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Spread of parasites transported with their hosts: case study of two species of cattle tick

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Summary
Like all parasites, ticks can be spread easily along with their hosts. Ticks are obligate parasites of vertebrates, to which they attach themselves for varying periods of time, and are well-adapted to this mode of transport. Once the transport stage is complete and they have detached at destination, they are also able to wait several months for the arrival of a new host on which they will continue their life cycle. This leads to the establishment of a secondary tick population. Two tropical cattle tick species, *Rhipicephalus microplus* and *Amblyomma variegatum*, have perfected this strategy of colonisation and occupation of favourable zones. *Rhipicephalus microplus*, which originated from South and Southeast Asia, is highly specific for ungulates, and thanks to cattle movements it has spread throughout the tropical belt, apart from the remotest areas. *Amblyomma variegatum*, which originated in Africa, was transported to Madagascar and the Mascarene Islands, as well as to the West Indies, during the time of the Atlantic triangular trade. These two ticks are vectors of particularly serious cattle diseases: babesiosis and anaplasmosis in the case of *R. microplus*, and heartwater (cowdriosis) in the case of *A. variegatum*. Anticipated climate changes are likely to modify the potential geographical range of these two parasite species and numerous others. Even now there are still many areas of the Americas, Asia and Oceania into which *A. variegatum* has not yet spread, but which it would find favourable. It could be spread not only by the transport of cattle, but also by the migration of some of its other hosts, such as birds. Surveillance – and know-how – is needed to identify these parasites when they first appear and to rapidly contain new outbreaks. Efforts should be made to raise the awareness of livestock professionals about the risks of transporting cattle. Regulations should be implemented and precautions taken to avoid such artificial expansion of the range of ticks and the diseases they transmit.

Keywords
Amblyomma variegatum – Climate change – Host – Parasite – Range – *Rhipicephalus microplus* – Tick – Tick-borne disease – Transport.

Introduction

In this era of successive influenza pandemics, it is common knowledge that disease is spread primarily by the transportation of healthy or sick hosts, on an altogether different scale from the local spread of the initial outbreaks.

Although not contagious, parasites are spread in much the same way as disease. Transport of the infested host can significantly expand the geographical range, which is limited only by the availability of hosts and, where appropriate, of vectors at the site of destination, and by a lack of physical environmental conditions that are favourable to the parasite's survival.

Environmental conditions vary from year to year or from one climate cycle to another, and a parasite species' failure to become established may be temporary if the transport of infested animals continues. As the earth's ecosystems seem to be facing climate changes that will result in rapid temperature increases (35), locations formerly unfavourable to a parasite may now become favourable (25, 26, 74, 76). The meat-production industry in these areas will suffer the deleterious effects of these migrations of parasites and pathogens (87). We also know that it is a spatially and temporally evolving process: although the zones favourable to these parasites may be gradually expanded, conversely, hitherto infested zones may well no longer suit them.

Clearly the processes leading to the spread of parasites and to shifts in their geographical range apply to all animal and plant parasites. A host carries a parasite that is able to become established anywhere it finds conditions compatible with its needs. Local movements (such as transhumance) ensure the spread not only of ticks and the diseases they carry, but also of every other parasite and pathogen (24). Humans (including producers and those working in livestock departments and on ranches and farms) are often responsible for transporting them over long distances. In the case of domestic animals, a sheep parasite as commonplace as the gastrointestinal nematode *Haemonchus contortus* is probably now present in all the world's temperate and tropical zones. And virtually all livestock parasites that have a direct life cycle and are moved throughout the world without taking special precautions are bound to be just as widespread.

As this summary on the transport of parasites by their hosts is not meant to be exhaustive, the authors make a case study of ticks, examining the history of two model tropical species that are of major veterinary interest and are therefore well known and extensively studied (Table I). The origin of both species is documented, their historical spread has been monitored and defined (in many cases mapped by tracking the diseases they carry) and their potential range has been the subject of analyses and hypotheses. One of the two ticks, the one-host species *Rhipicephalus (Boophilus) microplus*, comes from Asia; the other, a three-host species, *Amblyomma variegatum*, comes from Africa. (The situation may well be more complex, because *R. [B.] microplus* possibly consists of two different species: one [classical *R. microplus*] originating in India and Nepal, and the other [which should perhaps be called *R. australis*] in Indonesia, from where it was imported into Australia and later into New Caledonia [43]. No definitive proof has been provided and the biological comparison [cross breeding] is based on a single strain of '*R. australis*'. Moreover, Ongole zebus from India were present in Indonesia as from the 15th Century and were imported into Australia on a large scale in the 19th Century [47]. There has clearly been widespread intermingling of tick strains, if not of tick species.) They are among the species with the heaviest economic impact. Each has its own life-history traits and distinctive and specific means of spread (82). Unlike many other parasites, the spread of these ticks is worrying not only because of the direct damage they cause, but most importantly because of the diseases they transmit and are liable to spread (a large number of references, including 16). Heartwater is a case in point (1, 10, 15, 49, 65, 78).

