Onderstepoort J. vet. Res., 54, 405–417 (1987)

DANGER OF INTRODUCING HEARTWATER ONTO THE AMERICAN MAINLAND: POTENTIAL ROLE OF INDIGENOUS AND EXOTIC *AMBLYOMMA* TICKS

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ABSTRACT

BARRÉ, N., UILENBERG, G., MOREL, P. C. and CAMUS, E., 1987. Danger of introducing heartwater onto the American mainland: potential role of indigenous and exotic *Amblyomma* ticks. *Onderstepoort Journal of Veterinary Research*, 54, 405–417 (1987)

The existence of heartwater on 3 islands of the Central Lesser Antilles and the presence of an efficient vector originating from Africa, *Amblyomma variegatum*, on most of the islands of this region constitute a serious threat for livestock on the American mainland. The disease can be introduced there either by infected animals or infected ticks. The most likely way is probably the transportation of domestic animals which are heavily infested by ticks. Due to the low rate of infection of ticks in endemic areas and the low rate of infestation of wild animals by ticks, the risk of transportation by migratory birds (among which the cattle egret is the most important) seems negligible compared with domestic animals, especially ruminants and dogs.

The establishment and spread of the disease on the mainland could result from indigenous American *Amblyomma* species, of which at least 2, *Amblyomma cajennense* and, more especially, *Amblyomma maculatum*, are experimental vectors. The biological and ecological features of these ticks conform to some extent with the characteristics necessary for them to act as vectors. They are widespread and sufficiently well adapted to ruminants to ensure the continuation of the epidemiological cycle. Disease could evolve in wild life (deer) or, as seems more likely, in livestock, of which the population density is very high on most of the mainland. However, the establishment of the disease is more likely to occur if the well adapted vector of heartwater, *Amblyomma variegatum*, is introduced as well. This exotic species would find environmental conditions favourable for its survival and spread in most of the tropical and subtropical Western Hemisphere.

Protection of the American mainland and the disease-free islands of the area must be based on strict control of domestic animal movement in the Caribbean, on the decrease of the vector population by tick control campaigns and, if possible, on the eradication of *Amblyomma variegatum* from the focus of heartwater on the islands.

INTRODUCTION

Once the presence of heartwater in the Western Hemisphere had been confirmed (Perreau, Morel, Barré & Durand, 1980), the fundamental question of the risk of dissemination to neighbouring areas arose. Heartwater presents a serious threat to American livestock, and the danger of its introduction to the American mainland has clearly been pointed out (Uilenberg, 1977, 1982; Uilenberg, Barré, Camus, Burridge & Garris, 1984; Burridge, Barré, Birnie, Camus & Uilenberg, 1984). This justifies intensive research on the disease in the Caribbean region.

The Caribbean focus, although remote from countries with an important livestock industry (Antigua is 400 km south-east of Puerto Rico, Guadeloupe 580 km north of Venezuela), is less isolated than might appear. There are many islands interposed between the Caribbean and Florida, on the one hand, and Venezuela on the other. In this paper we speculate on the chance the disease has of spreading from its present focus and invading other islands or the mainland. Can cowdriosis invade other countries of the Western Hemisphere and if so, how can this threat be prevented? To answer these questions, 3 main points have to be examined: firstly the possibility of the disease being transported, and, secondly and thirdly, the chances of its subsequent establishment and of its spread in the new territory. Our speculation will be based on what is known of the epidemiology of the disease and the biology and ecology of the natural and potential vectors.

I. THE STATUS OF HEARTWATER IN THE WESTERN HEMISPHERE

1. Distribution of heartwater in the Caribbean (Fig. 1)

Heartwater was first diagnosed on Guadeloupe (French West Indies) in 1980 (Perreau *et al.*, 1980). A survey covering all of the Lesser Antilles was carried out from 1982 to 1984 by a French-US-Dutch team to determine the distribution of heartwater and its introduced African tick vector in the region. In addition to Guadeloupe, the disease has been discovered on 2 other islands, the one nearest to the north , Antigua, and the one nearest to Guadeloupe in the south, Marie-Galante (Camus, Barré, Birnie, Burridge & Uilenberg, 1984; Birnie, Burridge, Camus & Barré, 1985). Agriculture is the principal activity on these islands, which support a livestock population of about 110 000 cattle and 70 000 sheep and goats (FAO, 1984a). The cattle and goats are mainly of African origin and, with the exception of the more mountainous and wooded areas, are reared on small farms spread over the islands.

2. The vector of heartwater in the Caribbean (Fig. 1)

Originally, before human colonization, the Caribbean islands had no large animals and therefore no large animal ticks. The 4 tick species that occur on livestock there today, *Dermacentor nitens, Boophilus microplus, Amblyomma cajennense* and *Amblyomma variegatum,* have been introduced, the latter from Africa, the birthplace of heartwater, with Senegalese zebu cattle shipped to the French Antilles in approximately 1830 (Curasson, 1943). Guadeloupe and Antigua appear to have been the first islands colonized by *A. variegatum* (Morel, 1966). This tick has since spread to other islands, including one of the Greater Antilles, Puerto Rico (Maldona Capriles & Medina-Gaud, 1977; Garris, 1984, 1987) and most of the Lesser Antilles, where it has spread rapidly in recent years (Morel, 1966; Hourrigan, Strickland, Kelsey, Knisely, Crago, Whittaker & Gilhooly, 1969; Butler, 1975; Uilenberg *et al.*, 1984; Burridge *et al.*, 1984; Garris & Scotland, 1985; Burridge, 1985; USAID, USDA, IICA & FAO, 1986). Daubney (1930) was the first to demonstrate the role of *A. variegatum,* one of the most efficient vectors, in the transmission of heartwater.

