

THE LIFE CYCLE OF THE TWO-HOST TICK *RHIPICEPHALUS EVERTSI EVERTSI* NEUMANN, 1897, UNDER LABORATORY CONDITIONS (ACARINA: IXODIDAE)

J. G. H. LONDT⁽¹⁾ and ELEANORE B. VAN DER BIJL⁽²⁾, Veterinary Research Institute, Onderstepoort, South Africa

ABSTRACT

LONDT, J. G. H. & VAN DER BIJL, ELEANORE B., 1977. The life cycle of the two-host tick *Rhipicephalus evertsi evertsi* Neumann, 1897, under laboratory conditions (Acarina: Ixodidae). *Onderstepoort Journal of Veterinary Research* 44 (1), 21-28 (1977).

The life cycle of *Rhipicephalus evertsi evertsi* Neumann, 1897, is discussed under the following headings: larval feeding; larval drop; nymphal feeding; nymphal drop; nymphal moulting; adult feeding; adult drop; preoviposition period; oviposition period and incubation. Special attention has also been given to the development of both male and female reproductive organs, gametogenesis and mating.

Résumé

LA MÉTAMORPHOSE CYCLIQUE EN LABORATOIRE DE LA TIQUE À DEUX HÔTES, *RHIPICEPHALUS EVERTSI EVERTSI* NEUMANN, 1897 (ACARINA: IXODIDAE)

Les auteurs discutent le cycle de développement de la tique *Rhipicephalus evertsi evertsi* Neumann, 1897 sous les titres suivants: l'ingestion de sang par les larves; la chute des larves; l'ingestion de sang par les nymphes; la chute des nymphes; la mue des nymphes; l'ingestion de sang par les adultes; la chute des adultes; la période avant la ponte; la période de ponte et l'incubation. On a surtout étudié le développement des organes reproducteurs du mâle et de la femelle, la gamétogenèse et l'accouplement.

INTRODUCTION

Much information concerning the red tick, *Rhipicephalus evertsi evertsi* Neumann, 1897, has been published, though there is remarkably little detail about its life cycle. Adults of *R. e. evertsi* are common parasites of domestic animals including cattle, equines, goats and sheep. They have also been recorded, but much less frequently, from dogs, pigs and camels. *R. e. evertsi* has been collected as well from a number of wild antelope species. The immature stages of this 2-host tick commonly infest the same hosts as the adults, but may also be found on hares and elephant shrews (Hoogstraal, 1956).

The economic importance of *R. e. evertsi* is well established. This tick is a vector of East Coast fever (*Theileria parva*), benign bovine theileriosis (*T. mutans*) and spirochaetosis (*Borrelia theileri*) in cattle. It transmits equine piroplasmiasis (*Babesia equi* and *B. caballi*) in horses, mules and donkeys and causes spring-lamb paralysis in sheep (Hoogstraal, 1956; Neitz, 1956, 1958). The tick-bite fever pathogen of man (*Rickettsia conori*) has also been isolated from *R. e. evertsi* (Gear, 1954).

R. e. evertsi is difficult to control and cattle on even the best managed farms are often infested by this species. A number of explanations can be given for this. Firstly, the immature stages (larvae and nymphs) are found predominantly in the ear passages of cattle and goats (Baker & Ducasse, 1967, 1968), and consequently conventional dipping and spraying techniques often fail to control them. The fact that ear passages are usually greasy adds to the difficulty of wetting the ticks with an appropriate acaricide. Secondly, the immature stages are not infrequently encountered, often in very large numbers, on hares, and thus a natural reservoir of ticks is ensured. Thirdly, *R. e. evertsi* sometimes develops acaricide resistant strains (Whitehead & Baker, 1960, 1961; Pal & Kalra, 1965; Shaw & Stones, 1966; Brown, 1968).

Biological data concerning *R. e. evertsi* are limited to general observations on the life cycle (e.g. Bedford & Graf, 1935; Theiler, 1950; Gray, 1961), to the

seasonal incidence of adult stages on cattle (Jooste, 1966), to predilection sites of feeding stages (Thomas, 1962, Baker & Ducasse, 1967, 1968; Ducasse, 1969), to notes on the predatory actions of *Buphagus erythrorhynchus*, the oxpecker (Moreau, 1933) and to ecological notes on the occurrence of this tick in East and Central Africa (Wilson, 1953).

This paper deals with the feeding periods of all stages, the moulting of larvae and nymphs, nymphal and adult drop, the preoviposition and oviposition periods of engorged adult female ticks and the incubation of eggs under laboratory conditions. Special attention has been given to the development of the reproductive organs of both males and females throughout the nymphal and adult stages.

MATERIALS AND METHODS

A laboratory culture of *R. e. evertsi* was established from engorged female ticks taken from cattle at Soutpan (25° 24' S; 28° 05' E—a farm north of Pretoria). Immature ticks were fed on the ears of rabbits while adults were fed on and under the tails of Friesland calves. The mass of immature and adult male ticks was measured by means of a Cahn electrobalance and that of adult females on a Mettler single-pan balance. Ticks used in the study of reproductive organ development and gametogenesis were either superficially embedded in wax (immatures and adult males) or placed on double-sided masking tape (adult females), covered with saline and dissected under a Wild M5 stereomicroscope. Measurements of the reproductive organs were made as described by Londt & Spickett (1976) in a study of gametogenesis and reproductive organ development in *Boophilus decoloratus*. Other materials and methods are mentioned under the relevant sections.

