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Spatial and temporal variation in *Rhipicephalus appendiculatus* size in eastern Zambia

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Summary The size of *Rhipicephalus appendiculatus* collected at different altitudes in the Eastern Province of Zambia between February 1985 and May 1986 and between October 1994 and December 1996 showed distinct variation dependent on altitude and season. The ticks were smallest during the dry season and at the start of the rains, and specimens were larger as the rainy season progressed. Second-generation adults where on average smaller than first-generation ticks. At higher altitudes, where a one-generation-*per-annum* phenology dominates, ticks were larger than at intermediate altitudes, where two generations per year are common. Larger size, associated with increased survival, is also favoured in low-lying, drier areas. Selective mortality of smaller adult ticks in years with a delayed rainy season appears to play an important role in the variation in size between years.

keywords *Rhipicephalus appendiculatus*, distribution, abundance, size variation, Zambia

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Introduction

Rhipicephalus appendiculatus is the principal vector of *Theileria parva*, the causative agent of East Coast fever (ECF), an important cattle disease in eastern, central and southern Africa. The distribution and phenology of *R. appendiculatus* in the Eastern Province of Zambia were described by Berkvens *et al*. (1998). The area infested by this tick has been expanding westwards in a staggered manner for the past 15 years. Rapid expansions by up to 20 km in one season have been associated with ECF epidemics, movement of cattle to disease-free areas and abundant rainfall. The gentle slope of the plateau towards the Luangwa valley has probably facilitated adaptation to lower-lying drier areas to the west. The Eastern Province of Zambia is a transition zone for *R. appendiculatus* between the multigeneration phenology in eastern Africa and a single generation in southern Africa. Eastern Zambia provides a unique opportunity to study *R. appendiculatus* size variability because the full panoply of life histories is exhibited in a relatively small area.

Variation in size under the influence of environmental conditions and its considerable ecological implications for the life of an organism have been described for most arthropod classes (Roff 1981; Peters 1983; Schmidt-Nielsen 1984; Reiss 1989). Survival, generation interval and thus synchronization of reproduction with periods of favourable climatic conditions are all important life history characteristics that interact with size:, e.g. larger individuals thrive better than smaller ones in drier, desiccating conditions (Barker & Barker 1980; Chiera *et al*. 1985), while smaller size has been associated with nondiapausing cricket populations (Mousseau & Roff 1989), and for most insects temperature experienced during growth is inversely related to size attained at maturity (Atkinson 1994).

The size of *R. appendiculatus* has not been studied in its ecological context, with the exception of survival rates, which are lower for smaller individuals under unfavourable conditions (Chiera *et al*. 1985). Remarkably, Madder *et al*. (1996) demonstrated low heritability of size under laboratory conditions, but, as the authors point out, the implications of this finding for field conditions remain unknown. The influence of host resistance on *R. appendiculatus* size has been studied extensively under experimental conditions (Nuttall 1913; Chiera *et al*. 1985; Fivaz & Norval 1989; Walker *et al*. 1990), reaching the general conclusion that increasing host resistance significantly decreases size of instars.

Materials and methods

Preliminary observations

Between February 1985 and January 1988 *R. appendiculatus* males were collected monthly at Wafa and Genda (Table 1) from traditionally kept Zambian Angoni cattle (Williamson & Payne 1978). Ticks were collected from both ears, head (especially around the eyes and muzzle) and dewlap and stored in 70% alcohol. Several series of male ticks were measured with a micrometer mounted on a stereo dissecting microscope, giving a resolution of 1.25 μm. Only adult male ticks were measured because they were the most abundant in the collections and because it was easier to measure in a single antero-posterior plane. The maximum distance between the tip of the scapular processes and the distal end of the conscutum was used as a tick size index.

Formal surveys

Between October 1994 and December 1996 adult ticks were collected monthly, fortnightly or weekly from seven sentinel herds at different altitudes (Table 1) and measured as described above. Rainfall, temperature and relative humidity were recorded daily at Msekera Agricultural Research Station near Chipata. Scutal measurements were analysed in Stata 5.0 (StataCorp 1997), using standard regression techniques. A minimum significance level of 5% was used throughout.