Ticks, well-adapted stowaways

Ticks have numerous strategies for securing their transportation and establishment. For transport to be successful the parasitic stage must be longer than the journey time, or the tick must have been able to complete at least part of its life cycle during the journey. Ticks are obligate parasites that attach to the skin of their host to take their blood meal, which lasts for between 6 and 20 days, depending on the tick stage and species. These hosts, either transported by humans or moving independently, will become tick vectors if the ticks are still attached at the end of the journey, or if they have been able to complete a meal and moult en route and have re-attached at the next stage.

In view of the considerable expansion in commercial transport across the world in recent decades, the risks of spread have intensified. However, they have existed since time immemorial. For instance, *Amblyomma breviscutatum*, a swine tick from Southeast Asia, is present in Vanuatu and Fiji (South West Pacific), where no land mammals existed before the arrival of humans some 3,000 years ago. It can only have come with pigs transported in the dugout canoes of the first Austronesian migrants from Asia to settle in the Melanesian islands.

Although for one-host (monotropic) tick species with a predilection for certain animal species (such as *R. microplus* for *Bos*), only the transport of those particular animal species presents a risk, this is not the case with multiple-host ticks (three-host [telotropic] tick species). One host will transport the adult tick, while others will transport the immature stages, and such hosts may be extremely diverse. In Africa, for example, the three-host tick *A. variegatum* has three times more host species than the one-host tick *R. decoloratus* (21).

However, the transport of female ticks, which will go on to produce several thousand offspring each after detaching from the host (ranging from 2,000 in the case of *R. microplus* to 20,000 for *A. variegatum*) is much more effective than that of immature ticks. After dropping from

Table I
Biological characteristics of the main tropical tick species of economic importance to livestock, and the diseases they transmit (excluding arboviruses). *Amblyomma variegatum* favours the development of clinical dermatophilosis
Based partly on Morel (52)

Vector tick	Cycle	Hosts	Pathogen (and host)	Species (and disease)
Rhipicephalus (Boophilus) microplus	One-host (monotropic) tick	Cattle, other large mammals	Protozoans:	
			– Babesiidae (cattle)	*Babesia bovis, Babesia bigemina* (tropical bovine babesiosis)
			– Theileriidae (equids)	*Theileria equi* (equine theileriosis)
			Rickettsiales:	
			– Anaplasmataceae (cattle)	*Anaplasma marginale*
Amblyomma variegatum	Three-host (telotropic) tick	Cattle, large mammals (all stages); birds, carnivores (immature ticks)	Protozoans:	
			– Theileriidae (cattle)	*Theileria mutans, Theileria velifera* (benign theileriosis)
			Rickettsiales:	
			– Anaplasmataceae (ruminants)	*Ehrlichia ruminantium* (heartwater) *Ehrlichia bovis* (tropical bovine ehrlichiosis)
			– Rickettsiaceae (zoonoses)	*Rickettsia africae* (African tick fever)

the host and moulting, each immature tick will produce only one individual of the following stage (nymph or adult). Apart from parthenogenetic ticks, the resulting nymph or adult is unlikely to have many opportunities to meet sexual partners and produce offspring.

Once ticks have been successfully transported, another valuable adaptation for completion of their life cycle is the long survival period of the free-living stages, which they use to wait for a favourable host. Thus, the larvae of *R. microplus* (80) and *A. variegatum* (7) can live up to 5 months and 11 months, respectively, after the female detaches from the host and drops to the ground. This free-living period can be up to 20 months for the adults of *A. variegatum* originating from engorged nymphs detached from their host (7).