RESULTS AND DISCUSSION

Life cycle studies

Larval feeding

The mass of unengorged larval ticks was measured before their release onto a rabbit. Subsequently samples of ticks were removed from the host daily and mass measured. The results (Fig. 1) show that larvae lost mass over the first 24 hours on the host; thereafter they gradually regained this mass and by

⁽¹⁾ Present address: Natal Museum, Loop Street, Pietermaritzburg, South Africa

⁽²⁾ Present address: Murray and Roberts, P.O. Box 229, Manzini, Swaziland

Received 26 October 1976—Editor

Day 3 had exceeded their initial unengorged mass. From Day 3, larvae engorged rapidly until Day 9, when a maximum mean mass of 0,486 mg was recorded. The mean mass of larvae tended to decrease after Day 9, presumably owing to water loss through evaporation from the pharate nymphs as they do not feed while undergoing metamorphosis on the host. This mass decrease was also demonstrated in *B. decoloratus* by Arthur & Londt (1973) and in *B. microplus* by Londt & Arthur (1975). The mass measuring of larvae ceased on Day 13 as the larval population was very low by then. Larvae were present, however, till Day 15.

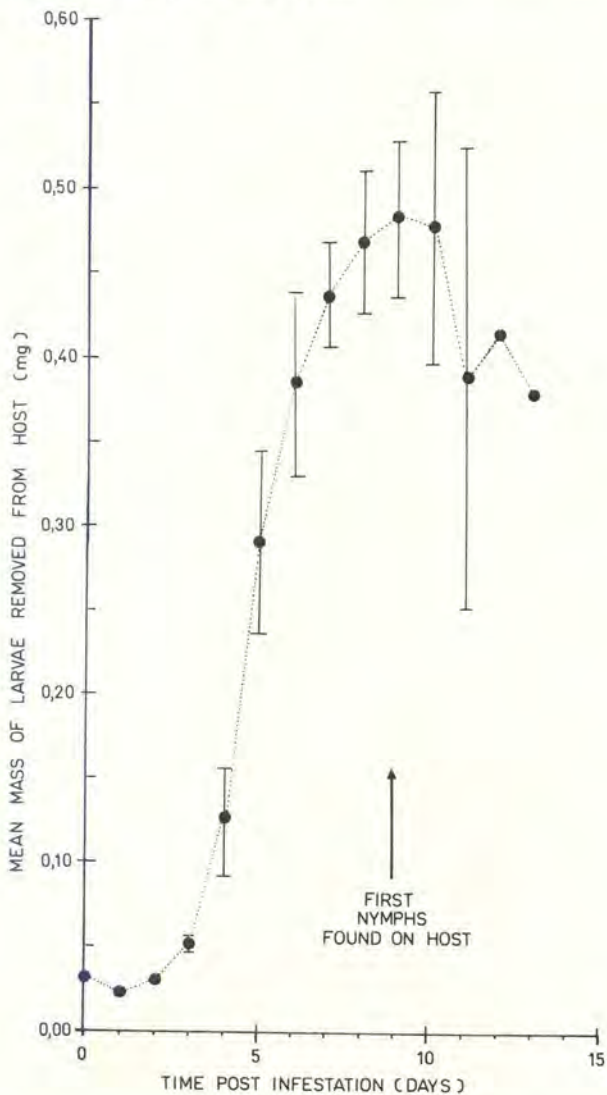


FIG. 1 Changes in mean mass of feeding *Rhipicephalus e. evertsi* larvae throughout their parasitic phase. Vertical lines indicate range

Larval drop

Although *R. e. evertsi* is regarded as a 2-host species, a number of larval ticks were shed daily by the host from about Day 4 onwards until none remained. These larvae were often semi-engorged and attached to pieces of the host's skin tissue. Sometimes, during the latter half of the larval phase, larvae were found embedded in lumps of wax secreted in the host's ear passages. It is therefore likely that larvae falling from the host are either scratched off, become detached owing to a breakdown of the

host's skin or are expelled by the copious secretion of wax. Arthur (1973) suggests that the production of copious amounts of wax by hares is a host reaction to the presence of ticks, a theory that is supported by this study. Although daily counts of larvae that had detached from the host were made, no significant relation emerged. A total of 1 359 larvae was counted, so the host's ability to free itself of ticks is considerable. A sample of 240 larvae that had become detached from the host on Day 6 was placed in an incubator (30 °C; 95% R.H.) to determine their possible fate. When they were examined 7 days later, 99 (41,3%) had moulted and the remainder were dead. Of these 99 nymphs, only 77 (77,8%) were still alive. On the 11th day after larval detachment, only 28,0% were alive, and on Day 13, 8,1%, and Day 15, 5,1% were alive. All were dead by Day 18. Nymphs moulting off the host therefore have very limited survival potential and would probably be unable to complete their life cycle under natural conditions.

