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# Distribution and phenology of ixodid ticks in southern Zambia

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**Abstract.** Distribution data for epidemiologically important ticks (Acari: Ixodidae) in the Southern Province of Zambia, one of the main cattle areas of the country, are presented. *Boophilus microplus* (Canestrini) was not recorded in southern Zambia, whereas *Boophilus decoloratus* (Koch) is present throughout the area. New distribution patterns for less economically important ixodid ticks are also discussed. Southern Zambia is a transition zone because it is the most northern area in Africa where mixed *Rhipicephalus appendiculatus* Neumann and *Rhipicephalus zambeziensis* Walker, Norval & Corwin populations were reported. Although a second generation of adult *R. appendiculatus*/*R. zambeziensis* was encountered, simulations indicated that this phenomenon is very rare in southern Zambia, mainly because of the colder temperatures during the early dry season and lower rainfall. These simulations were supported by a development trial under experimental conditions. Tick body size measurements showed that southern Zambian ticks are larger than eastern Zambian *R. appendiculatus*. It is hypothesized that body size is related to diapausing intensity in this species. The epidemiological consequences are that a different approach to control *Theileria parva* (Theiler) (Piroplasmida: Theileriidae) and other tick-borne diseases is needed in southern Zambia, compared to the one adopted in eastern Zambia.

**Key words.** *Rhipicephalus*, *appendiculatus*, *Rhipicephalus zambeziensis*, *Theileria parva*, epidemiology, ticks, Zambia.

## Introduction

Tick-borne diseases are a major constraint for livestock production in developing countries (Norval *et al.*, 1992). Theileriosis, caused by *Theileria parva* (Theiler), constitutes an especially serious threat to the traditional cattle sector in Zambia (D'Haese *et al.*, 1999). Its vectors, *Rhipicephalus appendiculatus* Neumann and *Rhipicephalus zambeziensis* Walker, Norval & Corwin, have been recognized as the most economically important tick species throughout eastern and southern Africa (De Vos, 1981). Other tick-borne diseases, such as anaplasmosis, babesiosis and cowdriosis, cause low mortality in the traditional sector because of an endemically stable situation (Moorhouse & Snacken, 1984; Berkvens, 1991; D'Haese *et al.*, 1999). They become important in the commercial sector whenever tick control is not optimal. Hence, although Jongejan *et al.* (1988) rightly indicate the secondary importance of babesiosis in north-eastern Zambia, the traditional cattle sector of Zambia focuses its control of tick-borne diseases on the control of theileriosis. Effective control of theileriosis depends on the knowledge of the distribution and dynamics of the vector (Norval *et al.*, 1992). For example, in eastern Zambia, a second peak of adult *R. appendiculatus* at the start of the dry season ensures a more continuous presence of vector

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competent nymphs and adults throughout the year, with peak numbers of adults on cattle in both January and May and peak numbers of nymph on cattle in May and September (Berkvens *et al*., 1998). The simultaneous presence of adults and nymphs on cattle can result in high levels of transmission from ticks to cattle and cattle to ticks and, perhaps more importantly, infection may be picked up from clinically ill cattle (Norval *et al*., 1991; Billiouw *et al*., 1999). Moreover, adult ticks of the second wave at the start of the dry season (May) are non-diapausing ticks, which transmit *T. parva* soon after moulting, when the parasite is still highly infective (Young *et al*., 1987). Under such epidemiological conditions immunization using the infection-and-treatment method is an effective way of controlling *T. parva* (Billiouw *et al*., 1999).

In the northern part of southern Zambia a strictly unimodal phenology has been observed with adults entering a behavioural diapause, induced by short day lengths at the start of the dry season (MacLeod, 1970; Pegram *et al*., 1986). This results in a more epidemic situation and control measures have to be adopted accordingly (Mulumba *et al*., 2000, 2001). Further south, in Zimbabwe, the activity of adult *R. appendiculatus* also appears to be restricted to the rainy season (Matson & Norval, 1977; Short & Norval, 1981; Minshull & Norval, 1982). The above indicates that the Southern Province of Zambia may form a transition zone where the phenology changes from multimodal to strictly unimodal. Cross-sectional surveys were conducted in the Southern Province of Zambia to update the knowledge of the distribution of ixodid tick species, emphasizing those of veterinary importance. An attempt was also made to map the occurrence of *R. zambeziensis*. Differences with available information on eastern Zambia are highlighted. In general, the importance of repeating an investigation of tick population dynamics 30 years after MacLeod (1970) and 10 years after Pegram *et al*. (1986) lies in the fact that it allows long-term comparisons. Changes in control methods (e.g. acaricides) and altered vegetation may alter tick populations. The phenology of the *R. appendiculatus*/*R. zambeziensis* complex was studied at various locations in the transition zone by means of longitudinal studies. A simulation model was developed to clarify differences in the phenology of *R. appendiculatus* between eastern and southern Zambia. Understanding the differences between eastern and southern Zambia in *R. appendiculatus* phenology is essential, as it assists in effective control programmes (e.g. immunization vs. vector control). A trial investigating the development periods under semi-natural conditions was used to support the simulation model. For the same reason, size measurements were undertaken to compare these with those reported by Chaka *et al*. (1999). The authors wish to stress that they use the specific names *R. appendiculatus* and *R. zambeziensis* for the sake of convenience (and brevity) only and that according to them it is still a matter of discussion whether the two entities constitute proper biological species, cryptospecies, subspecies or merely extreme morphs of a single species.