Finally, even when precautions are taken to prevent the spread of ticks when their hosts are transported, these parasites have developed mechanisms that limit the efficacy of such measures. In theory, an acaricide treatment prior to departure (for example with pyrethroid insecticides or the antiparasitic drug amitraz) should destroy attached ticks. However, numerous species, particularly single-host ticks, have developed resistance to most acaricides (33, 42). For example, the first reported case of acaricide-resistance in *R. microplus* dates back to 1947; now that it has developed resistance to 43 molecules, *R. microplus* is one of the top 20 most resistant arthropods (84). Not only will these drug-resistant tick species be transported, they will also establish colonies of acaricide-resistant parasites in the new migration sites that will be even more difficult to control.

A changing environment: sophisticated research tools become accessible

For ticks, which have no major capacities for movement and relatively sedentary hosts (livestock or zoo or companion animals), the only possibility for remote spread is the movement of their hosts, often by humans (1, 14). Birds can transport bird ticks, or multiple-host ticks whose hosts include migratory birds (particularly African ticks), to temperate Europe (12, 39). However, the ticks can become established and found a viable population only when the climatic conditions at the site of destination are favourable. Numerous studies to develop mathematical models and software, initiated by Sutherst and Maywald in 1985 (75) with their CLIMEX system, have attempted to predict these potential establishment locations and to define their boundaries and evolution in line with climate change scenarios (25, 26, 28, 29, 57, 58, 59, 72, 76).

The development and use of sizeable electronic databases, the widespread use of modern cartography tools with geographic information systems (GIS), and access to high-definition satellite images and aerial photos have greatly facilitated understanding of the distribution of ticks and their hosts in recent years (22). This makes it easier to predict potential establishment locations and, in certain areas, the veterinary authorities are able to implement measures (such as containment and protection zones and a zone with restricted animal movements) to prevent new parasites being introduced into these potentially favourable, but as yet parasite-free, zones.

Expansion of the geographical range of two model species

Because of their direct economic impact, and the number and seriousness of the diseases they transmit, these two species place a heavy strain on cattle production in tropical zones. The difficulty in eradicating them in secondary outbreaks (13, 19, 32, 61, 63, 64 and 73) justifies the efforts needed to implement and comply with drastic precautions to prevent the species from spreading. For each of the species, the authors describe its spread and the hypothetical reasons for it, starting with *R. microplus*. Tables I and II summarise the diseases they transmit and their possible modes of spread with their hosts.

Rhipicephalus (Boophilus) microplus

Rhipicephalus microplus, which has a virtually continuous pantropical distribution, is a tick that has adapted perfectly to livestock and has evolved an extremely simplified cycle, predisposing it to accompany its hosts in their natural or human-induced movements (Fig. 1). In this summary, mention of *R. microplus* (more commonly known under its former name of *Boophilus microplus*, revised in 2003 [53]) refers to the species that was widely accepted by acarologists until very recently. Experimental crossing and new information about divergences in certain mitochondrial DNA sequences of strains collected within its global range tend to support the existence of two species, *R. microplus* and *R. australis* (43, see earlier). The evidence suggests that *R. microplus*, which originated from India and Nepal, was transported to Africa and the Americas, and *R. australis*, which originated in Indonesia (Java), was imported into Australia and in there to New Caledonia.

Initial distribution and regional spread

The native home of *R. microplus* is acknowledged to be in tropical and subtropical Asia (Vietnam, Malaysia, the Philippines [77] and Indonesia [2]), where initially it must have infested wild cattle (banteng [*Bos javanicus*], gaur [*B. frontalis*] and kouprey [*B. sauveli*]), for whom these regions are also the original area of diversification (36). It spread from eastern Afghanistan to South Korea, including India, Bangladesh, Thailand and China (Tibet, Sichuan, Nanking: 70), and from there it must have spread to the southern Japanese islands of Ryukyu and Kyushu, the Philippines, Papua New Guinea (41), and Chinese Taipei (69).

Transport outside its range and initial distribution

Starting in the 16th and 17th Centuries, the tick spread by means of livestock introduced by the first settlers from South and Southeast Asia through most of the countries in

