Arch Virol (1990) [Suppl 1]: 303–322

Ecology of ticks as potential vectors of Crimean-Congo hemorrhagic fever virus in Senegal: epidemiological implications

J.-L. Camicas[1], M. L. Wilson[2,3], J.-P. Cornet[1], J.-P. Digoutte[2], M.-A. Calvo[2], F. Adam[1], and J.-P. Gonzalez[1,2]

[1]Institut Francais de Recherche Scientifique pour le Developpement en Cooperation (ORSTOM), Laboratoire ORSTOM de Zoologie medicale, Dakar
[2]Institut Pasteur, Dakar, Senegal
[3]Departments of Population Sciences and Tropical Public Health, Harvard School of Public Health, Boston, Massachusetts, U.S.A.

Accepted February 8, 1990

Summary. At least 30 tick species from 7 genera have been found naturally infected with Crimean-Congo hemorrhagic fever (CCHF) virus worldwide. To this list we add *Rhipicephalus guilhoni.* In the sub-saharan Africa, 17 tick species have been implicated as vectors, of which 12 are present in Senegambia or Mauritania. We studied the five principal species that appear to be the most important in CCHF virus transmission in Senegal, namely *Amblyomma variegatum, Hyalomma impeltatum, H. marginatum rufipes, H. truncatum,* and *Rhipicephalus guilhoni.* We report on the distribution, host associations, seasonal activity patterns and CCHF virus infection of these ticks, as well as the epidemiological implications for human disease. Despite similarities in ecological characteristics, not all of these species are equally likely to be important in the transmission cycle. The most important vectors in enzootic and epidemic transmission throughout Senegal appear to be *Hyalomma truncatum* and *Amblyomma variegatum.*

Introduction

The geographic distribution of Crimean-Congo hemorrhagic fever (CCHF) is astonishingly large for an arboviral zoonosis and includes most of Africa, southern Eurasia, southern Europe, and the Middle East [10]. CCHF virus transmission occurs in ecologically diverse sites of at least 30 different countries in the palearctic, oriental, and afrotropical biogeographic regions

[10, 23]. Equally astonishing is the number and diversity of ticks from which this virus has been isolated. Nearly 30 species from seven genera have been shown to be naturally infected [23]. It is precisely such diversity of potential vectors that represents a major obstacle to our understanding both of the ecology of CCHF virus and of the epidemiology of human outbreaks. In most settings, little is known about the important vector species and the conditions under which enzootic transmission is maintained. Which of these or other ticks are active in epizootic or epidemic transmission? What do the feeding patterns of the three stages of each tick species imply for vertebrate hosts of the virus? Which species competently transmit virus transovarially, transstadially and horizontally? Which tick stages and species can transmit the virus to humans? The diversity of tick species and stages that have been found infected in various faunal regions and habitats poses a formidable task for studies on CCHF virus transmission.

One common denominator appears to be the presence of *Hyalomma* spp. ticks. Despite CCHF virus isolations from numerous species of seven genera, active transmission has been most often linked to one or another species of *Hyalomma* ticks. Evidence of CCHF virus transmission is found only where these ticks are present, and epizootic or epidemic transmission corresponds with periods of increased abundance of *Hyalomma* spp. [23]. Conversely, enzootic transmission may be feeble or nonexistent where vector tick abundance is minimal or nil. However, this global relationship between tick species diversity and the magnitude of CCHF virus transmission has not been systematically studied within a defined geographic region.

Study sites and methods

In sub-saharan West Africa, CCHF virus has been isolated from ticks, domestic and wild vertebrates, and humans in Senegal, Mauritania, and Burkina Faso [3, 16–18]. This region of large ecological diversity is situated in a zone of transition between the Sahara desert in the north and rainforests in the south; the biota changes dramatically from north to south primarily in association with increasing rainfall. Annual precipitation, averaging 200–300 mm annually in the northern sahelian zone, is five times greater in the southern sudano-guinean and sub-guinean zones. The diversity and abundance of ixodid ticks is also varied [3, 6–8]. In this study, we analyse the potential of these ticks as vectors of CCHF virus in these zones and attempt to synthesize the ecological and epidemiological implications of these findings to determine risk of human infection.

Our analysis is based on experience and studies spanning nearly two decades. During this period, casual observations of host associations and CCHF virus infection have been increasingly directed toward systematic field observations of tick population dynamics, tick feeding patterns, and CCHF virus transmission cycles. In addition to anecdotal observations, we report on regular samples of domestic animals and wild rodents from the Senegal study sites in the villages of Bandia, Dahra, and Yonofere (Fig. 1). Many of our results and conclusions should be applicable to ecologically similar sites throughout the region.

Potential vector ticks

Worldwide CCHF virus infection of ticks

A total of 30 species of ticks (Acari: Ixodidae), have been found naturally infected with CCHF virus, including 28 species of ixodids ("hard" ticks) and 2 of argasids ("soft" ticks) [10, 19, 23]. The 28 ixodid species are distributed among 7 genera as follows: 11 *Hyalomma*, 8 *Rhipicephalus*, 4 *Boophilus*, 2 *Dermacentor*, 1 *Amblyomma*, 1 *Haemaphysalis*, and 1 *Ixodes* (Table 1). The 2 species of argasids belong to the genera *Argas* and *Alveonasus* (a subgenus of *Ornithodoros* for some taxonomists). The relevance of infection in these latter two "soft" ticks recently has been questioned by the experimental work of Shepherd et al. [19], who demonstrated CCHF virus replication in numerous ixodids, but could not show replication in 3 Argasina infected by intracoelomic inoculation. They concluded that strains obtained from the two argasid ticks may be merely surviving virus from recent viremic blood-meals, as was probably the case in the isolation from *A. lahorensis* [20]. Thus, CCHF virus appears to be primarily a virus transmitted by hard ticks (Ixodidae).

The biogeographic diversity of CCHF virus-infected ticks is striking. Five Ixodidae belong to the oriental biogeographical region, 17 ixodids and the 2 argasids to the palearctic region, and 18 or 19 ixodids plus 1 argasid are found infected in sub-saharan Africa. Note that the total is greater than 30, because some species are found in several faunal regions.

