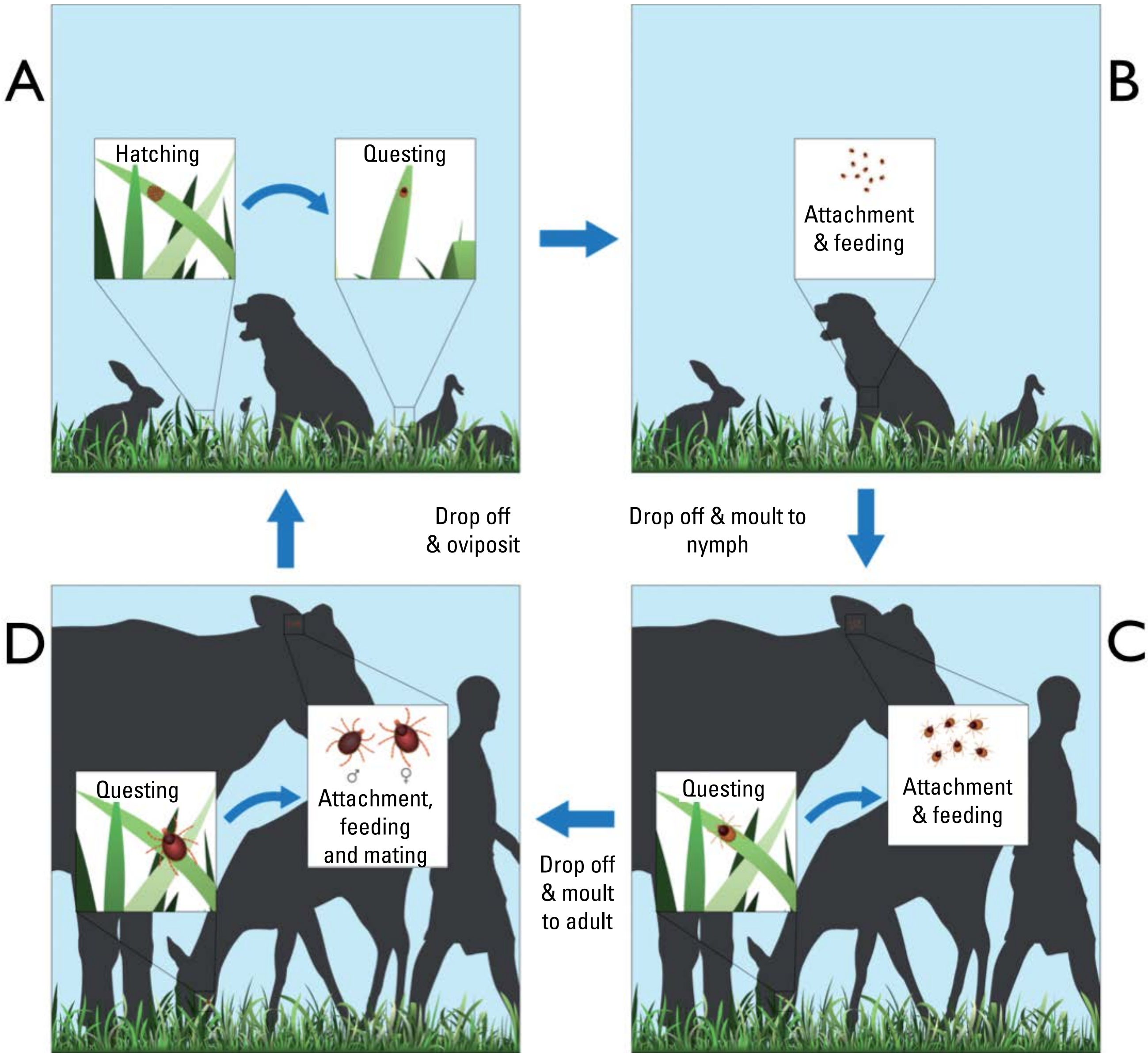

Fig. 2
The life cycle of a three-host tick
Larvae hatch from eggs, and quest in the vegetation for a host (A). After attachment and feeding (B), the larvae drop to the ground to moult, a process regulated by temperature and the availability of water. The nymphs quest again after moulting (C) and feed upon a second host. These engorged nymphs again drop to the ground for a final moult to the adult stage, which again quests, finds a suitable host, and drops to the ground to lay eggs (D)