Results

Climate

Climatic data (rainfall, mean temperature and relative humidity) for the period of observation between 1994 and 1996 are shown in Table 2. The 1994–95 rainy season was characterized by below-normal rainfall. Normal rains were experienced during the following two rainy seasons. Highly unfavourable climatic conditions occurred between July 1994 and December 1995, when the average vapour pressure deficit never dropped below 1 kPa.

Preliminary tick size study

Preliminary results indicated that ticks collected during the rains were larger than those collected during the dry season (Figure 1). Adults collected during the early part of the rainy season were smaller than those collected during the late rains. At higher altitudes (Genda) adults were on average larger than those collected at lower altitudes (Wafa).

Formal survey

Table 3 shows the numbers of male *R. appendiculatus*

Table 1 Co-ordinates of the sampling locations

Locality	Latitude	Longitude	Altitude (m)
Mwase	12°24 S	33°20 E	1200
Genda	13°41 S	32°41 E	1150
Lufu	13°51 S	32°24 E	1080
Nkholowondo	13°54 S	32°08 E	1080
Lupenga	14°21 S	31°54 E	1040
Wafa	13°35 S	32°29 E	980
Pwata	13°37 S	32°19 E	940
Langa	13°37 S	32°24 E	920

Table 2 Monthly total rainfall (mm), average daily temperature (°C) and average daily relative humidity (%), recorded at Msekera Agricultural Research Station, and calculated vapour pressure deficit (VPD in kPa)

Month	Rainfall	Temperature	Relative humidity	VPD
1994				
July		21.1	32	1.71
August		20.0	31	1.61
September		24.0	33	2.00
October	55.6	24.5	30	2.15
November	4.3	27.1	30	2.51
December	76.7	25.9	54	1.53
1995				
January	161.8	23.2	48	1.48
February	156.4	24.1	54	1.39
March	125.5	23.8	48	1.53
April		23.0	37	1.77
May		21.4	37	1.60
June		19.1	51	1.08
July		19.2	33	1.49
August		22.5	47	1.44
September		24.6	36	1.97
October		28.0	38	2.35
November	47.0	27.3	43	2.07
December	294.0	24.4	59	1.25
1996				
January	236.0	23.1	66	0.96
February	320.4	22.6	71	0.80
March	205.4	22.3	68	0.87
April		21.3	40	1.52
May	54.7	20.8	66	0.83
June		17.6	57	0.87
July		18.5	52	1.03
August		21.5	45	1.41
September		24.0	37	1.88
October	0.6	24.7	39	1.89
November	31.6	27.8	38	2.31
December	234.1	23.8	66	1.00
1997				
January	229.0	23.1	70	0.85
February	301.1	22.0	69	0.81
March	49.7	23.7	68	0.93

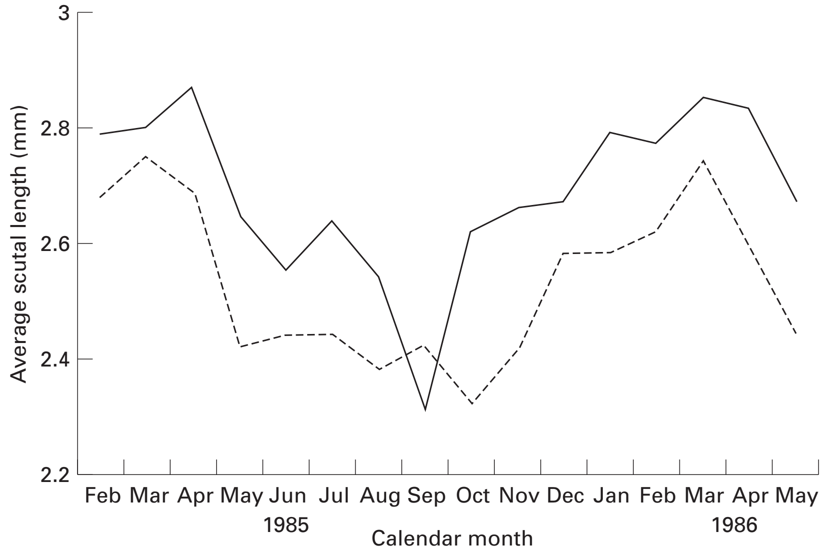

Figure 1 Results of preliminary study: average monthly male *R. appendiculatus* conscutal lengths at Genda (——) and Wafa (------) for the period February 1985 to May 1986.

collected and measured per month at the various localities. Because of the inclement weather conditions, tick numbers had dropped to a historical minimum by December 1995. The population recovered quickly during the first favourable rains and a second generation was observed immediately after the rains.