Nymphal feeding

The first nymphs to emerge on the host were found on Day 9 of the larval/nymphal parasitic phase, while the last nymph was recorded on Day 29. The changes in mean mass recorded for nymphs over this period are shown in Fig. 2. Nymphal ticks increased in mass only very slightly over the first 3 days of their parasitic phase. From Day 12, however, rapid engorgement took place until Day 17, when the numbers of fully engorged nymphs dropping from the host reached a peak. Thereafter, nymphs removed from the host showed no marked change in mass. A great range in mass was recorded each day, probably because of the different rates of feeding (and possibly larval moulting) of the larvae and nymphs.

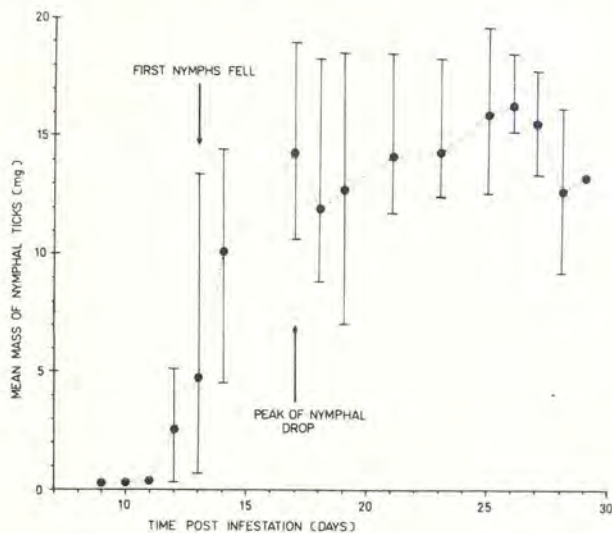


FIG. 2 Changes in mean mass of feeding *Rhipicephalus e. evertsi* nymphae throughout their parasitic phase. Vertical lines indicate range

Nymphal drop

The percentage of nymphs falling from the host on each successive day of the tick's parasitic cycle is shown in Fig. 3. As already mentioned, ticks fell from the host from Day 13 to Day 29. The mean parasitic period for the immature stages was 19,3

days and the ratio of larval : nymphal ticks found on each successive sampling day throughout this parasitic phase is shown in Fig. 4.

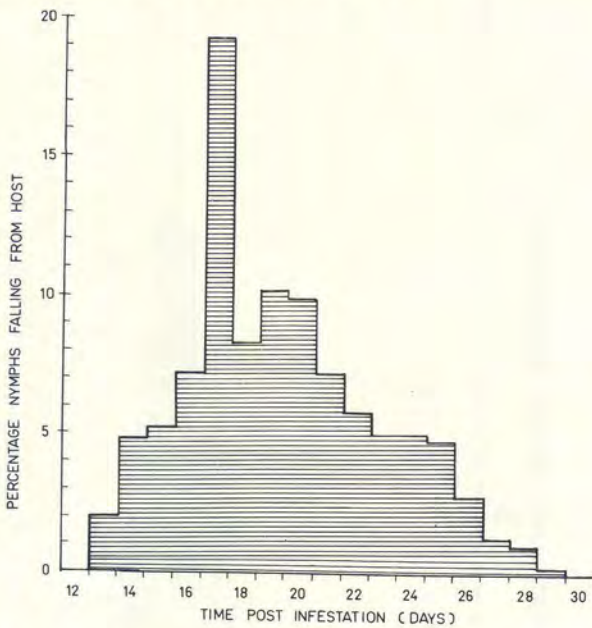


FIG. 3 Histogram showing number of *Rhipicephalus e. evertsi* nymphae which fell from host on each successive day of drop phase

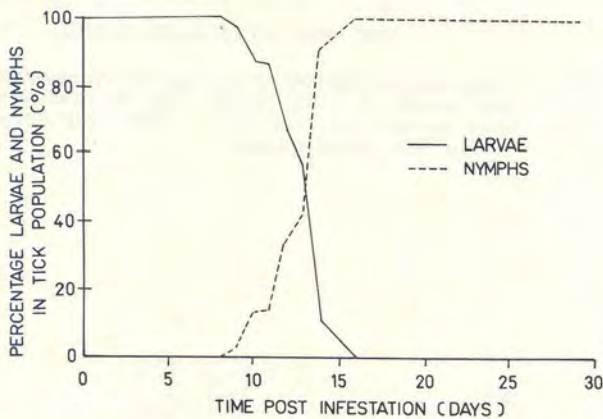


FIG. 4 Percentage of *Rhipicephalus e. evertsi* larvae and nymphae found on host on each day post larval infestation

Nymphal moulting

Nymphs which dropped from the host on Day 17 of the parasitic phase (i.e. the day on which the greatest number fell) were placed in an incubator (30 °C; 95% R.H.) to moult. The number of adult ticks emerging on each successive day after drop is shown in Fig. 5. The first appeared on Day 13 and the last on Day 20 (mean 15,3 days). Of the 110 nymphs studied, 95 (86,5%) moulted successfully, 64 (67,4%) of them into males and 31 (32,6%) into females.

To determine the ratio of males : females, the adults which emerged from each day's collection of nymphs were sexed and counted (Fig. 6). Of the total, 269 (62,1%) were males and 164 (37,9%) females, with nymphs falling in the first half of the drop phase tending to produce males and those falling in the second half tending to produce females (Fig. 6).