3. The origin of heartwater in the Caribbean

Heartwater has been diagnosed only recently in the Caribbean. However, the history of the introduction of its African vector and its distribution, as well as the fact that local breeds on the affected islands have a high

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Received 11 June 1987—Editor

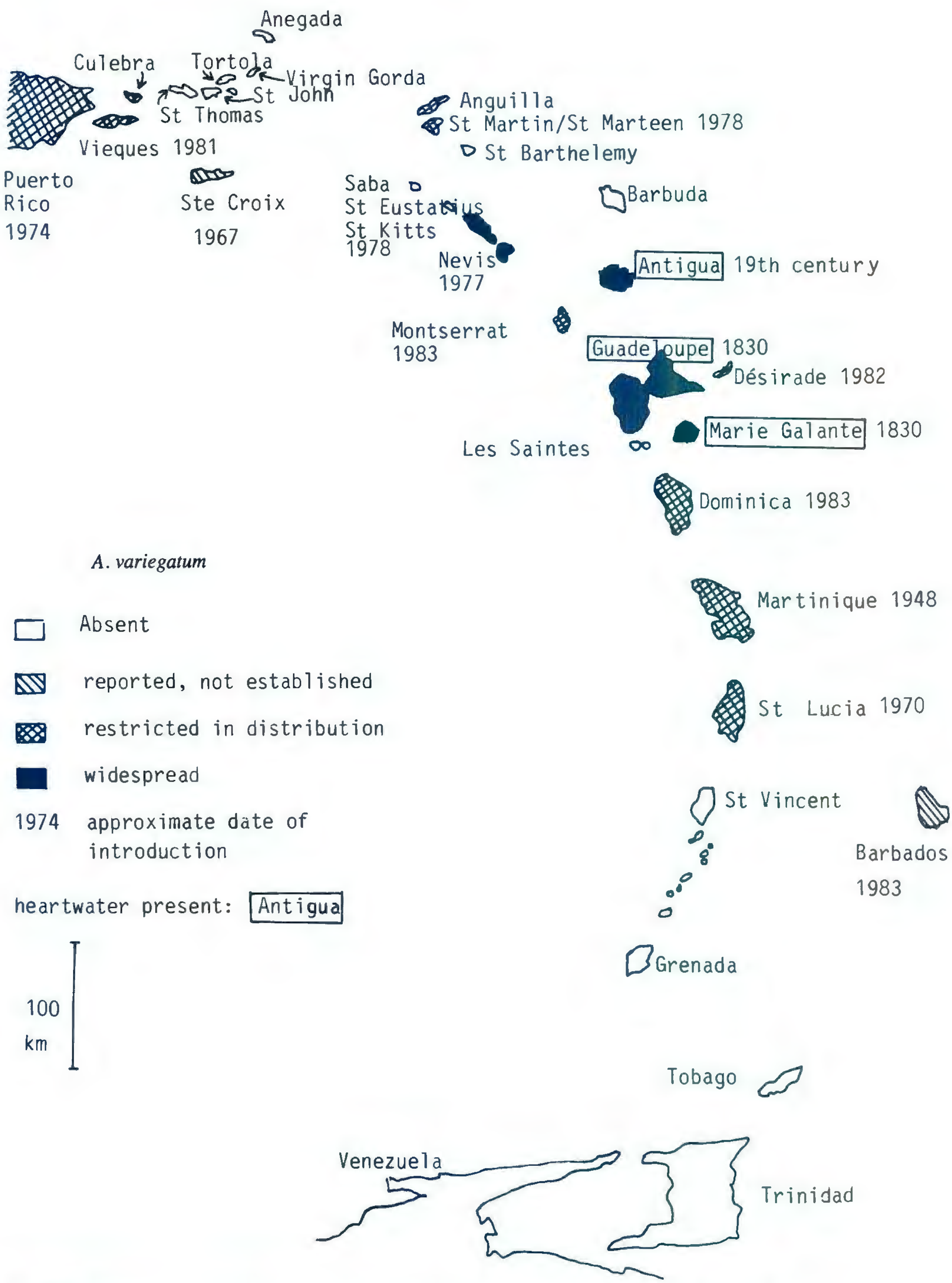

FIG. 1 Distribution of *A. variegatum* and heartwater in the Caribbean (from Uilenberg *et al.*, 1984 and USAID *et al.*, 1986)

innate resistance to the disease, make the hypothesis that it has been established there for a long time, at least on Guadeloupe, quite plausible. It would appear that it was introduced, together with its vector, with infected zebu cattle (Uilenberg *et al.*, 1984).

II. Possibilities of Transportation of Heartwater from the Caribbean Focus

Heartwater and new vectors may still be introduced to the American mainland from the African source, for example with infested exotic game animals, but by far the greater threat comes from the nearest focus, that in the Caribbean.

1. Transportation of the disease with infected ruminants

The Caribbean consists of closely scattered islands. Transportation of livestock is easy and probably not uncommon between the islands, even though it is usually illegal and in the case of Guadeloupe not mentioned in official reports (FAO, 1984b). (There are no data for Antigua.)

The risk of propagation from the 3 infected islands seems limited to domestic ruminants. There is little wildlife in the Lesser Antilles (Uilenberg *et al.*, 1984) and small mammals are unlikely to be reservoirs of the disease (Uilenberg, 1983a) even if some of them, like the mouse, can experimentally harbour the infection (Haig, 1952). The susceptibility of the mongoose (*Herpestes auropunctatus*), introduced from India to control rats and now widely spread in the Caribbean (Nellis & Everard, 1983), should be tested in view of the reported susceptibility of another carnivore, the ferret (Mason & Alexander, 1940). An attempt to infect the African slender mongoose (*Herpestes sanguineus ibeae*, referred to in the report as *Mungos ibeae*) has, however, failed (Anon., 1942). The possibilities of carriage by birds must also be studied since Bezuidenhout & Olivier (1986) have demonstrated recently the persistence of *Cowdria* in the blood of guinea-fowls for at least 16 days after experimental infection. The existence of reservoirs among migratory birds would modify fundamentally the risk of propagation. As far as we know at the present time, the threat in the region comes from cattle, goats and sheep. After infection and recovery, ruminants appear to remain infective to ticks for only a very limited period. Alexander (1931) succeeded in transmitting the disease with nymphs fed in the larval stage on an ox 14 days after its recovery. We have demonstrated that the infective period in goats usually does not exceed 3 days after recovery (Barré & Camus, 1987).

Ruminants transported during the incubation period of 10–30 days, the 1–8 days of the febrile reaction, and a short period of at most a few weeks after recovery, are the most dangerous. Recently recovered animals can be detected by serological tests, as can sick animals, after a period of quarantine. However, it is better to prohibit all introductions of ruminants from infected areas and to strictly control illegal movements of domestic animals, as relapses and rickettsaemia may occur after recovery (Neitz, Alexander & Adelaar, 1947; Neitz, 1968; Du Plessis, 1981; Uilenberg, 1983a; Du Plessis, Bezuidenhout & Lüdemann, 1984; Uilenberg, Camus & Barré, 1985).

