The global importance of ticks

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SUMMARY

Ticks and tick-borne diseases affect animal and human health worldwide and are the cause of significant economic losses. Approximately 10% of the currently known 867 tick species act as vectors of a broad range of pathogens of domestic animals and humans and are also responsible for damage directly due to their feeding behaviour. The most important tick species and the effects they cause are listed. The impact on the global economy is considered to be high and although some estimates are given, there is a lack of reliable data. The impact of ticks and tick-borne diseases on animal production and public health and their control are discussed.

Key words: Ticks, tick-borne diseases, global importance, animal production, zoonoses.

INTRODUCTION

Ticks transmit a greater variety of pathogenic micro-organisms, protozoa, rickettsiae, spirochaetes and viruses, than any other arthropod vector group, and are among the most important vectors of diseases affecting livestock, humans and companion animals. Moreover, ticks can cause severe toxic conditions such as paralysis and toxicosis, irritation and allergy. This chapter discusses the global importance of ticks and tick-borne diseases.

Whereas the importance of tick-borne diseases for humans and companion animals is measured by morbidity and mortality, the diseases transmitted by ticks to livestock are an additional major constraint to animal production predominantly in (sub)tropical areas of the world. In general, tick-borne protozoan diseases (e.g. theilerioses and babesioses) and rickettsial diseases (e.g. anaplasmoses and heartwater or cowdriosis) are pre-eminent health and management problems of cattle and small ruminants, as well as buffalo, affecting the livelihood of farming communities in Africa, Asia and Latin America. Recently, tick-borne diseases were again ranked high in terms of their impact on the livelihood of resource-poor farming communities in developing countries (Perry *et al*. 2002; Minjauw & McLeod, 2003). This is particularly relevant in parts of sub-Saharan Africa, Asia and Latin America where the demand for livestock products is increasing rapidly (Delgado *et al*. 1999).

Ticks and tick-transmitted infections have co-evolved with various wild animal hosts which often live in a state of equilibrium with them and constitute reservoir hosts for ticks and tick-borne pathogens of livestock, pets and humans. They have only become problems of domestic livestock when these wild hosts came into contact with them, either because man moved livestock into infested regions, or moved livestock infested with the ticks into previously uninfested regions. An example of man moving livestock into infested regions is the introduction of cattle into Africa where they came into contact with *Rhipicephalus appendiculatus*, the vector of *Theileria parva*, the causal agent of East Coast fever and related diseases; the African buffalo is the normal host of *T. parva* and the infection is normally subclinical in this animal. An example of man moving ticks and tick-borne diseases with livestock is the introduction of *Boophilus* ticks together with the livestock diseases they transmit into the American continent.

Whereas the global economic importance of ticks is particularly high for livestock, there is also a great impact on public health in the northern hemisphere, primarily due to Lyme borreliosis (LB) but also other zoonotic tick-borne illnesses, with those of viral origin, characterized by encephalitis and haemorrhagic fevers, causing the highest morbidity and mortality in man. Tick-borne pathogens of pets are of economic significance only in industrialized countries, whereas tick-borne pathogens infecting horses constitute important constraints to international trade and sporting events involving these animals.

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TICK TAXONOMY

Two special publications have appeared on tick taxonomy: Camicas, Harvy, Adam & Morel compiled a comprehensive list of the ticks of the world (Camicas *et al.* 1998) and Horak, Camicas & Keirans (2002) continued this endeavour by presenting a revised world list of valid tick names. According to this latter list of valid tick names, approximately 80% of the world's tick fauna are ixodid ticks (hard ticks) (683 species) and, with the exception of one species in the family Nuttalliellidae, the remainder are argasid ticks (soft ticks) (183 species). This list has formed the basis for an interactive database in access 2000, designated Tick*base*[1], containing the total of 867 currently known tick species. The world's argasid tick fauna is divided into four genera, namely *Argas*, *Carios*, *Ornithodoros* and *Otobius*, whereas the world's ixodid tick fauna consists of 241 species in the genus *Ixodes* and 442 species in the remaining genera. The most important genera of hard ticks are *Amblyomma*, *Dermacentor*, *Haemaphysalis*, *Hyalomma*, *Ixodes*, *Rhipicephalus* and *Boophilus*. Although the five species of the genus *Boophilus* have been placed in the genus *Rhipicephalus* by Horak *et al.* (2002), to reflect their close phylogenetic relationship and evolution, this change in nomenclature has kept the name *Boophilus* in common usage as a subgenus (Barker & Murrell, 2002; Horak *et al.* 2002). To avoid confusion, we continue to treat *Boophilus* separately from *Rhipicephalus* since ticks of the genus *Boophilus* are among the best-known in the world. A detailed account of modern tick systematics is given in the chapter by Barker & Murrell in this Supplement.

IMPORTANT TICKS OF THE WORLD

Most ticks have a preference for feeding on certain groups of wild animals, with some even being quite host specific. Consequently, the number of species pertinent to domestic animals and/or humans is limited. As a matter of fact relatively few species of ticks have successfully adapted to livestock or feed on a human subject, and these have developed into efficient vectors of a range of pathogenic micro-organisms, while virtually all human tick-borne diseases are zoonoses (Table 1).

The following ecological criteria were used to underpin the tick–host–pathogen relationships listed in Table 1. A tick species is considered a vector for a particular pathogen only if it (1) will feed on an infectious vertebrate host, (2) is able to acquire the pathogen during the blood meal, (3) can maintain the pathogen through one or more life stages, and (4) can pass it on to other hosts when feeding again (Kahl *et al.* 2002). In addition to information on well-established vector competence, Table 1 also includes ticks that can induce paralysis, toxicosis, severe local reactions such as forms of pruritus, secondary bacterial abscesses and a variety of reactions caused by immune-mediated responses. A detailed account of the biology of ticks is available in two classic monographs by Sonenshine (1991, 1993).

