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THE ECOLOGY OF THE AFRICAN VECTORS OF HEARTWATER, WITH PARTICULAR REFERENCE TO *AMBLYOMMA HEBRAEUM* AND *AMBLYOMMA VARIEGATUM*

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ABSTRACT

PETNEY, T. N., HORAK, I. G. & RECHAV, Y., 1987. The ecology of the African vectors of heartwater, with particular reference to *Amblyomma hebraeum* and *Amblyomma variegatum*. *Onderstepoort Journal of Veterinary Research*, 54, 381–395 (1987).

The hosts, sites of attachment, life cycle, habitat requirements and seasonal abundance of *Amblyomma astrion, Amblyomma cohaerens, Amblyomma gemma, Amblyomma hebraeum, Amblyomma lepidum, Amblyomma marmoreum, Amblyomma pomposum, Amblyomma sparsum, Amblyomma tholloni* and *Amblyomma variegatum*, the 10 potential vectors of heartwater in Africa, are listed. Factors influencing the distribution and abundance of the ticks as well as interactions with other species and the role of predators and pathogens are discussed.

INTRODUCTION

Information on the ecology of the 10 African species of *Amblyomma* ticks known to be capable of transmitting heartwater in Africa is widely scattered in the literature. Most of it comprises studies of a national or regional nature and thus is of limited value in view of the very wide geographical range occupied by some species. Moreover this literature deals mostly with surveys, and although these provide a great deal of observational information they seldom take more specialized experimental studies into account.

The present paper has 2 aims: Firstly to supply a broad summary of the general information related to the hosts, life cycle, climatic requirements, habitat preferences and population dynamics of each of the species and secondly to discuss this information, as well as that provided by experimental studies, as they relate to key areas of distributional, population and community ecology.

In addition particular attention will be paid to our understanding of *Amblyomma hebraeum* and *Amblyomma variegatum* as these 2 species represent the most important vectors of heartwater as well as being the most comprehensively studied.

METHODS

The references consulted generally date from after the review of ticks of the Sudan by Hoogstraal (1956), which cites earlier references and provides more or less detailed reviews of *Amblyomma cohaerens, Amblyomma lepidum, Amblyomma pomposum, Amblyomma tholloni* and *A. variegatum*. [Hoogstraal's designation of *Amblyomma marmoreum* was proved inaccurate by later taxonomic studies (Theiler & Salisbury, 1959)].

Data on hosts, preferred sites of attachment, life cycle, altitude, rainfall and habitat requirements, as well as seasonal dynamics are listed in the 1st section of the paper. Because of the widely varying amounts of information available some species can only be treated superficially while others are better known. In general the economically more important species, *Amblyomma gemma, A. hebraeum, A. lepidum*, and *A. variegatum*, have received the most attention.

The section on hosts comprises a more complex situation. Several recent works have pointed out the poor accuracy of the visual search methods for ticks on large hosts (Horak, Potgieter, Walker, De Vos & Boomker, 1983; Westrom, Lane & Anderson, 1985; MacIvor, Horak, Holton & Petney, 1987). In particular the small larval and nymphal stages stand a high chance of being overlooked by these methods. Moreover in many records the presence or absence of the particular species is often recorded without any indication of the importance of a particular host for that species. This information on general host associations, particularly for the immature stages, which also cause some problems with specific identification, is often poor.

Detailed host lists are not given as these are available in Hoogstraal (1956) and Theiler (1962). General lists are given with more precise information on those hosts usually recognised to be of major importance. Host lists are sequenced in 6 sections, 1 each for adults, nymphae and larvae on domestic hosts as well as 1 each for adults, nymphae and larvae on wild hosts.

The section on preferred attachment sites also suffers from limitations in sampling technique. It is sequenced in the order of adults, nymphae and larvae and quantitative data are supplied where available.

The life cycle data include the number of hosts required per cycle and, where available, the generation time and the time required for the completion of the various stages of the life cycle under laboratory conditions.

Altitude data have either been gleaned from existing references or calculated approximately from distribution data given by Walker & Olwage (1987). When information has been given in feet, it has been converted to the nearest 5 m. A similar situation applies to rainfall in that inches have been converted to the nearest 50 mm.

Habitat includes information on the general aridness of the environment. Where possible this is related to a graded series of conditions ranging from desert through arid, semi-arid, dry subhumid to humid (Pratt, Greenway & Gwynne, 1966). A general statement on vegetation type is also given. The latter is dependent on the information available in the literature but an attempt has been made to simplify this from particular floristic associations to specific growth forms. The references cited usually give much greater detail about the habitats in which the various species of *Amblyomma* are found than will be presented here.

The section on seasonal dynamics indicates the peak period of abundance where this is available. Data are supplied in the sequence of adults, nymphae and larvae.

THE TICKS

Amblyomma astrion Dönitz, 1909

Hosts: cattle and sheep have been recorded as domestic hosts (Serrano, 1963; Elbl & Anastos, 1966), and Uilenberg, Corten & Dwinger (1982) list it as a major

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parasite of domestic ruminants on São Tomé and Principe islands. Borght-Elbl (1977) records immatures from dogs and chickens. Adults and immatures are predominantly found on buffalo (Theiler, 1962; Serrano, 1963; Elbl & Anastos, 1966; Borght-Elbl, 1977).

Preferred sites of attachment: unknown.

Life cycle: 3-host tick; several generations p.a. are suggested for north-western Zaïre (Borght-Elbl, 1977).

Altitude: 0–1 000 m (Serrano, 1963).

Rainfall: 500–1 700 mm p.a. (Serrano, 1963; Borght-Elbl, 1977).

Habitat: wooded savannas (Theiler, 1962; Serrano, 1963) with a hot dry season varying from 60 to 100 days in length (Elbl & Anastos, 1966). Largely confined to regions occupied by Cape buffalo (*Syncerus caffer*) (Serrano, 1963).

Seasonal abundance: largely unknown. Elbl & Anastos (1966) recorded the largest collections during August, while Serrano (1963) found adults of both sexes on either buffalo or cattle in March, June, September, October and December. Larvae and nymphae are found in both autumn and spring in north-western Zaïre (Borght-Elbl, 1977).

Amblyomma cohaerens Dönitz, 1909

Hosts: domestic hosts are rarely infested in Tanzania and Kenya (Yeoman & Walker, 1967; Walker, 1974), although Hoogstraal (1956) indicates that *A. cohaerens* frequently attacks domestic cattle in areas where buffalo are or were common. Pegram, Hoogstraal & Wassef (1981) have recorded heavy infestations of *A. cohaerens* on cattle in western Ethiopia in an area which was probably originally occupied by buffalo. Small infestations have also been found on sheep, goats and mules (Pegram *et al.*, 1981). However, the specific status of *A. cohaerens* in Ethiopia has been questioned by Pegram (1979). Nymphae have been recorded from cattle but usually in low numbers (Morel & Rodhain, 1972; Morel, 1980). Except in Ethiopia, where domestic animals are important (Morel, 1980; Pegram *et al.*, 1981), the buffalo is the predominant host of adults (Hoogstraal, 1956; Theiler, 1962; Yeoman & Walker, 1967; Walker, 1974). Various other host species have been recorded in the areas in which buffalo are the preferred hosts but these are infrequent (Hoogstraal, 1956; Theiler, 1962). Ground-dwelling birds have been recorded for the immature stages (Theiler, 1962). Various mammalian species have also been recorded ranging from the buffalo to rodents (*Thamnomys dolichurus*) and including baboons (*Papio* sp.), warthog (*Phacochoerus aethiopicus*) and eland (*Taurotragus oryx*) (Theiler, 1962; Dinnik, Walker, Barnett & Brocklesbury, 1963). Borght-Elbl (1977) records larvae from wild pigs and buffalo as well as species of *Francolinus, Genetta, Thryonomys* and *Tragelaphus* and nymphae from a variety of birds, rodents, antelope and buffalo.

Preferred sites of attachment: Not recorded.

Life cycle: 3-host tick; 2 generations per year in suitable environments (Elbl & Anastos, 1966; Pegram, 1979).

Borght-Elbl (1977) gives the following life cycle details for individuals reared at 32 °C and 90 % relative humidity. She stresses that this information is a composite obtained from material from various infestations.

Pre-oviposition: 9 days.

Oviposition: 11 days.

Oviposition to hatching: 35 days.

Larval feeding: 5 days.

Nymphal premoult: 12 days.

Nymphal feeding: 4 days.

Adult premoult: 15 days.

Altitude: a highland species recorded from Tanzania and Kenya from 1 200–approximately 1 500 m (Yeoman & Walker, 1967; Walker, 1974).

Rainfall: 625–1 000 mm p.a. has been recorded in Kenya (Walker, 1974) with a similar (inclusive) range for Tanzania (Yeoman & Walker, 1967). However, Borght-Elbl (1977) and Morel (1980) indicate that *A. cohaerens* occurs predominantly in areas with a rainfall of above 1 000 mm p.a. Pegram *et al.* (1981) record 800 mm p.a. as the minimum rainfall for this species in Ethiopia with a maximum of 1 400 mm p.a.

Habitat: in Tanzania and Kenya *A. cohaerens* is found in dry subhumid to semi-arid bushland, wooded arid and bushed grassland (Yeoman & Walker, 1967; Walker, 1974), indicating that a litter or grass layer with scattered shade is important for its survival. In Ethiopia, however, *A. cohaerens* occurs predominantly in montane, moist evergreen forests (Pegram *et al.*, 1981), including tsetse infested valleys, as well as montane subtropical grassland (Morel, 1980). It is absent from the drier ecological zones of Ethiopia (Pegram *et al.*, 1981).

Seasonal abundance: peak activity of adult *A. cohaerens* in western Ethiopia occurs during April–May and October–December during the spring and autumn rains (Pegram *et al.*, 1981). Data from other areas are lacking as are data for the immature stages.