## Materials and methods

### *Study area*

Southern Province of Zambia is situated between 25°01′ and 28°40′ E and between 15°14′ and 17°42′ S. It covers a total area of about 85 300 km$^2$ (Fig. 1), and is bordered by

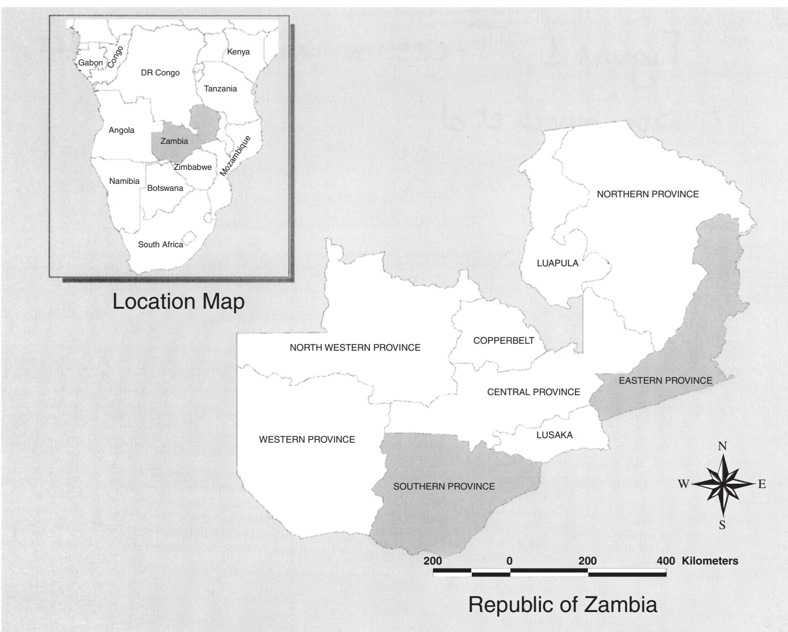


**Fig. 1.** The study areas in Zambia: Eastern and Southern Province.

 

the Zambezi River to the south and Lake Kariba to the east. To the north, the Province extends to the Kafue River, and the Central and Western Provinces border it in the west. The climate comprises three seasons: the warm rainy season from November to April, the cool dry season from May to August and the hot dry season from September to October. Woodlands and grassland dominate the vegetation. The predominant vegetation types are the *Brachystegia* spp. (Miombo) and *Acacia* spp. (Munga) woodlands on the plateau. *Colophospermum mopane* (Bentham) and scrub woodlands are found in the valley areas and on the Kalahari sands. Southern Province is the most important cattle area in Zambia, holding about 800 000 head (of a total of 2.9 million in Zambia; APHP, 1999). In communal areas tick-borne diseases are controlled by strategic vector control, immunization or curative treatment (D'Haese *et al.*, 1999). Eastern Province has been described by Berkvens *et al.* (1998) and is shown in Fig. 1.

*Surveys*

Tick surveys were conducted between February 1995 and August 1997, involving 75 sampling sites situated in all nine districts of Southern Province (Fig. 2). The majority of the surveys were carried out in February. The other months were chosen to allow for the possibility of a second wave of *R. appendiculatus* or *R. zambeziensis* adults. At each locality, one farmer with sufficient animals, not using any kind of tick-control was selected at random, and 20 animals were selected randomly from his herd. All ticks from both ears and dewlap of each animal were collected, stored in 70% ethanol and examined under a stereoscopic dissection microscope. The ticks were identified and life cycle stage and sex (where applicable) were determined. Distinction between *R. appendiculatus* and *R. zambeziensis* was based on Walker *et al.* (1981). Representative samples were sent to Dr Jane B. Walker and Dr Ivan G. Horak at the Onderstepoort Veterinary Institute (South Africa) for confirmation. Classification and Regression trees (CART) (Steinberg & Colla, 1995) were used to determine the effects of locality (district) and year of sampling on the tick numbers. Depending on the outcome of the analysis, tick densities were pooled.

*Longitudinal studies*

Sentinel cattle were sampled along a transect starting at an altitude of 900 m (Kafue Flats), climbing to 1200 m