2. Transportation of the disease with infected ticks

Introduced exotic ticks rarely establish themselves and usually disappear without being discovered by acarologists. However, the threat from exotic *Amblyomma* in the Western Hemisphere appears serious. *A. variegatum* is so far the only exotic *Amblyomma* to have succeeded in establishing itself in this part of the world. It has also been identified in the United States (Becklund, 1968; Wilson & Richard, 1984) and in Guatemala, French Guyana, Surinam and Venezuela (Neumann, 1899; Maldona Capriles & Medina-Gaud, 1977). Wilson & Richard (1984) report that from 1962 to 1984, 6 African vectors of *Cowdria* have been intercepted on 30 occasions on amimal products (12) or zoological animals (18), especially rhinoceros (9 of 18), imported from Africa into the United Sates. These include one of the major vectors, *Amblyomma hebraeum* (Diamant, 1965). In some cases, and like *A. variegatum* in the West Indies, these exotic *Amblyomma* were introduced in regions such as the southern United States and Central America, where climatic conditions were probably favourable for their establishment.

Infectivity of ticks

Only ticks of the genus *Amblyomma* (Neitz, 1968), and then only certain species of this genus (10 African and 2 American), are known at present to transmit the disease naturally or experimentally (Uilenberg, 1983a; Uilenberg *et al.*, 1985; Bezuidenhout & Olivier, 1986).

TABLE 1 Free stages and stages attached on a host representing a danger of transportation of heartwater

Host and/or ticks transported	Stages of *A. variegatum*		
	Larvae	Nymphs	Adults
Ruminant infected	Engorged larvae	Engorged nymphs	
Ruminant not infected		Engorged nymphs	If larvae fed on an infected host
Non-susceptible host		Engorged nymphs	(If larvae fed on an infected host)
Free stages		Flat nymphs — If larvae and/or nymphs fed on infected hosts	Flat adults — If larvae and/or nymphs fed on infected hosts

TABLE 2 Average number of *A. variegatum* found on some domestic animals in Guadeloupe
Bold numbers: stages potentially infected

	No. of hosts examined	% infested	Average no. of ticks recovered			
			Larvae	Nymphs	Adults	Total
Cattle	11	100	**266**	**36**	43	345
Goat	12	50	**547**	**12**	18	577
Feral dog	10	80	104	**8**	0	112

TABLE 3 Average number of *A. variegatum* found on errant or migratory birds in Guadeloupe
Bold numbers: stages potentially infected

	No. of hosts examined	% infested	Average no. of ticks recovered			
			Larvae	Nymphs	Adults	Total
Cattle egret	80	26	1,7	**0,05**	0	1,8
Shore birds	256	0	0	0	0	0

Infected ticks can, theoretically, be transported on vegetation (plants, vegetables, hay), with soil, compost, manure, etc. But undoubtedly the most effective way—which is assumed to account for the infestation of Guadeloupe (Perreau *et al.*, 1980; Uilenberg *et al.*, 1984) and also of Madagascar (Uilenberg, Hoogstraal & Klein, 1979)—is the transportation of ticks on their hosts. In the case of Guadeloupe the disease was introduced at the time of the sailing boats, when the duration of the journey from the West coast of Africa was a month. This means the ticks had time to detach from the animals and moult on the boat. They may have been introduced both with litter from the ship and/or on animals reinfested with moulted ticks on the ship.

Amblyomma species are 3-host ticks and, because transovarial transmission is exceptional (Bezuidenhout & Jacobsz, 1986), normally only free flat nymphs (infected in the larval stage) and adults (infected in the larval and/ or nymphal stage) can be infective. Attached larvae and nymphs also can be infective at the following nymphal or adult stage if they feed on a reacting host or, in respect of the latter, if the larvae have done so (Table 1).

For the transportation of the disease by attached ticks, one should distinguish between domestic animals, transported by man, and wild animals, especially migratory birds, which can move about freely.

Ticks on domestic animals

In a study of the hosts of *A. variegatum* in Guadeloupe, Barré, Camus & Salas (1985) and Barré, Garris, Borel & Camus (in press) found that 96,6 % of nymphs and 95 % of larvae feed on large domestic animals, especially cattle (36 nymphs and 266 larvae per animal) and goats (12 nymphs and 547 larvae). These 2 hosts, and horses, sheep and pigs, which were found infested in other surveys, could mainly be responsible for the transfer of infected ticks in view of their high rate and level of infestation (Table 2).

Other non-susceptible domestic animals could play a role by transporting nymphs, in particular dogs, which carry on average 8 nymphs per animal. This pet, which frequently travels with its owner, might be an unsuspected means of transport as veterinary services are concerned mainly with rabies.

Ticks on wild animals

Among mammals only the mongoose shows a low but significant level of infestation (0,3 nymph per animal). There is no serious risk that this host, and non-migrant birds such as the Caribbean grackle, (*Quiscalus lugubris*), which may carry 0,2 nymph per bird, will translocate ticks unless they are themselves transported by humans.

The situation is quite different for migratory birds. Some North American long-distance migrating species, such as the bobolink (*Dolichonyx oryzivorus*), plovers (*Pluvialis dominica, Squatarola squatarola, Charadrius vociferus*), snipe (*Gallinago gallinago*) and curlew (*Numenius phaeopus*), stop over on short pastures and mangrove swamps where they may be attacked by ticks.

FIG. 2 Bird migration routes: the example of the golden plover, *Pluvialis dominica*

They arrive in large numbers in the Caribbean each autumn and spring during their southward and northward migrations (Pinchon, 1976; National Geographic Society, 1979) (Fig. 2). Such birds could transport the disease over long distances. In 1 week (the average time of engorgement of immature tick stages) they could easily reach the United States in the north, or the Atlantic coast of Brazil in the south. However, of the 256 shore birds superficially examined (eyelids, base of the beak) in the autumn of 1983 (Table 3) none was infested (Barré *et al.*, in press), but this survey needs to be completed.