Amblyomma gemma Dönitz, 1909

Hosts: cattle seem to be the preferred domestic hosts of adult *A. gemma* but they have also been recorded from sheep, goats, camels, donkeys, horses and mules (Yeoman & Walker 1967; Walker, 1974; Pegram, 1976; Morel, 1980; Pegram *et al.*, 1981). Nymphs have been recorded from cattle (Bergeon & Balis, 1974; Morel, 1980) as well as camels and goats (Morel, 1980), but infestation levels are very low. Larvae have been collected from a domestic cow in Kenya (Borght–Elbl, 1977). Adults are regarded as parasites of large herbivores (Theiler, 1962; Yeoman & Walker, 1967; Walker, 1974). However, they have also been recorded from lion (*Panthera leo*) (Theiler, Walker & Wiley, 1956; Yeoman & Walker, 1967; Walker, 1974), baboon (*Papio doguera*) (Theiler, 1962) and once on a tortoise (Yeoman & Walker, 1967). Limited data are available for the immature stages. Nymphs have been recorded from the helmeted guinea fowl (*Numida meleagris*) (Yeoman & Walker, 1967); francolin (*Francolinus* sp.) (Morel & Rodhain, 1972; Morel, 1980), and lappet-faced vulture (*Torgos tracheliotus*), Cape hare (*Lepus capensis*) and warthog (*P. aethiopicus*) (Morel, 1980) as well as bovines and small carnivores (Borght–Elbl, 1977).

Walker (1974) has recorded nymphs in droppings under a *Quelea* roost and suggests that the larvae had engorged on these birds.

Preferred sites of attachment: adult *A. gemma* are found predominantly on the ventral surface of cattle, from the dewlap to the escutcheon, including the axillae and groin (Yeoman & Walker, 1967; Walker, 1974). They have also been recorded from the back and behind the ear of a warthog (Yeoman & Walker, 1967).

Life cycle: 3-host tick; Theiler *et al.* (1956) give the following details on the life cycle of *A. gemma* kept under laboratory conditions in Kabete, Kenya:

Pre-oviposition: 12 days.

Oviposition to hatching: 69 days.

Larval feeding: 5 days.

Nymphal premoult: 17 days.

Nymphal feeding: 6 days.

Adult premoult: 28 days.

Female feeding: 12 days.

Altitude: records for Tanzania and Kenya indicate that *A. gemma* is found predominantly from 0–1 830 m (Yeoman & Walker, 1967; Walker, 1974).

Rainfall: generally recorded as between 250–300 mm minimum–750 mm maximum p.a. (Yeoman & Walker, 1967; Walker, 1970, 1974).

Habitat: a tick of arid and semi-arid areas occurring in woodland, bushland, semi-arid bushland and wooded and bushed grassland (Yeoman & Walker, 1967; Walker, 1974). In Ethiopia it occurs mainly in semi-arid rangeland (Pegram *et al.*, 1981) while in northern Somalia it appears to be an obligate dweller of wooded highlands (Pegram, 1976).

Seasonal abundance: adults are found most frequently during the wetter months from May–September in northern Somalia (Pegram, 1976) and March–October in Ethiopia (Pegram *et al.*, 1981). The mean number of adults per host during the period of peak abundance in northern Somalia is about 5 individuals. No adults were found from October–April (Pegram, 1976). Pegram *et al.* (1981) report that *A. gemma* is never very abundant on cattle in Ethiopia. Wilson (1951, cited by Walker, 1974) records peak abundance from the Unoa area of the Machakos District in Kenya between March and April, while in the Kikumini area *A. gemma* is most prevalent during February, which is the hottest, driest month of the year, and again in July, October and November. Periods of peak rainfall in these areas occur from March–May and October–December.

Amblyomma hebraeum Koch, 1844

Hosts: cattle are the most important domestic hosts for adults (Zumpt, 1958; Norval & Lawrence, 1979; Paine, 1982) but this species also occurs on a wide range of other species including sheep, horses, donkeys and pigs (Theiler, 1962; Paine, 1982; Norval, 1983). Nymphae and larvae are also found on a wide variety of domestic hosts including cattle, sheep and goats (Theiler, 1962; Paine, 1982).

Adults attack a wide range of wild animal hosts including reptiles, birds and mammals (Theiler, 1962). They occur most commonly on large ungulates (Theiler, 1962; Minshull, 1981; Norval, 1983). In Zimbabwe, Norval & Lawrence (1979) indicate that the main host species differ from one area to another. They also point out that hosts of greater than 100 kg are regularly infested while hosts below this mass are not usually infested. The number of *A. hebraeum* adults present is correlated (non-linear) with host mass. They list giraffe and buffalo as carrying more adults than eland and warthog which in turn had more than kudu which had more than wildebeest, tsessebe and ostrich which had more than zebra, impala and bushbuck. No adults were collected from duiker, klipspringer or reedbuck. Unfortunately only 1 warthog, 1 bushbuck, 1 duiker and 1 klipspringer had been examined.

Theiler (1959) stresses the importance of birds as hosts for the immature stages, while Theiler (1962) records immatures from many species of birds and mammals as well as a few reptiles.

Nymphs and larvae utilize similar hosts to adults, but can be found on the smaller mammals such as hares and ground feeding birds (Howell, Walker & Nevill, 1978). Mountain tortoises *(Geochelone pardalis)* may also harbour large numbers of nymphae (Walker & Schulz, 1984; Dower, unpublished data, 1986).

Quantitative data are given for a variety of hosts for all parasitic life history stages by Horak, MacIvor, Petney & De Vos (1987).

Preferred sites of attachment: adults are usually found on the underside of the body (Howell *et al.*, 1978). On cattle 91 % of adults were found on the underside with 39 % of these around the perineum and 52 % on the axillae, sternum, belly and groin (Baker & Ducasse, 1967). Ducasse (1969) records 84 % of adults on goats from the belly, groin and sternum with the remaining 16 % on the limbs. Howell *et al.* (1978) recorded adults from the groin, axillae, sternum and perianal area of sheep.

Baker & Ducasse (1967) recovered 63 % of nymphae from the feet, 10 % from the axillae, 9 % from the sternum, 7 % from the belly and groin and 5 % from the legs of cattle. On goats 94 % were found on the feet (Ducasse, 1969). Howell *et al.* (1978) also indicate the feet as a preferred site.

Larvae are commonly found on the head (especially the muzzle) as well as the feet and legs of cattle. Baker & Ducasse (1967) recoverd 18 % from the muzzle of cattle, 12 % from the rest of the head and 36 % from the feet and legs. The remaining 34 % were widely scattered over the remaining body area. Ducasse (1969) records 63 % from the feet of goats, 13 % from the legs and 13 % from the pinnae of the ear.

Life cycle: 3-host tick; Rechav (1982) indicates 1 generation per year in the eastern Cape Province of South Africa with a possible split into 2 cohorts. However, Norval (1977a) suggests 1 generation per 3 years.

Norval (1974) gives the following data on the life cycle at 26 °C and 90 % relative humidity:

Pre-oviposition: 10–14 days.

Oviposition to hatching: 32–38 days.

Larval premoult: 54–61 days.

Larval feeding: 6–8 days.

Nymphal premoult: 14–25 days (mean 19,5 days).

Nymphal feeding: 5–13 days (rabbit), 6–9 days (sheep).

Adult premoult: 20–29 days (mean 23,4 days).

Adult feeding: male 4–6 days to sexual maturity
female 6–12 days from mating

Mean number of eggs laid per female (for 10 females) 14 711 with a range from 6 366–18 765 eggs.

Jordaan & Baker (1981) report that males can mate up to 42 times and remain on a host for 149–244 days (mean 177 days).

Altitude: 0–1 525 m in South Africa, but this is dependent on vegetation type. Ticks occur at the maximum altitude only in parkland but are not found above ± 1 000 m in tall grassland (Theiler, 1948). Purnell (1984) cites Norval as recording this species below 1 000 m in Zimbabwe.

Rainfall: the lower limit lies between 300 and 400 mm p.a. (Theiler, 1948; Paine, 1982; Purnell, 1984) and the upper at about 800 mm p.a. (Theiler, 1948; Paine, 1982).

Habitat: present in tall grass areas with trees or bush offering shade. Not present in open savanna, in steppe without tall plants or with only short grass, or in arid areas (Theiler, 1948, 1962; Zumpt, 1958). Larvae are restricted to well-drained shaded habitats with grass cover (Londt & Whitehead, 1972; Norval, 1977a; Rechav, 1982).

Seasonal abundance: Norval (1977a) and Rechav (1982, 1984) record peak abundance from February–March in the eastern Cape Province of South Africa, with the initial increase in numbers after the winter during the September/October rains. Minshull (1981) and Norval (1983) also record high adult numbers during the rainy season in Zimbabwe, with a peak from February–May, although adults are present throughout the year. However, in Natal the increase, which begins in September, falls off again more rapidly and numbers have declined by the end of January (Baker & Ducasse, 1967).

Nymphal peak activity was recorded from September until November/December in the eastern Cape Province of South Africa by Norval (1977a). However, Rechav (1982), working in the same region, recorded the 1st peak between June and August with a 2nd peak during October–November. In Natal peak numbers occurred between May and the end of September (Baker & Ducasse, 1967), while Paine (1982), in Botswana, records 2 peaks, 1 in December (hot rainy season) and 1 in June (cool, dry period). In the northern Transvaal, Schröder (1980) recorded nymphae from cattle during all months of the year, with peak numbers during October and November and a 2nd peak from January–April. In Zimbabwe nymphae have been recorded throughout the year from wild hosts but with peak activity varying between years (Minshull, 1981). Norval (1983) also recorded nymphae throughout the year in Zimbabwe, with a peak from August–November prior to the rains.