Infected ticks in Senegambia and Mauritania

Of the 17 ixodids implicated in published reports as potential vectors from sub-saharan Africa, (18 if *H. anatolicum anatolicum*, which may have been introduced into Nigeria, is included), 12 (13?) are present in Senegambia or Mauritania. Among these, 7 have been found naturally infected [3, 15, 18]. These include *Amblyomma variegatum*, *Boophilus decoloratus*, *B. geigyi*, *Hyalomma impeltatum*, *H. impressum*, *H. marginatum rufipes*, *H. truncatum*. To this list we add an eighth potential vector, *Rhipicephalus guilhoni* Morel & Vassiliades, 1963, from which CCHF virus was isolated in August, 1988 (Table 1). That isolation was made from a pool of 20 male *R. guilhoni* removed from sheep in Yonofere, Senegal (Fig. 1). The identity of the virus was confirmed at the WHO Collaborating Center for Arboviruses at the Pasteur Institute in Dakar. Thus, there is a total of 8 tick species from which CCHF virus has been isolated in Senegal or Mauritania (Table 1).

Other potential vectors that have been shown to be infected in other areas, and that exist in this region include *B. annulatus*, *H. dromedarii*, *H. nitidum*, *R. evertsi evertsi* and *R. sanguineus*. However, the low population densities of these species or the peculiarities of their feeding ecology suggest

Table 1. Potential vectors of CCHF virus in relation to geographic region

Genus, species	Pal	Ori	Afr	Sen
Hyalomma				
H. anatolicum anatolicum	○	○	+?	
H. asiaticum	○			
H. detritum	○			
H. dromedarii	○	+	+	+
H. impeltatum	+		○	○
H. impressum			○	○
H. marginatum marginatum	○	+		
H. marginatum rufipes			○	○
H. marginatum turanicum	○		+	
H. nitidum			○	+
H. truncatum			○	○
Rhipicephalus				
R. appendiculatus			○	
R. bursa	○			
R. evertsi evertsi			○	+
R. guilhoni			○	○
R. pulchellus			○	
R. pumilio	○			
R. rossicus	○			
R. sanguineus	○	+	+	+
R. turanicus	○		+	+?
Boophilus				
B. annulatus	○		+	+
B. decoloratus			○	○
B. geigyi			○	○
B. microplus		○	+	
Dermacentor				
D. daghestanicus	○			
D. marginatus	○			
Amblyomma				
A. variegatum			○	○
Haemaphysalis				
H. punctata	○			
Ixodes				
Ixodes ricinus	○			

Pal Palearctic region
Ori Oriental region
Afr Afrotropical region
Sen Senegal
\+ Tick species present
○ Tick species present and naturally infected

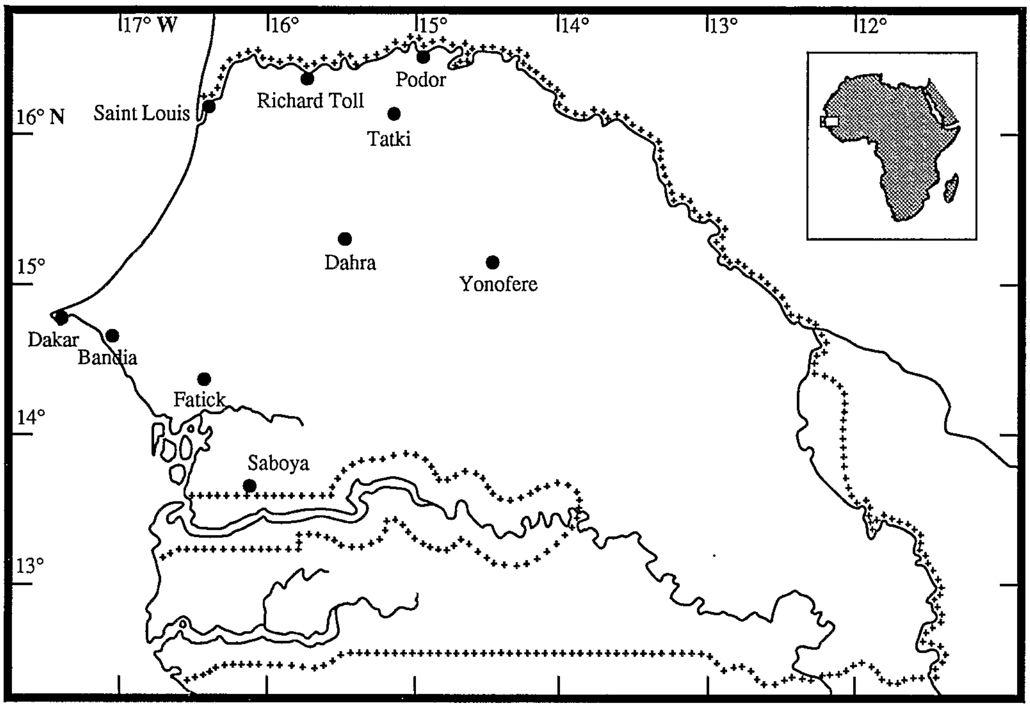
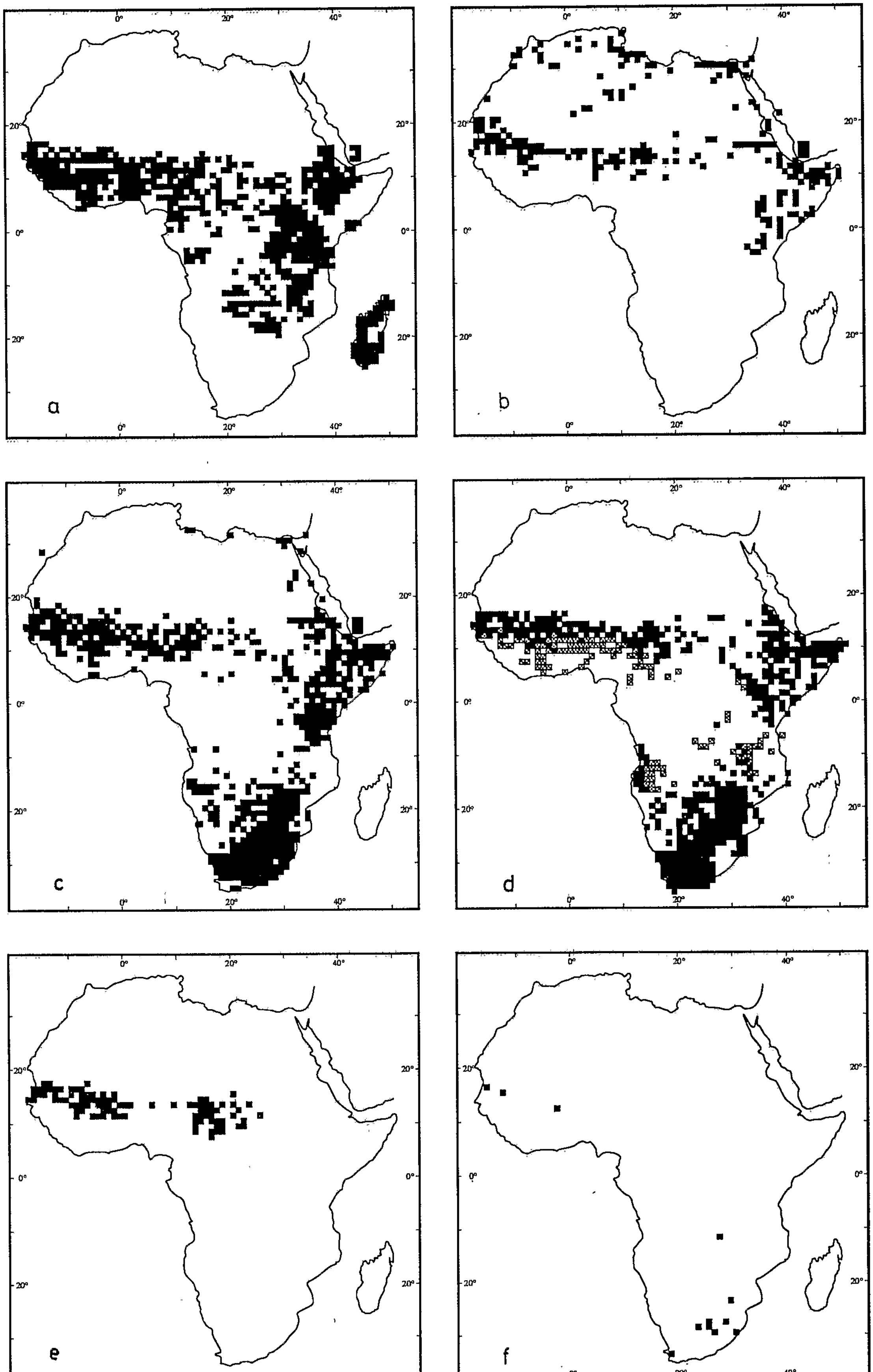