Another bird, the cattle egret (*Bubulcus ibis*), which colonized the Western Hemisphere during the late 19th century (Palmer, 1962; Albaine Pons, 1980), could be a more efficient vehicle. Even though the level of infestation by potentially infected stages is low [0,05 nymph per bird in our survey (Table 3)], the bird is abundant (about 11 000 in Guadeloupe, according to Edouard Benito-Espinal, personal communication, 1985). The cattle egret shows a marked preference for ruminants, near which it can pick up immature ticks and release engorged, potentially infected nymphs. While North American populations have become migratory, Caribbean populations seem to be resident (Rappole, Morton, Lovejoy & Ruos, 1983). Dispersing wanderers may spread to other areas when residents become overcrowded in a given area (Palmer, 1962). Apart from the introduction of infested domestic animals, this bird might well present the next most efficient way of disseminating both the tick and the disease. More studies are necessary to determine routes of migration or dispersion of the Caribbean population, in order to define more precisely the potential threat by this recent and very dynamic invader.

Simple control measures to prevent the movement of domestic animals would probably reduce the risk of spreading the disease to a very low level. Only about 1 in 20 cattle egrets carry nymphs. The rate of infection of adult ticks collected on hosts in endemic areas is low (Uilenberg, 1971; Du Plessis, 1984), of the order of 1 % (Camus & Barré, 1987). Assuming that the infection rate of nymphs might be about 2/3 that of adults (Table 4), 1 egret out of 6 250 would carry an infected nymph (Table 5). Taking into account the proportion of infected ticks and the average level of infestation of cattle, goats and dogs, it is estimated that each of the 2 ruminant hosts, and 1 out of 38 dogs, carry an infected larva or nymph. This makes them far more likely vectors of the disease than the egret (Table 5).

TABLE 4 Theoretical proportion of infected ticks attached on susceptible and non-susceptible hosts

Adult tick attached on *susceptible* host = 1 %	= 0,01*
Nymphs	0,0066
Larvae	0,0033
Adult tick attached on *non-susceptible* host	0,0066
Nymphs	0,0033
Larvae	0

* Observed; other data estimated

Transportation of the disease could, consequently, be frequent with translocated infested domestic animals, but the epidemiological situation in the Caribbean indicates that, because certain conditions are necessary for its success (see III), the risk of establishment and spread of the disease is in fact very low. Of the 28 islands visited by the French-US-Dutch team, 16 were infested with *A. variegatum* (Burridge, 1985; Burridge, Birnie, Barré, Camus & Uilenberg, unpublished data, 1986) but heartwater was found on only 3 of them. The 3 infected islands are those nearest to Guadeloupe, which was probably the initial focus of infection in the region. Trade and exchange of animals were presumably more extensive between Guadeloupe and the neighbouring islands than with the more remote ones.

III. Establishment of the Disease in a New Area

Once the disease has been introduced certain conditions are necessary for its establishment. These conditions are quite different when the source of infection is an infected animal free from ticks, and when infected ticks are involved.

1. Conditions necessary for the establishment of the disease after introduction of an infected animal

The disease is not directly contagious, therefore infected animals by themselves do not represent a risk if they are slaughtered immediately after introduction, or are introduced into a herd where vectors are absent.

The establishment of heartwater can only occur if the infected animals are introduced into an area where potential *Amblyomma* vectors occur in sufficient numbers and if there is an adequate density of susceptible hosts. Many of the livestock-growing areas of North, Central and South America could therefore be suitable, because of high host densities and the presence of potential vectors.

2. Conditions necessary for the establishment of the disease after introduction of infected ticks

If infected ticks are introduced on domestic livestock in sufficient numbers to produce an exotic vector population, establishment of the disease is likely to occur in the presence of susceptible hosts. If, however, the introduced exotic ticks cannot become established, an indigenous vector will be necessary to continue the infective cycle.

If non-parasitic infected ticks, or infected ticks on birds or other non-farm animals are introduced, there is rarely more than 1 tick involved, with little chance of establishing a population of the particular tick species. Moreover, the infection will not manifest itself unless the ticks infest a susceptible host. Infested dogs brought into towns, or migratory birds alighting elsewhere than on pastures with ruminants, do not therefore present a danger.

Migratory birds attracted to large mammals, such as the cattle egret, are more likely to be vehicles for the disease than other groups such as shore birds or passerine birds. Because all the potential bird hosts of exotic *Amblyomma* ticks live in open habitats, they are more likely to release ticks in pastures with domestic ruminants, than in forest habitats with wild ruminants. Nevertheless, the possibility of starting the disease in a forest habitat should be considered. Wild ruminants are much less abundant in tropical America than in the Old World, for they are represented only by Cervidae (*Odocoileus, Mazama*). At least 2 Eurasian species of this family, *Dama dama* (Hofmeyr, 1956) and *Cervus timorensis* (Poudelet, Poudelet & Barré, 1982) are susceptible to the disease. A wild cycle certainly occurs on Mauritius (Indian Ocean) among deer (Poudelet *et al.*, 1982). As far

TABLE 5 Theoretical average number of infected ticks per host in Guadeloupe
Data calculated from Tables 2, 3 and 4

Stage	Average number of infected ticks per host			
	Cattle	Goat	Dog	Cattle egret
Infected larvae	0,24	1,8	Not infected	
Infected nymphs	0,87	0,08	0,026	0,00016
Total number of infected ticks per host	1,1	1,9	0,026	0,00016
Average number of hosts carrying one infected tick	Every bovine	Every goat	1 out of 38 dogs	1 out of 6 250 cattle egrets

as the Wester Hemisphere is concerned, the susceptibility of the white-tailed deer (*Odocoileus virginianus*) to heartwater has also been demonstrated (Dardiri, 1984, cited by Logan, Endris, Birnie & Mebus, 1984).

The chances of tick and host meeting each other depend both on the density of the host and the mobility and survival time of the tick. Horizontal movement of free nymphs and adults of *Amblyomma* is very limited [about 10 m in 1 h for adult *A. variegatum* attracted to a CO_2 trap and 2 m for nymphs (Barré, unpublished data, 1986)]. The mobility of this tick slightly increases its chances of finding a host. Another adaptational characteristic greatly increases these chances. In favourable environmental conditions these ticks [which can remain infective for at least 15 months (Ilemobade, 1976)] can survive for a very long time. An experiment under natural conditions in Guadeloupe (Garris & Barré, unpublished data, 1986) showed a maximum survival period of more than 17 months for adults and 12 months for nymphal *A. variegatum*. Infected ticks, waiting for a host, can therefore remain a threat for a prolonged period.

Once the disease has been introduced, an adequate density of ticks and hosts is needed to establish and propagate it. The regional abundance of domestic animals can be obtained from agricultural data. Tick abundance is more difficult to quantify; it depends on host density, as well as ecological circumstances.