ARGASID TICKS

Argasid ticks of medical and veterinary importance belong to the genera *Argas*, *Ornithodoros* and *Otobius*. The Argasidae live near their favourite host (in its nest, pen, stable, hut, etc.) and the parasitic stages (nymphs are always parasitic, larvae and adults usually so) feed for a short period only on the host (a matter of minutes to, say, an hour) and then go back to their hiding place. Exceptions are the larvae of certain *Argas* spp. that attach and feed for some days on domestic poultry, and the immature stages of *Otobius* which are parasitic for long periods in the external ear canals of their hosts. Soft ticks often have several nymphal stages. Adult Argasidae mate off the host; the female (again with the exception of *Otobius* whose adults are non-parasitic) feeds several times and produces a small batch of eggs after each meal. *Argas miniatus* is widely distributed in the Neotropical region and both *A. persicus* and *A. reflexus* are found in southern Europe and central Asia; they usually feed on birds. *Argas monolakensis* is an important argasid tick of birds that can feed on humans in the Western USA (Schwan, Corwin & Brown, 1992). Other ticks such as *A. brumpti* and *Argas* (now *Carios*) *vespertilionis* cause extensive local lesions resembling bruising after feeding on humans. Larvae and nymphs of the spinose ear tick, *Otobius megnini*, can be found deep in the external ear canals of livestock, companion animals and, occasionally, man and may cause otitis. This tick occurs in the western parts of the USA and parts of South America. It is also found in the Afrotropical and Oriental regions. The widely distributed argasid genus *Ornithodoros* contains 38 species, with *O. moubata* and *O. porcinus* as important species in the relatively arid parts of Africa, where they find shelter in caves, rodent burrows, bird nests and also in cracks and crevices of huts and shelters of indigenous peoples and their domestic animals. Another species, *O. savignyi*, lives in sandy soil at the shaded resting sites of livestock in semi-desert areas and feeds on the legs of cattle, sheep, goats and camels, building up massive infestations (Hoogstraal, 1956).

IXODID TICKS

Ixodidae may be one-, two- or three-host species depending on the number of host animals they attach

[1] Tick*base* is a Global Species Database containing all valid names of the ticks of the world and is linked up with Species 2000 as part of an ongoing effort to produce an internet-based catalogue of life (www.species2000.org).

Table 1. Some of the economically most important ticks of the world, vector role or affections caused

Tick	Pathogen
Argasidae	
Argas brumpti Neumann, 1907	Extensive bruising; painful bites and severe pruritis in man
A. miniatus Koch, 1844	Avian borreliosis (*Borrelia anserine*)
A. monolakensis Schwan, Corwin & Brown, 1992	Mono Lake virus in man
A. persicus (Oken, 1818)	Avian borreliosis (*Borrelia anserina*); Aegyptianellosis (*Anaplasma* (*Aegyptionella*) *pullorum*) (1)
A. reflexus (Fabricius, 1794)	Loss of blood in pigeons; Aegyptianellosis (*Anaplasma* (*Aegyptionella*) *pullorum*)
A. walkerae Kaiser & Hoogstraal, 1969	Aegyptianellosis (*Anaplasma* (*Aegyptionella*) *pullorum*); paralysis toxin in birds
Ornithodoros asperus Warburton, 1918	Borreliosis (*Borrelia caucasica*)
O. coriaceus Koch, 1844	Bovine epizootic abortion; very painful bites
O. erraticus (Lucas, 1849)	African Swine Fever virus; borreliosis (*Borrelia crocidurae*)
O. hermsi Wheeler, Herms & Meyer, 1935	Borreliosis (*Borrelia hermsi*)
O. moubata (Murray, 1877)	*Borrelia duttonii* (African human relapsing fever); African Swine Fever virus
O. parkeri Cooley, 1936	Borreliosis (*Borrelia parkeri*)
O. savignyi (Audouin, 1827)	Loss of blood in domestic animals; severe pruritus in man
O. porcinus Walton, 1962	African swine fever; African human relapsing fever
O. tartakovskyi Olenev, 1931	Borreliosis (*Borrelia tatyschewii*)
O. tholozani Laboulbène & Mégnin, 1882	Borreliosis (*Borrelia persica*)
O. turicata (Dugès, 1876)	Borreliosis (*Borrelia turicatae*)
Otobius megnini (Dugès, 1883)	Severe otitis in livestock
Ixodidae	
Amblyomma americanum (Linnaeus, 1758)	Screw worm, tularaemia; human ehrlichiosis (*Ehrlichia chaffeensis*)
A. astrion Dönitz, 1909	Cowdriosis of ruminants (*Ehrlichia* (*Cowdria*) *ruminantium*)
A. cajennense (Fabricius, 1787)	Rocky Mountain Spotted Fever (*Rickettsia rickettsii*)
A. cohaerens Dönitz, 1909	Cowdriosis of ruminants (*Ehrlichia* (*Cowdria*) *ruminantium*); Benign African theileriosis of cattle (*Theileria mutans*)
A. gemma Dönitz, 1909	Cowdriosis of ruminants (*Ehrlichia*(*Cowdria*) *ruminantium*); Benign African theileriosis of cattle (*Theileria mutans*)
A. hebraeum Koch, 1844	Cowdriosis of ruminants (*Ehrlichia* (*Cowdria*) *ruminantium*); Benign African theileriosis of cattle (*Theileria mutans*); African tick-bite fever in man (*Rickettsia africae*); severe local reactions (secondary bacterial infections leading to loss of udder quarters in cattle)
A. lepidum Dönitz, 1909	Cowdriosis of ruminants (*Ehrlichia* (*Cowdria*) *ruminantium*); Benign African theileriosis of cattle (*Theileria mutans*)
A. maculatum Koch, 1844	Experimental vector of cowdriosis (*Ehrlichia* (*Cowdria*) *ruminantium*); Hepatozoonosis of dogs (*Hepatozoon americanum*); severe local reactions
A. marmoreum Koch, 1844	*Ehrlichia* (*Cowdria*) *ruminantium*
A. pomposum Dönitz, 1909	Cowdriosis of ruminants (*Ehrlichia* (*Cowdria*) *ruminantium*)
A. tholloni Neumann, 1899	*Ehrlichia* (*Cowdria*) *ruminantium*
A. variegatum (Fabricius, 1794)	Cowdriosis of ruminants (*Ehrlichia* (*Cowdria*) *ruminantium*); Benign African theileriosis of cattle (*Theileria mutans*); Associated with severe dermatophilosis of ruminants (*Dermatophilus congolensis*); Vector of Thogoto virus(2); African tick bite fever (*Rickettsia africae*) in man; severe local reactions in cattle (abscesses due to secondary bacterial infections leading to lameness and loss of udder quarters)
Boophilus annulatus (Say, 1821)	Bovine babesiosis (*Babesia bovis* and *Babesia bigemina*); Bovine anaplasmosis (*Anaplasma marginale*)
B. decoloratus (Koch, 1844)	Bovine babesiosis (*Babesia bigemina*); bovine anaplasmosis (*Anaplasma marginale*)
B. geigyi (Aeschlimann & Morel, 1965)	Bovine babesiosis (*Babesia bovis* and *Babesia bigemina*) (2)
B. microplus (Canestrini, 1888)	Bovine babesiosis (Babesia bovis and Babesia bigemina); Equine piroplasmosis (*Theileria equi*); Bovine anaplasmosis (*Anaplasma marginale*)
Dermacentor albipictus (Packard, 1869)	Bovine anaplasmosis (*Anaplasma marginale*); Severe alopecia (moose)