Fig. 1. Map of Senegal indicating major villages and the 3 sites (Bandia, Dahra and Yonofere) in which studies were done

that they are unlikely to play an important epidemiological role in the transmission of CCHF virus. The possibility that *R. sanguineus*, which typically infests canids, may be involved in a domestic cycle involving dogs remains to be ascertained. Thus, we consider there are five principal species (*A. variegatum*, *H. impeltatum*, *H. marginatum rufipes*, *H. truncatum*, and *R. guilhoni*) that are likely to be involved in either enzootic or epizootic transmission of CCHF virus because of their widespread distributions or relative densities.

For each of these ticks, we have analysed ecological factors that influence their potential as vectors of CCHF virus in Senegal, namely their distribution, host associations, and seasonal activity pattern. The classification scheme of Morel [13] has been employed to characterize the feeding ecology of ixodid ticks in terms of the types of hosts that larvae, nymphs, and adults feed upon during each of the three blood-meals, and the number of different individuals utilized while feeding. Ixodid ticks are considered as either mono-, di-, or triphasic signifying that the number of different individual hosts that they feed upon is either one, two, or three. The diversity of host types (e.g., ungulates, ground feeding birds and small mammals, carnivores) that are typically fed upon is characterized by the terms mono- or bitropic which indicate one or two host types, or telotropic for tick species whose



a
b
c
d
e
f
0°
20°
40°

immature stages utilize multiple host types while the adults are host type-specific. These factors influence the population dynamics of the vector and the possibilities for horizontal transmission of CCHF virus. Discussion of the distributions and host associations of these ticks is based on studies by Camicas et al. [1–3], Gueye et al. [6–8], and our unpublished observations.

Amblyomma variegatum

Distribution

This species exists, more or less abundantly, throughout most of Senegal (Fig. 2), its northern limit being the Senegal River basin [3, 7, 8]. It is rare in northeastern Senegal, particularly far from this river. This species tends to predominate where rainfall or humidity is more abundant. For adult ticks, the principal hosts are domestic ungulates, especially cattle which are typically ten times more parasitized than small ruminants (sheep and goats). Larval and nymphal ticks are found on practically all available terrestrial vertebrates including humans [2], although they seem to prefer small ruminants.

Host associations

A. variegatum typically exhibits a triphasic feeding cycle (i.e., each of the three stages engorge on and drop from a different individual host) and a telotropic host association pattern in which immatures are not host-specific and can be found on most available vertebrates, whereas adults feed principally on domestic ungulates.

Larval *A. variegatum* may intensely parasitize a very wide variety of vertebrate hosts. A study performed at Bandia, Senegal on a herd of 10 to 20 goats from 1976 through 1980, has shown a mean of about 500 larvae per animal during November of each year (Fig. 3). Ground-feeding birds are also important hosts for larvae because of their abundance and significant parasitic load. Indeed, we have occasionally found intense infestations of tens or hundreds of larvae on birds such as the red-beaked hornbill (*Tockus erythrorhynchus*), Senegal coucal (*Centropus senegalensis*), grey-breasted helmet guinea-fowl (*Numida meleagris galeata*), double-spurred francolin (*Francolinus bicalcaratus*), and long-tailed glossy starling (*Lamprotornis*

Fig. 2. Geographic distributions of 5 potential CCHF virus vector ticks and of naturally acquired human hemorrhagic CCHF cases in Africa. Tick species include *Amblyomma variegatum* (**a**), *Hyalomma impeltatum* (**b**), *H. marginatum rufipes* (**c**), *H. truncatum* (■) (☒ *H. truncatum* and/or *H. nitidum*) (**d**), and *Rhipicephalus guilhoni* (**e**), Natural human hemorrhagic cases (**f**)