In the eastern Cape Province larval activity occurs from February–May/June with a peak in April and occasionally again in August/September (Rechav, 1982, 1984). Baker & Ducasse (1967), in Natal, also record a peak from February to mid May. However Norval (1977a), also working in the eastern Cape Province, found activity high between September and January. In Zimbabwe the period of minimum abundance on wild hosts was during the hot, dry period from September–December while the period of maximum abundance varied from year to year (Minshull, 1981). Norval (1983) found that the period of peak larval abundance in Zimbabwe coincided with that of the nymphae from August–November, prior to the start of the rains.

Amblyomma lepidum Dönitz, 1909

Hosts: cattle are the most important hosts for the adults (Hoogstraal, 1956; Yeoman & Walker, 1967; Yeoman, 1968; Pegram, 1979). Other domestic hosts are less common but include sheep, goats, horses, mules, camels and dogs (Hoogstraal, 1956; Karrar, Kaiser & Hoogstraal, 1963; Yeoman, 1968; Walker, 1974; Morel, 1980). Camels may have quite heavy infestations (Walker, 1974; Pegram *et al.*, 1981).

Yeoman & Walker (1967) record nymphae from cattle in Tanzania, but both Hoogstraal (1956) and Karrar *et al.* (1963) regard cattle as rare hosts in the Sudan.

Adults infest a wide range of wild hosts but are found predominantly on ungulates and other herbivores (Hoogstraal, 1956; Theiler, 1962; Yeoman & Walker, 1967; Walker, 1974). Theiler (1962) reports immatures from birds and a spotted hyena *(Crocuta crocuta)* as well as ungulates and other herbivores. Morel (1980) lists carnivores and ungulates as well as hares, monkeys and birds as hosts for the immature stages.

Nymphae have been found on ungulates and birds (Hoogstraal, 1956; Karrar *et al.*, 1963; Yeoman & Walker, 1967) with a single record from a migratory thrush *(Turdus merula)* as far north as Cyprus (Kaiser, Hoogstraal & Watson, 1974). Detailed information on larval hosts has not been reported.

Preferred sites of attachment: adults are predominantly found on the ventral surface of the host from the lower dewlap to the escutcheon, including the axillae (Yeoman & Walker, 1967; Walker, 1974). They are less common on the prepuce and scrotum (Yeoman & Walker, 1967). Walker (1974) also records adults from the hocks and heels.

Nymphae occur on the same sites as the adults but have a preference for the heels (Yeoman & Walker, 1967; Walker, 1974).

Life cycle: 3-host tick. Walker (unpublished data, 1952) recorded the following life cycle data, with the free-living stages kept as 23–29 °C, at Muguga, Kenya:

Pre-oviposition: 18–20 days.
Oviposition to hatching: 6–70 days.
Larval feeding: 8 days (rabbit), 11 days (sheep).
Nymphal premoult: 31 days.
Nymphal feeding: 19 days (rabbit), 10 days (sheep).
Adult premoult: 27–32 days.

Karrar *et al.* (1963) report that 13 fully engorged nymphae held at 22–27 °C and 60 %–80 % relative humidity moulted in 29–45 days (mean 35 days) after collection.

Altitude: in Kenya *A. lepidum* occcurs from 0–1 525 m with a few records from as high as 2 440 m (Walker, 1974). In Tanzania the range of altitudes fits within the above ranges (Yeoman & Walker, 1967). Pegram *et al.* (1981) list records at 2 000 m in Ethiopia.

Rainfall: usually reported as less than 750 mm p.a. (Yeoman, 1968; Walker, 1974) but in some areas may be as high as 1 250 mm p.a. (Hoogstraal, 1956; Walker, 1974). In Ethiopia 1 000 mm p.a. is regarded as the maximum rainfall (Pegram *et al.*, 1981). Minimum rainfall requirements seem to be as low as 250 mm p.a. (Walker, 1974; Pegram *et al.*, 1981) although Yeoman & Walker (1967) report 350 mm p.a. as being the minimum in Tanzania.

Habitat: A. lepidum is a tick of arid and semi-arid areas including semi-desert (Karrar *et al.*, 1963; Walker, 1974; Hoogstraal, 1985). Contrary to the opinion of Lewis (1939) it does not occur in desert conditions (Hoogstraal, 1956; Morel, 1980). It occurs in woodland, bushveld and grassland with either trees or bushes present (Yeoman & Walker, 1967; Walker, 1974). In Tanzania, *A. lepidum* characteristically occurs in areas with short rainy seasons, prolonged droughts and little vegetational cover (Yeoman & Walker, 1967; Yeoman, 1968).

Seasonal abundance: in Tanzania peak adult abundance occurs between October and February with the increase beginning either shortly before or after the onset of the rainy season (mid-December) (Yeoman & Walker, 1967). Male numbers usually increase before females, but there is considerable variation in both timing of the peak and numbers present (Yeoman, 1968). Peak abundance was recorded on animals at the Hungamarwa site in Tanzania by Yeoman (1968) during October 1959 and January 1960, with mean infestations of 23,6 and 39,3 adult *A. lepidum* per beast respectively. A maximum of 98 adults per beast was recovered. Samples from the same site and during the same months of the 1958/1959 season yielded only 2,0 and 5,7 adults/host respectively (Yeoman, 1968). In general infestations were well below 5 adults per beast at all times of the year for this and other sites sampled (Yeoman, 1968). Similar results were found in Tanzania 15 years later (Easton & Tatchell, 1981; Tatchell & Easton, 1986), with a mean infestation of 20,5 adults per beast at Lalago but more usual numbers being around 1 tick per beast at other localities. No seasonal variation was found for *A. lepidum* adults in Tanzania in the latter studies (Tatchell & Easton, 1986), although Yeoman (1968) suggests that adults peak in November–February like *A. variegatum*. Pegram *et al.* (1981) indicate that adult numbers peak during the rainy season in Ethiopia (May–June). A maximum adult load of 322 per beast was recorded by these workers. Nymphae in Tanzania peak from May–October after the rainy season (Yeoman & Walker, 1967). Data for larvae are not available.

Amblyomma marmoreum Koch, 1844

Hosts: adults very rarely feed on domestic stock. Nymphae and larvae have been recorded from cattle, sheep, goats and dogs (Norval, 1975; Horak & Knight, 1986). Larval infestations in particular may be quite substantial (Horak & Knight, 1986). Hoogstraal & Aeschlimann (1982) list *A. marmoreum* as being a monotropic species with both adults and immatures specific for the same limited host group.

Adults are regarded as specific for reptiles, particularly tortoises and large varanids (Theiler & Salisbury, 1959; Theiler, 1962; Norval, 1975). Nymphae also occur on tortoises (Norval, 1975, 1983; Dower, 1986). They have also been recorded from ground-frequenting birds and small mammals (Norval, 1975; Horak *et al.*, 1987). Larvae have been recovered from tortoises, birds, lagomorphs, ungulates and carnivores (Norval, 1975; Horak & Willams, 1986; Horak, Knight & De Vos, 1986).

Preferred sites of attachment: on tortoises adults attach preferentially to the rear, soft, thigh region and fleshy areas around the tail as well as the front axillae and head area (Walker & Schulz, 1984). On large varanids the cloacal area is a common site of attachment (Petney, unpublished data, 1986).

Life cycle: 3-host tick; 1–2 generations p.a. (Norval, 1975). Norval (1975) gives the following life cyle data, with the free-living stages maintained at 26 °C and 90 % relative humidity in complete darkness.

Pre-oviposition: 12–15 days.

Oviposition to hatching: 30 days.

Larval premoult: 37 days (from start of oviposition).

Larval feeding: 6–12 days (sheep), 30 days (tortoise).

Nymphal premoult: 14–21 days.

Nymphal feeding: 8–20 days (sheep), 51 days (tortoise).

Adult premoult: 21–28 days.

Female feeding: 60 days (tortoise).

Altitude: 0–1 500 m (Petney, unpublished data, 1986).

Rainfall: 250–900 mm (Petney, unpublished data, 1986).

Habitat: absent from very arid habitats (Theiler, 1962; Norval, 1975). Occurs in grassland with scrub or trees but not open grassland (Theiler, 1962). Larvae and nymphae are most numerous in humid, tree protected habitats but absent from dry habitats (Norval, 1975).

Seasonal abundance: this is rather difficult to estimate as the active period of the tortoise hosts is restricted to certain seasons and tortoises have seldom been sampled in large numbers. In Zimbabwe tortoises have been collected in the warmer months (September–May) and were usually infested by both adults and immatures (Norval, 1983). This is similar to the situation for the eastern Cape Province of South Africa where peak adult abundance was found from December–March (mid to late summer) (Norval, 1975).

Limited collections of attached and of free-living nymphae from the eastern Cape Province indicate that nymphal activity is highest from August–March (Norval, 1975).

Collections of free-living larvae in the eastern Cape Province indicate that maximum activity occurs during April and May (late summer) with little activity during winter, spring and early summer (Norval, 1975). Most larvae were collected from tortoises in April and May (Norval, 1975; Dower, 1986).

Amblyomma pomposum Dönitz, 1909

Hosts: Hoogstraal (1956) indicates that cattle are the dominant domestic host, although *A. pomposum* has also been found on sheep, goats, donkeys, mules, horses and dogs. The paucity of *A. pomposum* on cattle in Zambia (Matthysse, 1954; MacLeod, 1970; MacLeod & Mwanaumo, 1978) probably indicates an unsuitable environment.

Wild hosts of adults are mainly Artiodactyla (Hoogstraal & Aeschlimann, 1982). MacLeod (1970) records the following hosts in an area marginal for *A. pomposum:* buffalo *(S. caffer)*, eland *(T. oryx)*, kudu *(T. strepsiceros)*, sable antelope *(Hippotragus niger)* and roan antelope *(Hippotragus equinus)*. Theiler (1962) adds topi *(Damaliscus korrigum)* and hartebeest *(Alcelaphus lichtensteini)* as well as zebra *(Equus burchelli)* and warthog *(P. aethiopicus)*. Serrano (1963) adde red lechwe *(Kobus lechwe)* and a banded mongoose *(Mungos mungo)* while Colbo (1973) adds bush pig *(Potamochoerus porcus)*.