Source: Image prepared by Alex McAuley, University of Texas Medical Branch, Galveston, United States of America

host. This contributes to the fixing of the tick, and is called 'cement'. A few hours after the tick has become attached to the host's skin, a complex sequence of events begins, mainly originating in the salivary glands of the tick. The feeding tick begins a series of peristaltic movements that inoculate saliva through the mouthparts into the so-called 'feeding cavity'. At the same time, a dramatic series of changes occurs in the tick's salivary glands, whose cells are deeply transformed, adapting their physiology and pharmacological secretions to the new 'active' status. The inoculation of several dozen pharmacologically active compounds (33, 34) contributes to the sustained flow of blood into the feeding cavity, lysis of the cells surrounding the feeding place, and evasion of the host's immune response. Transmission of pathogens is likely to start approximately 24 h after a tick begins to feed, but may start sooner in some cases. After each blood meal, ticks detach and drop to the ground, where they moult. The engorged females do not moult and they lay thousands of eggs, which are left among the decaying vegetation at protected sites where a high relative humidity will ensure their survival.

Feeding ticks concentrate the blood meal by removing excess water. This helps to accommodate the large blood intake (several millilitres) in the relatively small body of the engorging tick. The immature stages (larvae and nymphs) commonly feed for three to six days, while the adults may feed for as long as two weeks. Digestion of the blood may start during the first few hours after the beginning of feeding, and usually lasts for several weeks or even months. While digestion takes place, possible pathogens acquired from the hosts cross the gut wall, become incorporated in the haemolymph circulation of the tick, and invade the cells of the body tissues. After feeding, the tick will moult; after the moult is complete it takes several days for the cuticle to harden completely, and the tick will then actively quest for a new host.

The diagram in Figure 2 refers to a three-host cycle. In this type of life cycle, each stage feeds on a different host. A few species complete their life cycle by feeding only on two hosts, larvae and nymphs feeding on the same individual and adults on a different one after completion of the moult. Some species may complete their entire life cycle on only one host. These different types of life cycle have importance in the survival of the ticks. Given that weather regulates tick development and the mortality rates during moulting, as well as questing rates, ticks that complete their cycles in fewer 'steps' (i.e. fewer moults off the host) have less dependence on the environment. These features are of importance for the transmission of pathogens. For a tick-transmitted pathogen to persist in the environment it must be acquired from an infected host, passed into the next active stage of the tick, and then be successfully transmitted to a new host (35). This complicates the dynamics of a pathogen in the field, which therefore depends upon both the survival and activity rates of the tick and the composition of the community of hosts (36).

Ticks spend long periods between meals in the environment, during which they are exposed to the weather. There are two key processes in the life cycle of any species of tick: the development processes, which include moulting and oviposition, and periods of questing activity. Weather regulates the development rates (moulting, oviposition), which are dependent on the temperature, as well as the mortality rate, which depends on loss of water (regulated by the relative humidity and the air saturation deficit). During the winter, low temperatures prevent rapid development, and development progresses slowly until temperatures rise in the spring. Large numbers of active ticks appear in the vegetation in the spring in temperate regions, as a consequence of the synchronous development of moulting ticks driven by the rise in temperature after the winter.

How ticks find a host

Both the microclimate (e.g. the climate within the lower layers of vegetation) and the abundance and availability of hosts shape the seasonality and abundance of ticks, a feature known as 'phenology'. Each tick stage prevails at definite times of the year, according to the specific combination of climate and seasonal changes in host abundance. In the process of finding an animal to feed upon, ticks actively quest for a host after gaining a vantage point on the vegetation. The restriction of the questing activity of ticks in the temperate regions of the world to a defined period is a consequence of the seasonality of the climate and regional variations in weather.