3. Host abundance and susceptibility

Important regions of animal production in North and Central America (Fig. 3) are in the southern USA, the slopes of the Rocky Mountains, the Mexican plateau between the 2 Oriental and Occidental Sierra Madre, the area from Yucatan to Panama, and in South America the Orinoco basin in Venezuela and Colombia, the vast area of the Brazilian plateau (Campos, Caatingas), the Parana basin across Uruguay and northern Argentina to Paraguay, and the Patagonian steppe (Serryn & Blasselle, 1973). Host density can be as high as 1,9 ruminants per ha in Uruguay. In most countries of the mainland the density is between 0,1 and 0,5 per ha (FAO, 1984a), which indicates fairly intensive farming activity.

FIG. 3 Areas of ruminant production in the Western Hemisphere

Venezuela, which possesses an important livestock industry and is close to the Caribbean focus of heartwater, is more threatened than any other mainland country, especially in view of the migration routes of birds. Another favourable factor for the establishment of the disease on the mainland is the fact that the ruminant population is entirely susceptible to the disease. In contrast with animals in endemic areas, where most are immune and will not become infective to ticks after reinfection (Barré & Camus, 1987), every individual of the ruminant populations on the mainland, with no previous experience of heartwater, will react if infected and become infective to ticks.

IV. SPREAD OF THE DISEASE ONTO THE AMERICAN MAINLAND

Two possibilities have to be examined: (i) spread by means of an American *Amblyomma* species, or (ii) spread with an introduced African vector.

A. POSSIBILITIES OF SPREAD BY AN INDIGENOUS VECTOR

This requires the presence of a local *Amblyomma* species able to transmit *Cowdria* and of which at least 2 stages commonly feed on ruminants. An adequate population of susceptible hosts is, of course, also essential to ensure the infection of the vector population. Ticks of the genus *Amblyomma* are well represented in America with half of the known species [52 out of 102 (Dias Lopez, 1983)] living in tropical, subtropical and temperate areas.

(a) The transmission capability of American *Amblyomma* species

Our knowledge on this point is derived from studies by Uilenberg, who was the first to point out the possible danger of extension of heartwater to the mainland by indigenous vectors. The results of his experimental work, carried out with several *Cowdria* strains including one strain (Gardel) isolated in Guadeloupe, are summarized in Table 6.

Out of 5 American *Amblyomma* species tested, 2 proved to be vectors experimentally, namely *Amblyomma maculatum* and *A. cajennense*, the former being more efficient than the latter. A potential danger therefore exists. However, these 2 *Amblyomma* species of the Western Hemisphere appear to be less effective as vectors than African ones. Thus it is not at all certain that the disease could maintain itself and be spread by indigenous ticks, particularly *A. cajennense*, which appears to be a poor vector (Uilenberg *et al.*, 1985). Further experiments are necessary to define more precisely the potential role of the above species and that of any other species with a suitable biology.

(b) Biological and ecological characteristics of African vectors of heartwater

These data, brought together by Morel (1969), Uilenberg (1983a), Walker (1987) and Petney, Horak & Rechav (1987), are useful to define the characteristics which appear to be important for the transmission of heartwater, and thus identify American species of *Amblyomma* that could be involved.

We can formulate a set of rules that govern the effectiveness of vectors of heartwater:

TABLE 6 Results of transmission experiments with *Amblyomma* of the Western Hemisphere

Tick species	Tick strain	*Cowdria* strain	Passage	Transmission	Reference
A. variegatum	Togo & Tanzania	Nigeria	L-N	+	1
	Togo & Tanzania	Ball. 3	L-N	−	1
	Guadeloupe	Gardel	L-N	+	3
	Guadeloupe	Gardel	L-(N)-A	+	3
A. maculatum	Texas	Zeerust	L-N	+	1
	Texas	Nigeria	L-N	+	1
	Texas	Gardel	L-N	+	3
	Texas	Zeerust	L-(N)-A	+	1
	Texas	Nigeria	L-(N)-A	−	1
	Texas	Gardel	L-(N)-A	−	3
	Texas	Gardel	N-A	−	3
A. cajennense	Mexico	Zeerust	L-N	−	1
	Mexico	Zeerust	L-N	−	1
	Mexico	Umm Baneim	L-N	+	2
	Mexico	Gardel	L-N	−	3
	Mexico	Gardel	L-N	−	3
	Mexico	Umm Baneim	L-(N)-A	−	2
	Mexico	Umm Baneim	N-A	−	2
	Mexico	Gardel	N-A	−	3
A. imitator	Mexico	Gardel	L-N	−	3
	Mexico	Gardel	L-N	−	3
	Mexico	Gardel	N-A	−	3
A. americanum	Texas	Nigeria	L-N	−	1
	Texas	Ball 3	L-N	−	1
	Texas	Zeerust	L-N	−	1
	Texas	Gardel	L-N	−	3
	Texas	Gardel	L-N	−	3
	Texas	Gardel	N-A	−	3
A. neumanni	Argentina	Gardel	L-N	−	3
	Argentina	Gardel	N-A	−	3

1. Uilenberg, 1982
2. Uilenberg, 1983a, b
3. Uilenberg *et al.*, 1985

L = larvae
N = nymphs
A = adults

- Only *Amblyomma* ticks are known to be involved.
- Those best adapted to ruminants, which feed commonly in at least 2 stages on susceptible domestic hosts, are the most effective.
- Ticks of open habitats are more likely to be vectors than ticks of forest habitats.
- Among suitable vectors, those having the widest distribution are the most effective.
- The situation with regard to tick vectors is susceptible to change with ecological modifications such as deforestation and replacement of large wild animals by domestic ruminants.

(c) American *Amblyomma* species with the biological characteristics necessary for vectors of heartwater

1. *Host specificity*

Because of the natural relative scarcity of wild ruminants in the Western Hemisphere, no *Amblyomma* species have specifically evolved on these hosts. The 2 subgenera best represented on mammals in the New World are *Amblyomma* and *Anastosiella*. The first subgenus evolved primarily on large rodents, Edentata, tapirs and peccary and the second on Carnivora. None is essentially adapted to ruminants, except possibly 2 species of *Anastosiella, Amblyomma (Anastosiella) parvitarsum* and *Amblyomma (Anastosiella) neumanni* which are more specific for llama and vicugna on plateaux and mountain habitats with Andino-Patagonic and Chaco Serrano vegetation (Morel, unpublished data, 1986). However, some species are either sufficiently ubiquitous to have a wide host range, including ruminants, or sufficiently flexible in their ecological requirements to infest, particularly in marginal habitats, species not normally included in their host range.