Effect of year of collection

Ticks collected at Wafa, Nkholowondo and Pwata at start of the rainy season (October to December) were significantly smaller in 1994 than in 1995 and 1996 (Figure 2, $F(2\ 848) = 4.02$, $P = 0.018$).

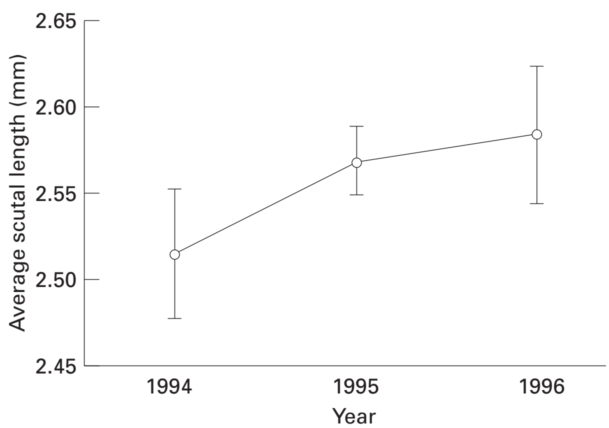

Figure 2 Average male *R. appendiculatus* conscutal lengths (± standard error) for the period October to December in the years 1994, 1995 and 1996.

Effect of altitude

Over the entire year mean tick size from each locality showed a distinct relationship with altitude. The smallest males were found at Wafa (980 m). Ticks were significantly larger both at higher (Mwase) and at lower altitudes (Pwata and Langa) (Figure 3, $F(6\ 4872) = 18.21$, $P < 0.001$).

Monthly variation of size

The month of collection also exerted a significant effect (Figure 4, $F(11\ 4390) = 10.70$, $P < 0.001$). Ticks were smaller at the beginning of the tick season (October to November), grew as the rains progressed, and reached maximum size in February and March. Scutal length decreased in April, and second-wave adults at the start of the dry season were smaller than those collected during the first wave. Different patterns were observed in the middle of the dry season in Mwase (Figure 4b) and the rest of the Province (Figure 4a): both in 1995 and 1996, a significant increase in size was recorded at Mwase in August.

Discussion

The preliminary study showed that size in *R. appendiculatus* varied seasonally and there was a strong indication that altitude had an influence. Similar observations were reported for cricket populations in transition zones between multigeneration and single-generation phenologies (Mousseau & Roff 1989). These authors further report a direct correlation between diapausing behaviour and size. The observation made for *R. appendiculatus* could theoretically also be correlated with phenology: smaller adults were collected at lower

Table 3 Number of adult *R. appendiculatus* measured per locality per month.

	Wafa	Nkh*	Pwata	Lupenga	Lufu	Mwase	Langa	Total
1994								
October	7	0	0	nc	nc	nc	nc	7
November	12	7	1	nc	nc	nc	nc	20
December	76	52	11	nc	nc	nc	nc	139
1995								
January	152	172	3	nc	30	69	16	442
February	54	73	52	25	106	61	20	391
March	13	16	11	nc	29	53	9	131
April	30	15	5	33	6	nc	1	90
May	22	14	3	39	6	nc	0	84
June	3	4	0	nc	8	nc	1	16
July	7	2	1	nc	3	nc	0	13
August	3	0	0	nc	3	30	0	36
September	6	0	1	2	2	12	0	23
October	3	1	0	nc	2	14	1	21
November	11	4	2	nc	0	22	1	40
December	475	22	20	29	21	137	0	704
1996								
January	234	29	62	66	50	279	27	747
February	117	27	46	28	60	184	12	474
March	38	7	7	30	47	110	8	247
April	100	3	22	15	10	64	6	220
May	182	18	55	nc	19	76	3	353
June	66	7	9	nc	10	32	7	131
July	21	0	3	45	3	14	5	91
August	12	1	1	13	4	9	3	43
September	6	1	0	nc	3	11	0	21
October	0	2	1	nc	0	17	0	20
November	6	0	0	nc	5	30	0	41
December	101	18	19	nc	40	223	6	407
Total	1757	495	335	325	467	1447	126	4952

* Nkh, Nkholowondo; nc, no collection

altitudes with two generations *per annum*, larger ticks were found at higher altitudes where a single generation per annum is the norm (Berkvens *et al*. 1998).