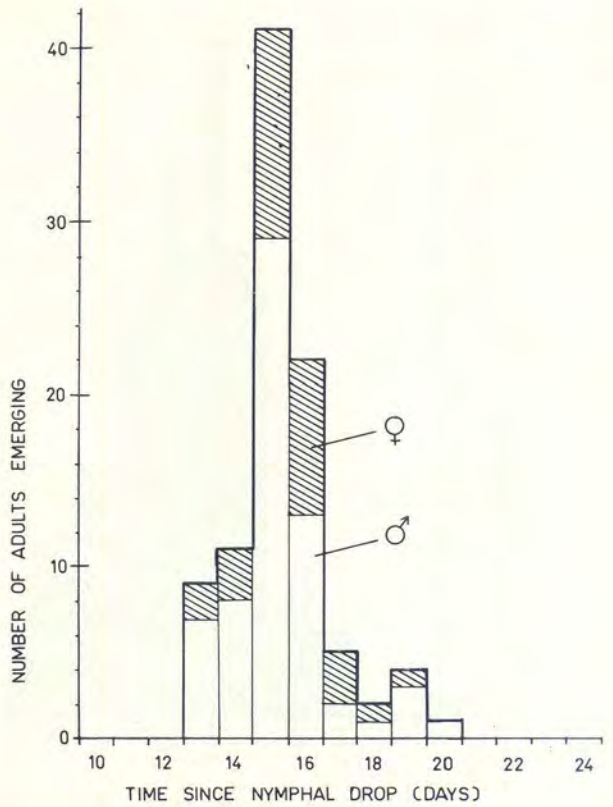


FIG. 5 Histogram showing number of *Rhipicephalus e. evertsi* adults, emerging on each day of emergence phase, and ratio of males : females. Nymphae were held at 30 °C and 95% R.H. throughout their period of metamorphosis

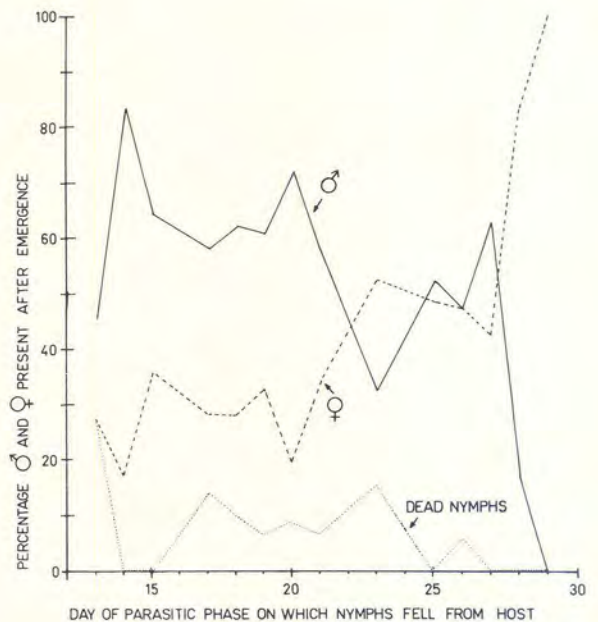


FIG. 6 Percentage of *Rhipicephalus e. evertsi* adult males and females emerging from nymphae that fell from host on each successive day of the drop phase

A histogram showing the engorged mass distribution of nymphal *R. e. evertsi* that fell on Day 17 of the parasitic cycle is given in Fig. 7. Nymphs ranged in mass from 4, 11-19, 37 mg (mean 12, 14 mg).

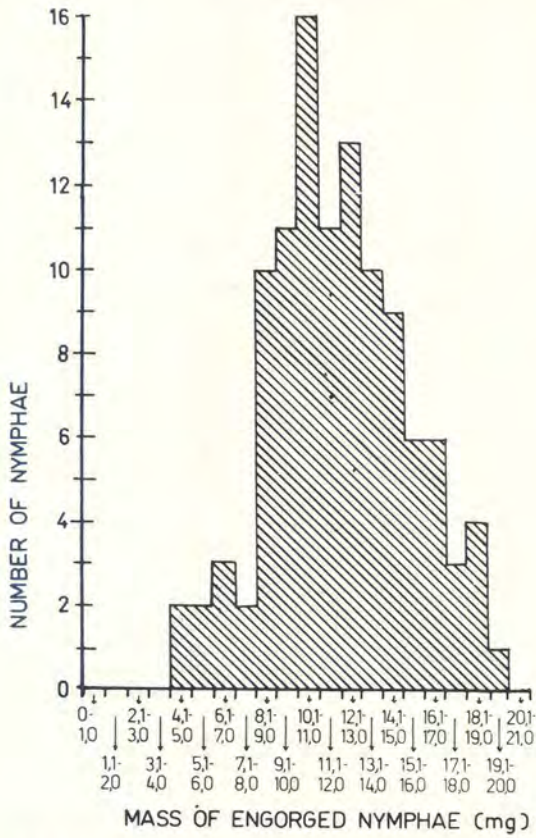


FIG. 7 Mass distribution histogram for fully engorged *Rhipicephalus e. evertsi* nymphae fallen from host