Records listing immatures are infrequent. Theiler (1962) records immatures from reptiles (*Agama* sp.) as well as the vervet monkey *(Cercopithecus aethiops)*. MacLeod & Mwanaumo (1978) record 49 nymphae from Lichtenstein's hartebeest *(A. lichtensteini)* and 1 from warthog *(P. aethiopicus)* in Zambia.

Records of larvae are not available.

Preferred sites of attachment: adults prefer the underside of cattle, especially the udder, scrotum, groin and axillae (Serrano, 1963).

Life cycle: 3-host tick; 1 generation p.a. (Serrano, 1963). Serrano (1963) gives the following data for life cycle studies carried out at 26 °C and 80 % relative humidity. (Data given in weeks and months have been converted to days).

Pre-oviposition: 11–18 days.

Oviposition to hatching: 30–60 days.

Larval feeding: 5–10 days (rabbit and sheep).

Nymphal premoult: 21–28 days.

Nymphal feeding: 7–12 days (rabbit and sheep).

Adult premoult: 28–35 days.

Female feeding: 10–20 days.

Altitude: a highland tick (Theiler, 1962). Serrano (1963) indicates that *A. pomposum* occurs above 1 200 m in Angola. In the Congo Elbl & Anastos (1966) state that the regions of maximum abundance are located between 1 400 and 1 700 m which is in general agreement with other data from Zambia and Angola.

Rainfall: in Angola *A. pomposum* is recorded from areas receiving from 800–2 000 mm p.a. (Serrano, 1963). However, in the Congo Elbl & Anastos (1966) indicate that it occurs where annual rainfall is less than 1 200 mm. In both areas the upper rainfall limit is high when compared with other vectors of heartwater.

Habitat: tropical and humid temperate highlands (Serrano, 1963), characterized by savannas (Hoogstraal, 1985) and forested savannas (Elbl & Anastos, 1966). In Zaïre the area occupied is characterized by a tropical climate with a 5–7 month dry period (Elbl & Anastos, 1966).

Seasonal abundance: adults occur predominantly from September–March during the rainy period, with maximum infestations during November and December (Serrano, 1963). Nymphae are found from October–December (Serrano, 1963). Serrano also points out that substantial variations occur in seasonal abundance, depending on the region and climate. Data on larvae are not available.

Amblyomma sparsum Neumann, 1899

Hosts: A. sparsum is rare on domestic hosts. Yeoman & Walker (1967) record 2 males only from cattle and Walker (1974) a single unconfirmed collection from a goat and a single confirmed collection from a dog. Norval (1983) states that small numbers of nymphae may occur on cattle, sheep and goats in Zimbabwe. In the Zambezi valley *A. sparsum* is usually found in wildlife reserves in the absence of domestic stock (Norval, 1983).

A. sparsum is unusual in that adults are commonly found both on large reptiles and certain mammalian hosts. It has frequently been recorded on tortoises, large varanid lizards and large snakes (Theiler & Salisbury, 1959; Theiler, 1962; Yeoman & Walker, 1967; Walker, 1974). Although Hoogstraal & Aeshclimann (1982) regard it as totally specific for reptiles with only some adults found on mammals quite a lot of data indicate that the black rhinoceros *(Diceros bicornis)* and possibly buffalo *(S. caffer)* also represent important hosts. Additional records come from elephant *(Loxodonta africana)*, hippopotamus *(Hippopotamus amphibius)* and bushpig *(P. porcus)* (Theiler & Salisbury, 1959; Theiler, 1962; Elbl & Anastos, 1966; Yeoman & Walker, 1967; Walker, 1974; MacLeod & Mwanaumo, 1978; Norval, 1983).

Theiler (1962) lists immatures from reptiles, including varanid lizards, birds (Coraciformes, Galliformes) and small mammals including insectivores, lagomorphs and rodents. Nymphs have been found on buffalo *(S. caffer)* and tortoises (Theiler & Salisbury, 1959; Morel, 1980; Norval, 1983). Hosts for the larvae have not been recorded.

Preferred sites of attachment: the adults attach to the axillae and caudal folds of tortoises and have been recorded from the brisket, groin and escutcheon of buffalo (Yeoman & Walker, 1967).

Life cycle: 3-host tick. Walker & Parsons (1964) give the following data for life cycle studies. Egg laying, hatching of larvae and moulting of engorged larvae and nymphae took place at 24–27 °C and 80 % relative humidity. Unfed larvae, nymphae and adults were kept at about 21 °C. Ranges in times for the first generation of Walker and Parson's strain are given.

Pre-oviposition: 19–22 days.

Oviposition to hatching: 48–57 days.

Larval feeding: 6–10 days (rabbit host).

Nymphal premoult: 11–20 days.

Nymphal feeding: 6–11 days (rabbit host).

Adult premoult: 30–33 days.

Time to engorge after mating: 26 days (tortoise host).

Altitude: Walker (1974) records *A. sparsum* from sea level to 1 830 m in Kenya while Yeoman & Walker (1967) record it from 1 065–1 525 m in Tanzania.

Rainfall: Walker (1974) records 250–1 250 mm p.a. in Kenya. The range recorded in Tanzania between 500 and 1 000 mm falls within the Kenyan range (Yeoman & Walker, 1967). Elbl & Anastos (1966) list a rainfall of approximately 1 000 mm p.a. in Zaïre.

Habitat: predominantly in arid and semi-arid habitats containing a wide variety of wooded and wooded savanna areas (Elbl & Anastos, 1966; Yeoman & Walker, 1967; Walker, 1974; Morel, 1980). In regions where rainfall is less than 500 mm p.a. this species probably survives in very humid microhabitats such as marshland and areas along streams, rivers and lakes susceptible to inundation (Borght-Elbl, 1977).

Seasonal abundance: in Zambia adults were commonly found on hippopotamus from June–August and on buffalo from June–November with periods of highest infestation from June–August (MacLeod & Mwanaumo, 1978). This represents the dry season in the districts sampled. In Zimbabwe Norval (1983) found no well-defined peak in adult activity. He did, however, record a nymphal peak from April–August.

Amblyomma tholloni (Neumann, 1899)

Hosts: domestic stock are not common hosts (Yeoman & Walker, 1967; Walker, 1974; MacLeod, Colbo, Madbouly & Mwanaumo, 1977). However, larvae and nymphae have been recorded from cattle, sheep and goats in Zimbabwe (MacKenzie & Norval, 1980; Norval, 1983). Hoogstraal (1956) lists references for horses and dogs.

Adults of *A. tholloni* are found predominantly on the African elephant (Hoogstraal, 1956; Theiler, 1962; Yeoman & Walker, 1967; Walker, 1974; Hoogstraal & Aeschlimann, 1982). It is also found, but much less frequently, on other large herbivores such as black rhinoceros *(D. bicornis)* (Walker, 1974) and hippopotamus *H. amphibius)* (Dinnik *et al.*, 1963; Norval, 1983). Theiler (1962) lists a variety of less common hosts.

Immatures have been recorded from reptiles ("large lizard" and *Kinixys belliana*), birds and elephants as well as 2 species of artiodactyls (Theiler, 1962), although Santos Dias (1948) and Elbl & Anastos (1966) report that both nymphae and larvae are uncommon on elephants. Elbl & Anastos (1966) consider birds as major hosts of the immatures.

Nymphae have been recorded from elephants as well as hippopotamus and buffalo (Dinnik *et al.*, 1963; Borght-Elbl, 1977; Norval, 1983). Hoogstraal (1956) records nymphae from passerine birds and a single specimen from a chameleon. Birds are also recorded by Borght-Elbl (1977).

Larval records are rare but a single individual has been found on a bird *(Pitta reichenowi)* (Hoogstraal, 1956), while hippopotamus have also been recorded as being infested (Hoogstraal, 1956; Norval, 1983). Borght-Elbl (1977) records the elephant as a host.

Preferred sites of attachment: adults may occur on any part of the elephant (Hoogstraal, 1956; Elbl & Anastos, 1966; Norval, 1983), though Walker (1974) singles out the area behind the ears, the axillae and abdomen as sites of particular importance. Norval (1983) has records from the inside of the mouth of elephants and the nostrils of hippopotamus.

No data are available on the sites of attachment of the immature stages.

Life cycle: 3-host tick. Norval, Colborne, Tannock & MacKenzie (1980) have recorded data on the life cycle at 25 °C and 85–87 % relative humidity. Information is also given by Santos Dias (1948) but that of Norval *et al.* (1980), with closely controlled humidity and temperature conditions, is preferred.

Pre-oviposition: 14–29 days (mean 18,4 days).

Oviposition: 24–44 days (2 871–10 347 eggs/female; mean 5 805 eggs).

Oviposition to hatching: 50–59 days.

Larval feeding: mean 6,69 days (rabbit), mean 6,10 days (sheep).

Nymphal premoult: 16–28 days (mean 20,2 days).

Nymphal feeding: mean 6,29 days (rabbit), mean 5,42 days (sheep).

Adult premoult: 23–28 days (mean 25,7 days).

Female feeding: 8–18 days.

Altitude: A. tholloni is found from 0–1 525 m (Yeoman & Walker, 1967; Walker, 1974) although some records from Kenya are from over 1 825 m (Walker, 1974).

Rainfall: rainfall maxima of 1 250 and 1 750 mm p.a. have been recorded in Kenya and Tanzania respectively (Yeoman & Walker, 1967; Walker, 1974). The minimum rainfall is less than 500 mm p.a. in Kenya with about half the records of *A. tholloni* occurring on or below this value (Walker, 1974). In Tanzania the minimum is recorded as 500 mm (Yeoman & Walker, 1967). Aeschlimann (1967) records *A. tholloni* as occurring in areas with 1 000 mm p.a. or less in the Ivory Coast.