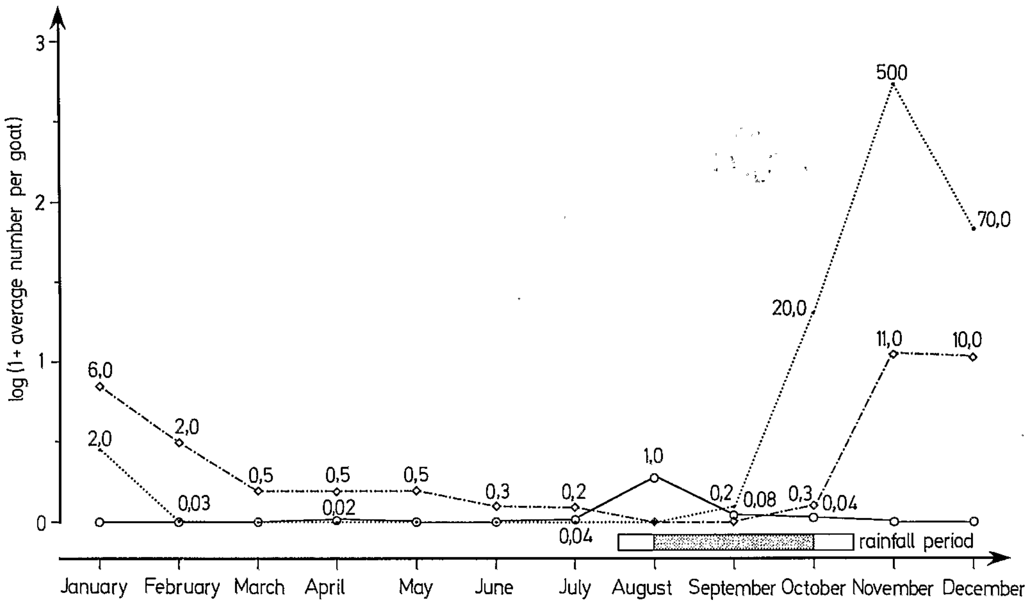


Fig. 3. Seasonal activity cycle of *Amblyomma variegatum* larvae (● · · · · ●), nymphs(◇–·–◇), and adults(○—○) at Bandia, Senegal. Average number of ticks per goat per month during 1976 through 1980. Rainy season during the 1972–86 drought (dark bar) was shorter than the typical rainy period (lighter extension)

caudatus). Several species of medium and small mammals may be heavily parasitized by *A. variegatum* larvae. Except for myomorph rodents, which are never parasitized by this tick, larvae can be found on most small mammals. We have found numerous larvae on the common jackal (*Canis aureus*), the serval (*Felis serval*), and Crawshay's hare (*Lepus crawshayi*). Primates may be parasitized, including the green monkey (*Cercopithecus aethiops sabaeus*) and the patas monkey (*Erythrocebus patas*).

Preferred hosts of nymphal *A. variegatum* are large and small ruminants, as well as large rodents, lagomorphs and primates. We have removed nymphal *A. variegatum* from the above-mentioned monkeys, hares, and the ground squirrel *Xerus erythropus*. Some birds have also been found infested.

Adult *A. variegatum* prefer ungulates, and particularly (zebu) cattle. In addition, they occasionally can be found on carnivores, especially domestic dogs. There appears to be a tendency toward monotropism on ungulates and dog.

Seasonal activity

The seasonal pattern of *A. variegatum* in Senegal indicates that it is univoltine [2]. Adults are most active on ungulates during the rainy season, typically from June or July through September and October (Fig. 3). The larval population is at its maximum just after this period, particularly in

November; larvae usually cannot be found in February and March. The nymphal activity peak follows that of larvae by about a month. Nymphs, however, do not disappear abruptly; they persist in low numbers until the next rainy season. Unlike larvae and adults, which are highly hygrophilous, nymphs of this species are much more tolerant of dryness, and are found in reduced numbers on vertebrates throughout most of the dry season.

Epidemiological implications

Because immature *A. variegatum* exhibit a strong anthropophily (personal observations of 5 people infested with a total of 129 larvae and 12 people with 14 nymphs), they may be able to transmit CCHF virus to humans. Transmission by larvae should be rather exceptional because this would have required that the larva be previously infected by transovarial transmission of the virus, an apparently rare event. Alternatively, nymphs, infected by the transtadial route from larvae fed on viremic hosts, could be important vectors to humans. Adults, emerged from nymphs infected mainly by feeding on ruminants, may transmit CCHF virus to other ungulates, thereby supporting viral circulation and amplification. These adults, however, are of no direct importance in human infection because they almost never feed on humans.

Hyalomma impeltatum

Distribution

The geographic range of *H. impeltatum* (Fig. 2) was first described by Morel [13] who noted that this tick "does not belong to the Ethiopian fauna but constitutes in Oriental and Occidental Africa a Mediterranean Palearctic component". The southern limit of the distribution of this species in coastal West Africa is at about 14° N. Adult *H. impeltatum* are abundant on cattle in northern Senegal where rainfall is low, averaging ca. 500 mm or less. This boundary extends east-southeast reaching 10° N in Mali [22] and even 9° N in Nigeria [13]. In Oriental Africa, the phytoclimatic situation is quite different and parallel bands of increasing rainfall and corresponding vegetation do not exist. There the species will be found as far south as the latitude 5° S. In Senegal, this species is rarely found at the Bandia station (14°30′ N); we found immature stages in 1967 and 1970 on *Lepus crawshayi* and again two larvae on the rodent *Arvicanthis niloticus* in 1988.

Host associations

H. impeltatum is typically pholeo-exophilic ditropic, that is, its immatures feed principally on small mammals, while adults most often infest ungulates and carnivores [13]. Specifically, the major hosts of adults are domestic ungulates, particularly zebu cattle, and to a lesser extent sheep and goats. The hosts for both larvae and nymphs appear to be similar, principally myomorph rodents of the genera *Acomys*, *Arvicanthis*, *Gerbillus*, *Psammomys*, *Jaculus*, as well as hares (*Lepus crawshayi*) and hedgehogs (*Erinaceus*) [1, 9; Morel, pers. comm.].

Seasonal activity

The seasonal population dynamics of *H. impeltatum* has been studied in Dahra (Fig. 1) where, each month, 50 randomly selected sheep were examined, 10 from each of 5 different flocks. Adults were most numerous from the beginning of January through August, showing increased activity during the dry season (Fig. 4). Interestingly, a similar study of sheep in Yonofere, about 80 km due east of Dahra (Fig. 1), indicates that this tick is rarely found there (ML Wilson, unpubl.).

Observations on immature *H. impeltatum* are scarce, although it appears that most immatures are active just after the rainy season. Except for two larvae found in mid-February 1988 in Bandia, the six other findings of immatures on rodents and hares were in November and December. Nymphal activity occurs typically a month or two following that of larvae. Perhaps those eggs that are laid during the rainy season have a greater chance of hatching. Yet larvae, nymphs and adults, which are xerophilous, are active during the dry season. Thus, it may be that members of this species reproduce one generation per year.