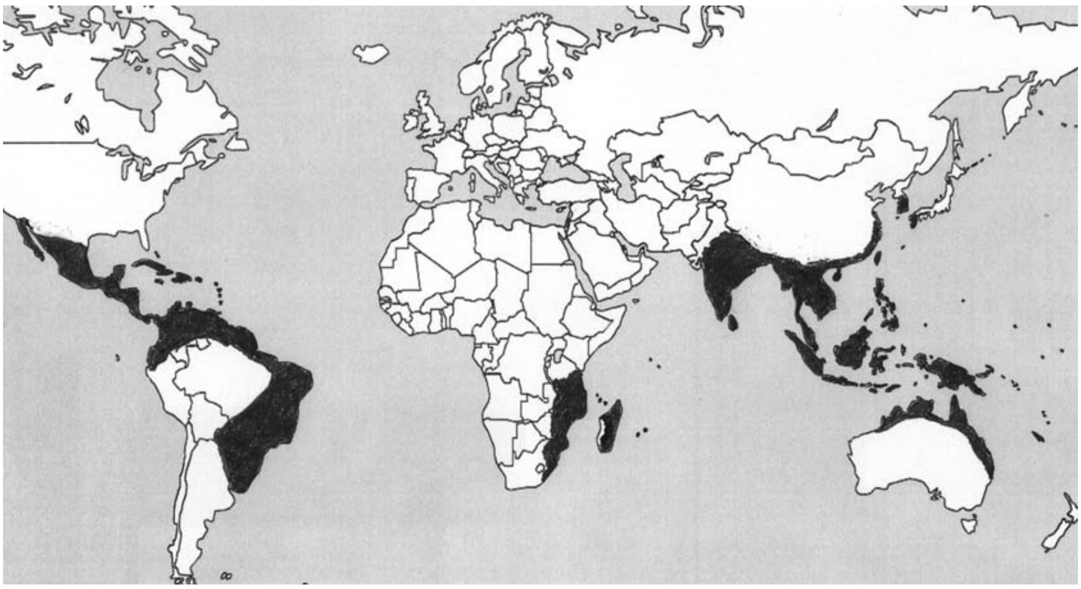

Fig. 1
Global distribution of *Rhipicephalus*
The original range of *Rhipicephalus microplus* covers continental and insular South and Southeast Asia. From there it was transported with livestock to eastern and southern Africa, to the Comoro Islands, Madagascar and the Mascarene Islands, Central and South America, northern and eastern Australia, New Caledonia and French Polynesia (86). It is the most widely distributed tropical tick and the one that causes the heaviest losses to the cattle industry because of the diseases it transmits (babesiosis, anaplasmosis)

Table II
Different scenarios for the spread of ticks and tick-borne diseases

	Spread of ticks and of healthy livestock **Healthy bovine infested with a non-infected tick**	
Origin	**Transport of infested livestock**	**Establishment of the non-infected tick**
Guadeloupe: bovine infested with non-infected *A. variegatum*	Transport of infested cattle to Martinique (1948)	Martinique: new area with cattle infested with *A. variegatum*
Marie Galante: goats infested with non-infected *A. variegatum*	Transport of two goats to Dominica (1983)	Dominica: new area with cattle infested with *A. variegatum*
Australia: cattle infested with non-infected *R. microplus*	Transport of infested mules to New Caledonia (1942)	New Caledonia: new area with cattle infested with *R. microplus*
	Accidental transport of ticks	
Guadeloupe: non-infected *A. variegatum*	On vagrant or migratory birds (cattle egret)	Nevis: new area with cattle infested in 1977
Hypothetical case	Engorged females on the ground; larvae in bedding	New area infested with ticks
	Spread of ticks and of infected livestock **Case of heartwater**	
Origin	**Transport of infested livestock**	**Establishment of the healthy tick**
West Africa: cattle carrying heartwater and infested with *A. variegatum*	Transport of cattle and ticks, or bedding with ticks (1828)	Guadeloupe: new area with cattle infested with *A. variegatum* and infected with heartwater. Heartwater cycle set in motion on the island Followed by secondary outbreaks in Antigua, Marie Galante and elsewhere
East Africa: cattle carrying heartwater and infested with *A. variegatum*	Transport of cattle and ticks to Madagascar	Madagascar: new area with cattle infested with *A. variegatum* and infected with heartwater. Heartwater cycle set in motion Followed by secondary outbreaks in Reunion Island (1980) and Mauritius (1982)
Guadeloupe: free-living infected immature *A. variegatum*	Transport of infected immature ticks by vagrant or migratory birds	American continent: infestation and infection of susceptible cattle. Subsequently, transmission of the infection is taken over by the competent local tick *A. maculatum*. Cycle set in motion (possible theoretical case)
Zambia: *A. sparsum* infected with *Ehrlichia ruminantium* on a leopard tortoise	Transported to Florida (2000)	Interception of the tortoise, positive PCR analysis on the ticks. (Hypothetical) risk of establishment of the tick and of heartwater in livestock, or of transmission by a competent local tick vector
Guadeloupe: bovine (or small ruminant) carrying *Ehrlichia ruminantium*	Transported to the American continent or the Greater Antilles (theoretical case)	Infestation of the animal by a competent local tick vector (*A. maculatum*) or a tick that might become one (other American *Amblyomma*). Cycle set in motion
	Spread of ticks and of infected livestock **Case of babesiosis (*Babesia bovis*)**	
Origin	**Transport of infested livestock**	**Establishment of the healthy tick**
Southeast Asia (Indonesia): livestock carrying babesiosis and infested with *R. microplus*	Transported to Australia	Establishment of vector ticks and of babesiosis. Cycle set in motion
Australia: healthy livestock carrying babesiosis	Transported to New Caledonia (theoretical case)	Presence of competent vector ticks. Cycle set in motion
Australia: vaccinated livestock, live babesiosis vaccine	Transported to New Caledonia (2007 episode)	Presence of competent vector ticks. Cycle set in motion