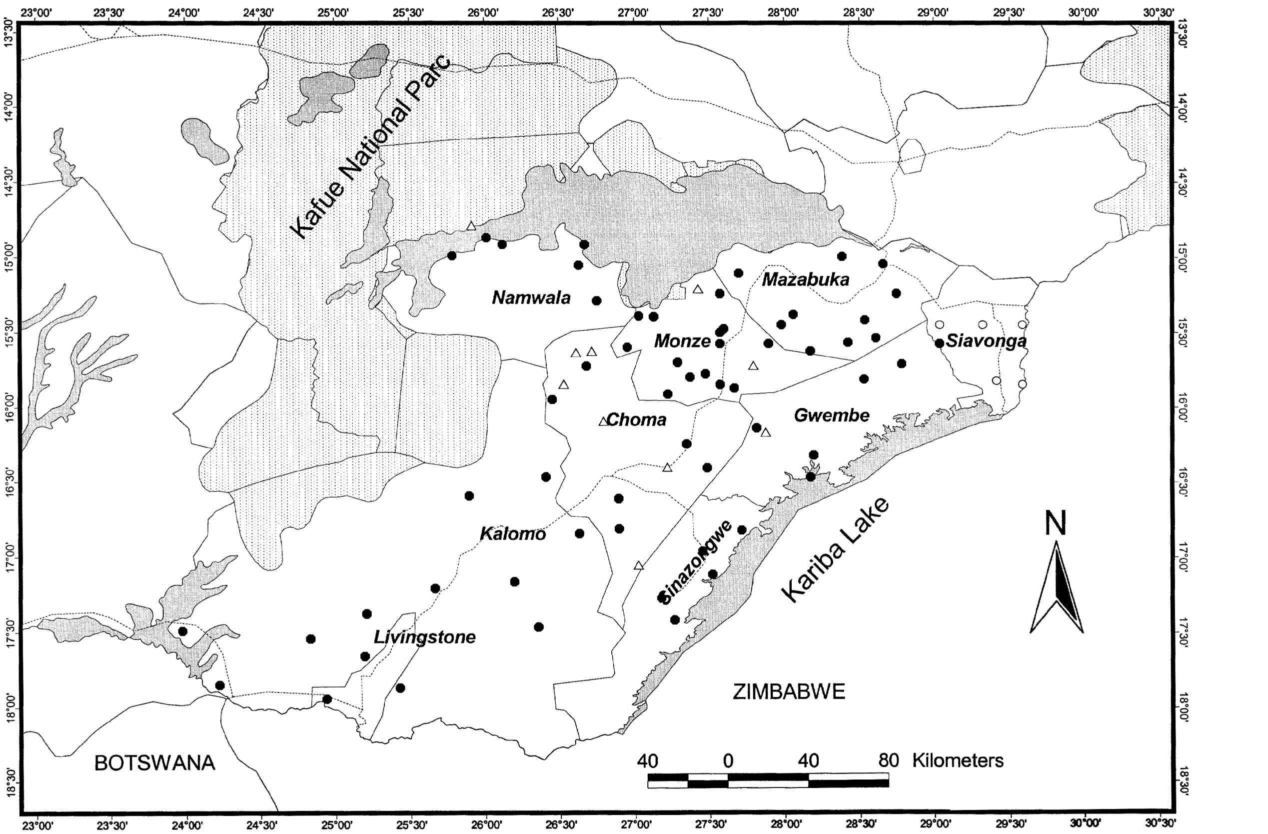


**Fig. 2.** Survey localities ($n = 75$) where *R. turanicus*, *B. decoloratus* and *R. supertritus* were found (△, $n = 10$), where *R. turanicus* and *B. decoloratus* were found (●, $n = 60$) and where none of these species were found (○, $n = 5$).

(Monze) and descending to 600 m (Gwembe-valley) in order to determine seasonal dynamics of the *R. appendiculatus*/*R. zambeziensis* complex. The Livingstone area (900 m) was added to investigate the influence of this specific microclimate caused by the nearby Victoria Waterfalls. Samplings were conducted at 12 localities between December 1993 and May 1998 (Fig. 3). One farmer was selected at each location and about 25 cattle from different age categories were identified and ear-tagged. The sentinel animals were kept under traditional management practices and not treated with acaricides. Ticks were collected monthly from the sentinel cattle in the way described above.

### *Population modelling (simulations)*

A simulation model was developed to identify factors responsible for the difference in *R. appendiculatus* phenology between southern and eastern Zambia. Magoye Research Station near Monze (16°05′ S) and the Msekera Agriculture Research Station near Chipata (13°39′ S) were chosen as localities representative for southern and eastern Zambia, respectively. For the sake of simplicity, these localities are further referred to as Monze and Chipata. In eastern Zambia, Berkvens *et al.* (1998) and Chaka *et al.* (1999) found a second wave of adults at the start of the dry season under similar climatic conditions. Climate data were rainfall, temperature and relative humidity averages obtained from records collected between 1994 and 1998 (Monthly Bulletins of the Meteorological Department, Lusaka).

Development times were calculated based on the principle of fractional development as described by Gardiner & Gettinby (1981), using development parameters of Branagan (1973). Due to the lack of detailed records, average temperatures were used, which may slightly overestimate the development periods. A vapour pressure deficit (VPD) of 1004 Pa was used as the critical equilibrium humidity (CEH) for larvae (Londt & Whitehead, 1972). The simulations were all carried out in EXTEND 3 (Imagine that, 1995), a simulation tool. A deterministic model was developed simulating the development from one stage to another. To validate the simulation model for southern Zambia, a full generation of field ticks was allowed to develop under quasi-natural conditions.