Epidemiological implications

H. impeltatum probably is incidental to infection of humans. Although Hoogstraal [9] mentioned that humans are fed upon by adult and immature

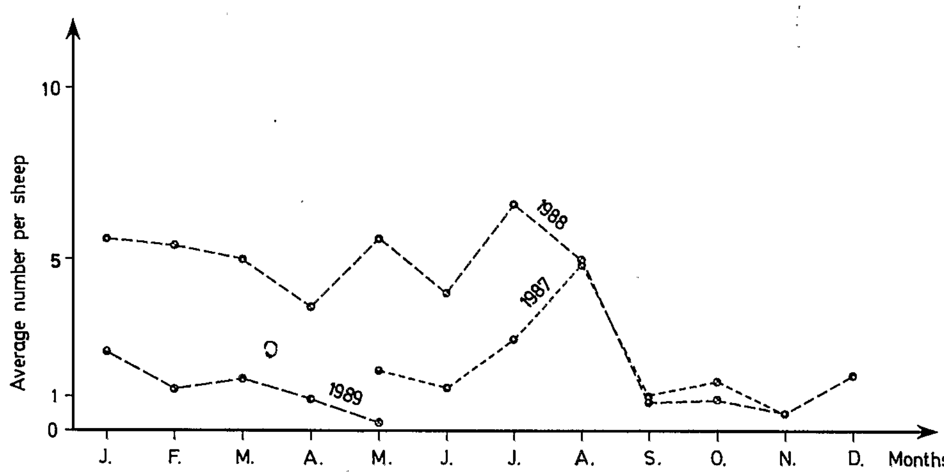


Fig. 4. Seasonal activity cycle of adult *Hyalomma impeltatum* on sheep in Dahra, Senegal. Monthly mean number of ticks from 50 randomly selected sheep (10 from each of 5 herds) examined monthly from May 1987 through May 1989

stages, we have never noticed such occurrence in Senegambia during the past two decades. Infected immature ticks may transmit CCHF virus between small mammals (rodents and lagomorphs). Larval *H. impeltatum*, however, would be able to infect small mammals only if they had been infected transovarially. Nymphs that emerge from larvae engorged on a viremic rodent may be able to infect a naive rodent. Adults that develop from infected nymphs are possible vectors, particularly to ungulates that could become infected at any point during the year, more likely during the dry season. To the extent that *H. impeltatum* adults feed on humans, transmission would occur during the period from November through June.

Hyalomma marginatum rufipes

Distribution

In his study, Morel [13] explained that "the normal habitat of the species is situated between the isohyets 150 and 750 mm of annual rainfall" (Fig. 2). *H. marginatum rufipes* disappears where annual rainfall exceeds 1250 mm, except in southern Senegal and western Guinea. In this area, despite abundant precipitation (ca. 2,000 mm per year), the seven-month long dry season apparently creates acceptable conditions. In Senegal, this tick is present nearly everywhere. Despite widespread distribution, *H. marginatum rufipes* is never very abundant, typically much less abundant than *A. variegatum* and *H. truncatum.*

Host associations

H. marginatum rufipes typically exhibits a biphasic ditropic cycle in which engorged larvae molt on the host producing nymphs that feed on the same individual; adults, however, feed on another type of host. Immatures most often parasitize birds or lagomorphs, while adults usually infest ungulates. A 1969 study showed that 23% of birds were parasitized in Bandia and 4.5% in Saboya (JL Camicas et al., unpubl.). Ground-feeding birds that are often infested by immature *H. marginatum rufipes* include Levaillant's cuckoo (*Clamator cafer*), spotted eagle-owl (*Bubo africanus*), broad-tailed roller (*Eurystomus glaucurus*), red-beaked hornbill (*Tockus erythrorhynchus*), long-tailed glossy starling (*Lamprotornis caudatus*), and the common garden bulbul (*Pycnonotus barbatus*). In addition, terrestrial monkeys (e.g., *Erythrocebus patas*), hedgehogs (*Erinaceus* [*Atelerix*] *albiventris*), and hares (*Lepus crawshayi*) have been found heavily infested. The major hosts of adults are ungulates, particularly zebu cattle.

Seasonal activity

The monthly mean number of adult *H. marginatum rufipes* on natural hosts shows little seasonality; they are present, though not abundant, throughout