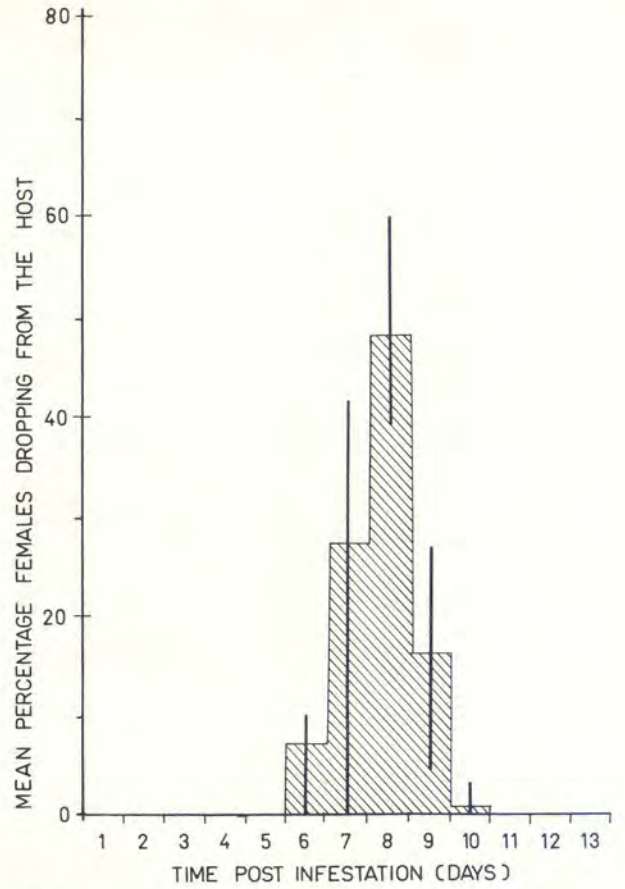


FIG. 9 Histogram showing mean percentage of fully engorged *Rhipicephalus e. evertsi* females that fell from their hosts on each successive day of their drop phase. Vertical lines indicate range

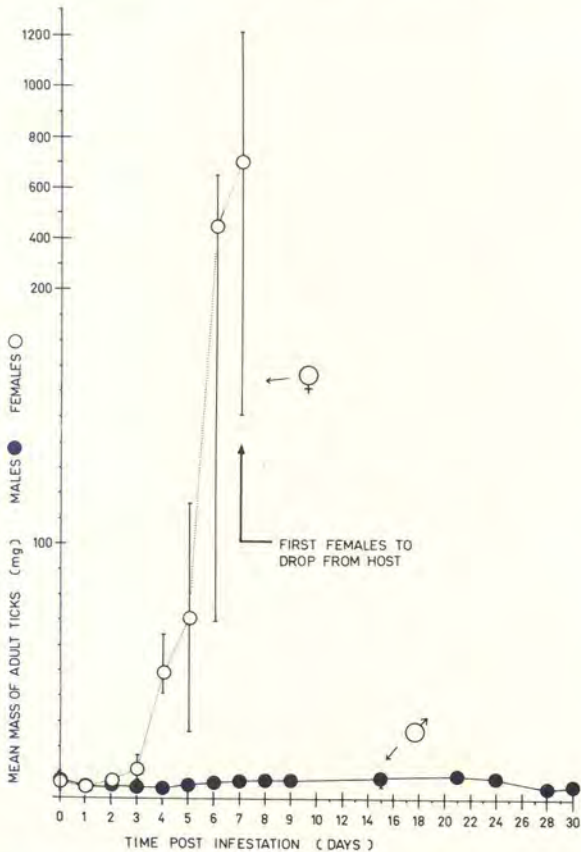


FIG. 8 Changes in mean mass of feeding *Rhipicephalus e. evertsi* adult males and females throughout their parasitic phase. Vertical lines indicate range

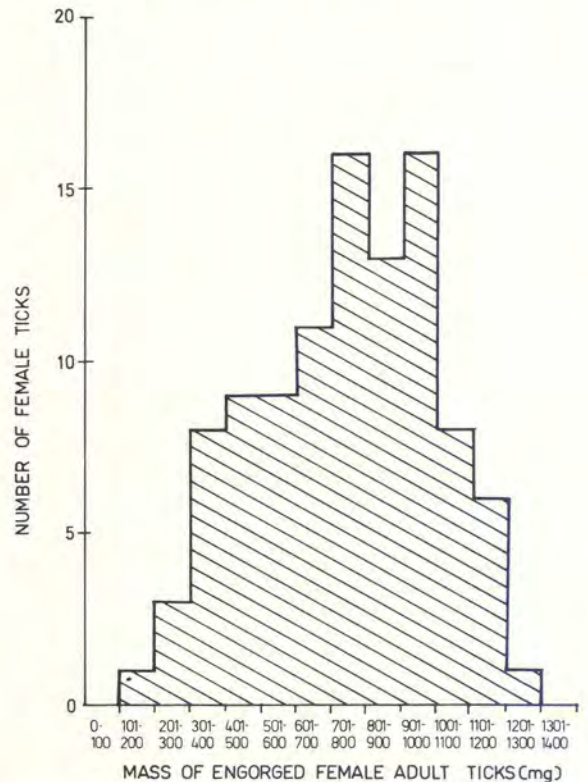


FIG. 10 Mass distribution histogram for fully engorged *Rhipicephalus e. evertsi* adult females fallen from their hosts