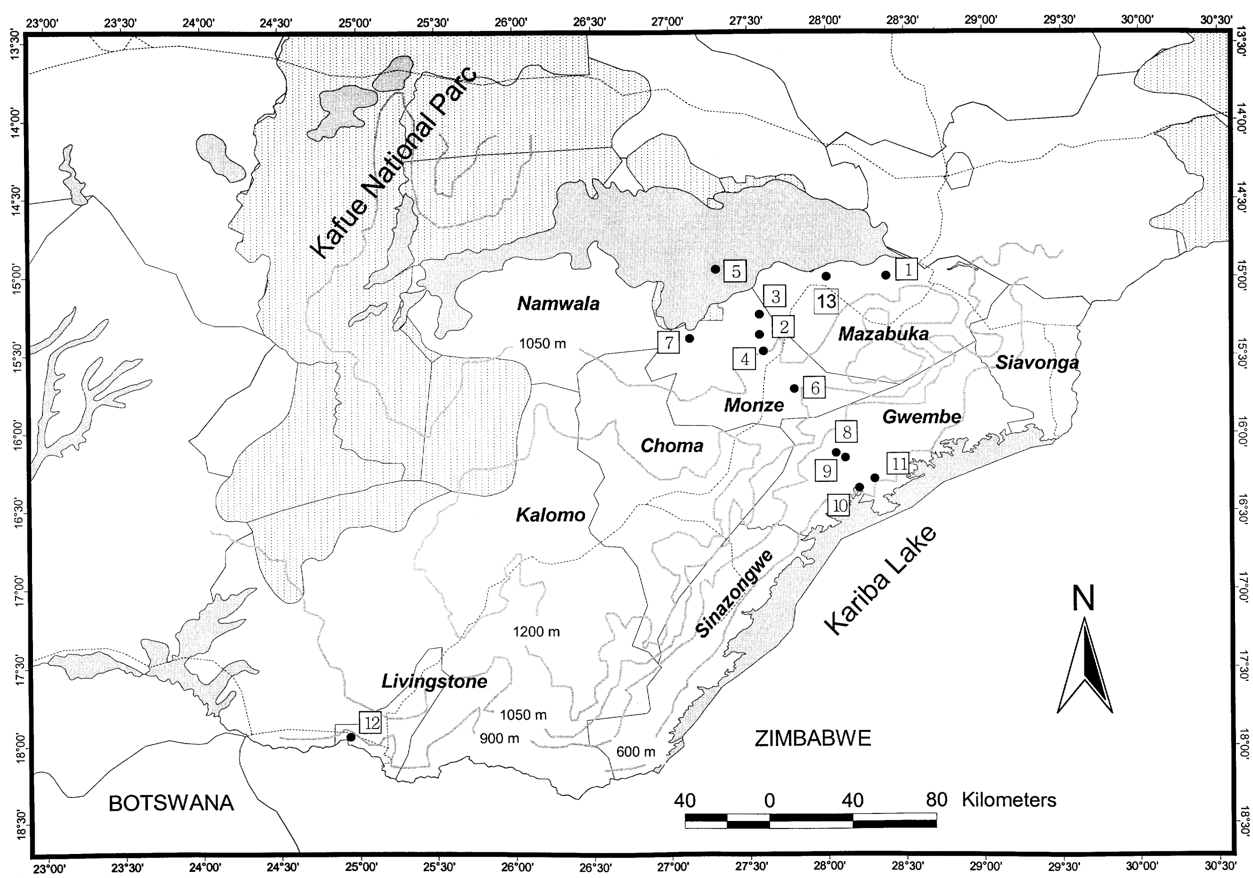


**Fig. 3.** Location of sentinel herds in Southern Province Zambia used in the longitudinal study. 1 = Nega-Nega (1010 m), 2 = Nteme (1050 m), 3 = Keemba (1050 m), 4 = Kayuni (1100 m), 5 = Kafue Flats (950 m), 6 = Sikabenga (1160 m), 7 = Nakasagwe (1020 m), 8 = Lukonde (700 m), 9 = Halubilo (800 m), 10 = Siabwengo (600 m), 11 = Sinafala (550 m), 12 = Simonga (990 m); grey = flooded area, dotted = National Parks.

In December 1995, engorged females were collected from the sentinel herd at Nteme (Fig. 3) and placed at ground level in an experimental plot in Mazabuka (Fig. 3). They were confined in open-ended plastic rings (diameter 1 cm) sealed with gauze and covered by about 1 cm of soil and leaf litter. The ticks were followed up daily and their developmental stage was recorded. Temperature at ground level was measured using a Rolog® climate data logger (Kritech, Eupen, Belgium). After hardening, larvae were fed on rabbits. Engorged larvae, moulting to nymphs, and afterwards engorged nymphs were treated in the same way as the engorged females. Pre-oviposition, pre-eclosion and pre-ecdysis times were determined. *Rhipicephalus appendiculatus* body size was measured to allow comparison with results reported by Chaka *et al.* (1999). The maximum distance between the tip of the scapular processes and the distal end of the conscutum was used. Ticks for measurements came from collections in February and March when peak *R. appendiculatus* adult numbers are expected in Siabwengo (herd 10), Simonga (herd 12) and Nteme (herd 2). A series of 30 male ticks were measured with a micrometer mounted on a stereoscopic dissection microscope, allowing a resolution of 1.25 μm. The analysis of the sizes was done by regression analysis and Scheffé multiple-comparison test.

## Results

### *Surveys*

Ticks were found at all sampling sites, with the exception of a few localities near Kariba Lake in Siavonga District. The rainy season distribution of ixodid ticks is in line with previous observations made in the northern part of Southern Province by MacLeod (1970) and Pegram *et al.* (1986). *Boophilus decoloratus* (Koch) was present in all areas except for Siavonga (Fig. 2). *Amblyomma variegatum* (Fabricius) was absent in the Gwembe area and in Siavonga. *Hyalomma truncatum* Koch was absent in Gwembe, Namwala and Siavonga. *Hyalomma rufipes* Koch was absent in Gwembe and Sinazongwe. *Rhipicephalus supertritus* Neumann was observed at various localities (Fig. 2). *Rhipicephalus turanicus* Pomerantsev was widely distributed (60 localities) and *Rhipicephalus evertsi evertsi* Neumann was found throughout Southern Province except in Siavonga. *Rhipicephalus lunulatus* Neumann, *Rhipicephalus simus* Koch, *Rhipicephalus kochi* Dönitz., *Rhipicephalus* sp. near *pravus* Donitz and *Rhipicephalus* sp. near *punctatus* Warburton were only encountered sporadically.

Regression tree analysis classified *R. appendiculatus* and *R. zambeziensis* burdens on animals at the different sampling sites in Southern Province according to the district of collection, rather than the year of collection. Hence, tick density data from 1995 to 1997 were pooled. The average numbers of adult *R. appendiculatus* collected in February between 1995 and 1997 are presented in Fig. 4, also showing areas where either *R. zambeziensis* or *R. appendiculatus* or both were collected. Mixed populations of *R. appendiculatus* and *R. zambeziensis* were mainly found at altitudes below about 1100 m. Most of the homogeneous *R. appendiculatus* populations occurred at higher altitudes. In Livingstone, near the Victoria Waterfalls, homogeneous *R. appendiculatus* populations were found at an altitude of 900 m. The highest numbers of ticks were found in Monze and neighbouring localities in Gwembe, parts of Choma and Livingstone Districts. In the surveys, mean adult tick numbers per animal in February ranged from zero to 63 in Siavonga and Simonga, respectively. During the cold dry season, relatively high numbers of adults were collected only at Nakasagwe in Namwala District (average burden (mean ± SD) of five (4.9 ± 3.10) and four (4.0 ± 4.51) in June 1995 and August 1997, respectively, compared to 0.72 (±2.72) and 0.16 (±0.97) for the other localities), suggesting a special phenology for the *R. appendiculatus*/*R. zambeziensis* complex at this locality.

### *Longitudinal studies*

Figures 5 and 6 show *R. appendiculatus*/*R. zambeziensis* burdens in the different sentinel herds. All samples in the longitudinal studies except those from Livingstone and Sikabenga (where only *R. appendiculatus* was found) contained both *R. appendiculatus* and *R. zambeziensis*. In general, a strict monomodal adult activity pattern was observed throughout the province. Adults feed during the rainy season and nymphs are seen throughout the cold season. Numbers of larvae found were insufficient to draw conclusions. Peak average adult numbers in February vary between nearly zero in Lukonde (Gwembe) and 190 in Simonga (Livingstone). Within some localities (e.g. Nteme), peak tick numbers seemed to vary little over the years. A second wave of adults at the start of the dry season was only observed at Nakasagwe (unfortunately this study could not be continued due to the lack of collaboration on the part of the farmer) and Nega-Nega (Mazabuka District). Nymphs were never found at Nakasagwe and very low numbers of nymphs were seen in Keemba. In the Gwembe valley only marginal populations were seen at intermediate altitude (*c.* 700–800 m), whereas at lower altitudes (500–600 m) higher numbers was present. At Siabwengo, the adult *R. appendiculatus*/*R. zambeziensis* peak occurred later during the rains (March–April).