the neotropics, including Brazil and Colombia (G. Bechara, personal communication, 2008), although it is not known whether the infestation came directly from South Asia or via Africa. The American and African strains share the same genetic characteristics, which are indeed identical to those of the strains found in South Asia (43).

Even though no reliable data have been found on the introduction of the tick into the Americas, it seems reasonable to assume that more recent introductions were made by Indian zebus, such as the Girs in Brazil (1890), the Kankrej zebu (called Gujerá in Brazil) (as from 1870), and the Ongole zebus (Nelore in Brazil) (as from 1895). These zebus also contributed to the creation of several American breeds, notably the Brahmans in North America (introduction of zebus from India starting in 1906 and from Brazil starting in 1924) (47, 85). Moreover, it is not impossible for the American *R. microplus* species to have had multiple origins (at least Asia and Africa) during different periods. Two ticks of the *Rhipicephalus* (*Boophilus*) subgenus (*R. [B.] microplus* and/or *R. [B.] annulatus*), spread to the southern United States, where, in 1907, they were established in California, and from North Carolina to Texas. They were eradicated from there for the first time in 1943 (13), but re-invasions of Texas from Mexico necessitated costly new eradication programmes (32). *Rhipicephalus (B.) microplus* became established throughout Central America and from Colombia and Venezuela as far as Uruguay and Argentina (27). It is widespread in Brazil, except in a few north-eastern regions and in the mountains of Rio Grande do Sul, probably because of heavy rainfall and low temperatures (30), and in Amazonia, where the conditions are too humid and the tick would be able to persist only by means of sporadic introductions (27). There are some indications (G. Bechara, personal communication, 2009) that the tick may have arrived in southern Brazil in the early 17th Century with livestock bought in Chile (from where it is currently absent). The tick is associated with the biomes of the Chaco and Pampas of Argentina, the Wet Andes of the centre and north, the Atlantic forests and the Mesoamerican formations (27).

The tick is also present in the savannas of French Guiana (31) and in almost all the islands of the West Indies, including Puerto Rico where it was first reported in 1899 (19). In Morel's review of the infestation of the Greater and Lesser Antilles by *R. microplus* (50), he states that it was imported from Central or South America, having originated in continental or insular Eastern Asia before being transported with livestock across the Pacific (meaning that it had arrived via the western coast of the Americas). After Puerto Rico, the first reference is to Cuba (1906), followed by Jamaica (1909), Antigua, Saint Kitts, Nevis, Montserrat, Saint Vincent (1914), Trinidad (1926), Guadeloupe (1938), Martinique (1946) and Saint Martin (1966) (50).

In Africa, where several *Rhipicephalus (Boophilus)* species coexist, *R. microplus* is present in the most easterly and southerly part, from Tanzania in the north to South Africa (27), where its range overlaps with that of *R. appendiculatus* (21). It has recently been discovered in Côte d'Ivoire in West Africa, which is a long way from its previously known range (45). Its origin on the African continent is unknown: there were imports of Indian Sahiwal cattle to Kenya, but only as from 1939, whereas *R. microplus* (under the name of *B. australis*, and later *B. fallax*) was already known in South Africa as from 1899 (Fuller, cited by Hoogstraal [38]).