At this point, it should be noted that some *Amblyomma* species have been well-studied, while the biology of others remains obscure, especially concerning the hosts of the immature stages. Until it has been demonstrated that the immatures of these latter species do not infest ruminants, these ticks have to be considered potential vectors.

The diversity of hosts and tick species does not allow a detailed discussion of all of them.

As shown in Table 7, 4 species that infest ruminants frequently in all developmental stages, *A. neumanni, A. cajennense, A. maculatum* and *Amblyomma americanum,* have the characteristics of suitable vectors. *A. neumanni,* primarily a parasite of llamas, appears to be the best adapted to cattle at all stages (Guglielmone & Hadani, 1981, 1982). *A. maculatum* and *A. americanum* have a wide host range in the immature stage (coyote, fox, dog, racoon, rodents, lagomorphs, ground birds) and in the adult stage (coyote, fox, dog) and are found in all stages of development on *Odocoileus* deer (Cooley & Kohls, 1944; Brennan, 1945; Bishopp & Trembley, 1945; Hair & Howell, 1970; Clymer, Howell & Hair, 1970; Lancaster, 1973; Cooney & Burgdorfer, 1974; Patrick & Hair, 1977; Garnett & Ahrens, 1979) and also on cattle, goats and sheep (Bishopp & Hixon, 1936; Hixon, 1940; Cooley & Kohls, 1944; Hoffman, 1962; Lancaster, 1973; Semtner & Hair, 1973a; Barnard, 1981; Barnard, Jones & Rogers, 1982; Diaz Lopez, 1983; Goddard & Norment, 1985).

A. cajennense has a very wide host range, due partly to its wide distribution and presence in regions supporting a greater variety of possible hosts. Most of its hosts are wild, non-susceptible animals, but deer (*Odocoileus, Mazama*) and particularly domestic ruminants are also often parasitized, especially in regions where wildlife is scarce or absent (Cuba, Jamaica). Many authors have

TABLE 7 Degree of specificity for ruminant hosts of *Amblyomma* of the Western Hemisphere

Amblyomma species	Subgenus	Experimental transmission	Immature stages ( ) usual hosts	Adult stages ( ) usual hosts
			Most on ruminants	*Most* on ruminants
A. variegatum	Xi	+	(goat, cattle)	(cattle)
A. neumanni	An	–	(llama, cattle)	(llama, cattle, peccary)
			Numerous on ruminants	*Numerous* on ruminants
A. cajennense	Am	+	(cattle, deer, peccary)	(cattle, deer, peccary)
			Some on ruminants	*Numerous* on ruminants
A. maculatum	An	+	(birds, rodents, cattle)	(cattle, deer, carnivora)
A. americanum	Am	–	(rodents, carnivora, cattle)	(cattle, deer, carnivora)
			Few on ruminants	*Some* on ruminants
A. parvum	Ad		(rodents, carnivora, cattle)	(carnivora, armadillo, cattle)
			Not on ruminants or hosts poorly known or uknown	*Some* on ruminants
A. tigrinum	An		rodents?	(carnivora, rodents, cattle)
A. triste	An		?	(carnivora)
A. ovale	An		(rodents, tapir)	(carnivora, tapir)
A. parvitarsum	An		?	(llama, cattle)
A. inornatum	Ad		(rodents, ground birds, armadillo)	(carnivora, rodents, armadillo, peccary)
A. coelebs	Am		(armadillo)	(rodents, tapir)
A. incisum	Am		(rodents)	(tapir, deer)
A. oblongoguttatum	Am		?	(tapir, peccary, deer)
A. imitator	Am		?	(peccary, carnivora)

(Subgenus: Xi = *Xiphiastor*, An = *Anastosiella;* Am = *Amblyomma;* Ad = *Adenopleura*
From P. C. Morel, unpublished data, 1986)

pointed out the role of domestic ruminants in the life cycle of *A. cajennense* (Newstead, 1910; Cooley & Kohls, 1944; Floch & Fauran, 1958; Hoffmann, 1962; Fairchild, Kohls & Tipton, 1966; Prieto, 1974; Prieto & Delgado, 1975; Smith, 1975; Guglielmone & Hadani, 1982; Serra Freire, 1982; Diaz Lopez, 1983).

Finally another species, *Amblyomma parvum,* has been found on cattle in its immature stages (Guglielmone & Hadani, 1980, 1982). These authors and Aragão (1936), Fairchild *et al.* (1966) and Diaz Lopez (1983) recorded adults on deer and cattle.

Of the last 9 species in Table 7, the adults can infest ruminants but the immature stages have not been reported on these animals, or their hosts are not known. More studies on the hosts of these ticks are needed, before excluding them from the list of potential vectors.

2. *Habitats*

The habitats of the ticks listed have rarely been described except for the North American species.

A. americanum has received special attention because of its importance as a vector of human Rocky Mountain spotted fever and the possibilities of control by modification of the vegetation cover. This tick is primarily a species of wooded pastures and forests with dense underbrush. Grassy and herbaceous areas in open fields are less favoured than woody areas (Bishopp & Trembley, 1945; Hair & Howell, 1970; Semtner, Barker & Hair, 1971; Semtner & Hair, 1973b; Lancaster, 1973; Mount, 1981).

A. maculatum lives in grasslands with scattered clumps of trees or shrubs in patches within the prairies (Hooker, Bishopp & Wood, 1912; Bishopp & Hixon, 1936; Semtner & Hair, 1973a; Fleetwood & Teel, 1983). *Amblyomma tigrinum* has the same habitat in Paraguay (Morel, unpublished data, 1986).

A. cajennense is encountered in widely different biotopes and shows a great adaptability to a wide variety of ecological zones, from savannah open grasslands covered with tall grasses to equatorial forest with dense tree shade and sparse undergrowth (Newstead, 1910; Prieto, 1974; Smith, 1975; Guglielmone & Hadani, 1982; Diaz Lopez, 1983).

A. neumanni and *A. parvum* have been studied in Argentina (Guglielmone & Hadani, 1982), and the latter species also in Panama (Fairchild *et al.*, 1966). They are found in xerophilic forests more or less modified by grazing and forest exploitation, and in mountain steppes.

There is insufficient precise information on other potential vectors but, considering their host range, it can be assumed that most of them are adapted to forest habitats.