### Rhipicephalus appendiculatus *life cycle simulation*

The start of the rains does not differ much between eastern and southern Zambia (Fig. 7) but rains end earlier in southern Zambia and total rainfall is lower there, except for 1995 (year with little rainfall). Simulations showed that females engorging in early January in southern Zambia could produce questing females by 23 April and in Eastern Province by 28 April. Day lengths (as defined by List, 1951) are identical at both localities at that time of the year

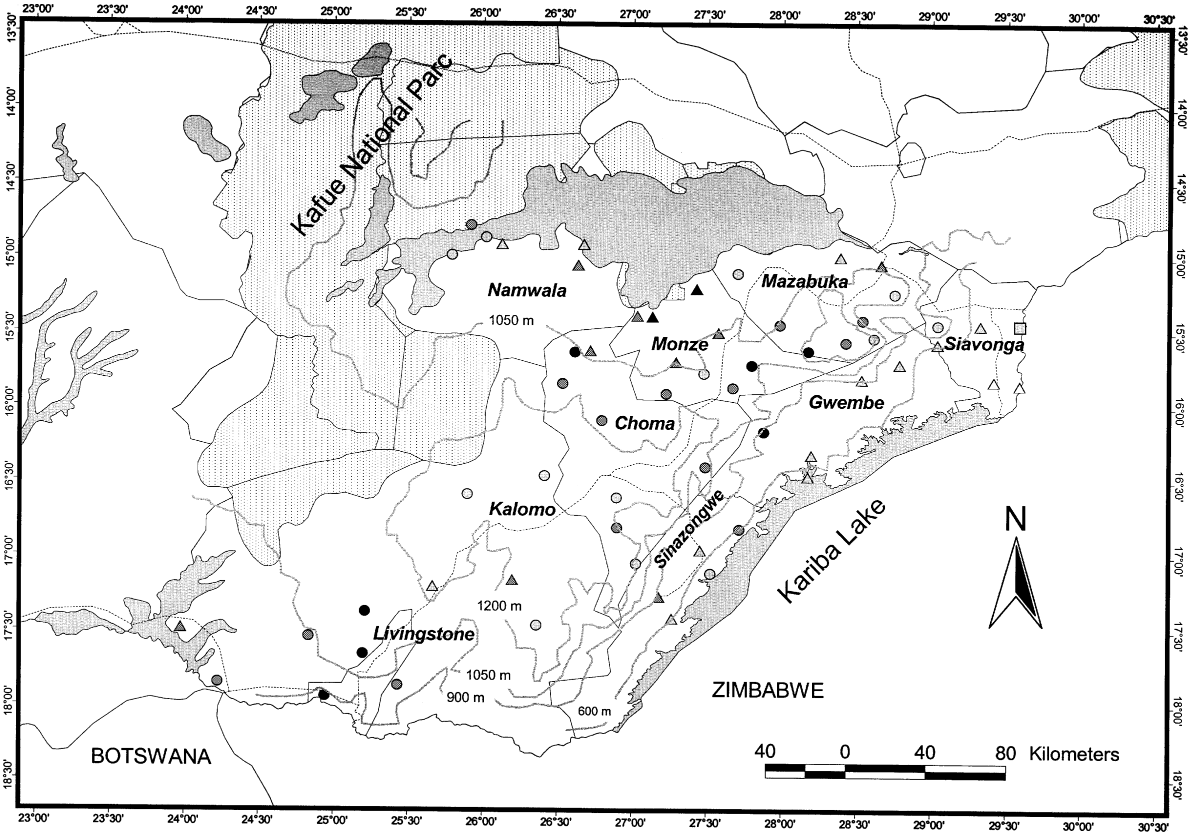


**Fig. 4.** Average cattle burdens of *R. appendiculatus*/*R. zambeziensis* found in Southern Province, Zambia. Circle = *R. appendiculatus*, triangle = mixed *R. appendiculatus*/*R. zambeziensis*, square = *R. zambeziensis*; white = 0, light grey = 1–5, grey = 6–20, black = >20.

(11 h 39 min and 11 h 38 min for Chipata and Monze, respectively). The principal difference between the two areas is found in the cold-season temperatures, which are considerably lower in southern Zambia, mainly due to the strong differences in minimum temperatures (Fig. 8). A newly moulted population of adult *R. appendiculatus* in early May develops much slower in Monze than in Chipata. Using the development parameters obtained by Branagan (1973), this population results in larvae by 7 July in Chipata, when relatively low VPD values (987 Pa) and morning dew are recorded, enabling the larvae to survive and quest, and by 17 August in Southern Province when the hot dry season starts with very inimical conditions for the larvae (VPD = 1347 Pa).

The results of the development trial (Table 1) indicate that the engorged females collected from animals in the field in December 1995 resulted in new females by the beginning of May. Predictions made using recorded temperatures at ground level and the relations between temperatures and development rates found by Branagan (1973) show a good fit.

Male *R. appendiculatus* found on cattle in Southern Province are larger than those encountered in Eastern Province, which range from 2.57 to 2.70 mm (Chaka *et al.*, 1999). The sizes of male adults measured in February and March were (mm mean ± SD): Nteme: 2.84 ± 0.36; Simonga: 3.23 ± 0.30; Siabwengo: 2.76 ± 0.51; Nega-Nega: 3.10 ± 0.33; Nakasagwe: 2.710 ± 0.33. Using the data from Eastern and Southern Provinces together in a regression analysis revealed significantly larger ticks in Southern Province ($P < 0.001$). Using a Scheffé multiple-comparison test, sizes in Simonga were significantly higher ($P < 0.05$) than sizes in all localities except Nega-Nega. Sizes in Nega-Nega were significantly higher ($P < 0.05$) than sizes in Nakasagwe but not higher than sizes in the other localities and there were no significant differences in the sizes of Nteme, Siabwengo and Nakasagwe.