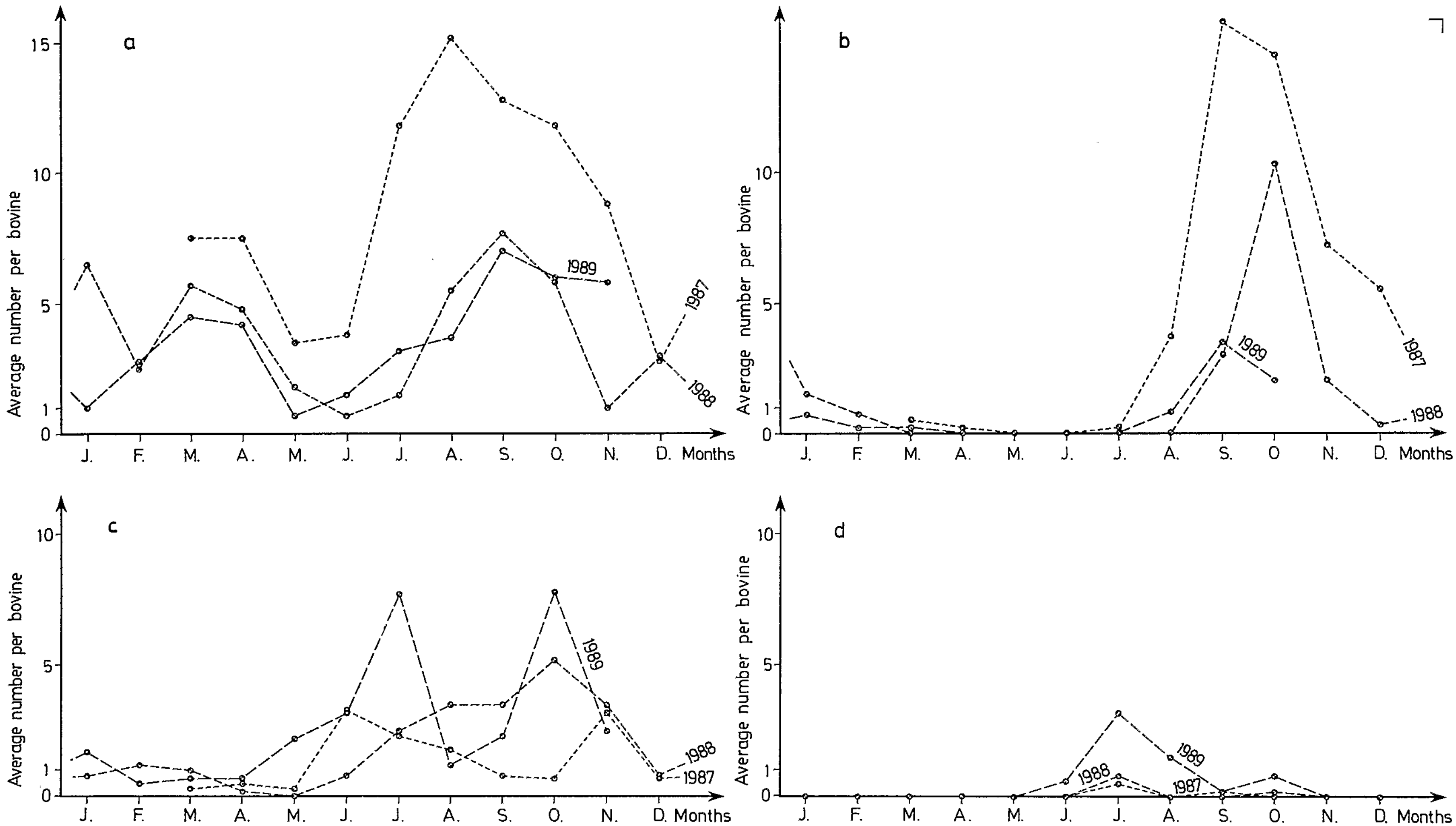


Fig. 5. Seasonal activity cycle of adult *Hyalomma truncatum* (**a**), *Rhipicephalus guilhoni* (**b**), *H. marginatum rufipes* (**c**), and *Amblyomma variegatum* (**d**) in Bandia Senegal. Monthly mean number of ticks from bovines examined three times each month from March 1987 through November 1989

the year (Fig. 5). Similarly, we have not been able to determine a seasonal pattern for immatures, either because infestation levels are low or because of annual variation in weather. Thus, it has been impossible to determine whether *H. marginatum rufipes* has one or more generations per year, or does not follow any seasonal cycle in Senegal.

Epidemiological implications

From an epidemiological point of view, the rarity of human infestation by adult *H. marginatum rufipes* suggests that this species plays a minor role in human infection. Moreover, as birds apparently are unable to develop significant viremias with CCHF virus, and as the proportion of immature ticks that feed on mammals is very small, *H. marginatum rufipes* may be of little epidemiological importance unless transovarial transmission of the virus is a frequent phenomenon.

Hyalomma truncatum

Distribution

In West Africa, *Hyalomma truncatum* is found predominantly in areas with annual rainfall between 400 and 1,000 mm, although its range extends to regions with annual precipitation ranging from 150 mm to 2,000 mm [13]. The southern boundary of the recognized distribution of this species perhaps should be revised in view of the possible confusion with *H. nitidum* Schulze, 1919, a more hygrophilous species. According to our observations, *H. nitidum* is not found in Senegal west of 13° W, whereas *H. truncatum* is found throughout the region southward to areas experiencing 1,500 mm of annual rainfall. Our observations indicate that *H. truncatum* exists throughout Senegal (Fig. 2). In the southeast *H. truncatum* coexists with *H. nitidum.* In Senegal *H. truncatum* is, by far, the most abundant and widespread member of the genus *Hyalomma.*

Host associations

H. truncatum is a species with a triphasic-ditropic cycle. Specifically, hosts of larvae tend to be ground-feeding birds, rodents, hedgehogs, and hares. The resulting nymphs typically feed on a different individual host, but these also tend to be rodents, hares and hedgehogs. The principal hosts of adult *H. truncatum* are cattle and sheep.

Seasonal activity

Our studies of *H. truncatum* infestations of cattle in Bandia suggest that they produce only one generation per year. With the first significant rains of July,