It can be deduced from their preferred habitats that most of the American *Amblyomma* species are dependent on woody ecosystems, even if some of them, especially *A. cajennense* and perhaps also *A. neumanni,* and to a lesser extent *A. americanum,* live in open habitats or on forest edges where they can feed on domestic animals.

However, like some African *Amblyomma* species, some of the American species which evolved with non-susceptible hosts, or are restricted to remote habitats, may adapt to susceptible domestic animals where pastures and livestock are extended at the expense of the forest.

3. *Distribution*

The most important potential vectors are those having the widest distribution.

A. cajennense (Fig. 4) is the most widely distributed *Amblyomma* species of the Western Hemisphere (Fig. 4) as it occurs from southern Texas through the Caribbean and Central America, as far south as Buenos Aires (Neumann, 1899, 1911; Newstead, 1910; Cooley & Kohls, 1944; Bishopp & Trembley, 1945; Floch & Fauran, 1958; Aitken, Omardeen & Gilkes, 1958; Fairchild *et al.*, 1966; Jones, Clifford, Keirans & Kohls, 1972; Guglielmone & Hadani, 1982). It is considered the 2nd species of economic importance in Latin America (Luque, 1978).

Some of the other species are fairly limited in their distribution. *A. neumanni, A. parvitarsum* and *Amblyomma triste,* for instance, are confined to the north of Argentina and Uruguay (Boero, 1957; Guglielmone & Hadani, 1981, 1982). The latter species is also, but in our opinion doubtfully, reported from Mexico by Diaz Lopez (1983). *Amblyomma inornatum* (Eads & Borom,

FIG. 4 Distribution of *A. cajennense*

FIG. 5 Distribution of *A. maculatum*

1975; Gladney, Dawkins & Price, 1977; Diaz Lopez, 1983) and *Amblyomma imitator* (Kohls, 1958; Diaz Lopes, 1983) are restricted to the Gulf Coast on both sides of the United States-Mexican border, and in the Yucatan in the south for the latter species.

Between these 2 extremes other ticks have a fairly wide range:

A. americanum: North America as far as Maine and northern Central America (Neumann, 1911; Cooley & Kohls, 1944; Bishopp & Trembley, 1945; Hair & Howell, 1970; Lancaster, 1973).

A. maculatum (Fig. 5): southern and central North America and Central America to Colombia and Venezuela (Cooley & Kohls, 1944; Bishopp & Trembley, 1945; Jones *et al.*, 1972; Lancaster, 1973). This tick, which has extended to the north-east in central North America (Semtner & Hair, 1973a; Goddard & Norment, 1983, 1985) and to the north along the Atlantic coast (Anderson & Magnarelli, 1980), has often been confused with *A. tigrinum*, its relative in the southern subcontinent (Kohls, 1956).

A. tigrinum occurs from Venezuela and Colombia to Argentina (Neumann, 1899; Floch & Fauran, 1958; Jones *et al.*, 1972; Guglielmone, Mangold & Hadani, 1982), where it has a similar distribution to that of *A. incisum* (Aragão, 1911; Floch & Fauran, 1958).

Most of the other species are nearly as widespread as *A. cajennense*, occurring in Central and South America, for instance *Amblyomma coelebs*, *Amblyomma oblongoguttatum*, *A. parvum* and *Amblyomma ovale* (Aragão, 1935, 1936; Boero & Prosen, 1955, cited by Floch & Fauran, 1958; Hoffmann, 1962; Fairchild *et al.*, 1966; Jones *et al.*, 1972; Evans, 1978; Guglielmone & Hadani, 1982; Diaz Lopez, 1983). The last mentioned species also occurs in the southern Caribbean, in Grenada (Nellis & Everard, 1983) and Trinidad (Morel, 1966; Nellis & Everard, 1983).

TABLE 8 Features of American *Amblyomma* species favourable for the spread of heartwater

	Experimental transmission	Infestation of ruminants	Open habitats	Wide distribution	On migratory routes	
					South	North
A. neumanni	−	++	++	+	+	−
A. cajennense	+	++	++	+++	++	+
A. maculatum	++	++	++	++	+	++
A. americanum	−	++	+	++	−	++
A. parvum		+	++	+++	++	−
A. tigrinum		±		++	++	−
A. triste		±		+	+	−
A. coelebs		±		+++	++	−
A. ovale		±		+++	++	−
A. incisum		±		++	+	−
A. imitator	−	±		+	−	−
A. inornatum		±		+	−	−
A. oblongoguttatum		±		+++	++	−
A. parvitarsum		±		+	+	−

If we postulate an introduction of heartwater by birds, ticks on the southern route of migration in Venezuela, Guyana and Brazil and those present on the northern route in Florida and along the North American Atlantic Coast are more likely to be involved in transmission.

The more efficient vectors should not only be capable of transmitting *Cowdria* but should also combine the biological and ecological characteristics necessary for achieving transmission under natural conditions. Table 8 is an attempt to summarize the importance of each American *Amblyomma* species as regards its potential role in the transmission of the disease. It can be seen that, in addition to its ability to transmit the disease experimentally, *A. maculatum* is also quite well adapted to ruminants, and capable both of establishing itself in habitats where it can find susceptible hosts and of spreading the disease to quite a large region. However, the southward migratory route that crosses the Caribbean is considerably more frequented by birds than the northward one [birds go north mainly via Central America (Pinchon, 1976)], and *A. maculatum* has a very limited distribution in South America (Jones *et al.*, 1972). Consequently the establishment and extension of the disease on the mainland is more likely to occur by means of its introduction with infected domestic animals from the Caribbean than with migratory birds carrying infected ticks.

A. cajennense, which is abundant on the mainland south of the Caribbean, could be more dangerous and take over the role of a vector, after ticks brought by birds from the Caribbean introduced the infection, but it seems to be a poor experimental vector. Other species are either not experimental vectors (*A. americanum*, *A. neumanni*) or, as far as we know, do not have the biological characteristics necessary to ensure transmission. They may hardly be concerned in the epidemiological process.

B. POSSIBILITIES OF SPREAD WITH AN EXOTIC VECTOR

Even though only some of the 3 developmental stages of *Amblyomma* can introduce the disease, a population can become established at any stage if the adults can meet and mate. However, in the *A. variegatum* strain introduced into Puerto Rico in 1974, 20 % of the female ticks can reproduce by parthenogenesis (Garris, 1984). The hazard of not meeting with another adult would thus be avoided for the pioneer population, consequently increasing the likelihood of establishment.