Table 1. (*cont.*)

Tick	Pathogen
D. andersoni Stiles, 1908	Powassan encephalitis virus; Colorado Tick Fever virus; Bovine anaplasmosis (*Anaplasma marginale*); Rocky Mountain Spoted fever (*Rickettsia rickettsii*); paralysis toxin
D. auratus Supino, 1897	Forested parts of the Himalayas: notorious for tick annoyance
D. marginatus (Sulzer, 1776)	Canine babesiosis (*Babesia canis*); Human rickettsiosis (*Rickettsia slovaka*); Human Q-fever (*Coxiella burnetii*)
D. nitens Neumann, 1897	Equine babesiosis (*Babesia caballi*)
D. nuttalli Olenev, 1928	Human rickettsiosis (*Rickettsia sibirica*)
D. occidentalis Marx, 1892	Bovine anaplasmosis (*Anaplasma marginale*)
D. reticulatus (Fabricius, 1794)	Equine babesiosis (*Babesia caballi*); canine babesiosis (*Babesia canis*); Siberian tick typhus (*Rickettsia sibirica*); human rickettsiosis (*Rickettsia slovaka*)
D. variabilis (Say, 1821)	Bovine anaplasmosis (*Anaplasma marginale*); Rocky Mountain Spotted Fever in humans (*Rickettsia rickettsii*); paralysis toxin in animals and man
Haemaphysalis flava Neumann, 1897	*Rickettsia japonica*
H. concinna Koch, 1844	*Rickettsia sibirica*
H. leachi (Audouin, 1826)	*Babesia rossi* (Canine babesiosis)
H. longicornis Neumann, 1901	Bovine babesiosis (*Babesia ovata*); East Asian bovine theileriosis (*Theileria buffeli*); Canine babesiosis (*Babesia gibsoni*); Human rickettsiosis (*Rickettsia japonica*)
H. punctata Canestrini & Fanzago, 1878	Bovine babesiosis (*Babesia major*); Babesiosis of small rumninants (*Babesia motasi*); Cosmopolitan benign bovine theileriosis (*Theileria buffeli*)
H. qinghaiensis Teng, 1980	Small ruminant theileriosis (China)
H. spinigera Neumann, 1897	Kyasanur Forest Disease virus in humans
H. turturis Nuttall and Warburton, 1915	Kyasanur Forest Disease virus in humans
Hyalomma anatolicum anatolicum Koch, 1844	Bovine tropical theileriosis (*Theileria annulata*); Theileriosis of small ruminants (*Theileria lestoquardi*)
H. anatolicum excavatum Koch, 1844	Bovine tropical theileriosis (*Theileria annulata*)
H. asiaticum asiaticum Schulze and Schlottke, 1930	Bovine tropical theileriosis (*Theileria annulata*); Human rickettsiosis (*Rickettsia mongolotimonae*) (3)
H. detritum detritum Schulze, 1919	Bovine tropical theileriosis (*Theileria annulata*)
H. dromedarii Koch, 1844	Bovine tropical theileriosis (*Theileria annulata*)
H. lusitanicum Koch, 1844	Bovine tropical theileriosis (*Theileria annulata*)
H. marginatum marginatum Koch, 1844	Bovine tropical theileriosis (*Theileria annulata*); Crimean-Congo Haemorrhagic Fever virus in humans
H. marginatum rufipes Koch, 1844	Crimean-Congo Haemorrhagic Fever virus in humans
H. truncatum Koch, 1844	Crimean-Congo Haemorrhagic Fever virus in humans; sweating sickness (*toxicosis in domestic animals*); Human rickettsiosis (*Rickettsia mongolotimonae*)
Ixodes cookei Packard, 1869	Powassan Encephalitis virus
I. hexagonus Leach, 1815	Lyme borreliosis (*Borrelia burgdorferi* s.l.)
I. holocyclus Neumann, 1899	Paralysis in animals and man; *Rickettsia australis*; holocyclotoxin
I. ovatus Neumann, 1899	*Rickettsia japonica*
I. pacificus Cooley & Kohls, 1943	Lyme borreliosis (*Borrelia burgdorferi* s.l.)
I. persulcatus Schulze, 1930	Tick-borne encephalitis virus; Lyme borreliosis (*Borrelia burgdorferi* s.l.)
I. ricinus (Linnaeus, 1758)	Tick-borne encephalites in man and animals, including Louping ill virus in sheep; Lyme borreliosis (*Borrelia burgdorferi* s.l.); Babesiosis in cattle and sporadically in man (*Babesia divergens*); human babesiosis (*Babesia microti*); Tick-borne fever or pasture fever in ruminants and human granulocytic ehrlichiosis (*Anaplasma* (*Ehrlichia*) *phagocytophilum*); *Rickettsia helvetica*
I. rubicundus Neumann, 1904	Tick paralysis (important in sheep) (Karoo paralysis toxin) (4)
I. scapularis Say, 1821	Lyme borreliosis (*Borrelia burgdorferi* s.l.) human granulocytic ehrlichiosis and equine ehrlichiosis (*Anaplasma* (*Ehrlichia*) *phagocytophilum*; human babesiosis (*Babesia microti*)
Rhipicephalus appendiculatus Neumann, 1901	East Coast Fever and Corridor Disease in cattle (*Theileria parva*); Benign bovine theileriosis (*Theileria taurotragi*); Nairobi Sheep Disease virus; Thogoto virus (5)
R. bursa Canestrini & Fanzago, 1878	Babesiosis of small ruminants (*Babesia ovis*); bovine babesiosis (*Babesia bigemina*); bovine anaplasmosis (*Anaplasma marginale*); Anaplasmosis of small ruminants (*Anaplasma ovis*)