Results obtained from empirical studies confirm that the questing activity of ticks is regulated by the climate (5, 37, 38, 39, 40, 41, 42, 43). This can be applied to every species of tick for which field or laboratory data are available, with small variations resulting from particular features of their biology. Most ticks are inactive at the lowest layers of vegetation before they begin to quest. The process of questing is triggered by specific combinations of climate and photoperiod, i.e. the ratio of the hours of light and darkness in a day (44). Photoperiod may act on the moulting stages, activating or delaying moulting until more favourable conditions are available, or on the questing stages, activating or delaying the onset of activity. This is believed to ensure the success of the population by allowing ticks to find a host, feed and enter the moulting period before the onset of winter, and then stopping any activity until the beginning of the next spring.

During questing, ticks may lose water, which they normally regain by descending at intervals to the litter zone (the layer of dead leaves, grass, twigs, etc. covering the soil) (39) where they can reabsorb water vapour from the atmosphere (45, 46). When they are hydrated, they climb the vegetation again. The seasonal activity of ticks is thus characterised by several cycles of ascending and descending movements in the vegetation, regulated by temperature and losses of water. The energy reserves of the tick, its ability to retain water, the content of water in the air, and the temperature are therefore some of the factors regulating the questing and survival of ticks in the field. Temperature plays a central role in the regulation of the tick life cycle. However, mortality rates while questing are related to the water content of the air: if the relative humidity drops below a species-specific limit, under which ticks are not able to absorb water from the atmosphere, the saturation deficit can control the mortality rate. The saturation deficit also depends on the temperature.

Factors affecting the abundance of ticks

The microclimate in the layers of vegetation populated by ticks is an important factor regulating the abundance of their populations. The weather also regulates the periods of the year when ticks are active (47). Climate therefore has various, not yet totally quantified, effects on the mortality and development rates of the population of ticks, and also on the phenological component of the cycle (e.g. activating a cohort of questing ticks earlier or later in the year). Ticks are responsive only to the microclimate, e.g. the temperature and water content recorded between the litter and the height at which the ticks quest. In the summer in temperate areas, long periods of high temperatures (together with the high desiccating power of the air) may promote a rise in the mortality rates of ticks in the moulting or questing stages. Long winters or abnormally low minimum winter temperatures may induce high mortality in the population of ticks overwintering in the ground. However, it is well known that long periods of snow cover on the ground may confer a protective effect, by insulating ticks overwintering in the ground from very low temperatures.

Short-term changes in regional weather may also promote variations in the seasonal pattern of tick populations. For example, mild temperatures in autumn and winter may affect the development rates of ticks, and newly moulted ticks might begin questing in the vegetation a few days earlier than they would if the temperatures were cooler. Similarly, if winter temperatures are high enough to promote questing behaviour, ticks may quest outside the periods in which they have been recorded. This was reported in Germany for the unusually warm winter of 2006, when adult *Ixodes ricinus* were collected while questing throughout the whole winter, a period when they are not commonly active (38, 48, 49).

The effects of the weather on the observed seasonality of ticks in the field are not yet completely understood, because of the many uncertainties operating at the smallest scale. Several studies have attempted to quantify the effects of different combinations of temperature and relative humidity on each of the processes for several species of tick, expressing such effects as equations describing a physiological response (50, 51, 52). However, we do not yet know how the long-term trend in a variable (e.g. the yearly average temperature) affects the complete life cycle of ticks and their ability to persist in the field. Studies suggest that seasonal changes in critical periods of the tick's life cycle might have more impact on its fitness than long-term averages or extreme values of these weather variables (40, 52).

As the climate roughly delineates the habitats that can be colonised by populations of ticks, the availability of hosts shapes the density of their populations and the phenology. It has long been evident that patterns of land use can have an important influence on the risk of tick bites, at least for humans. In this particular field of research, landscape epidemiology, studies have demonstrated that a territory may have a greater risk of transmission of pathogens either because it is more visited by humans or because larger populations of ticks and reservoirs of the pathogen are established in it. In either case, the structure of the landscape may be largely responsible for such an increased risk. This has been empirically demonstrated for the pathogens transmitted by the tick *I. scapularis* (53, 54). It has also been demonstrated that the structure of the landscape accounts for the abundance of the tick *I. ricinus*, probably because the movements of the animals acting as hosts follow a well-defined pattern according to the fragmentation of the territory (55). It has been suggested that the spatial structure and relationships of these fragmented patches of vegetation are of importance in defining the abundance of such tick species (56). Animals use the land in different ways, and may have a tendency to visit particular sites with high densities of ticks.