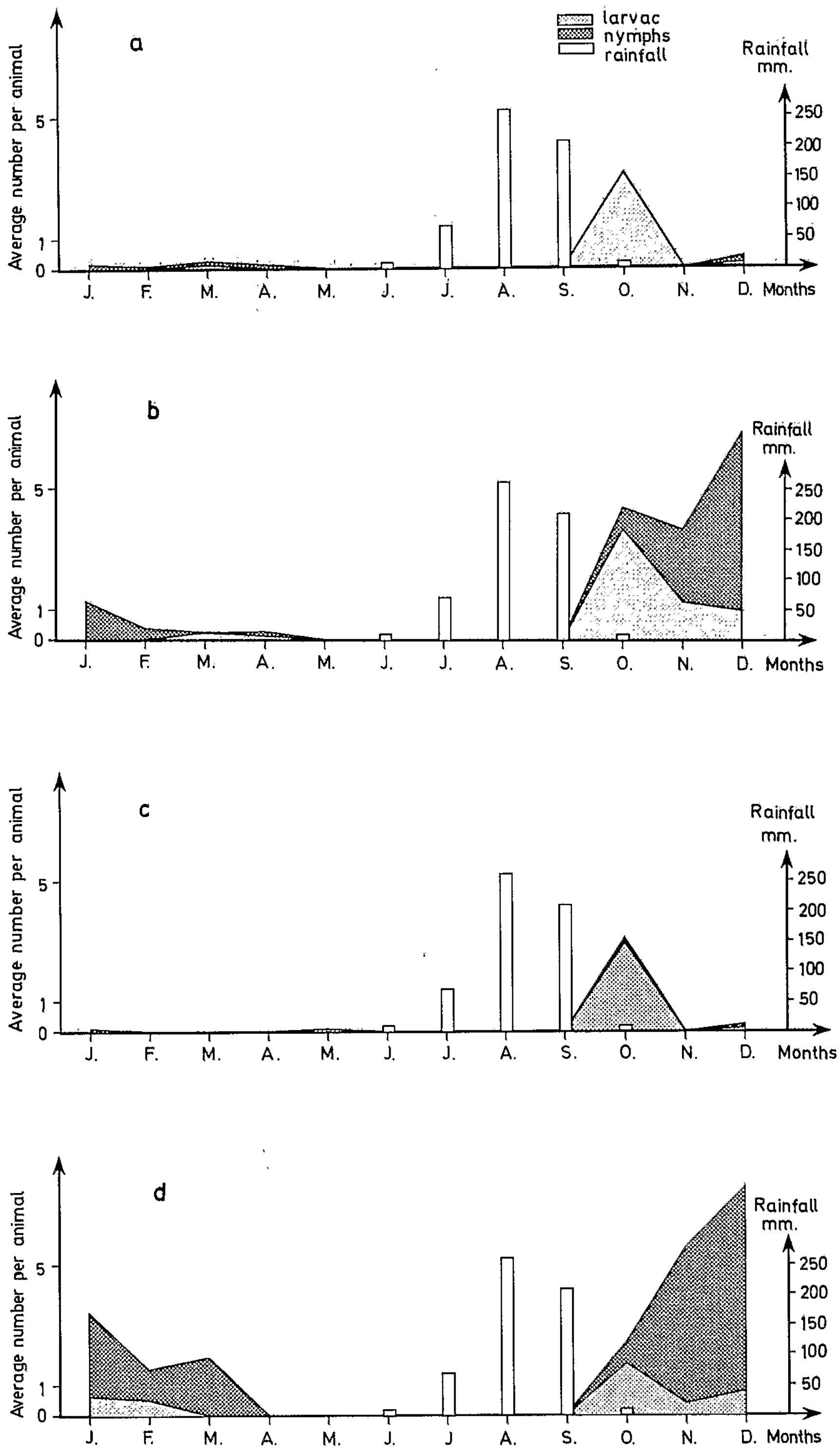


Fig. 6. Seasonal activity cycle of larval and nymphal *Hyalomma truncatum* attached to *Mastomys erythroleucus* (**a**) or *Arvicanthis niloticus* (**b**), and of *Rhipicephalus guilhoni* attached to *M. erythroleucus* (**c**) or *A. niloticus* (**d**) in Bandia, Senegal. Monthly mean number of ticks from rodents were examined monthly from March 1987 through December 1988

adults appear in large numbers and become progressively more scarce through June of the following year (Fig. 5). Parasitism of rodents, determined by holding captured rodents until all ticks have detached, indicates that larvae are in maximum abundance on these hosts in October, and nymphs in December (Fig. 6). Occasionally, we have found a few larvae in March. However, because adult *H. truncatum* feed throughout the year, it may be that engorged females produce eggs that emerge as larvae at that time. Larvae emerging in October from females engorged one or two months earlier find optimal conditions of temperature and relative humidity. Later, as the dry season progresses, the hygrometric conditions become unfavourable and probably lead to a high mortality of laid eggs or emerged larvae and nymphs. The occasional appearance of some larvae on rodents in March and April may correspond to momentarily favorable conditions due to erratic rains that can occur at this period of the year [11].

Epidemiological implications

H. truncatum may be an important vector of CCHF virus to humans in Senegal for several reasons. First, it is among the most abundant and widely distributed of potential vectors. Second, tick infection by horizontal transmission may be relatively more common because a proportion of immatures feed on small mammals that are liable to harbor CCHF virus such as *Erinaceus albiventris* [4] and *Mastomys* sp. [5]. Recent experimental results have shown that larva can be infected by feeding on viremic new-born laboratory mice, and that adults are transstadially infected and transmit virus to guinea pigs [12]. Finally, *H. truncatum* adults have been found to feed on humans (four personal observations). Our studies in Yonofere indicate a strong correlation between IgG antibodies to CCHF virus in humans and their reports of being bitten by adult *H. truncatum*, but not by adult *A. variegatum* or *Rhipicephalus guilhoni* (L. Chapman et al., unpubl.).

Rhipicephalus guilhoni

Distribution

The recognized distribution of *R. guilhoni* is limited to habitats between the isohyets of 250 mm and 750 mm annual rainfall [13] (Fig. 2). In Senegal, this species is found from the Senegal River in the North, south to 14° N. Our collections are consistent with this distribution. Our most southern findings of *R. guilhoni* are in Bandia, where this species is abundant.

Host associations

R. guilhoni shows a triphasic ditropic cycle. The major hosts of its adults are domestic ungulates, particularly cattle, sheep and goats; on goats, it is the dominant *Rhipicephalus.* Adults bite humans having close contact with ruminants (3 personal observations). The immature stages feed essentially on rodents, particularly *Arvicanthis niloticus.*

Seasonal activity

Analysis of the mean number of *R. guilhoni* on cattle and goats of Bandia provides clear evidence for the existence of only one annual generation (Fig. 5). In Bandia, May and June are the only months during which adult *R. guilhoni* are not found. They appear in small numbers after the first significant rains of July. The annual peak abundance is attained two months after the beginning of the rainy season, generally in September. This is different from *A. variegatum* and *Hyalomma* spp., which appear to increase activity immediately following the beginning of the rainy season, usually in July. Then, as with the *Hyalomma* spp., *R. guilhoni* adults are seen during much of the dry season, typically until April.

Studies of the seasonal abundance of immature *R. guilhoni* on rodents *Arvicanthis niloticus*, and *Mastomys erythroleucus* have shown a cycle nearly identical to that observed for immature *H. truncatum* (Fig. 6). For both species, maximum larval activity occurs in October; two months later, nymphs are at their maximum. Both immature stages usually disappear by April.

Epidemiological implications

R. guilhoni is implicated in the natural cycle of CCHF virus transmission in Senegal by our isolation of a strain from adults collected in 1988. The role of this species in the epidemiology of human infection may be similar to that of *H. truncatum.* Although immatures are not believed to bite humans, infected adult *R. guilhoni* may be capable of transmitting CCHF virus to humans.

Conclusions

Of the 17 African hard ticks found infected with CCHF virus, 12 are present in Senegambia or Mauritania and eight have been shown to be infected there. Yet, the widespread and focally prevalent nature of CCHF virus transmission suggests that those tick species that are neither widely distributed nor abundant are unlikely to play a role in enzootic transmission. Furthermore, the particular feeding patterns of some ticks, such as monophasic-monotropism, would limit the possibility of horizontal transmission by such species. Even those ticks that become infected but are rarely anthropophilic would not be important in transmission to humans. Thus we consider only five ticks as potential enzootic vectors.

For each of these ticks, we have compared those ecological factors that may influence their status as vectors of CCHF virus in Senegal. These factors include their population dynamics, seasonal activity, and host associations. Of the five tick vectors of potential importance in the epidemiology of CCHF in Senegal, each, with the possible exception of *H. marginatum rufipes*, has a similar population cycle of one generation per year. For *A. variegatum*, it is the adults that influence the timing of reproduction by becoming active only after the first significant rains (July); adult *A. variegatum* disappear with the beginning of the dry season (November). For *H. impeltatum*, *H. truncatum*, and *R. guilhoni*, adults, which are more xerophilous, engorge on ruminants during the first half of the dry season. Climatic conditions following the end of the rainy season (October–December) permit development of these species during this period. As the dry season progresses, only adult ticks continue to feed on ruminants, laying eggs that may not develop. Larvae that emerge during this dry period probably die before finding a host.