TABLE 1 Preoviposition, oviposition and incubation period durations of *Rhipicephalus e. evertsi* at 3 different temperature levels

Incubator setting	Tick No.	Tick mass (mg)	Preoviposition period (Days)	Oviposition period (Days)	Incubation period (Days)
30 °C; 95% R.H.....	1	853,2	4	25	25
	2	919,6	4	22	26
	3	1 049,5	5	Died	27
	4	948,4	4	27	25
	5	748,7	6	14	26
	Mean	903,9	4,6	22,0	25,8
23 °C; 95% R.H.....	1	774,1	7	15	Died
	2	1 073,4	7	13	39
	3	910,5	8	25	40
	4	986,5	5	29	39
	5	846,0	7	18	39
	Mean	917,9	6,8	20,0	39,3
15 °C; 95% R.H.....	1	907,8	88	Not studied	Not studied
	2	1 006,7	Died		
	3	842,5	Died		
	4	1 154,7	57		
	5	926,0	Died		
	Mean	967,5	77,5		

Adult feeding

The changes in mean mass of adult males and females throughout their parasitic phase are shown in Fig. 8. In the particular experiment illustrated, males, did not show significant mass changes whereas females increased rapidly in mass after fertilization and the first fell from the host on Day 6 after infestation.

Adult drop

The mean percentage (of 3 series) of adult female ticks dropping on each successive day is shown in Fig. 9. Female ticks dropped from Day 6–Day 10 following infestation, with the peak on Day 8, when 48,2% fell from the host. The mass of 110 engorged female ticks (Fig. 10) ranged from 167,6–1 274,1 mg (mean 796,1 mg).

Preoviposition period

The mass of engorged female ticks was measured and the ticks were placed in 3 different incubators (30 °C, 95% R.H.; 23 °C, 95% R.H.; 15 °C, 95% R.H.) to oviposit. Their preoviposition periods (Table 1) are dependent on temperature as was shown for *B. decoloratus* by Londt (1974). Of the 5 ticks held at 15 °C, only 2 produced eggs and their mean preoviposition period was 77,5 days—about 10 times longer than that of ticks held at 23 °C.

Oviposition period

The oviposition periods of female ticks held at constant temperatures of 30 °C and 23 °C are shown in Table 1. Ticks held at 30 °C completed egg production in 22 days, but those held at 23 °C finished laying in 20 days, though for some unknown reason they did not appear to produce their full complement of eggs. The oviposition pattern of females at 30 °C is shown in Fig. 11. Egg production reached a peak on Day 4, after which it gradually decreased. This pattern is very similar to that described for *B. decoloratus* by Londt (1977).

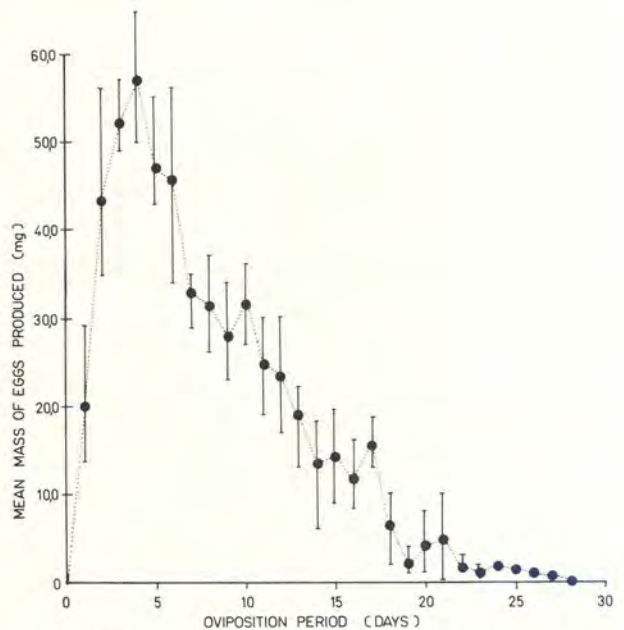


FIG. 11 Oviposition pattern of *Rhipicephalus e. evertsi* females held at 30 °C; 95% R.H. Vertical lines indicate range

The relation between the mass of individual engorged females and that of eggs produced at 30 °C is shown in Fig. 12. This is a linear relationship similar to that shown for *Amblyomma hebraeum* by Norval (1974) and *B. decoloratus* by Londt (1977). The percentage of the engorged female's mass converted into eggs ranged from 49,1% to 63,6% (mean 59,5%).

Incubation

The incubation periods of eggs produced and incubated at constant temperatures of 30 °C and 23 °C (and 95% R.H.) are shown in Table 1. They too appear to be dependent on temperature as was shown by Londt (1977) for *B. decoloratus*. As for *B. decoloratus*, the percentage hatch was greater

for eggs produced during the first half of the oviposition period than for those produced in the second half (Fig. 13).