1. *Introduction of* A. variegatum

Observations have been made on specimens of *A. variegatum* recovered erratically from areas outside its normal range such as Guatemala, Surinam, French Guyana, Venezuela (Neumann, 1899; Maldona Capriles & Medina-Gaud, 1977), United States (Wilson & Richard, 1984), France (Lamontellerie, 1954), Italy (Albanese, Bruno-Smiraglia & Lavagnino, 1971), Bulgaria (V. Levy, cited by Kaiser, Hoogstraal & Watson, 1974), Turkey (Mimioglu & Yarer, 1961) and Israel (Tsafrir & Rauchbach, 1973). Hoogstraal, Traylor, Gaber, Malakatis, Guindy & Helmy (1964) and Kaiser & Hoogstraal (1974), who found immature *A. variegatum* on migrating pipits (*Anthus* sp.) in Egypt and Cyprus, believe that migrating birds are important disseminators of ticks and arboviruses.

So far as the Caribbean region is concerned we have pointed out the potential role of the cattle egret, of which individuals were found carrying as many as 104 larvae and nymphs of *A. variegatum*. Sedentary wild mammals or birds are not involved in tick dissemination, but domestic animals are often heavily infested [maxima of 2 603, 641 and 610 ticks on goats, cattle and dogs respectively in our survey (Barré *et al.*, in press)]. These

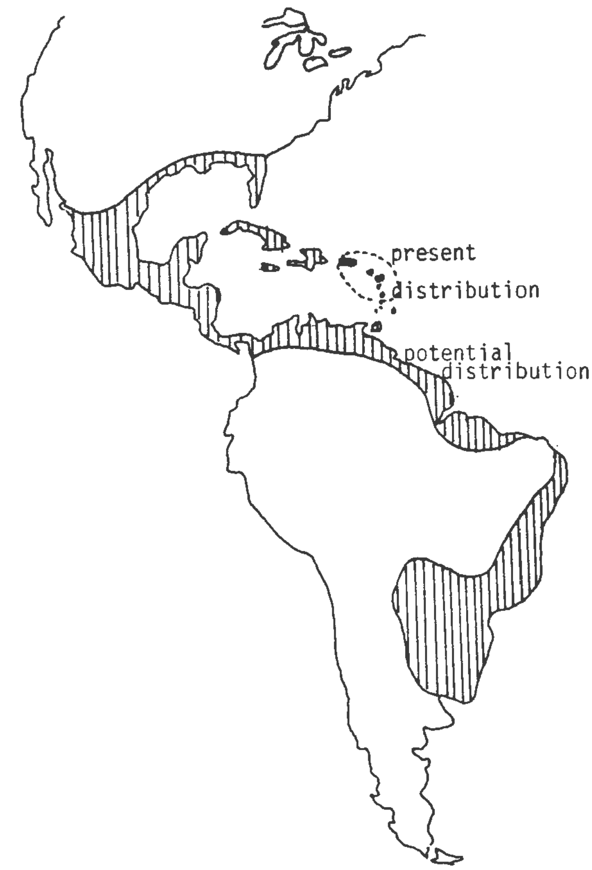

FIG. 6 Present and potential distribution of *A. variegatum* in the Western Hemisphere (USAID *et al.*, 1986 adapted from Sutherst & Maywald, 1985)

animals present a much more serious threat of creating a viable surviving population, particularly with engorged females, if they are introduced in new areas. Infestation of most of the islands of the Lesser and Greater Caribbean is certainly due to movement of livestock as we have observed in 1982 for Desirade Island (Uilenberg *et al.*, 1984).

The wind is also a possible method of transporting ticks, particularly the larvae. Part of the tick fauna of Cuba has been brought from the mainland by aerial and marine currents (De la Cruz, 1978).

2. *Establishment and extension of* A. variegatum

This fairly ubiquitous species has invaded many regions of the tropical zone outside its normal distribution, such as Madagascar, the Mascareignes, the Caribbean area (Neumann, 1899) and the Arabian peninsula (Hoogstraal & Kaiser, 1959). Environmental conditions, among which temperature and humidity appear to be the most crucial parameters, must be favourable to the accomplishment of its life cycle. Based on vegetation type and satellite imagery, Hugh-Jones & O'Neill (1986) successfully characterized the distribution of *A. variegatum* in St Lucia. Using an ecoclimatic index integrating biological data and geographical distribution, Sutherst & Maywald (1985) predicted the suitability of areas all over the world for some tick species, including *A. variegatum* (Fig. 6). This species would find favourable conditions in the Greater Antilles, Florida and other parts of the southern United States, Central America, Venezuela and Brazil from the north-east, to the Parana basin in Uruguay, Argentina and Paraguay. In our opinion, this tick could also become established in the coastal savannahs of French Guyana and probably also in the humid woody savannahs of the Mato Grosso plateau, where there is an important livestock population.

As in Africa, Madagascar, the Mascareignes and the Caribbean, *A. variegatum* would be a very efficient vector of the disease on the mainland, certainly more efficient than any indigenous *Amblyomma* species.

Furthermore, as in the multivectorial cycle in Africa, an epidemiological cycle with *A. variegatum* on the American mainland could be extended to a cycle among indigenous *Amblyomma* species.

CONCLUSION

The danger of the establishment of heartwater on the mainland from the Caribbean focus is a serious possibility which has to be prevented. The more animals infected and vectors in the focus, and the wider the infected and infested area, the greater the danger of propagation of the disease and the tick vector. From this point of view, tick control in all infested islands is beneficial. Strategy must be based on the protection of areas not yet contaminated by the disease and the vector. Restrictions on the movements of domestic animals from the Caribbean and African foci need to be enforced. Translocation of ruminants from areas where *A. variegatum* is present but heartwater is absent, and movements of non-susceptible animals from the heartwater focus or from the *A. variegatum* focus, should be authorized only if these animals are subject to an efficient acaricidal treatment. Susceptible animals from the heartwater focus should not be introduced into areas where *Amblyomma* ticks are established. They may be in the incubation phase of the disease, or recovered and immune, but in the latter case they can relapse and develop a rickettsaemia.

Finally, the most drastic and efficient way to end the risk of dissemination of the disease is to eradicate the disease in the focus by eradicating, if it is possible, its tick vector.

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