Table 1. (*cont.*)

Tick	Pathogen
R. evertsi evertsi Neumann, 1897	Equine piroplasmosis (*Babesia caballi*; *Theileria equi*); bovine anaplasmosis (*Anaplasma marginale*); tick paralysis in animals (toxin)
R. sanguineus (Latreille, 1806)	Canine ehrlichiosis (*Ehrlichia canis*); canine babesiosis (*Babesia vogeli*); canine hepatozoonosis (*Hepatozoon canis*); Tick bite fever in humans (*Rickettsia conorii*)
R. simus Koch, 1844	Bovine anaplasmosis (*Anaplasma marginale*; *Anaplasma centrale*)
R. zambeziensis Walker, Norval & Corwin, 1981	East Coast fever, Corridor Disease in cattle (*Theileria parva*); Benign bovine theileriosis (*Theileria taurotragi*)

General note: This table is meant to provide an overview of the most important and well established tick–host–vector associations only.
(1) old name between brackets; (2) suspected vector role; (3) not clear whether other subspecies of *H. asiaticum* are also vectors; (4) many other tick species can induce tick toxicosis; (5) many other tick species involved.

to during their life cycle. Larvae and nymphs feed once to engorgement and then moult. One-host ticks moult twice on the same host animal, from larva to nymph and from nymph to adult. Two-host ticks moult once on the host, from the larval to the nymph stage; the engorged nymph drops off, moults off the host and the resulting adult has to find a second host animal (which may or may not be of the same species as the first). Three-host ticks do not moult on the host; the engorged larva drops off, moults to a nymph, which then has to find a second host animal on which it engorges and drops off again to moult to the adult stage, which attaches to a third host animal. Adult Ixodidae usually mate on the host, the female then feeds to engorgement, drops off, lays a large batch of eggs and dies (while the male may remain on the host for several months). Logically, the egg batches of one-host ticks contain on average far fewer eggs than those of three-host ticks, as the latter have to run the gauntlet of finding a new host three times in their life cycle, and the former only once. Two-host ticks run less risk than three-host species but more than one-host ticks, and their egg batches are intermediate in size.

Some characteristics of seven important genera of ixodid ticks (*Amblyomma*, *Boophilus*, *Dermacentor*, *Haemaphysalis*, *Hyalomma*, *lxodes* and *Rhipicephalus*) are summarized below.

Amblyomma

There are 129 species of *Amblyomma* ticks. They are characterized by long mouthparts and, usually, beautifully coloured 'ornamented' scuta. Eyes are present, in most species not housed in sockets. These three-host ticks are widespread in tropical and subtropical zones where they parasitize a wide variety of mammalian hosts and also reptiles and amphibians. Immature stages of some species infest birds and these can play an important role in dispersing the ticks. *A. variegatum* is the most important species on most of the African continent as it is well adapted to domestic livestock and has the widest distribution throughout tropical sub-Saharan Africa. *A. hebraeum*, which inhabits the south-eastern part of the African continent, is another important pest of livestock. Other species of more local importance are *A. lepidum*, *A. astrion*, *A. gemma*, *A. pomposum* and *A. cohaerens*. In addition to its widespread distribution in Africa, *A. variegatum* has been introduced into the Caribbean region, presumably in the 18th or 19th century with cattle from West Africa. To date, *A. variegatum* is the only African *Amblyomma* to have successfully established itself outside the African continent (Camus & Barré, 1990). Several species (including *A. americanum*, *A. cajennense* and *A. maculatum*) are of economic significance on the American continent as their adults prefer to feed on cattle.

Boophilus

Boophilus are one-host ticks which take about three weeks to complete their cycles on the host from unfed larva to engorged female, preferably on cattle (except for *B. kohlsi*, a Near/Middle Eastern species with a predilection for small ruminants). Although *Boophilus* ticks have short mouthparts, damage to hides is considerable as the preferred feeding sites are often of good leather potential. *B. microplus* is the most important species. Originating from South-East Asia, this species has spread throughout the tropics including Australia, East and Southern Africa, and South and Central America. *B. annulatus* is present in the Mediterranean region, and occurs in southern Russia as well as in the Near and Middle East; this species has also extended its distribution southwards into Africa in a belt from West Africa to southern and central Sudan (Hoogstraal, 1956). Furthermore, *B. annulatus* has been introduced into Mexico, together with *B. microplus*, subsequently spreading into the southern USA before being successfully eradicated there. However, continued surveillance is required to prevent reintroduction. To date, two other species, *B. decoloratus* and *B. geigyi*, have remained confined to Africa. In addition to cattle, *B. decoloratus* readily feeds on a large variety of wild ruminants. *B. geigyi* is common on ruminants in West and central Africa. As *Boophilus* spp. are one-host ticks, they may become very numerous on cattle herds, particularly those with a low degree of resistance, and cause considerable direct damage.