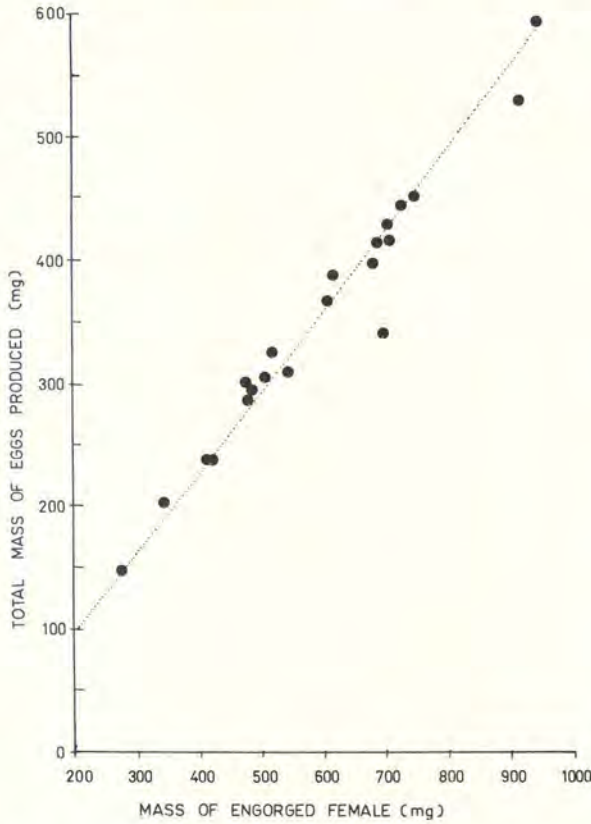


FIG. 12 Linear relation between mass of fully engorged *Rhipicephalus e. evertsi* adult females and total mass of eggs they produced

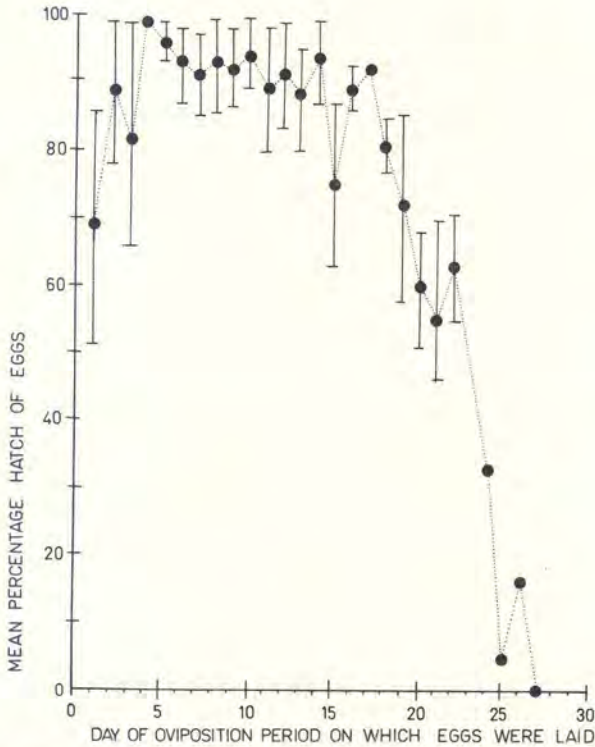


FIG. 13 Mean percentage hatch of *Rhipicephalus e. evertsi* eggs produced on each successive day of oviposition period. Vertical lines indicate range.

DEVELOPMENT OF REPRODUCTIVE ORGANS, GAMETOGENESIS AND MATING

Male

The morphology of the male reproductive organs is very similar to that described for *B. decoloratus* by Londt & Spickett (1976) except that the testes and accessory glands appear to be longer in *R. e. evertsi*. Male nymphs and adults were dissected on various days throughout the life cycle. The changes recorded in the overall length of the dissected ticks (Fig. 14) and the lengths of their testes and accessory gland complexes (Fig. 15) are illustrated. Larval ticks were not dissected. Measurements were made as described by Londt & Spickett (1976).

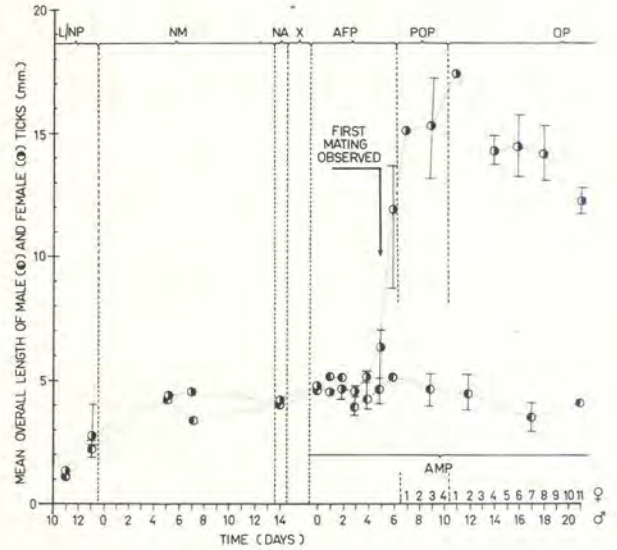


FIG. 14 Changes in mean overall length of male and female *Rhipicephalus e. evertsi* ticks throughout their larval/nymphal and adult phases. Vertical lines indicate range. AFP=Adult female parasitic phase. AMP=Adult male parasitic phase. L/NP=Larval/nymphal parasitic phase. NA=Newly-emerged adult ticks. NM=Nymphal metamorphosis in laboratory incubator (30 °C; 95% R.H.). OP=Oviposition period. POP=Preoviposition period. X=2-week-period in incubator between adult emergence and introduction to host