Habitat fragmentation describes the emergence of discontinuities (fragmentation) in the environment, which can be observed at different scales. For example, large patches of forest may become fragmented because of agricultural activities, leaving several smaller patches of forest immersed in a matrix of other habitat classes. Habitat fragmentation can be caused by natural processes that slowly alter the layout of the physical environment or by human activities such as land conversion. The area of the patch is the primary determinant of the number of species and the abundance of animals (57). The area will thus influence the number of species that are present when the fragment is initially created, and will also influence their ability to persist. Of importance regarding habitat patchiness and ticks is that small patches will probably remain unconnected after fragmentation, meaning that animals will not move among the patches. Habitat fragmentation thus has additional effects on the modulation of the abundance of ticks and their hosts, and therefore on the transmission rates of pathogens. However, these studies have only been partially extended to ticks that transmit pathogens to domestic animals. Empirical evidence from field studies suggests that the abundance of *I. ricinus* is related to a vegetation index that takes into account the abundance of trees and bushes on the edge of pastures. The proportion of pasture perimeters with a high vegetation index is significantly associated with a higher prevalence of babesiosis in cattle (58).

In summary, trends in climate obviously can promote changes in the habitat, but large effects resulting from human activities are much faster and may not be directly linked to the climate. Such activities are known to have a profound impact on the transformation of the biotopes, which may, or may not, influence the rate at which pathogens infect ticks.

The climate and its effects on ticks

Like any other arthropods, ticks are expected to respond to changes in medium- and long-term weather variables. It has been predicted that the forecasted trends in weather will increase either the range of ticks or their local or regional abundance, in different ways. It has commonly been thought that this will result in a higher risk of pathogen transmission to either animals or humans. However, the response of ticks and transmitted pathogens to changes in climate is not simple, and depends also on changes in the populations of vertebrates. Human actions that change the landscape, modifying the habitats in which vectors, hosts and pathogens coexist, may have deeper effects on the epidemiology of tick-transmitted pathogens than climate change (58).

The interest in capturing the effects of climate on the distribution of ticks has fuelled recent research in which observations of their current range are compared with the historical records of ticks. It has been reported that the milder winter periods recorded in recent decades in northern Europe, the northern United States (USA) and southern Canada have promoted the spread of some species of tick to northern latitudes. *Ixodes ricinus* has been reported to have spread northwards in Sweden (59, 60), Norway (61) and Finland (62). These data were collected along the fringes of tick distribution and do not apply to the core distribution areas. In Sweden, it is known that the spread into northern latitudes is not only shaped by the milder winter temperatures in these areas, but has also occurred because some species of wild ungulate that feed the adult ticks are becoming more abundant in these territories (63). In the case of such large hosts, just one animal can provide a blood meal for hundreds of female ticks. Thus, both the warmer winters and an unprecedented abundance of large hosts seem to have driven the reported spread of *I. ricinus* into northern latitudes in Scandinavia. A similar scene has been reported in the Czech Republic, where the trends of climate in recent decades have promoted the upward movement of *I. ricinus* in mountain ranges, allowing it to colonise biotopes that were formerly too cold to support permanent populations of the tick (64). In southern Canada and the northern USA, *I. scapularis* is being recorded further north than its historical distribution (5). The driver of such northerly spread seems to be warmer temperatures in winter. Migratory birds fly from the USA to Canada, and these carry immature stages of the tick. A warmer climate facilitates the colonisation of areas in northern Canada by ticks that would not have been able to survive in these areas had the temperatures remained low (5).

Similar concerns have been raised regarding the tick *Hyalomma marginatum* in the Mediterranean region and areas at higher latitudes in Europe. This is a common species in steppe Mediterranean habitats, where it is involved in the transmission of some prominent pathogens to livestock (e.g. the protozoan *Theileria* spp.) and in the transmission of the Crimean-Congo haemorrhagic fever virus to humans (65). The finding of immature stages of the tick feeding on migratory birds is well known (66). However, adult ticks of the same species have been recorded only occasionally at sites in Central Europe (67), probably as a result of the importation of immature ticks by migratory birds and because warmer weather has allowed the imported engorged nymphs to moult. It is currently not known how many immature ticks are introduced each year by migratory birds and how many of them manage to survive as a consequence of warmer weather at the periphery of their current range of distribution, although estimates have been provided (2, 68). Therefore, it is not yet possible to evaluate the impact of weather on this tick in terms of the survival of invading specimens. Adults of other species of the genus *Hyalomma* have also been reported outside their main range (69). The presence of adult ticks suggests that there is an established population of such species feeding on livestock, far north of the reported distribution range.