Rhipicephalus microplus (under the name of *Boophilus fallax*) was reported in Madagascar for the first time by Minning (48). According to Hoogstraal (37), G. Theiler (correspondence) thought that the tick had been introduced into Madagascar from Africa at about the same time as *A. variegatum* (Neumann reports *A. variegatum* in Madagascar in 1899 [54]). *R. microplus* is now well established there; it is also present in the Comoros Islands of Anjouan, Moheli and Grande Comore (68 and F. Stachurski, personal communication, 2010).

It is reasonable to assume that the Mascarene Islands were infested from Madagascar with the introduction of 'moka' cattle, but this would mean that Madagascar had been infested earlier than Minning testified (48). *Boophilus decoloratus* was reported in Mauritius in 1915 (18) and in Reunion Island in 1949 (34). It should be noted that, in 1901, Neumann considered *R. decoloratus*, *R. australis* and '*Haemaphysalis micropla*' to be synonymous with *R. annulatus* (55) and in 1911 he even considered both *B. microplus* (under the name of *australis*) and *B. decoloratus* to be subspecies of *B. annulatus* (56). Moreover, Hoogstraal (37) also said that Neumann had reported *B. caudatus* (= *B. microplus*) in Reunion Island as early as 1897. As well as collecting *B. microplus* from livestock in Mauritius and Reunion Island, the authors of the present paper have also collected it on Rodrigues (9).

Parsonson notes that cattle from South Africa and zebus from India were introduced into the south-east Australian state of New South Wales – which for the most part is unsuited to the development of *R. microplus* – in the late 18th Century (60). The same author also mentions the introduction into northern Australia of buffalos (*Bubalus bubalis*) from the Dutch East Indies in 1824, and of bantengs (*Bos javanicus*) between 1829 and 1849, which may have introduced the tick (44). During this period, Indian cattle were also transported to northern Australia. This may not, however, have been how *R. microplus* entered the country. According to Parsonson (60), it is more likely to have been introduced on zebus imported into northern Australia from Java in 1872, because it is only from around 1881 that severe losses from 'tick fever' were reported. A detailed history of the arrival in Australia of *R. microplus* and babesiosis (redwater), of which it is a vector, and their subsequent spread is also provided by Angus (3), who believes that epizootics of babesiosis occurred there earlier. Based on the text of Letts (44), she thought that the tick had very probably been introduced with bantengs (*Bos sondaicus*) imported into Darwin from Timor and maybe from Bali between 1829 and 1849, and indeed cases of redwater were reported there as from 1870 (J.A.G. Little, cited by Angus [3]). From the region of Darwin, the tick spread to northern Kimberley (in Western Australia) between 1879 and 1885 and to the Gulf of Carpentaria in the east in 1891, where once again it manifested itself in severe losses from babesiosis. It quickly invaded Queensland in spite of the disease protection measures implemented on the 20th parallel, which were shifted southwards to the 22nd parallel in 1892 and to the 24th parallel the following year. By 1897 *R. microplus* had reached the far south of Queensland and in 1907 it entered New South Wales (see also Rainbow [67]), the northern part of which is still its most southerly boundary (3, 71, 86). In 1926 the tick occupied the whole of Kimberley in the west (3). This means that, in spite of measures to contain it, *R. microplus* was able to travel 4,500 km in the space of 100 years (45 km per year!) and conquered all of Australia's favourable zones.

Rhipicephalus (B.) microplus was introduced into New Caledonia from Australia during the Second World War (in 1942) by American troops with equids, 1,384 of which – some with ticks from the outset – were taken on board at Brisbane (11, 66, 81). From there the tick spread throughout the island in just a few years, despite attempts to eradicate it. *Rhipicephalus microplus* was also introduced into several French Polynesian islands with cattle from the Americas (66), as well as into Guam in 1912 (40) and into the Solomon Islands on cattle transported from northern Australia (11).

Potential range

Rhipicephalus (B.) microplus has such a capacity for spread that it seems reasonable to assume that it has colonised virtually all of its potential favourable range, except perhaps in West Africa (45) and Central Africa, unless other indigenous *Rhipicephalus* (*Boophilus*) have hindered its establishment. Some remote locations, particularly islands, still remain unaffected, and they can be spared by observing restrictions on livestock imports (at least the Pacific islands of Loyalty, Vanuatu, Tonga and Fiji). The tick could also return to areas of the southern United States where it was established in the early 20th Century (13), if efforts to control its spread from Mexico are relaxed. Simulations for Latin America predicting a temperature increase suggest that areas in the most southerly parts of the continent, as well as the foothills of the Andes and in Mexico, which are currently too cold for *R. microplus*, might suit it one day. By contrast, the tick might desert zones that have become too arid (25, 28).