Dermacentor

The genus *Dermacentor* comprises 33 species with ornate scuta, short palps and eyes, and usually follows a three-host life cycle. *Dermacentor* spp. occur on all continents, except Australia. In Eurasia several species (e.g. *D. marginatus* and *D. reticulatus*) infest livestock and other domestic animals, while in North America *D. variabilis* and *D. andersoni* are important ectoparasites of livestock. In Africa, however, *Dermacentor* spp. do not play a significant role on livestock.

Haemaphysalis

The genus *Haemaphysalis* contains 168 species. They are easy to differentiate from other genera by the characteristic lateral projection of palpal article 2 beyond the margins of the basis capituli. All *Haemaphysalis* spp. are eyeless, three-host ticks. Only a few species have adapted to domestic livestock and these are important on livestock in Asia, Europe and, to some extent, Australia. For example, *H. bispinosa* occurs on cattle on the Indian subcontinent, while *H. longicornis*, an East Asian species that occurs on cattle and other domestic animals, has been introduced into Australia, New Zealand and New Caledonia. In Europe *H. punctata* is common on ruminants.

Hyalomma

Hyalomma spp. are medium-sized to large ticks with long hypostomes and eyes typically in sockets. *Hyalomma* species parasitize domestic and wild mammals and birds, and are abundant in semi-arid zones. The genus *Hyalomma* comprises 30 species, most of which follow a three-host life cycle. However, some species undergo either a two-host or a three-host cycle, depending on the host species, while *H. scupense* is a one-host tick. Unlike most other ixodid ticks, which wait on the vegetation for a host to pass, adult *Hyalomma* actively run out from their resting sites when a host approaches.

Ixodes

Ixodes is the largest genus of hard ticks with 241 species. These are characterized by the anal groove curving anteriorly to the anus, a scutum lacking ornamentation and lack of eyes. They have a three-host life cycle and many species inhabit nests or burrows. Relatively few *Ixodes* species parasitize larger mammals, but the genus is widely distributed throughout wooded or grassy environments. The most important species in Europe and Asia are *I. ricinus* and *I. persulcatus*, whereas *I. scapularis* is the most common *Ixodes* in North America. *I. persulcatus* attacks humans far more aggressively than does *I. ricinus*. The indiscriminate feeding behaviour of *I. ricinus* and *I. persulcatus* on a variety of hosts, makes them important vectors of a large number of zoonotic tick-borne diseases.

Rhipicephalus

The genus *Rhipicephalus* comprises 70 species. These small to medium-sized ticks with short, broad palps that are usually inornate and have eyes and festoons. Most *Rhipicephalus* spp. are found on mammals on the African continent. They are usually three-host ticks, although some have a two-host cycle (e.g. *R. evertsi*). Taxonomic identification of rhipicephalid group ticks may cause difficulties and the reader is referred to a recent revision of the entire genus (Walker, Keirans & Horak, 2000). *R. appendiculatus*, the brown ear tick, is the most important rhipicephalid tick in East and Southern Africa where it occurs on a wide variety of domestic and wild ruminants. This tick prefers to feed on the ears of its hosts in the adult stage of its three-host life cycle.

IMPACT ON LIVESTOCK

Without acting as vectors of disease, ticks can be harmful to livestock and of great economic importance simply because of their direct effects. Much depends on the circumstances, on the tick species involved, on the local climatic conditions (favourable or unfavourable to the ticks) and, to a large extent, on the susceptibility to tick infestation of the livestock in the region. Resistance to tick infestation, or at least the capability of developing an effective immunological response to infestation, is genetically determined. This is particularly important where one-host *Boophilus* spp. are implicated. Uncontrolled *Boophilus* infestations in climatically favourable conditions severely affect European cattle, but have little effect on zebu cattle. Such infestations *per se*, even when no diseases are transmitted by the ticks, can limit productivity of European *Bos taurus* cattle to the extent that a choice has to be made between simply renouncing the use of such cattle, or applying intensive and expensive chemical tick control, which usually leads rapidly to resistance against the acaricides used. For example, on the island of New Caledonia the tick *Boophilus microplus* has been introduced without the diseases it transmits elsewhere, namely babesioses and anaplasmosis. However, highly favourable climatic conditions throughout the year and a large population of susceptible European beef cattle breeds have made it necessary to develop intensive acaricidal treatment programmes, which have led to an enormous problem of widespread multi-acaricide resistance, with resistance having successively developed to the various groups of chemicals used (Bianchi, Barré & Messad, 2003). Hence, it may be far more economical to make more use of *Bos indicus* breeds, pure or cross-bred, as has been done in many instances in Australia, where zebu cattle have proved to be much more resistant to tick infestation than European cattle.

The damage caused by tick bites also diminishes the value of skins and hides for the manufacture of leather; even ticks with a short hypostome, such as *Boophilus*, may be important in this respect when present in large numbers on susceptible cattle. Ticks with long and massive hypostomes, such as *Amblyomma* and to some extent *Hyalomma* spp., may induce abscesses because of secondary bacterial infections. In this way *Amblyomma* spp. may cause loss of teats or lameness, depending on the site of attachment. In turn loss of teats will lead to increased calf mortality.

The saliva of certain tick species contains paralysing toxins; examples of this are *D. andersoni* in Canada and the USA that can cause death even in adult cattle, *I. rubicundus* that induces a severe form of paralysis in sheep in southern Africa, and *I. holocyclus* in Australia, that usually feeds on bandicoots, but can also feed on domestic animals, tropical bats (*Pteropus* spp.) or humans, and is considered a very important tick with respect to tick toxicosis (Gothe, 1999). Another form of tick toxicosis is 'sweating sickness', a generalised eczema-like condition of calves and other species of livestock in Africa, induced by the saliva of certain lines of *Hyalomma truncatum*. A detailed account of tick salivary toxins is given in the chapter by Mans, Gothe & Neitz in this Supplement.