Habitat: A. tholloni has been found in a wide variety of woodland, bushland and bushed or wooded savannas from the arid zone through to subhumid and humid areas (Yeoman & Walker, 1967; Walker, 1974). It is generally regarded as occurring almost throughout the range of its main adult host, the African elephant (*L. africana*) (Hoogstraal, 1956; Yeoman & Walker, 1967; Norval, 1983).

Seasonal abundance: few data are available, but Norval (1983) has recorded large numbers of nymphae from domestic stock during August and September in Zimbabwe.

***Amblyomma variegatum* (Fabricius, 1794)**

Hosts: A. variegatum is one of the major tick parasites of cattle over a wide area of Africa. Sheep and goats are infested to a lesser degree than cattle (Hoogstraal, 1956). *A. variegatum* adults have also been found on camels, horses and donkeys (Yeoman, 1968; Walker, 1974; Pegram *et al.*, 1981) as well as on dogs, cats and pigs (Hoogstraal, 1956; Yeoman, 1968; Walker, 1974).

Hoogstraal (1956) reports nymphae from all domestic stock. Sheep and goats are reported to be better hosts for this stage than for adults (Yeoman, 1968). Cattle also act as hosts (Yeoman, 1968, MacLeod, 1970; Walker, 1970). Camels are rarely attacked (Pegram, Hoogstraal & Wassef, 1982). Larvae have been found on sheep, goats and cattle (Yeoman & Walker, 1967). Nymphae occur more commonly on cattle than do larvae (MacLeod & Colbo, 1976).

Adults occur on a very wide range of mammals. Theiler (1962) gives records from Proboscoidea, Perissodactyla and Artiodactyla, and lists single records from Lagomorpha and Rodentia. However, *A. variegatum* adults are most prevalent on medium and large herbivores (Hoogstraal, 1956; Theiler, 1962; Yeoman & Walker, 1967; Walker, 1974; Hoogstraal & Aeschlimann, 1982). It is usual for *A. variegatum* adults to be less common on wild hosts than on cattle (Colbo, 1973; MacLeod *et al.*, 1977).

Theiler (1962) records immatures from lizards, birds and mammals (Insectivora, Primates, Carnivora, Perissodactyla, Artiodactyla, Lagomorpha and Rodentia). Theiler (1959) and Walker (1974) stress the importance of ground-feeding birds although workers in Zambia found few immatures on these hosts (Colbo, 1973; Colbo & MacLeod, 1976).

Hoogstraal (1956) gives a detailed host list for nymphs and larvae. He lists medium and large mammals as well as birds as being frequent hosts of nymphs while larvae are recorded predominantly from birds and small mammals. Hosts as large as zebra (*Equus* sp.) have been recorded for larvae.

Preferred sites of attachment: adults and nymphae occur commonly on the ventral surface of the host including the lower dewlap, brisket, abdomen, axillae and genitalia (Hoogstraal, 1956; Yeoman & Walker, 1967, Walker, 1974; MacLeod, 1975; MacLeod *et al.*, 1977). Kaiser, Sutherst & Bourne (1982) list 78 % of males, 76 % of females and 67 % of nymphae from the abdomen of cattle. MacLeod (1975) lists 87 % of adults from the ventral surface (dewlap, chest, axillae, abdomen and groin) while MacLeod *et al.* (1977) recovered 84 % from the chest and abdomen. Yeoman & Walker (1967) indicate that *A. variegatum* forms clusters, as would be expected given the presence of an aggregation/attachment pheromone (Norval & Rechav, 1979).

Nymphae are also found on the heels (Walker, 1974), elbows, hocks and elsewhere on the legs where few adults are present (Yeoman & Walker, 1967).

Larvae have been recorded from the head, including the ears, of cattle (Wilson, 1948, 1949, cited by Hoogstraal, 1956). MacLeod *et al.* (1977) list 36 % of larvae from the ears of cattle while the remaining 64 % were scattered over the rest of the animal except the tail. In contrast Kaiser *et al.* (1982) do not record larvae from the ears, but 29 % were found on the dewlap, 45 % from the back and 18 % from the abdomen with only 4 % from the head.

Walker (1974) records immatures from the head and around the eyes and ears of birds.

Life cycle: 3-host tick. In places with a single rainy season 1 generation occurs p.a. (Wilson, 1950; Hoogstraal, 1956; Elbl & Anastos, 1966). However, where there are 2 rainy seasons 2–3 generations p.a. are possible (Hoogstraal, 1956).

Life cycle data from Walker, as cited by Hoogstraal (1956) are given. The ticks were maintained at 25–27 °C. These data conform reasonably well with those reported by Lewis (1932) and CIBA SA (cited by Aeschlimann, 1967).

Pre-oviposition: 12 days.

Oviposition to hatching: 53 days.

Larval feeding: 5 days (rabbit).

Nymphal premoult: 14 days.

Nymphal feeding: 5 days.

Adult premoult: 19 days.

Female feeding: 12 days.

Lewis (1934) reports that females bury themselves in the soil before laying eggs.

Altitude: found from sea level to 2 590 m (Hoogstraal, 1956; Elbl & Anastos, 1966; Walker, 1974) although it is not common at sea level in Kenya (Walker, 1974). Records from other authors fall within this range. Thus in the Yemen Arab Republic *A. variegatum* is most commonly found on cattle from 1 300–2 000 m (Pegram *et al.*, 1982) whereas in Angola it occurs around 1 200–1 500 m (Serrano, 1963). Schoenaers (1951) and Elbl & Anastos (1966) in Rwanda were not able to find *A. variegatum* in mountain forest above 2 000 m.

Rainfall: minimum rainfall appears to be between 400–750 mm p.a. (Elbl & Anastos, 1966; Yeoman & Walker, 1967; Walker, 1970, 1974; Pegram, 1976; Pegram *et al.*, 1981; Paine, 1982). At low rainfall (400 mm to between 750–1 000 mm in Tanzania) *A. variegatum* becomes less common (Yeoman & Walker, 1967).

Maximum rainfall recorded is 2 050 mm p.a. in Kenya and 2 800 mm p.a. in Tanzania (Walker, 1974, and Yeoman & Walker, 1967, respectively).

Habitat: A. variegatum is absent from drier, arid areas but can be found in semi-arid and humid areas (Walker, 1974) where it occupies a wide variety of different habitat types, mainly with tree and/or bush cover (Yeoman & Walker, 1967; Walker, 1974; Morel, 1980). It also occurs in cultivated steppe and grassland with a high grass cover but not where the grass cover is low (Yeoman, 1968; Walker, 1970). In Northern Somalia it is an obligate dweller of wooded highlands (Pegram, 1976) while in Ethiopia it is commonly present in humid sub-highlands but rare in highland and lowland areas (Pegram *et al.*, 1981). Paine (1982) has also recovered *A. variegatum* from swamp grassland in Botswana. Elbl & Anastos (1966) have recorded it from Equatorial Rain Forest.

Seasonal abundance: the seasonal abundance of *A. variegatum* is dependent on the region (Theiler, 1962). In general adult abundance is greatest during the rainy season. Thus in Tanzania (Yeoman & Walker, 1967; Yeoman, 1968; Tatchell & Easton, 1986), Zambia (MacLeod, 1970; MacLeod *et al.*, 1977; MacLeod & Mwanaumo, 1978; Pegram, Perry & Schels, 1984; Mulilo, 1985; Pegram, Perry, Musisi & Mwanaumo, 1986) and Malawi (Wilson, 1946; 1950) peak abundance occurs from November/December–January. Yeoman (1968) presents data from Tanzania showing substantial variation in the maximum abundance and in the exact timing of peak occurrence between years. Numbers may begin to increase in October with males starting sooner than females, before the commencement of the rains (Wilson, 1946; Yeoman & Walker, 1967; Tatchell & Easton, 1986). Females engorge and oviposit during the months of highest rainfall (Wilson, 1950; Theiler, 1962). In Zambia (Pegram *et al.*, 1986) and Tanzania (Tatchell & Easton, 1986) substantial differences in maximum abundance occur between regions with different climatic characteristics.

In Ethiopia adults occur from March–July, during the spring rains (Pegram *et al.*, 1981). In the Yemen Arab Republic adults are also most abundant from March–July, but camels seem to be infested later than cattle although they occur in the same habitat (Pegram *et al.*, 1982). In northern Somalia peak abundance occurs during the April–May rainy season (Pegram, 1976). In Nigeria adults peak in the May–June rainy season (Bayer & Maina, 1984).

At the southern end of its distribution in Zimbabwe adult *A. variegatum* occurs throughout the year, but heavier loads are present on cattle in the warmer, rainy season from September–May (Norval, 1983).

Levels of adult infestation may be high. Yeoman & Walker (1967) record a maximum single infestation of 458 adults for cattle in Tanzania. Kaiser *et al.* (1982) record a mean infestation of 42,7 males and 20,0 females/beast from January 1976–March 1977 in southern Uganda. Pegram *et al.* (1986) recorded a maximum of about 200 adults/beast in November/December 1981 in one of their study herds. On other herds studied adult ticks increased from less than 10 to about 75/beast usually during December or January. Easton & Tatchell (1981) record a maximum mean infestation of 122,8 adults/beast on the Malampaka herd in Tanzania in November 1973. In their study substantial annual variation occurred and in November 1974 the mean infestation was 11,4 adults/beast. In Ethiopia maxima of 438 adults/beast and 403 adults/beast have been recorded (Pegram *et al.*, 1981).

Nymphal and larval peaks vary in line with the variation found in the timing of adult peaks. When the adult peak falls in the period November-January, peak nymphal abundance occurs during the following dry season, usually between April and August (Wilson, 1950; Hoogstraal, 1956; Yeoman & Walker, 1967; MacLeod *et al.*, 1977). In Zambia Pegram *et al.* (1986) recorded peak nymphal abundance from May–September. In Tanzania nymphae peak from June–August at the Tabora site of Tatchell & Easton (1986) but possibly have a double peak (March–May, depending on locality, and in November) in Sukumaland. In Ethiopia, where the adults peak later than in other regions, immatures are most active between November and April (Pegram, 1979) while in Zimbabwe nymphae peak from June–December (Norval, 1983). Kaiser *et al.* (1982) record a mean of 72,0 nymphae/beast from January 1976–March 1977 in southern Uganda.