Amblyomma variegatum

Initial distribution

Amblyomma variegatum is present in more than 30 countries of Africa between latitude 17° north, practically following the 500 mm isohyet (which corresponds to the boundary of the dry savanna), and latitude 20° south (Fig. 2). It is the species of the genus with the widest distribution on the African continent (22, 29, 52, 83). With 2,586 locations in the Cumming database (21), it ranks third among the ten most collected species in Africa. It occupies all the climatic zones, limited in the north only by the arid conditions (< 400 mm) found on the edge of the Sahel and in the Horn of Africa, and in the south by the cooler temperatures prevailing in the subtropical regions of the continent. In equatorial regions, where the maximum rainfall that the ticks can tolerate is around the 2,750 mm isohyet, *A. variegatum* is scattered thinly and remains confined to clearings (88). At high altitude, it has become established only on hot plateaus with abundant rainfall (51). Its absence from certain regions within the boundaries of the apparently favourable range is probably explained by competition with an already established tick species, such as *A. hebraeum* in southern Africa or *A. pomposum* in the Angolan savannas (57). Throughout its range in Africa, as well as in Yemen at the southern tip of the Arabian Peninsula, *A. variegatum* occupies a wide diversity of habitats, ranging from dry grass steppes and mountain grasslands to the moist tree savanna bordering the equatorial forest.

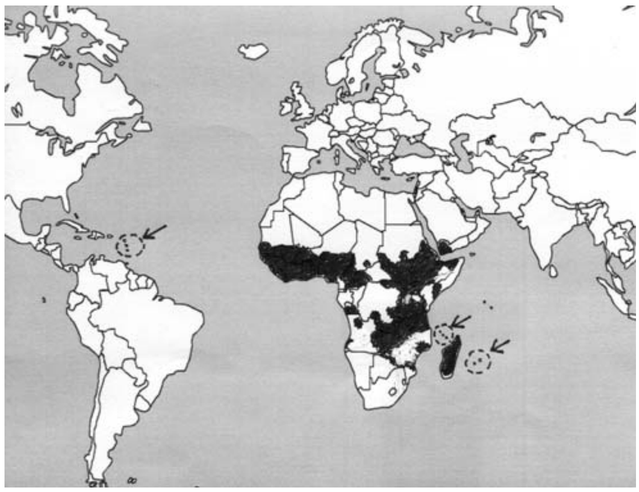

Fig. 2
***Amblyomma variegatum* is the most widely distributed African tick on the African continent**
It was transported to the Lesser Antilles with livestock from Senegal or The Gambia – from where it was able to spread and become established in the Greater Antilles and on the continent. From East Africa it spread to the Comoro Islands, Madagascar and the Mascarene Islands (29). It is a vector of heartwater, which it has carried everywhere

This wide distribution, together with its marked tropism for the large herbivores, including livestock, makes *A. variegatum* a species that can easily spread and become established outside its native range. The history of its recent expansion confirms this.

Transport outside its range and secondary distribution

From Africa, two zones were colonised: one was the West Indies and the other Madagascar and the Mascarene Islands.

The infestation of the West Indies with the tropical bont tick *A. variegatum* – which is referred to in those parts as the 'Senegalese' tick – happened long ago as a result of the flourishing Atlantic triangular trade between the ports of Europe, the trading posts of Africa and the American colonies. Initiated in the 16th Century and developed by the West India Company, apart from slave trafficking – which was abolished in 1848 – this triangular trade consisted of transporting livestock from Europe and especially West Africa (Senegal, Gambia, Guinea) to the West Indies. It continued until the 19th Century for the importation of African livestock and the transport of European migrants (46).