There is also at least one example of a tick-associated disease which is not transmitted by ticks. This is severe bovine dermatophilosis induced by the presence of adult *Amblyomma variegatum* which, in certain regions of the tropics, may prevent upgrading of local cattle with highly susceptible imported breeds (Ambrose, Lloyd & Maillard, 1999).

The most important diseases transmitted by ticks, particularly in domestic ruminants, are babesioses, theilerioses, anaplasmoses and cowdriosis (see chapters in this Supplement on babesiosis by Bock *et al.*, theileriosis by Bishop *et al.* and anaplasmosis by Kocan *et al.*). Recovered animals retain the infection and remain immune for long periods, sometimes for life. In general, where such diseases are endemic, the local livestock has been exposed to a long process of natural selection and has, to various degrees, become tolerant, but not refractory to the infection. Furthermore, young animals are generally more tolerant than adults. The combination of natural tolerance and age-associated tolerance may result in an endemically stable situation which, at best, means that the prevalence of infection may be 100% but that the disease is not clinically apparent. In other cases, endemic stability may be less perfect and there may be some mortality following primo-infections in young animals, but older stock that have survived the infection are immune. Obviously tick numbers are important as endemic stability can only be attained where adequate numbers of infected ticks are present to infect all animals while they still possess their age-associated tolerance. For example, in regions where cowdriosis is endemic the situation may be endemically stable in local cattle, but not in local breeds of small ruminants, probably because fewer *Amblyomma* (at least adult ticks) feed on them. Climatic conditions are among the main factors influencing tick numbers and endemic stability is thus not attained in areas which are climatically marginal for the vector tick species.

Exotic livestock, introduced from disease-free regions in which they have not been exposed to natural selection, are far more susceptible to most tick-borne diseases and even though mortality in young stock of such breeds is less than in adults, endemic stability can often not be achieved. This is certainly true for cattle and theilerioses (at least tropical theileriosis, *Theileria annulata*, and East Coast fever caused by *T. parva*), babesiosis caused by *Babesia bovis*, and cowdriosis (*Ehrlichia* (*Cowdria*) *ruminantium*). However, there may be little difference in susceptibility to anaplasmosis (*Anaplasma marginale*) and babesiosis caused by *B. bigemina* between local and exotic cattle. Particularly theilerioses and cowdriosis may make it impossible, or at least uneconomical, to keep exotic ruminant breeds unless management and veterinary infrastructures are adequate. The same considerations apply to indigenous breeds of animals that have never been exposed to a particular pathogen. For instance, translocation of indigenous goats from the north of Mozambique to the south into *Amblyomma hebraeum*-infested areas were highly risky because of cowdriosis (Bekker *et al.* 2001).

Anyone involved with livestock in tropical and subtropical areas of the world recognises that ticks and tick-borne diseases are important, but there are few if any reliable global figures of the costs involved. Young, Groocock & Kariuki (1988) considered the control of ticks and tick-borne diseases as the most important health and management problem in Africa, presenting a problem of equal or greater magnitude than tsetse fly and trypanosomosis. Various estimates of effects are tentative, sometimes rather different, and moreover depend on variables, including annual climatic variations, fluctuating exchange rates and inflation. The global costs of tick and tick-borne disease control has been estimated at US$ 7 milliard ($=7\times10^9$) by McCosker (1979). This amount, still sometimes quoted, is certainly hugely underestimated because it was based on Australian figures taking only the tick *B. microplus* and its role as a vector into account, multiplied by the world cattle population exposed to ticks and tick-borne diseases. Some other economic estimates of the cost of ticks to the livestock industry only concern certain diseases and particular regions and, although we do quote a few of them, we are under no illusion as to their accuracy. Mukhebi *et al.* (1999) estimated that the national annual loss due to cowdriosis in Zimbabwe could attain 5·6 million US$, while a questionnaire study in 1991 by Meltzer, Perry & Donachie (1996) arrived at a figure of about 6·5 million US$ in cattle alone on large-scale commercial farms in Zimbabwe, most of this amount being the cost of dipping. Recently, Minjauw & McLeod (2003) have made a great effort at producing figures, tables and maps on the importance, the distribution, the numbers of animals at risk and the cost of the various diseases in eastern and southern Africa, also to some extent in sub-Saharan Africa as a whole, and of tropical theileriosis in India. They estimate the annual cost of tropical theileriosis in India at 384·3 million US$, of East Coast fever in the smallholder dairy system in Kenya and Tanzania at 54·4 million US$ and 4·41 million, respectively, in the traditional system in Kenya and Tanzania at 34·1 and 129·5 million, respectively. An older figure is 168 million US$ annually as the cost of *Theileria parva* in eastern, central and southern Africa (Mukhebi, Perry & Kruska, 1992).

IMPACT ON COMPANION ANIMALS

Companion (or pet) animals, in particular dogs, pay a heavy toll to tick-borne diseases. Again, we will only mention a few of the more important ones. In tropical and subtropical regions, but even in many of the temperate zones, there are several babesioses of which some are highly pathogenic to dogs. Ehrlichioses occur in many regions of the world and infection with *Ehrlichia canis* is often fatal. Dogs belonging to tourists travelling to warm regions are liable to contract (sub)tropical tick-borne diseases, which usually only become apparent after returning home. In Europe in particular ehrlichiosis and babesiosis are acquired by dogs travelling to the Mediterranean region. Moreover, *Hepatozoon canis*, with its peculiar life cycle wherein the vector has to be ingested by the dog, is found with increasing frequency in dogs returning to the northwest of Europe. From the viewpoint of the animal health industry, acaricides for companion animals are seen as an increasingly important part of their market portfolio and focus (see chapter by Leach-Bing *et al.* in this Supplement).