## Discussion

### *Surveys*

*Boophilus microplus* (Canestrini) is still absent from Southern Province of Zambia in contrast to Eastern Province, where *B. decoloratus* has been replaced by *B. microplus* (Berkvens *et al.*, 1998). The traditional herd in Southern Province thus still has not been exposed to *Babesia bovis* (Babès) (transmitted by *B. microplus* but not by *B. decoloratus*). Anaplasmosis, transmitted by *B. decoloratus*,

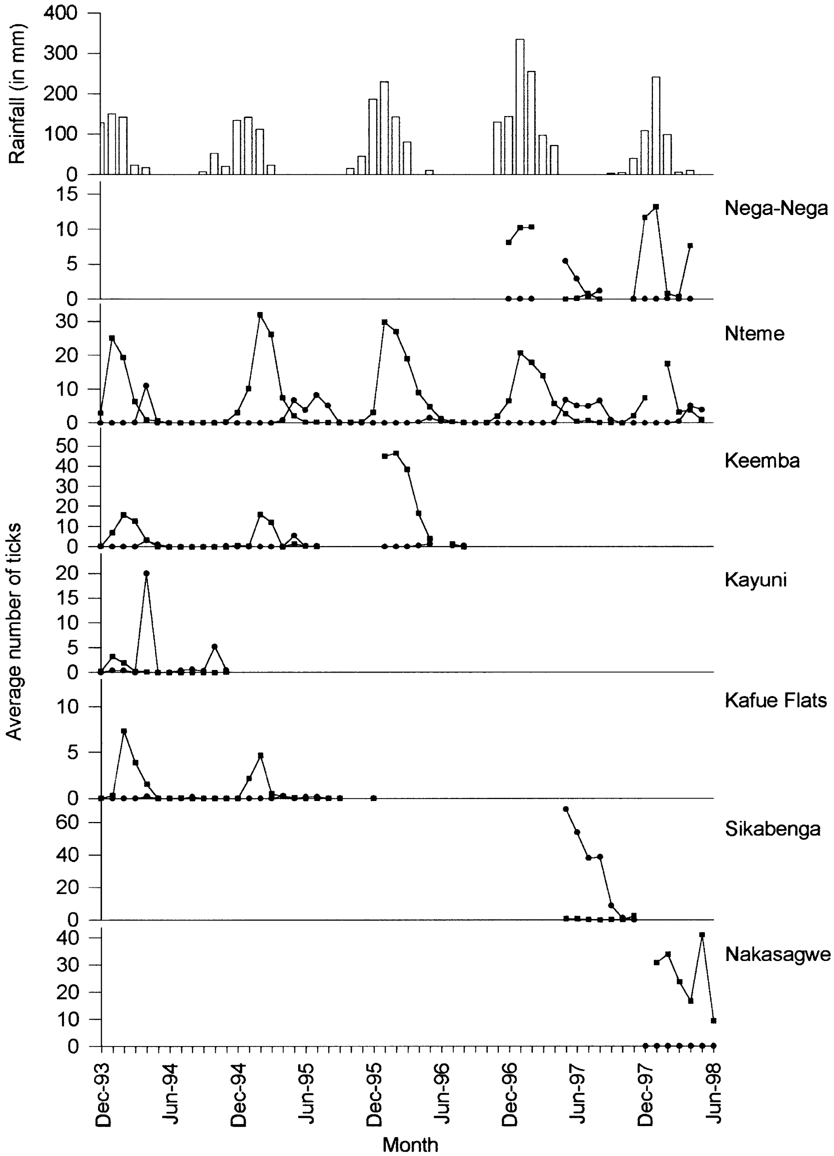


**Fig. 5.** Rainfall and average *R. appendiculatus*/*R. zambeziensis* burdens in Mazbuka and Monze Districts of Southern Province, Zambia: adults (■) and nymphs (●).

is endemic in the traditional sector, but in the commercial cattle sector important losses due to it have been reported. *Rhipicephalus supertritus* was present in relatively high numbers near Choma, whereas previously it was only reported in a limited area in Central Province (MacLeod *et al.*, 1977). *Rhipicephalus turanicus* was found in considerable numbers in southern Zambia compared to the low numbers in eastern Zambia (Berkvens *et al.*, 1998). Figure 3 considerably extends the area, infested by this species, as shown in Walker *et al.* (2000).

Despite differences in their ecological requirements (Norval *et al.*, 1982), both *R. appendiculatus* and *R. zambeziensis* were found in most parts of Southern Province below 1100 m. Adult numbers were generally low in areas where mixed populations occurred. Areas with mixed populations are ecological transition zones and small changes in the climatic conditions (e.g. higher rainfall) may benefit one entity (*R. appendiculatus*) and disfavour the other (*R. zambeziensis*). The importance of humidity in the distribution of both entities is clearly demonstrated in the Livingstone area. Despite the low altitude (below 1000 m), only *R. appendiculatus* occurred, very likely due to the presence of the Victoria Waterfalls that create a microclimate of high humidity. Differences in the species composition within a population may have important epidemiological repercussions. In areas where mixed populations occur, adult transmission of *T. parva* (rainy season) only occurred when climatic conditions were optimal for *R. appendiculatus*, as