The modifications of the dynamics of tick-transmitted pathogens are often accounted for as though they were driven only by environmental factors. (70). However, the drivers of change in the epidemiology of tick-transmitted pathogens are likely to be dependent on socio-demographic factors, agricultural development (or abandonment), deforestation, and the extent to which humans or other animals come into contact with the ecosystem of the disease (70). This introduces a high degree of uncertainty when attempting to capture the local or regional risk of pathogen transmission by considering only the weather. The circulation of tick-transmitted pathogens is focused in small areas with particular conditions of weather, reservoirs, and vector species. This is why the term 'foci of transmission' is accurate when applied to the spatial distribution of tick-transmitted pathogens. These foci are not only defined by the microclimate, but also by the presence and abundance of key reservoir hosts necessary for the maintenance of the pathogens in the field. The weather, physical features (e.g. slopes) or plant composition of transmission foci (71) affect pathogen dynamics at the local scale, because of effects on both the survival of ticks and the presence of key reservoir hosts. The focal distribution of hosts also affects the reliability of process-driven models (see below) intended to produce estimates of tick density, because they are built using data on host density, which may change greatly with space or time. To achieve an adequate understanding of how climate shapes the transmission cycles of tick-borne disease agents there must be more rigorous analysis, which is prevented by the current lack of data.

Even with the acknowledged limitations that restrict our ability to capture the complete set of factors that shape the distribution of ticks, efforts are being made to produce regional maps of the probability of ticks persisting as permanent populations. Such estimations of the effects of the weather on the phenology and distribution of ticks and pathogens (including the extension of their historical distribution areas) are commonly based on:

– evaluation of the 'abiotic niche' of the ticks and the building of so-called correlative models (41), and

– development of process-driven models that aim to capture the complete life cycle, based on equations aimed at explaining each process (development and mortality rates, questing activity, etc.) in separate 'boxes' (72, 73).

Correlative models are based on the idea that populations of living organisms are constrained to areas with particular environmental conditions (74). Such a niche is defined in terms of values of abiotic variables, such as temperature and water availability, at which populations have variable fitness but always show positive growth. Thus, within these climate restrictions, species may vary in abundance along environmental gradients that together correspond to optimal and less optimal conditions. This concept, applied to ticks, assumes that the factors that drive the tick life cycle in the field are mainly related to weather. Therefore, correlative models identify possible niches by comparing data on occurrence of the tick with data summarising climate and/ or other abiotical constraints. If presence records suggest that, at some stage, individuals of that species were able to develop, survive to the adult stage and successfully reproduce in that location, then climate is also geo-referenced to that site, and is then inferred to be within the tolerance range of that species. This trains the coefficients of the model such that other sites with similar conditions are considered more likely to contain tick populations and are weighted accordingly, ultimately defining a space of suitable environmental conditions. The prevalence of a tick-transmitted pathogen is strongly dependent upon the availability of reservoir hosts and is therefore not only modulated by the climate. Tick-transmitted pathogens are thus restricted to sites where adequate reservoir hosts exist, although climate can indirectly affect the presence and abundance of both the reservoir and the vector (36).

Another approach to understanding the effects of climate on ticks and their transmitted pathogens is the development of process-driven models (4, 50, 51, 72, 73). These models aim to capture every 'process' (egg development, density-dependent mortality, etc.) of the tick life cycle with equations that define the response of the tick to given combinations of the components of the environment. This is assumed to represent tick distribution more reliably, by capturing the sites where permanent populations are expected to exist. Correlative models assume that the presence of ticks results from a combination of the physiological processes of the tick and they do not look at how each individual process affects their presence. However, process-driven models address each physiological step separately and look at the effect of different weather conditions and environmental features on each process of the life cycle. Process-driven models are built upon observations of the life cycle carried out under laboratory or field conditions.