Greater mean tick size observed during the period October to December in 1995 and 1996 (compared to 1994) is likely due to selective mortality of smaller ticks because of the particularly dry conditions until December 1995 (Knülle & Rudolph 1982; Chiera *et al*. 1985).

The lowest average conscutal length was observed at Wafa at an altitude of 980 m. Two generations per year are generally encountered at this locality. At altitudes above 1000 m, size increased with altitude. This is in agreement with previous reports for other ectotherms. The question whether this difference is a consequence of different life histories as a response to a shorter season at higher altitude, and thus no possibility of a second generation (Roff 1981), or due to a direct influence of temperature on development rates and size at maturity (Atkinson 1994) is not clear, although the former is the more logical explanation. Size differences of the magnitude observed during this study have not been obtained under different temperature regimens in the laboratory (unpublished observations).

At altitudes below 950 m, size increased again, reaching the highest recorded annual average at Langa (920 m), on the edge of the species' range in the Eastern Province. The need to survive hot and dry conditions during most of the year appears the likely cause for the larger size observed here. The total rainfall for the 1994/95 season was below normal, with the season being unusually short despite an early start, and the period after the rains in 1995 was very dry. The second wave of adults was largely absent in 1995, probably as a response to conditions unfavourable for eclosion and survival of larvae. An appreciable number of smaller-sized second-wave adults were found with the return of favourable con-

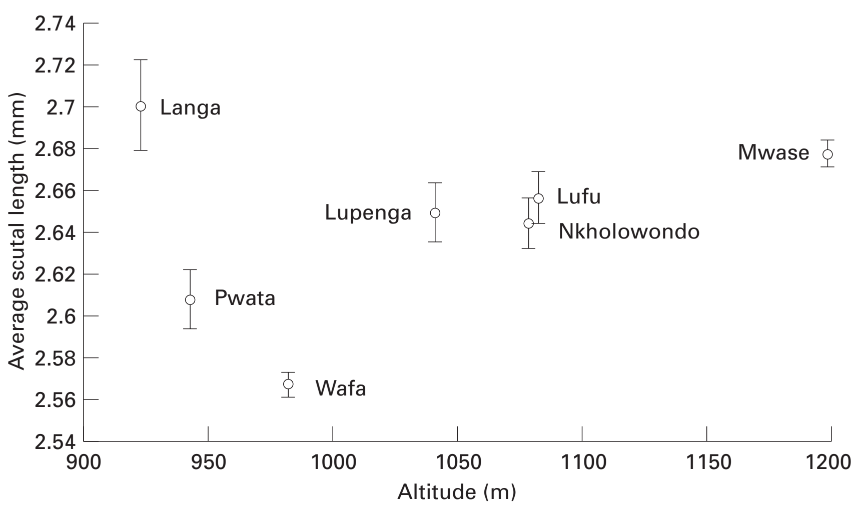

Figure 3 Average observed male *R. appendiculatus* conscutal lengths (± standard error) in function of altitude of sampling locality.