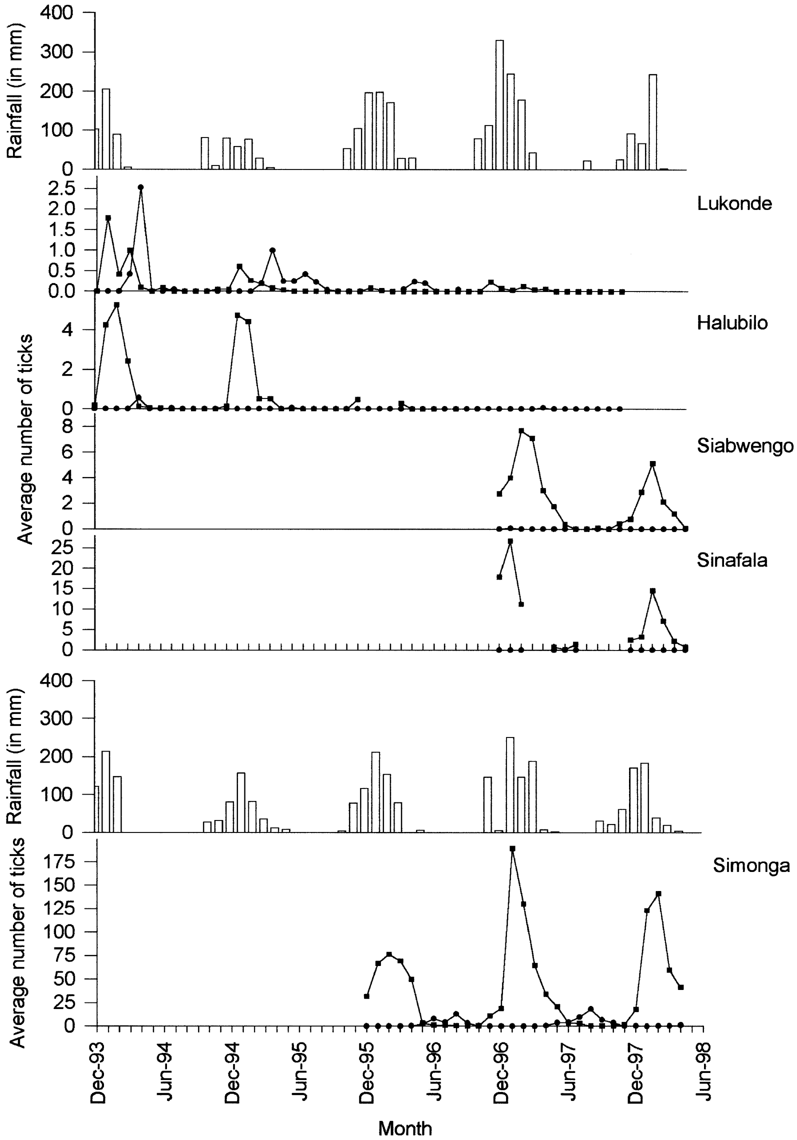


**Fig. 6.** Rainfall and average *R. appendiculatus*/*R. zambeziensis* burdens in Gwembe and Livingstone Districts of Southern Province, Zambia: adults (■) and nymphs (●).

was the case in Nteme in 1997 and 1998 (Mulumba *et al.*, 2001). Lower transmission occurred during the drier years (e.g. 1995 and 1996), when conditions were more favourable for *R. zambeziensis* (Mulumba *et al.*, 2000). Until now, this difference has been explained entirely by climatic conditions (Young & Leitch, 1981a, 1981b; Mulumba *et al.*, 2000, 2001), but it is theoretically possible that differences in species composition of the vector population play a role as well. It can be noticed that although the vector competence of *R. zambeziensis* is not known, Lawrence *et al.* (1983) have indeed demonstrated differences in vectorial capacity of different instars of *R. appendiculatus* and *R. zambeziensis*. Further research under controlled conditions is indicated to allow distinction between climate effects and vector species effects.

### *Longitudinal studies*

Peak *R. appendiculatus*/*R. zambeziensis* adult burdens recorded on cattle varied little from year to year, despite the unfavourable weather conditions during 1995 and 1996 compared to 1997 and 1998 (Mulumba *et al.*, 2000, 2001). The unimodal phenology observed at most localities in southern Zambia confirms the results of Pegram *et al.* (1986). Occasionally two waves were noted in nymph burdens on cattle (May–June and August), which can be explained by the low temperatures during the cold season delaying the development of engorged larvae. Indications of a second wave of adult ticks were only found at Nakasagwe and Nega-Nega (Fig. 5). It thus appears that the transition between the east African multimodal phenology and the

 

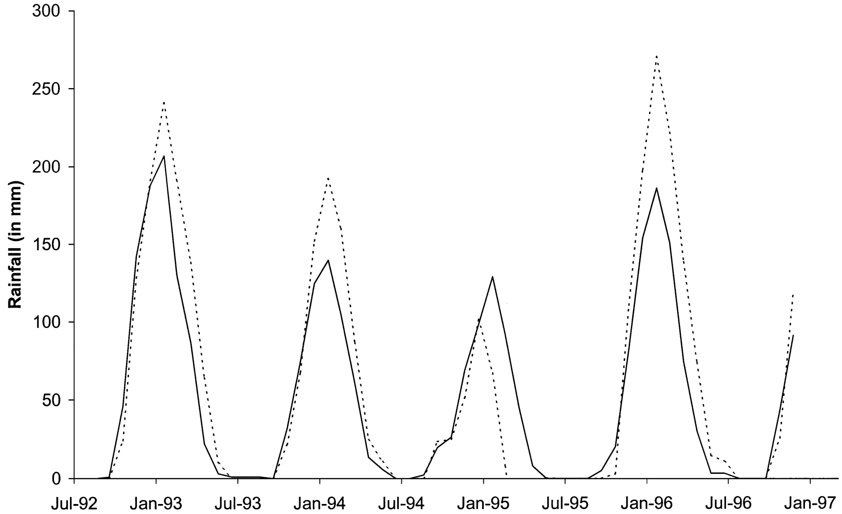


**Fig. 7.** Rainfall moving averages (period = 3) in Chipata (dotted line) and Monze Districts of Southern Province, Zambia (full line) for the period 1992–1997.

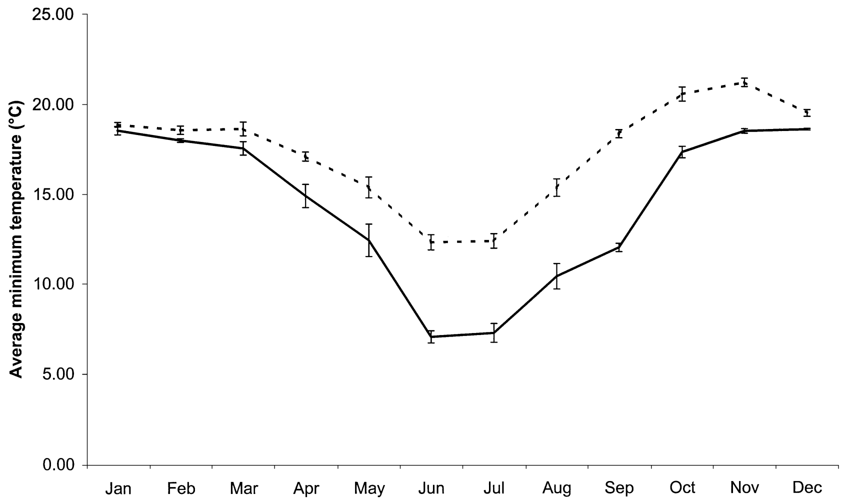


**Fig. 8.** Monthly minimum temperature averages (with standard error bars) in Chipata (dotted line) and Monze (full line) Districts of Southern Province, Zambia for the period 1992–1997.