In Tanzania larvae peak twice in Sukumaland (March and November) but once (April) at Tabora (Tatchell & Easton, 1986). In Zambia peak larval abundance occurs from March–May (Pegram *et al.*, 1986), towards the end of the rainy season. Such March–April/May peaks are common when the adult peak occurs from November–January (MacLeod, 1970; MacLeod & Colbo, 1976; Yeoman & Walker, 1967; MacLeod *et al.*, 1977). Hoogstraal (1956) indicates that larvae engorge only during the dry season.

Kaiser *et al.* (1982) give a mean larval burden of 29,0/beast from January–March 1977.

Host Relationships and Heartwater Epidemiology

The *Amblyomma* species reviewed above can be divided into 3 reasonably well-defined groups according to their importance as vectors of *C. ruminantium* to domestic hosts.

(1) The major vectors are *A. hebraeum* and *A. variegatum*. Both these species have wide distributions, occur in large numbers and use cattle as preferred hosts for their adults. Sheep and goats are important hosts for the immature stages.

(2) Vectors of secondary importance are *A. astrion, A. cohaerens, A. gemma, A. lepidum* and *A. pomposum*. These species either have a limited distribution and/or occur in only small numbers on domestic stock. They may be locally important as vectors.

(3) Accidental vectors are *A. marmoreum, A. sparsum* and *A. tholloni*. These species do not normally feed on domestic stock and their influence is thus limited by their host range. The role of their nymphae as potential vectors may be of greater significance than that of their adults but this largely remains to be determined. *A. marmoreum* may be of greater importance than the other 2 species because when infected ticks are fed on tortoises, transmission of the organism to uninfected *A. marmoreum* can occur (Oberem, 1987). In addition *A. hebraeum* nymphae, which are efficient vectors, commonly use tortoises as hosts in some areas (Walker & Schulz, 1984; Dower, 1986), and any *A. marmoreum* feeding on these tortoises at the same time could become infected.

Our knowledge of host range is generally good for the adults of most species. However, considering the previous limitations in sampling technique, very little reliable, quantitative information is available for the immature stages of any species except *A. hebraeum* and *A. marmoreum*. Moreover, very little information is available on the relative success of natural infestations in terms of survival to the next moult or to egg laying. The importance of this information may be judged by the findings of Dower (1986). She determined that 14 leopard tortoises (*G. pardalis*) from Grahamstown, South Africa, harboured a total of 678 *A. hebraeum* nymphae and 18 *A. marmoreum* nymphae. However, only 48,7 % of the former moulted successfully, while 94,4 % of the latter species did so. Thus although the tortoises had a high natural infestation of *A. hebraeum* they were not particularly suitable as hosts.

TABLE 1 The habitats of the *Amblyomma* species capable of transmitting heartwater

Amblyomma spp.	Altitude (m)	Rainfall (mm)	Habitat*
A. astrion	0–1 000	500–1 700	wooded savanna
A. cohaerens	1 000–1 500	650–1 400	woodland, bushland and bushed grassland
A. gemma	0–1 830	250– 750	woodland, bushland, wooded and bushed grassland
A. hebraeum	0–1 525	300– 800	wooded and bushed grassland
A. lepidum	0–1 525	250– 750	woodland, bushland, wooded and bushed grassland
A. marmoreum	0–1 500	250– 900	wooded and bushed grassland
A. pomposum	1 200–1 700	800–2 000	highland wooded savanna
A. sparsum	0–1 830	250–1 250	wide range of wooded and grassland vegetation
A. tholloni	0–1 525	500–1 750	woodland, bushland, wooded and bushed grassland
A. variegatum	0–2 590	400–2 800	woodland, bushland, wooded and bushed grassland

* Habitat classification is highly simplified

A. hebraeum is also less successful at attaching to cattle than are species such as *Rhipicephalus appendiculatus* and *Rhipicephalus evertsi evertsi* (MacLeod, 1975), although this study did not measure relative engorgement success of those individuals which did attach.

Most parasites are not randomly distributed within their host population (Anderson & Gordon, 1982; Anderson & May, 1985). Ticks seem to be no exception. Kaiser *et al.* (1982) showed that some cattle consistently carried a higher load of female *A. variegatum* than did others. Thus 25 % of the herd carried 50 % of the female ticks. This pattern is consistent both within different life history stages of the same species and between different tick species. Thus the number of *A. variegatum* females found by Kaiser *et al.* (1982) was significantly positively correlated (at the 1 % level of significance) with the numbers of males and nymphae and larvae on the same animal. The number of *A. variegatum* females was also positively correlated with the number of female *R. appendiculatus*, *Boophilus decoloratus* and *Rhipicephalus simus* (1 % level of significance) and *R. evertsi evertsi* (5 % level of significance).

Such patterns of overdispersion may be generated by a number of different environmental mechanisms involving either the host or the free-living environment (Anderson & Gordon, 1982). These may include differences in the immune response of different hosts or non-random distribution of free-living ticks so that some hosts are more likely to come into contact with them than are others.

Factors Influencing Tick Distribution

The distribution of *A. tholloni* is largely the same as that of the host of its adults, namely the African elephant (*L. africana*). The only localities in which both have not been found together are the Bahr El Ghazal and Upper Nile provinces of the Sudan (Hoogstraal, 1956). At present *A. tholloni* is also not found in isolated southern populations of elephants such as that in the Addo Elephant National Park (eastern Cape Province, South Africa). The presence or absence of its main host must therefore be considered as the key factor influencing the distribution of *A. tholloni*.

A. astrion, *A. cohaerens*, *A. marmoreum* and *A. sparsum* also have relatively limited host ranges. However, the distributions of neither *A. astrion* nor *A. cohaerens* cover more than a fraction of the range of their buffalo host (Smithers, 1983; Walker & Olwage, 1987). Thus although the buffalo may be essential for the maintenance of populations of these species, some other factor(s) must determine their restrictions to a subset of the host's range.

A. marmoreum occupies a similar range to that of one of its main hosts, the leopard tortoise (*G. pardalis*) in southern and eastern South Africa (Grieg & Burdett, 1976; Walker & Olwage, 1987). As yet there are no published records of this tick from parts of the western regions of South Africa or South West Africa where the tortoise is also present. *A. sparsum* occurs in areas where suitable reptile and/or rhinoceros hosts are present. The distributions of *A. sparsum* and *A. marmoreum* abut in northern Zimbabwe (Norval, 1983; Walker & Olwage, 1987). This area defines the southern limit of *A. sparsum* and the northern limit of *A. marmoreum*. Neither hosts, climate, nor vegetation seem likely to prevent the southern and northern expansions of these species respectively.

A. gemma, *A. hebraeum*, *A. lepidum*, *A. pomposum* and *A. variegatum* all have wide host preferences and it is unlikely that their distributions are in any way limited by host availability.

Environmental preferences reflected by habitat and climate probably are of considerable importance in limiting distribution. Table 1 briefly summarizes the environments utilized by each species. Only *A. variegatum* occurs above 2 000 m above sea level with most species not exceeding 1 500–1 800 m. Rainfall seems to have a considerable influence with no species able to survive in areas with less than 250 mm p.a. Similarly all species seem to require ground covered by vegetation which can probably provide both litter and shade. Although Yeoman (1968) indicates that *A. variegatum* can exist in long grass without bush or tree cover, he does point out that it does not occur in short grass. MacLeod (1970) suggested a reduction in ground cover as a possible control mechanism for *A. variegatum*. The association between ticks and particular vegetation types can probably be explained in terms of the need for suitably cool, humid environments to permit successful moulting and egg laying as well as prolonged survival (Norval, 1977a; 1977b).

The association of a species with certain environmental characteristics should not be considered as necessarily causal. *A. hebraeum* had previously been thought to be limited on its northern boundary either by *Brachystegia-Julbernadia* vegetation (Theiler, 1962) or by higher rainfall (Jooste, 1967 cited by Norval, 1983). Neither of these hypotheses is correct as *A. hebraeum* has in fact extended its range into areas containing such vegetation and with higher rainfall (Norval, 1983). This expansion may have been made possible by the increased grass and scrub cover consequent to heavy stock losses (Norval, 1983).

One feature of distribution emphasized in Table 1 is the remarkable similarity in environmental requirements of all the *Amblyomma* vectors of heartwater. Differences do, however, exist. *A. lepidum* and *A. gemma* are usually found in more arid conditions than *A. variegatum* (Yeoman & Walker, 1967; Yeoman, 1968; Walker, 1974). *A. pomposum* is restricted by a higher threshold altitude than the other species although the range of altitudes at which it is found still falls largely within that of most other species. Although distributional boundaries frequently coincide with environmental limits this is certainly not universally true.

A number of species share more or less well-defined boundaries at which little or no overlap occurs. These boundaries seem not to occur in regions of major climatic or vegetational change. Thus *A. marmoreum* and *A. sparsum* have allopatric distributions except in northern Zimbabwe (Norval, 1983; Walker & Olwage, 1987). *A. hebraeum* and *A. variegatum* show a similar pattern (Norval, 1983; Walker & Olwage, 1987). *A. variegatum* and *A. pomposum* have more convoluted distributions, however, species ranges seem to abut in eastern Angola, Zaïre, Zambia and southern Tanzania (Walker & Olwage, 1987). *A. variegatum* overlaps the distributions of *A. lepidum* and *A. gemma* further north. *A. astrion* and *A. cohaerens* occur in west and east Africa respectively with distributions approaching each other in the north of Zaïre (Walker & Olwage, 1987). Few of these boundary areas have been mapped in detail and the degree of overlap between the species has not been quantified.