Considering their seasonal activity patterns, host ranges, proclivity for human-biting, and CCHF virus infection rates, the ticks that appear to be the most likely vectors to humans in Senegal are nymphs of *A. variegatum* and adults of *H. truncatum*. Such human infection should occur predominantly during periods of maximal vector activity: November through February if nymphal *A. variegatum* are vectors, or during July through November if adult *H. truncatum* transmit. Nymphal *A. variegatum* derived from larvae that fed on viremic hosts or that were infected transovarially could transmit to humans. Transovarial transmission of CCHF virus by this tick has not yet been recognized; however, horizontal transmission by infection of vertebrates that also serve as hosts for nymphal *A. variegatum* may occur. Adult *A. variegatum* that emerge from such nymphs could transmit CCHF virus to other ungulates; however, they would not directly influence risk of human infection because they almost never feed on people.

H. truncatum appears to be an important vector of CCHF virus to humans in Senegal because it is among the most abundant and widely distributed of infected ticks, immatures feed readily upon small mammals that have been shown to be infected, experimental evidence has demonstrated horizontal and transstadial transmission [12], and adult ticks bite humans. Furthermore, the distribution of CCHF virus antibody seroprevalence among humans in Africa, and of naturally acquired hemorrhagic cases, fits more closely the distribution of *H. truncatum* than that of *A. variegatum* (Fig. 2). Thus, we suggest that *H. truncatum* is likely to be the principal anthropo-zoonotic vector in Senegal.

The natural cycle of this virus contains numerous links, some of which could change considerably the dynamics of virus maintenance and transmission to humans (Fig. 7). Other hypothetical links remain to be identified. Adding to these complex interactions are temporal and spatial variations in antibody prevalences [24], the unknown protective properties of neutralizing antibodies, variation in the timing and magnitude of viremia among vertebrates, differences in the vector competence of ticks, and changing

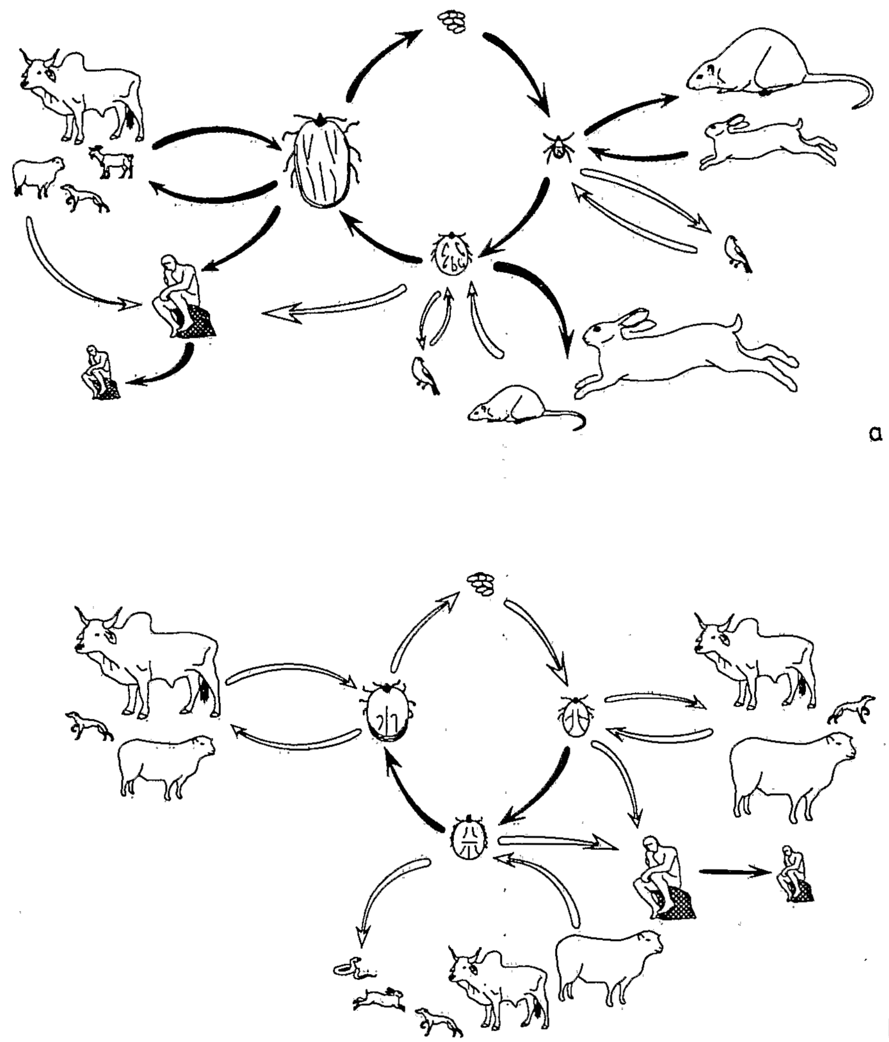


Fig. 7a, b. Scheme of the transmission cycle of Crimean-Congo hemorrhagic fever virus among vector ticks and vertebrates. The sizes of vertebrates represent their relative importance as hosts to the tick. Demonstrated transmission (solid arrows), suggested transmission (open arrows). Virus may be vertically transmitted among eggs, larvae, nymphs and adults, or horizontally transmitted to and from vertebrates. Transmission cycles for *Hyalomma truncatum* (**a**) and *Amblyomma variegatum* (**b**) are illustrated

infection rates. Schematic diagrams of CCHF virus transmission (Fig. 7) are useful tools in conceptualizing the potential pathways and interactions, both deriving from and guiding research on longterm transmission dynamics under natural conditions. We lack, at present, sufficient observations of this sort to paint a satisfactory picture of the ecology of CCHF virus throughout most of its range.

Acknowledgements

Funding of this research was provided through grant DAMD 17-87-G-7003 from the U.S. Army Medical Research Institute of Infectious Diseases (USAMRIID), Ft. Detrick, Frederick, Maryland, U.S.A. We thank Khalilou Ba, Mamoudou Diallo, Abdoulaye Diouf, Elizabeth Dykstra, and Ibrahim Samb for technical assistance. We are grateful to Drs. Arona Gueye and Racine Sow of the Institut Senegalais de Recherches Agricoles (ISRA) for their cooperation and for permission to work at the ISRA research station at Dahra.

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Authors' address: J.-L. Camicas, Institut Pasteur, B.P. 220, Dakar, Senegal.

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