According to Curasson (23), zebus from Senegal were imported into the French West Indies and Guiana in 1828 and 1830. He points out (p. 272) that the zebus also brought piroplasmosis to the West Indies, along with *A. variegatum* (which he also referred to as the 'Senegalese' tick, saying that it had now become one of the biggest pests in Guadeloupe). He blamed the transport of livestock for the presence of this African tick in the Caribbean and there is little doubt that he was right. Although 1828-1830 is the first ever reference to the tick in Guadeloupe, and the date generally accepted for its introduction (6), *A. variegatum* could have been introduced earlier in view of the frequency and long history of trade (46). Taking into account the length of the voyage by sailing ship (around one month) and the maximum duration of the parasitic stage (18 days for females: Barré [unpublished]; 7), Guadeloupe could have become infested either when tick-infested bedding was unloaded, or from livestock in the hold infested by ticks that had detached at the previous stage and moulted in the bedding during transportation (6). From Guadeloupe, Marie Galante was infested in around 1835 (6), Antigua before 1895 (5) and Martinique in 1948, where the introduction of six bulls from Guadeloupe led to the establishment of the tick in Le Lamentin (50). The infestation of the West Indies then grew to include 14 islands, from Saint Croix in 1967 to Saint Vincent in 1988. The transport, legal or otherwise, of cattle (La Desirade, Saint Lucia, Saint Kitts and Anguilla), goats (Dominica), dogs (Barbados) and cattle hides (Saint Martin) is sometimes blamed. However, the accelerated spread of *A. variegatum* should also be seen in connection with the arrival (in the 1950s), rapid spread and subsequent growth of sedentary and migratory populations of cattle egret (*Bubulcus ibis*) (4), which is often a host of the immature stages of the *A. variegatum* tick (6, 8, 20). This spread was a cause of serious concern because of the tick's role not only in favouring the development of clinical dermatophilosis but particularly as a heartwater vector, and because American *Amblyomma* spp. had proved to have this competence and were able to transmit the disease (78). Although an eradication programme (Caribbean Amblyomma Programme) co-ordinated by the Food and Agriculture Organization of the United Nations (FAO) was set up in the Lesser Antilles in 1994 (62, 63, 64), it had to be abandoned in 2006 because of the high cost (US$24 million), failure to meet its objectives and problems in implementing the programme (61).

In the Indian Ocean, *A. variegatum*, probably from East Africa, colonised neighbouring islands, including the Comoro Islands (Anjouan) and Madagascar (54, 68, F. Stachurski, personal communication, 2010), and from there the Mascarene Islands. The first references to the tick in Mauritius are by Neumann (54, 56) and de Charmoy (17), and in Reunion Island by Gillard (34). There is little doubt that the tick had been introduced with live animals transported by boat. In Reunion Island, the 'moka' zebu from Madagascar had formerly been imported as a draught animal before anti-tick products existed. In addition, Uilenberg *et al.* (79) collected this tick in Madagascar from rusa deer (*Cervus timorensis russa*) from Mauritius. In Madagascar (79) and the Mascarene Islands (9), the tick is confined to relatively dry, low-lying savanna regions. Although a few specimens were collected in Madagascar on the plateaus (1,000 m to 1,400 m) (79), the authors blamed transhumant livestock for the persistence of *Amblyomma* at high altitude and doubted that they could become established permanently without continual introductions from zebus travelling from coastal regions.

Potential range

Simulations have been conducted since 1985 primarily to assess which areas of the American continent are favourable to *A. variegatum*, i.e. areas which could be struck by heartwater and where severe forms of dermatophilosis could develop. The first predictive models were obviously too lax (75), with a very extensive potential range covering areas that were probably climatically unsuitable for the tick. More recent models, based on the climatic conditions found in its range in the West Indies, have restricted it to Hispaniola in the north, between Yucatan and Panama in the east and as far as the coastal zones of Colombia and Venezuela in the south (29). No recent assessment exists for the rest of the world. However, it seems reasonable to assume that *A. variegatum* would find suitable ecological conditions at least in the southern part of the Indian Peninsula, in insular and continental Southeast Asia, in Papua New Guinea and in Australia's Northern Territory and Queensland. It goes to show what a serious risk this tick poses to an extensive geographical area.

Conclusion

The authors trust that these two examples have demonstrated how easily parasites can spread throughout the world with their hosts, to anywhere where they find suitable ecological and climatic conditions. While such conditions obviously have no influence on internal parasites, except for their stages outside the host (such as helminth eggs and larvae or coccidia oocysts), they do impact heavily on ectoparasites, on parasitic stages, and even more on non-parasitic stages. An example of the influence of climate is that the cattle that introduced *A. variegatum* into the West Indies from Senegal and/or The Gambia must also have been infested with ticks of the (xerophilic) *Hyalomma genus*, but the latter failed to become established in the West Indies, not having found the climatic conditions at their sites of destination to be favourable back then.

Parasite ranges are not definitively established and a special effort must be made to improve knowledge and to implement appropriate biosecurity regulations in order to prevent the spread of parasites to areas that are still free.

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■

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