Since only 10% of the world's horse population resides in areas free from *Babesia caballi* and *Theileria equi*, piroplasmosis certainly has a great economic impact on the horse industry. Although these diseases are endemic throughout the (sub)tropics and even in some temperate regions, a disease-free status is required for any horse entering North America, Canada, Japan or Australia. Hence there have been many complications for horses harbouring either one of these parasites but fit to compete for instance at one of the Olympics Games (Atlanta, USA, 1996; Sydney, Australia, 2000) or at any other sporting event.

EMERGING ZOONOSES AND PUBLIC HEALTH IMPACT

Reviews of human tick-borne diseases have been published by Parola & Raoult (2001 *a*, *b*), who reported that 15 novel bacterial pathogens have been described since the discovery of *B. burgdorferi* in 1982. Cunha (2000) edited a book encompassing the diagnosis and management of human tick-borne infectious diseases, while the literature pertaining to ticks feeding on humans has been reviewed by Estrada-Peña & Jongejan (1999). Recently, Gray *et al.* (2002) edited a volume dealing comprehensively with the complex biology and ecology of Lyme borreliosis in a worldwide context.

The mounting array of tick-borne zoonotic diseases emerging in the temperate parts of the world poses an ever increasing public health risk. There is a clear correlation between the increase in the USA and much of western Europe in abundance of deer (main host for adult *I. scapularis* and *I. ricinus*) with tick density. This is due to conversion of agricultural land into habitat suitable for the maintenance of large populations of deer, contributing to a sharp increase in tick numbers. Increased recreational activities in rural tick-infested areas have resulted in an increased number of humans who are bitten by ticks in the USA as well as in western Europe. To put another perspective on this, in some rural parts of Tanzania people prefer to sleep outdoors to avoid attack by the indoor-dwelling soft ticks and tick control is practised by spraying infested houses with pesticides to reduce the incidence of tick-borne relapsing fever (Talbert, Nyange & Molteni, 1998).

Human tick-borne diseases have gained enormously in notoriety since the discovery of Lyme borreliosis (LB) two decades ago (Burgdorfer *et al.* 1982), which stimulated a considerable quantity of research. Spirochaetes of the *B. burgdorferi* sensu lato complex consist of more than 10 different genospecies transmitted by ticks of the genus *Ixodes* (Gray *et al.* 2002). LB is now recognized as the most commonly reported arthropod-borne disease in North America and Europe, accounting for tens of thousands of new cases yearly in both regions. The complications of untreated LB in humans can be severe and disabling, but reports of LB as a cause of death are mostly unsubstantiated (Dennis & Hayes, 2002). The costs for medical care of LB patients, disease surveillance and laboratory diagnostics must of necessity be very high, but no accurate figures are available. A detailed account of Lyme borreliosis in Europe and the USA is given in the chapter by Piesman & Gern in this Supplement.

Some of the major human diseases transmitted by argasid ticks (mainly *Ornithodoros*) are caused by other *Borrelia* species, which induce relapsing fevers. In large areas of Africa and elsewhere, where soft ticks transmit such *Borrelia* spirochaetes to humans, the infections may be confused with malaria and consequently are much underestimated human tick-borne diseases in terms of morbidity and impact on public health.

Man-biting *Ixodes* spp. transmit viral infections causing European tick-borne encephalitis and the more severe Russian spring summer encephalitis. Other viral infections, such as Crimean-Congo haemorrhagic fever, transmitted by *Hyalomma* spp., occur sporadically throughout vast areas of Africa, Asia and Europe, and can cause mortality. Another potentially deadly flavivirus, which causes Kyasanur forest disease in India, is transmitted by *Haemaphysalis* spp., and claims many victims annually. A detailed account of tick-borne viruses is given in the accompanying chapter by Labuda & Nuttall in this Supplement.

The tick-borne rickettsiosis, Rocky Mountain spotted fever, caused by *Rickettsia rickettsii*, a life-threatening but treatable rickettsial disease, is widespread in most of the United States and beyond, and is transmitted by *Dermacentor* spp. Another rickettsial infection, fièvre boutonneuse, caused by *Rickettsia conorii* and transmitted by *Rhipicephalus sanguineus* and other tick species, occurs mainly in Europe. In Africa, *Amblyomma* spp. transmit *Rickettsia africae*, whereas *Dermacentor reticulatus* transmits *R. sibirica*, the causative organism of Siberian tick typhus, in the former Soviet Union. Two other tick-borne rickettsioses of humans, monocytic and granulocytic ehrlichiosis, caused by *Ehrlichia chaffeensis* and *E. phagocytophila* (or *Anaplasma phagocytophila* according to Dumler *et al.* (2001), rectified to *A. phagocytophilum* (Anonymous, 2002)), have recently emerged. *E. chaffeensis* is transmitted by *Amblyomma americanum* and *E. phagocytophila* by *Ixodes scapularis* in the USA and by *Ixodes ricinus* in Europe.

Protozoan diseases also play a role in human public health. Babesiosis is transmitted by *Ixodes* spp. in the USA and Europe. Traditionally thought to be caused by *Babesia microti* in the USA and by *B. divergens* in Europe, this view of human babesiosis may be over-simplified since it appears that not all of the approximately 300 cases reported in the USA thus far are due to *B. microti*. Other parasites, distinct from *B. microti*, have now been identified and some of them are *B. divergens*-like (Kjemtrup & Conrad, 2000; Beattie, Michelson & Holman, 2002). Although the role of *B. microti* needs to be established, clinical cases in Europe have mostly been attributed to *B. divergens*, but perhaps wrongly so (Herwaldt *et al.* 2003). Human babesiosis appears to be on the increase, with more than half of the cases in the literature reported since 1985. A further dimension is added if one considers the incidence of human babesiosis transmitted by blood transfusions which also appears to be on the increase. Since 1980 over 20 cases have been reported including recent cases from Japan (Saito-Ito *et al.* 2000) and Canada (Bu Jassoum *et al.* 2000). It is currently the second most common parasitic infection (after *Plasmodium*) acquired by blood transfusion and the risk of becoming infected by blood transfusion has been estimated at six per 1 million units of blood collected (McQuistion *et al.* 2000). The chapter by Telford & Goethert in this Supplement describes new and re-emerging human tick-borne diseases.