In Tanzania the distributions of *A. variegatum* and *A. lepidum* have twice been studied in detail at an interval of 15 years (Yeoman, 1968; Tatchell & Easton, 1986). Although the overlap is only about 30 km, the actual site of the boundary had moved about 130 km from Lake Victoria into the more arid areas of the country.

Such abutting distributions of ticks have previously been found. Thus *Ixodes ricinus* occurs in Europe while *Ixodes persulcatus* occurs in Asia with the boundary, including areas where both species are found together, running along the Urals in Russia (Smorondintsev, 1958). The best studied boundaries, however, occur between the reptile ticks *Amblyomma limbatum, Amblyomma albolimbatum* and *Aponomma hydrosauri* in Australia (Smyth, 1973). Bull and his co-workers have made detailed analyses of these boundaries using the working hypothesis that they were caused by some form of interaction between the species (Bull, Sharrad & Petney, 1981; Bull, 1986). To date no conclusive proof of this hypothesis has been presented although Andrews, Petney & Bull (1982) have demonstrated that the simultaneous occurrence of females of 2 of the species on the same host precluded successful mating of either species, perhaps through interference between their pheromone systems.

No comparable body of data has been built up for any of the abutting species pairs of *Amblyomma* in Africa. Nevertheless Tatchell & Easton (1986) suggest that the movement of the boundary between *A. lepidum* and *A. variegatum* was initially induced by the high rainfall years from 1961–1964 reducing the suitability of habitat for *A. lepidum* and allowing *A. variegatum* to move in. Subsequent maintenance of the boundary is thought to be due to some form of interspecific competition. Although data to support this contention are not available it is perhaps significant that both *A. lepidum* and *A. variegatum* share similar hosts, use the same preferred sites of attachment and occur at the same time of the year. It is worth noting that Tatchell & Easton (1986) state: "The distribution limits of ticks are not fixed and constant. They are determined by a complicated interplay of factors such as climate, vegetation, host density, susceptibility, grazing habits, etc. We are rarely able to appreciate more than the simplest relationships".

The boundary between *A. variegatum* and *A. hebraeum* has been studied in some detail by Norval (1983). *A. hebraeum* appears to have extended its distribution northwards with considerable rapidity between 1975 and 1980. Nevertheless *A. hebraeum* and *A. variegatum* have little significant overlap in spite of their preference for similar habitats. Previous reports suggest that *A. hebraeum* did not occur in Zimbabwe until introduced from South Africa early in the century (Jack, 1942), hence it is unlikely that the present boundary has existed for more than a short time. Nevertheless Norval (1983) suggests that interspecific competition between the 2 species may be responsible for the exclusion of *A. hebraeum* from the north-western area of Zimbabwe where conditions are otherwise suitable. It seems unlikely that the same type of reproductive interference occurs between these species as between the Australian reptile ticks because aggregation/attachment pheromones of both species have little interspecific activity (Norval & Rechav, 1979) and given a choice each species prefers to mate intraspecifically (Rechav, Norval & Oliver, 1982). Both species do, however, have similar preferred sites of attachment and similar seasonal maxima.

Too little information is available at present to determine whether interactions between *Amblyomma* species influence their distributions. Detailed maps of boundary areas are needed to determine how much overlap occurs and whether both species can be found on the same hosts. Once this information is available it would then be necessary to determine how the species interact.

Species of *Amblyomma* which occur sympatrically usually occur on different hosts. Species occurring on similar hosts are usually allopatric. Thus in general the main cattle parasites *A. hebraeum, A. lepidum, A. pomposum* and *A. variegatum* occupy different distribution ranges as do the 2 main tortoise parasites *A. marmoreum* and *A. sparsum* and the 2 main buffalo parasites *A. astrion* and *A. cohaerens*.

FACTORS INFLUENCING ABUNDANCE

An understanding of the factors influencing both the timing and the level of infestation reached during peak periods of abundance is of considerable epidemiological importance. Dipping strategies must relate to the timing of the peaks (Sutherst, Norton, Barlow, Conway, Birley & Commins, 1979), while the numbers of ticks attaching per host give some indication of the likelihood of an individual contracting heartwater.

Adequate information on seasonal abundance, however, is not available for *A. astrion, A. cohaerens, A. pomposum* or *A. tholloni*, while data are limited for either time, space and/or life history stage for *A. gemma, A. lepidum, A. marmoreum* and *A. sparsum*. Only *A. hebraeum* and *A. variegatum* have been studied for extended periods in different areas with data for larvae, nymphae and adults being collected. Most of the following discussion will therefore deal with the latter 2 species.

Adult abundance of the main herbivore parasites (*A. gemma, A. hebraeum, A. lepidum, A. variegatum*) is highest during the period of rains. This is independent of the timing of the rainy season. When more than 1 rainy season occurs p.a. it is possible for more than 1 generation to occur (*A. variegatum;* Hoogstraal, 1956). Peak larval numbers do not necessarily occur soon after the drop off of engorged females. Both Rechav (1982, 1984) working on *A. hebraeum* and Pegram *et al.* (1986) working on *A. variegatum* demonstrated larval peaks well after the time of first detachment of engorged females. In both species the delay is related to delayed oviposition by engorged females. *A. hebraeum* females do not lay eggs at temperatures below 14 °C (Rechav, 1984). This diapause has also been found in *Amblyomma nuttalli* and *A. sparsum,* which use reptiles as hosts (Belozerov, 1982). Belozerov has also indicated the possibility of diapause in embryonating eggs of *A. hebraeum* and *A. variegatum*. In the eastern Cape Province diapause in female *A. hebraeum* leads to 2 separate larval peaks. The one occurs soon after female detachment, while the other is delayed (Rechav, 1982, 1984). These peaks are mirrored in later nymphal peaks, but do not progress further, so that only a single adult peak occurs (Rechav, 1982, 1984).

The seasonal dynamics of reptile parasitizing *A. marmoreum* and *A. sparsum* may also include delays. The time taken to engorge is dependent on host temperature (Sweatman, 1970; Norval, 1978). Hence in *A. marmoreum* periods of attachment to the leopard tortoise of 104 days for larvae and 47 days for nymphae have been recorded during the cooler months (Dower, 1986). These attachment times are underestimates, as the ticks originated from natural infestations on the tortoises which were brought into the laboratory, and no estimate could be made of the time the ticks had already been attached.

The timing of peak abundance may vary annually by several months and actual abundance may also vary substantially both between sites within years and for the same site between years (Yeoman, 1968; Rechav, 1982; Pegram *et al.*, 1986; Tatchell & Easton, 1986). This presumably reflects differences either in factors controlling development, survival or activity. Development and survival in *A. hebraeum* is dependent on climatic conditions with the pre-oviposition period, nymphal premoult period and adult premoult period being determined by temperature (Norval, 1977b). Relative humidity seems to have little influence on the duration of any of these phases. The activity of *A. hebraeum* may, however, also be controlled by climatic factors. Norval (1977a) found substantial differences in which climatic factors were correlated with activity for different developmental stages. Larvae showed no significant relation between activity and weekly rainfall, temperature or daylength. Nymphal activity was significantly negatively correlated with daylength, temperature and rainfall in descending order of importance. It is also likely that there is an intercorrelation between daylength and temperature as well as rainfall. Rechav (1984) suggests that temperature is the main factor regulating seasonal activity in *A. hebraeum*.

Information on seasonal factors influencing the timing of *A. variegatum* peaks is lacking. This is a pity as the distribution of *A. variegatum* covers a very wide area which includes several quite different climatic zones. However, as the number of generations p.a. is directly related to the number of rainy seasons and as the months of maximum adult abundance vary widely, depending on when rain falls, it seems that rainfall is the key factor determining the seasonal cycle. As male activity begins before the onset of rains (Yeoman, 1968), the factor leading to increased activity is again likely to be climatic, such as daylength or temperature.

The factors controlling the peak population size attained at a specific sample site are also poorly understood. The microclimatic conditions experienced by the free-living life history stages of the ticks are thought to be of major significance. Thus the distribution of *A. hebraeum* larvae is largely confined to areas with ground cover and leaf litter, with the highest density occurring in shaded habitats with grass cover and well-drained soil (Norval, 1977a). Lateral movement of larvae is very limited (Rechav, 1979), hence they are unable to migrate to a more favourable habitat, so only females detaching in a suitable habitat are likely to have offspring. Thus population density is likely to be regulated by the amount of suitable habitat available for survival of the free-living stages as well as the time spent in this habitat by hosts during the main detachment phases of the tick (Rechav, 1978a). The number of hosts available is also important (Sutherst & Dallwitz, 1979; Norval, 1979). Rechav (1982) has shown that the population size of *A. hebraeum* is substantially higher in the humid coastal areas of the eastern Cape Province of South Africa, where summer temperature is lower and there is more vegetation, than in the drier, hotter, less vegetated inland areas. Pegram *et al.* (1986) suggest that the large number of *A. variegatum* present at Kabile in Zambia is probably related to the favourable habitat present in this site.

In a detailed laboratory study Norval (1977b) demonstrated that the percentage of *A. hebraeum* eggs hatching, as well as the percentage of larvae and nymphae successfully moulting and the survival time of larvae, nymphae and adults, are determined by saturation deficit and temperature. In general the smaller the life history stage the lower the saturation deficit and temperature needed for maximum survival.

PATHOGENS, PREDATORS, COMPETITORS AND INTERACTIONS WITH OTHER SPECIES

Very little information is available on the role of these factors in reducing the numbers of ticks present at a given time. This is true not only for the *Amblyomma* species discussed here, but for ticks in general.

Bacillus thuringiensis is pathogenic for a number of tick species including *A. hebraeum*. Females affected by this bacteria turn black and die without laying eggs, although engorgement does not seem to be influenced (Fiedler, 1969). In the north-western Transvaal up to 30 % of *A. hebraeum* females may be affected during May and June (Fiedler, 1969). Larvae and nymphae may also be affected (Petney, unpublished data, 1986). *B. thuringiensis* is a commonly used, commercially available agent for destroying insects.