**Table 1.** Results of the development trial starting from engorged *R. appendiculatus* females collected from field animals.

| Stage | Time | Expected time‡ |
|---|---|---|
| Collection engorged females | 21 December 1995 | |
| Eggs | 26 December 1995 | 27 December 1995 |
| Larvae | 1 February 1996 | 31 January 1996 |
| Hardened larvae applied to rabbit | 13 February 1996 | |
| Engorged Larvae | 16 February 1996 | |
| Nymphs | 6 March 1996 | 1 March 1996 |
| Hardened nymphs applied to rabbit | 25 March 1996 | |
| Engorged nymphs | 3 April 1996 | |
| Adults | 1 May 1996 | 27 April 1996 |

‡Based on Branagan (1973) and temperature logger data.

southern African unimodal phenology in the *R. appendiculatus*/*R. zambeziensis* complex occurs in Zambia. Berkvens *et al.* (1998) had suggested that this occurred in Eastern Province but the present observation shows that it may happen at least as far south as Southern Province. A behavioural diapause during the dry season, as demonstrated for *R. appendiculatus*, has never been found in *R. zambeziensis* (Berkvens *et al.*, 1995; Madder *et al.*, 2002). The latter authors, working with *R. appendiculatus*/*R. zambeziensis* from Southern Province were able to demonstrate a compulsory diapause in *R. appendiculatus*-like stocks and absence of diapausing behaviour in *R. zambeziensis*-like stocks. The second wave at Nakasagwe and Nega-Nega can thus possibly be explained by the presence of *R. zambeziensis* adults. *Rhipicephalus zambeziensis* shows heavier punctuation than *R. appendiculatus* (Walker *et al.*, 1981). Specimens, recorded on cattle during the early dry season, were heavily punctuated and both herds are situated in areas with mixed *R. appendiculatus*/*R. zambeziensis* populations. The higher numbers of both adult *R. appendiculatus* and *R. zambeziensis* at lower altitudes in Siabwengo (altitude 600 m) is possibly due to the higher numbers of cattle in this area, compared to the valley slopes (Mulofwa *et al.*, 1994). The fact that peak numbers of adults on cattle occur later during the rainy season (March–April) in Siabwengo cannot readily be explained at present. An effect of seasonal cattle movement because of flooding of grazing grounds is a possibility, but this remains to be demonstrated. The highest numbers of adults were seen on animals in Sikabenga and Livingstone, two areas where the surveys yielded homogeneous *R. appendiculatus* populations.

### *Simulation of* R. appendiculatus *life cycle*

The ecology of *R. appendiculatus* is complex, and, consequently, modelling should be regarded as an important tool in its study. The central parameter of interest in the simulation is the so-called season length, defined in the present context as the period of the year during which the most vulnerable stages (e.g. eggs and larvae) can survive long enough to allow development and questing. Season length is the ultimate determining factor in the tick's phenology, causing certain populations to cycle through two generations per year and others to enter a diapause at the start of the dry season. The factors affecting the season length, as shown in the case of Zambia are numerous and their interactions are very complex. In general, two factors play an important role in determining the season length in the transition zone in southern Zambia, compared to eastern Zambia: lower total rainfall and considerably lower temperatures during the cold dry season. The much longer development periods in drier conditions would result in smaller number of emerging larvae at a time (August) when survival is seriously compromised. This probably means that a two-generation-per-annum strategy is not an effective adaptation under standard Southern Province conditions and that synchronization of adult questing with the rains must be achieved either through diapause or quiescence of the adults during the dry season.

*Rhipicephalus appendiculatus*/*R. zambeziensis* adults from Southern Province are larger than their counterparts in Eastern Province. The larger size allows ticks to survive more adverse conditions (Chiera *et al.*, 1985). A larger size also appears to be correlated with a more intense diapause: increasing latitude is associated with increasing body size as well as with diapausing propensity (Chaka *et al.*, 1999; Madder *et al.*, 2002). The strength of this relationship should be verified under experimental conditions. Another possibility enabling survival during inimical conditions would be a more radical one, namely a mutation affecting a basic enzyme. In the case of *R. appendiculatus* and *R. zambeziensis*, glucose phosphate isomerase (GPI, EC5.3.1.9) has been shown to be a good species indicator (Wouters *et al.*, 1987; Wouters, 1989) and GPI isomorphs have been shown to have different molecular functions in *Colias* butterflies (Watt *et al.*, 1996). Our own unpublished observations under experimental conditions have shown that *R. zambeziensis* does indeed survive longer under drier conditions, but that *R. appendiculatus* survives longer under more humid conditions. The absence of diapause in *R. zambeziensis* may result in an organism that can react immediately to favourable climatic conditions, even allowing for a second generation per year if conditions permit. Provided that better survival under more extreme conditions and the lower reproductive capacity are confirmed, *R. zambeziensis* is a specialist species, surviving climatic conditions that *R. appendiculatus* cannot, but being out-competed by it under conditions favourable for the latter (much like *B. decoloratus* and *B. microplus*; Berkvens *et al.*, 1998)

Theileriosis control in Southern Province is a more complex matter than in Eastern Province, where the situation has so far always evolved towards endemicity, allowing immunization (Billiouw *et al.*, 1999). The more adverse climatic conditions and the presence of mixed *R. appendiculatus*/*R. zambeziensis* populations result in a more unstable epidemiology, and immunization will have to proceed with caution, ensuring that protection lasts long enough between epidemic episodes. Up to 3 years between two infections are possible in some animals, as can be deduced from figures in Mulumba *et al.* (2001). Tick control also has to be adjusted to the most important vector stage (adults in the case of *R. appendiculatus* and favourable climate and nymphs in the case or *R. zambeziensis* and drier conditions).

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