Process-driven models are the only way to capture the importance of each environmental variable for any tick stage, as well as the time of year at which it operates. We should remember that ticks are affected not only by the average and extreme values of the weather at any point, but also by the time of year at which a precise combination of abiotic conditions occurs. This is the factor that defines the phenology of the ticks (75), and process-driven models are oriented towards its capture. In any case, there is always a degree of uncertainty around estimations of the properties of the foci of ticks and associated pathogens, because of their inherent plasticity. This does not mean that we cannot capture the precise meaning of the epidemiological relationships occurring in the foci of tick-transmitted pathogens, but caution is required when interpreting the results of short-term field experiments in which adequate integration of the numerous variables affecting the ecology of ticks has not occurred (35, 36). Climate undoubtedly has a direct impact on populations of ticks and the reported changes in the incidence of tick-transmitted pathogens. However, simplistic observations may obscure subtle relationships of ticks with the reservoirs of pathogens, and these relationships must be explored if we are to develop a complete framework for evaluating the rates of change.

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Les tiques en tant que vecteurs : taxonomie, biologie et écologie

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Résumé

Les tiques sont des parasites importants de l'homme et des animaux et des vecteurs efficaces pour les agents pathogènes. L'auteur expose et illustre les principales caractéristiques morphologiques des tiques appartenant aux familles Ixodidae et Argasidae et résume les composantes essentielles de leur cycle évolutif, en mettant l'accent sur les processus de développement et les causes de mortalité des populations de tiques, afin de décrire à grands traits les processus de régulation de ces populations dans la nature et les modalités de transmission des agents pathogènes dans ce contexte. En outre, il examine les effets des événements météorologiques sur ces cycles, ainsi que les effets sur la densité des populations de tiques d'autres facteurs biotiques, en particulier la présence et l'abondance des hôtes et l'influence des éléments qui modèlent les paysages. Il souligne également l'incertitude inhérente à tout ce qui a trait à la transmission des agents pathogènes par les tiques, ce processus étant le résultat d'une relation souvent complexe entre le vecteur, le climat et la présence et densité des hôtes. Après avoir mis l'accent sur la nécessité d'obtenir de sources sûres des données de terrain concernant cette relation avant de tirer des conclusions sur l'effet isolé de chacune de ses composantes, l'auteur consacre toute une partie de son article aux répercussions probables (mais non entièrement élucidées) des tendances climatiques sur la propagation des tiques, ainsi qu'aux possibilités de les analyser et d'en assurer le suivi.

Mots-clés

Biologie – Climat – Composition de la population d'hôtes – Composition du paysage – Écologie – Tique.

Las garrapatas como vectores: taxonomía, biología y ecología

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Resumen

Las garrapatas son importantes parásitos y eficaces vectores de patógenos humanos y animales. El autor expone e ilustra las principales características morfológicas de las garrapatas de las familias Ixodidae y Argasidae, y resume los componentes fundamentales de su ciclo vital, centrándose básicamente en los procesos de desarrollo y la mortalidad en las poblaciones de garrapatas, a fin de describir a grandes rasgos la regulación de esas poblaciones en la naturaleza y el modo en que los patógenos pueden transmitirse en tales circunstancias. Además, examina los efectos de la meteorología sobre esos ciclos, y al modo en que otros factores bióticos, en particular la presencia y abundancia de los anfitriones y la influencia de los elementos que configuran el paisaje, pueden repercutir en la densidad de población de las garrapatas. También subraya la incertidumbre inherente a todo lo que rodea la transmisión de patógenos por las garrapatas, proceso que resulta de la relación, a veces compleja, entre el vector, el clima y la presencia y densidad de anfitriones. Tras hacer hincapié en la necesidad de obtener sobre el terreno datos fidedignos acerca de esa relación antes de extraer conclusiones sobre el efecto aislado de cada uno de los componentes del sistema, el autor dedica toda una sección a las presumibles (y aún no comprendidas del todo) repercusiones de las tendencias climáticas en la propagación de garrapatas y a la forma en que es posible analizarlas y seguirlas.

Palabras clave
Biología – Clima – Composición de la población de anfitriones – Composición del paisaje – Ecología – Garrapata.

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