Finally, human international travel, one of the largest and most rapidly evolving industries world-wide, has a significant impact on health care. Travel-associated tick-borne diseases have emerged as common subjects of international travel medicine. For instance, African tick-bite fever, a spotted fever group rickettsiosis caused by *Rickettsia africae*, transmitted by *Amblyomma* spp., is present in many countries in sub-Saharan Africa, as well as in the Caribbean region. Although the clinical course of African tick-bite fever is usually mild, complications may occur. In addition, the infection may easily be overlooked or confused with other tropical diseases such as malaria (Jensenius *et al.* 2003).

TICK CONTROL ON LIVESTOCK

Within the limits of this review, it is possible to outline only briefly the various aspects of tick control and discuss various new developments. Except on islands, where successful campaigns have sometimes been implemented, eradication of ticks is generally not feasible. Although the eradication of *Boophilus* spp. from the USA remains a notable exception, eradication of ticks on large islands and on continents is in most cases not a realistic goal. In the case of the USA, eradication was possible through the stringent application of legislative measures and particularly because *Boophilus* spp. are one-host ticks with a distinct preference for cattle. Luck may also have played a role in that acaricide resistance was not a complicating factor during the campaign. It is, however, now becoming increasingly difficult to prevent the ticks from becoming re-established from neighbouring Mexico, partly because of acaricide resistance and the presence of large numbers of deer. Acaricide resistance was probably also one of the main reasons for the failure to eradicate *B. microplus* in New South Wales, Australia. Because wild animals act as reservoirs or preferred hosts for economically important ticks, it is generally unrealistic to consider eradicating ticks, including those such as *I. ricinus*, which parasitize many animals in addition to domestic livestock in temperate regions.

Control of tropical tick-borne diseases, especially in more susceptible and productive exotic or upgraded breeds of livestock, still depends mainly on intensive tick control using acaricides (see chapter in this Supplement by George *et al.*). However, these chemicals are toxic, leave residues in meat and milk and cause environmental pollution. Moreover, acaricides are costly and require expenditure in foreign currencies, thus constituting a major economic strain on the development of the livestock industry, particularly in developing countries. Finally, the resistance of ticks to acaricides poses an increasing threat to livestock production. Consequently intensive (and thus expensive) dipping or spraying programmes have been largely unsuccessful in eradicating ticks and tick-borne diseases.

Integrated tick control strategies are therefore advocated. Such strategies have been preferred for quite some time (e.g. Young *et al.* 1988) and are based on host resistance to ticks and to the diseases they transmit, strategic tick control (taking into account the seasonal dynamics of tick infestation), the availability of vaccines against tick-borne diseases and cost/benefit analyses of acaricidal application. Accurate data on tick ecology (e.g. geographical distribution, seasonal occurrence and host preference) are required, together with data on the prevalence of tick-borne diseases within both traditional and commercial livestock production systems. Epidemiological data, combined with tick ecological data, form a basis for a sustainable tick control programme. Detailed accounts of tick ecology by Randolph and the application of GIS tools for tick-borne disease surveys by Daniel, Kovar & Zeman are given in separate chapters in this Supplement.

Sometimes solutions to specific tick-related problems are available but not implemented. For instance, it is feasible to keep susceptible highly productive cattle breeds in areas infested with *Hyalomma* spp. that are infected with *Theileria annulata* through vaccination using attenuated cell cultures derived from the *Theileria* parasites. This approach, successfully implemented in a number of countries, should be further examined and developed, in particular in northern Africa and in the Sudan.

New opportunities have been created with the development of anti-tick vaccines (Willadsen & Jongejan, 1999). Although this subject is discussed in detail by Willadsen elsewhere in this Supplement, the very high efficacy of available anti-*Boophilus microplus* vaccines (TickGARD and GAVAC) against *Boophilus annulatus* in two independent trials with two different vaccines is interesting to note (Fragoso *et al.* 1998; Pipano *et al.* 2003). This result indicates that it may actually be possible to eradicate *B. annulatus* from particular areas.

Progress in the Caribbean *Amblyomma* Programme to eradicate *A. variegatum* with the aim of increasing food security in the Caribbean and prevent tick introduction onto the American mainland is showing encouraging results with several islands declared provisionally free of the tick (Pegram & Eddy, 2002). However the programme will only truly be successful if the tick is eradicated from all the infested islands.

Acaricidal control of soft ticks on poultry is very difficult because of the particular hiding behaviour of the ticks in the housing. The poultry industry nowadays has become a large professional agribusiness using improved housing facilities; this is also the case in the tropics and certainly in most Latin American countries. These modifications have diminished the possibility of ticks being able to hide inside. On the other hand, free-range egg production is an emerging trend in response to concerns about the welfare of poultry kept in strict confinement in large farm complexes and *Argas* may yet strike again.

Tick control on dogs in particular is advocated by the use of acaricide-impregnated collars, whereas individual treatment for horses usually consists of synthetic pyrethroid pour-on compounds.

CONCLUDING REMARKS

The impact of tick feeding and tick-transmitted diseases and their control should be much better defined in economic terms. Tick control on livestock remains to a large extent based on acaricides but their use in possible combination with anti-tick vaccines and utilization of host resistance to ticks should reduce dependency on chemical tick control. Research into novel, ecologically sound, practical tick control methods should be intensified and implementation of existing methods to vaccinate against tick-borne diseases is recommended, as well as intensified research towards developing novel vaccines and delivery systems.

Much progress is expected in the next few years by the use of tools available in the post-genomic era. It can also be expected that new tick-borne pathogens will continue to be discovered. Furthermore, in the future we may be able to exploit for medical purposes some of the considerable number of bio-active molecules of the fascinating largely undisclosed tick pharmacy (see chapter by Valenzuela in this Supplement).

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