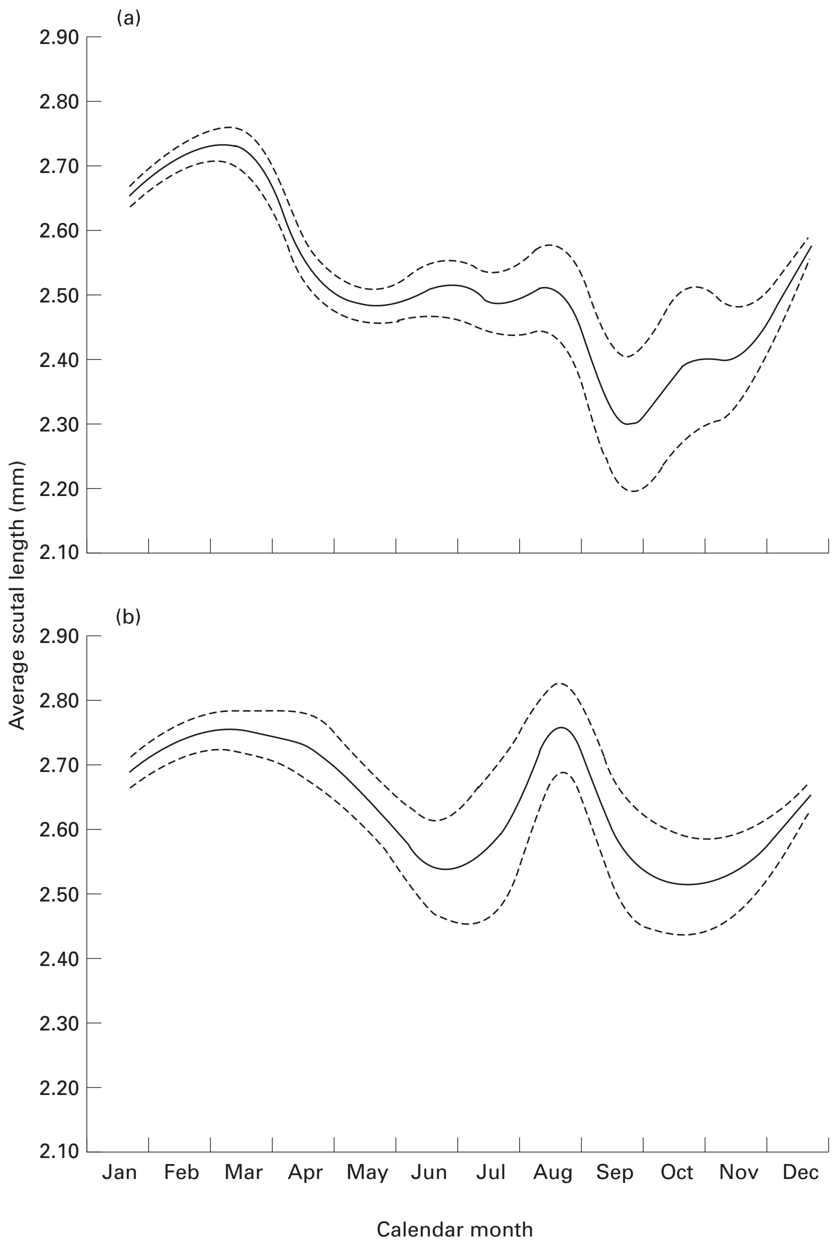

Figure 4 Seasonal variation in average male *R. appendiculatus* conscutal lengths collected at (b) Mwase and (a) the other sampling points. —— fitted regression, ------- 95% confidence interval.

ditions in 1996. The higher number of ticks collected during the 1995–96 rains (compared to 1994–95) indicates that mortality also is considerable during the rainy season: tick numbers at the start of the 1995–96 rainy season cannot have been higher than at the start of the very dry preceding season.

There are more smaller ticks feeding at the beginning of the tick season (October to November) than later during the rains, indicating a possible relationship between size of questing ticks and the occurrence of first substantial rains. Two factors may influence the size of ticks feeding at this time of the year: a weakened diapause because of older physiological age in smaller ticks, and faster restoration of water balance in smaller ticks during night time, permitting more questing activity during the day (Knülle & Rudolph 1982).

The sharp drop in tick size observed with the start of the dry season is most likely due to dwindling numbers of the larger ticks of the rainy season and an increasing number of smaller emerging ticks of the second generation. This observation further supports the presumed link between life history and size: smaller size is correlated with a two-generation-per-year phenology, larger size with one generation per year. The ticks observed in Mwase in August (both in 1995 and 1996), which were larger than during the rainy season, are an exception. This may be due to the possible longer growing season in Mwase due to lower mean temperatures during the rains and the dry season and higher humidity during the cold dry season compared to the rest of the Province (FAO 1984).

An alternative explanation for the seasonal variation of size could be variation in host resistance to ticks. This, however, remains to be demonstrated in the field. Such seasonal fluctuation would have to be synchronized in all possible hosts of *R. appendiculatus* for it to result in such obvious seasonal differences in adult size. A quantitative assessment of the effect of tick infestation fluctuations on resistance profiles in the field is required.

The effect of temperature on several morphometrical traits observed in most ectothermic organisms will have to be tested in *R. appendiculatus*. This will have to be done within the possible thermal range for complete development of this species. Only then will a distinction between the possible theoretical causes of the size differences observed in the field be possible. Either way it remains essential to elucidate this important relationship between phenology and size in order to understand fully the species' ecology in the framework of integrated ECF control programmes.

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