Two parasitoids of the genus *Hunterellus* have been found to parasitize ticks of the genus *Amblyomma*. One undescribed species has been recorded from *A. nuttalli*, a reptile tick, from the Ivory Coast (Graf, 1979). The other, *Hunterellus hookeri*, has been recorded in South Africa, predominantly from ticks of the genera *Hyalomma* and *Rhipicephalus* (Cooley, 1934; Fiedler, 1953). Santos Dias (1948) has also recorded it from *A. tholloni* from Maputo, Moçambique. In both cases nymphae were infested. No parasitoids were found in *A. variegatum* collected at the same site as *A. nuttalli* by Graf (1979).

No parasitoids were found in the 11 487 male and 7 223 female *A. hebraeum* studied by Rechav (1978b). However, most authors have recorded the insects from nymphal and sometimes larval ticks, not adults (Cooley, 1934; Smith & Cole, 1943; Fiedler, 1953; Hoogstraal & Kaiser, 1961; Doube & Heath, 1975; Graf, 1979). Cooley (1934) did not record any parasitoids from *A. hebraeum* collected in South Africa. Given the lack of records on parasitoids of *Amblyomma* species it seems unlikely that these insects have any real influence on population levels.

The presence of the dipteran *Megaselia scalaris* infesting a laboratory colony of *A. variegatum* (Garris, 1983) seems of little consequence for free-living ticks.

Amblyomma species parasitic on large herbivores of the Perissodactyla, Artiodactyla and Proboscidae are subject to predation by the red and probably yellow-billed oxpeckers, *Buphagus erythrorhynchus* and *Buphagus africanus* (Moreau, 1933; Attwell, 1966; Bezuidenhout & Stutterheim, 1980). Moreau (1933) records 16 of his sample of 58 red-billed oxpeckers collected in Tanzania as having eaten 186 *A. variegatum* between them; the life history stage was not given. In the Kruger National Park 51 of 53 red-billed oxpeckers had *Amblyomma* sp.

in their stomach contents (Bezuidenhout & Stutterheim, 1980). These included all possible life history stages (7 males, 13 females, 643 nymphae, and 1 531 larvae). Maxima of 68 nymphae and 272 larvae were recorded from individual birds. Nevertheless *Amblyomma* was less important in the birds' diet than either *Boophilus* or *Rhipicephalus*. Under experimental conditions the birds preferred *B. decoloratus*, *R. appendiculatus* and *Hyalomma truncatum* adults to *A. hebraeum* adults. Engorged female *A. hebraeum* were too large for birds to swallow (Bezuidenhout & Stutterheim, 1980). Nevertheless the daily food intake of 14,7 g (equal to 7 195 engorged *A. hebraeum* larvae), and the possibility of numerous birds feeding on a single host, indicate that oxpeckers may exert some pressure on population numbers.

Very little information is available on the role of the yellow-billed oxpecker as a tick predator. Other species of birds have not been recorded as major predators of *Amblyomma* species.

Predation of free-living stages is almost unknown in a quantitative or qualitative sense. Norval & McCosker (1983) recorded a rainbow skink (*Mabuya quinguetaeniata margaritifer*) eating an engorged female *A. hebraeum* in Zimbabwe. Another species of skink (*Gerrhosaurus flavigularis*) was observed eating 2 *A. hebreaum* nymphs on grass stems in South Africa (Norval, 1976). This seems to be the sum total of information available.

It seems intrinsically likely that predation of free-living stages is much higher than recorded. Predation has been considered in very few publications as it is difficult to observe, thus lack of opportunity or interest has probably contributed to the paucity of information. However, an engorged larva, nymph or female tick is a slow moving, blood-filled object with high protein content and would presumably be a highly suitable meal for a predator. Certain studies of other species have indicated the potential of invertebrates and more particularly ants as important predators of ticks. Wilkinson (1970a) explains the scarcity of *Boophilus microplus* from certain zones in Australia, which are otherwise suitable for its survival, because of ant predation. He lists 15 species of ants from 10 genera as predators. In Moreles State, Mexico the fire ant (*Solenopsis geminata*) is a common predator of *B. microplus*, with substantial numbers of females experimentally exposed being eaten (Butler, Camino & Perez, 1979). The actual percentage eaten is dependent on the habitat in which the tick is exposed, with less predators occurring in bush or woody vegetation. *Amblyomma americanum* is also a victim of fire ant predation. Eggs and engorged larvae released in an ant infested plot in Louisiana U.S.A. were largely destroyed over a 72 h period while a similar release in a plot treated with formicide showed very small losses (Harris & Burns, 1972). Engorged females also survived significantly better in the plot treated with formicide. The density of *A. americanum* decreased rapidly as fire ant density increased (Burns & Melancon, 1977).

In Australia *A. limbatum* and *Ap. hydrosauri* have a higher mortality in cages allowing predator access than in closed cages (Bull, 1986). Ant species found in the area of these experiments will prey on both tick species in the laboratory (Bull, unpublished data, 1986). Other potential tick predators include spiders (Wilkinson, 1970a; Ault & Elliot, 1979), lizards (Wilkinson, 1969, 1970a), toads (Verissimo, Rocha, Ferrari, Garcia, Martucci & Homan, 1985), birds (Wilkinson, 1970b; Theiler, 1975) and mammals (Short & Norval, 1982). This list is not intended to be comprehensive but is rather aimed at showing that predation of free-living stages may be of consequence in determining population levels.

The influence of self-grooming by rodents and primates on infestation levels has not been assessed.

No evidence exists to indicate that competition is important in regulating populations of *Amblyomma*. Serious competition with members of the same genus over much of their range seems unlikely given the separation between the species either through different host preferences or geographically. In particular, the *Amblyomma* parasites of large herbivores seem to occupy largely allopatric distributions with the exception of *A. gemma* and *A. lepidum*.

Richardson (1930) indicates that *A. cohaerens* and *A. variegatum* may occur together in large numbers on cattle which are occupying old buffalo grazing grounds. In the absence of recent records it is doubtful whether this finding is of much consequence. It would be interesting to look for interactions between *A. gemma* and *A. lepidum* as both species are reasonably common on cattle in Tanzania (Yeoman & Walker, 1967). Both are most abundant as adults during the rainy season and both prefer to attach to the ventral surfaces of the cattle.

The potential for interaction between the various *Amblyomma* species, should they occur together, seems high as peak seasonal abundance is usually linked with the rainy season and all species have similar preferred attachment sites on their hosts.

Competition with other species of ticks is unlikely as the other species occurring in large numbers often attach to different areas of the host. Thus, while *A. variegatum* adults prefer to attach to the ventral abdomen, *B. decoloratus* uses the back and abdomen, *R. appendiculatus* the ears, *R. evertsi evertsi* the anal/vulval area and *R. simus* the hooves (Kaiser *et al.*, 1982).

THE COMMUNITY OF TICKS

The *Amblyomma* vectors of heartwater comprise only a part of the tick fauna found on any individual host. Although members of this genus may be the dominant tick parasites in certain areas, this is not universally true and both *B. decoloratus* and *R. appendiculatus* may far outnumber them.

From the epidemiological point of view it is important to know which species of ticks occur in the same area and whether different species of ticks interact with one another.

The similarity in distribution patterns between *A. variegatum* and *R. appendiculatus* has frequently been noted (Hoogstraal, 1956; Yeoman, 1968; Tatchell & Easton, 1986). *R. appendiculatus* is more sensitive to aridity than *A. variegatum* and does not extend as far into arid areas (Yeoman, 1968; Walker, 1974; Tatchell & Easton, 1986). In Tanzania although *A. variegatum* is always present where *R. appendiculatus* is present, *R. appendiculatus* is always present only where *A. variegatum* is abundant (Yeoman & Walker, 1967). *R. appendiculatus* is also found in much the same regions as *A. hebraeum* in southern Africa (Howell *et al.*, 1978). Concurrent infestations of each species pair on the same host are common as the maximum period of abundance falls at approximately the same time (Rechav, 1982; Tatchell & Easton, 1986).

The distribution of *A. lepidum*, which is largely found in drier areas than *A. variegatum*, overlaps with those of *A. gemma*, *Hyalomma albiparmatum*, *Hyalomma marginatum rufipes* and *Rhipicephalus pravus* (Yeoman & Walker, 1967).

Such distributional overlap between species is often associated with a preference for different feeding sites or host species, thus limiting the potential for interactions. In a detailed study of the relationships between tick species attacking Zebu cattle in southern Uganda, major differences in the attachment sites of the 5 commonest tick species occurred (Kaiser *et al.*, 1982). Over 65 % of adult *R. appendiculatus* occurred on the ears, over 75 % of *A. variegatum* on the abdomen, over 70 % of *B. decoloratus* on the back or abdomen, over 90 % of *R. evertsi evertsi* on the anal/vulval area and over 70 % of *R. simus* from around the hooves.

FUTURE PROSPECTS

The large number of surveys which have already been conducted and which include data on the more important *Amblyomma* vectors of heartwater provides a strong baseline of data. However, there is a surprising lack of information on basic ecological factors likely to influence either the distribution or the abundance of the species concerned.

The recent improvement in techniques for quantifying the importance of different host species as vectors of immature stages of *Amblyomma* opens up the possibility of substantial increases in our knowledge in this area. In general our understanding of the ecology of the immature stages is much poorer than that of the adults.

More attention should be paid to the possibility that interactions between species of the genus influence distributional limits. The possibility of interactions with predators and pathogens in limiting abundance should also be considered in more detail. Both of these areas are open to experimental analysis.

Little attention has been paid to the distribution of any members of the genus *Amblyomma* within the host population. The importance of knowing such distribution patterns in epidemiological research has recently been stressed (Anderson & May, 1985). Both models of heartwater transmission as well as implementation of control strategies would benefit by such information.

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