Between Day 11 (2 days after the first nymphs moulted on the rabbit) and Day 13 of the nymphal parasitic phase, nymphs increased rapidly in length through engorgement (Fig. 14, 15). At the same time the testis also lengthened. The accessory glands however, grew only slightly. Fully engorged nymphs that had dropped from the host on Day 14 were placed in an incubator (30 °C; 95% R.H.) to moult. During metamorphosis no marked changes were observed in the ticks except that the accessory gland complex lengthened. Newly-emerged adults were similar in overall length to metamorphosing nymphs and the length of their testes was also much the same. Both male and female adults were kept in the incubator for 2 weeks, during which time growth took place in both the accessory gland complex and the testes. They were then placed on a calf to feed and during the following 5 days further enlargement of these organs took place. Pairing of the sexes was first observed on Day 5 and all ticks were paired by Day 6. Maximum development of both testes and accessory glands was recorded on Day 6, showing that these organs grow mainly during the first 5-6 days of feeding. Thereafter, a decrease

in the length of the testes appeared to take place, but, as males dissected over this period tended to be smaller, this decrease was probably apparent rather than real. The last males to be dissected were removed from the host on Day 21. A few males were left on the calf until they died or dropped off naturally. The last of these disappeared on Day 43 after infestation.

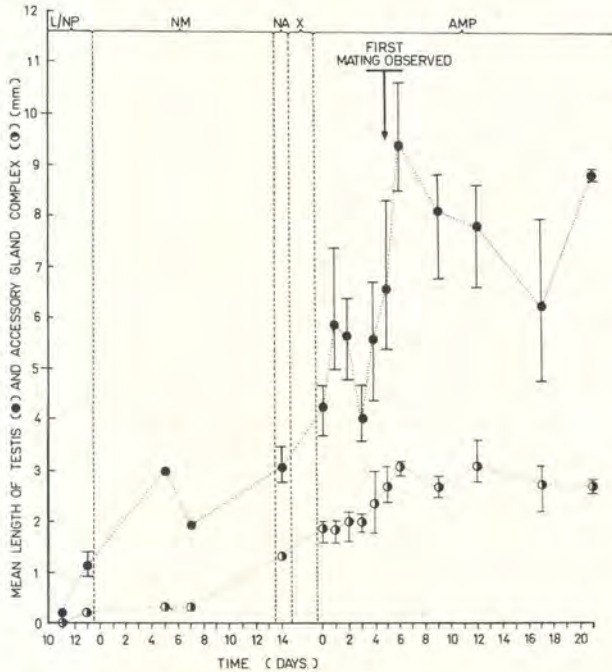


FIG. 15 Changes in mean length of male *Rhipicephalus e. evertsi* testis and accessory gland complex throughout larval/nymphal and adult phases. Vertical lines indicate range. Abbreviations as in Fig. 14

Spermatogenesis followed the same basic pattern as shown for *B. decoloratus* by Londt & Spickett (1976). The males have a diploid chromosome complement of 20 autosomes and 1 long x-chromosome. No chromosomes could be extracted from nymphal ticks or pharate adults. Meiosis and mitosis were first observed 24 hours after adult attachment to the host. Spermatid transformation was first seen on Day 4 of the adult parasitic phase and on this day all stages of transformation were noted as in male *B. decoloratus*.

Males began fertilizing females on Day 5 and counts, made of the number of spermiophore capsules found in the seminal receptacles of 18 females, were as follows: 1 capsule—5 ♀♀; 2 capsules—8 ♀♀; 3 capsules—0 ♀♀; 4 capsules—2 ♀♀; 5 capsules—1 ♀; 6 capsules—2 ♀♀. It appears, therefore, that 2 capsules are usually produced by males at a single impregnation, although a single capsule may be produced. Five females possessed more than 2 capsules, suggesting that multiple mating is possible. These observations parallel those reported for *B. decoloratus* by Londt & Spickett (1976).

Female

The morphology of the female reproductive organs is similar to that described for *B. decoloratus* by Londt & Spickett (1976). The changes recorded in the overall length of the dissected ticks (Fig. 14) and the lengths of their ovaries and oviducts (Fig. 16) are illustrated. As in the case of males, larvae were

not dissected. All measurements were made as described by Londt & Spickett (1976). During nymphal feeding and metamorphosis very little growth in the reproductive organs took place. Newly-emerged adult females were similar to pharate adults. Adult ticks, kept for 2 weeks in an incubator (30 °C, 95% R.H.) and before their release on a calf, showed some growth of the reproductive organs. A clear distinction between ovary and oviduct was first noted in adult females just before they were put on the host. During the first 3 days of attachment little change was recorded in ovary or oviduct length, then both grew rapidly during Days 4, 5 and 6. The first few females, fertilized on Day 5, began falling from the host on Day 6. Those females dissected on Day 6, however, were pulled off the host,

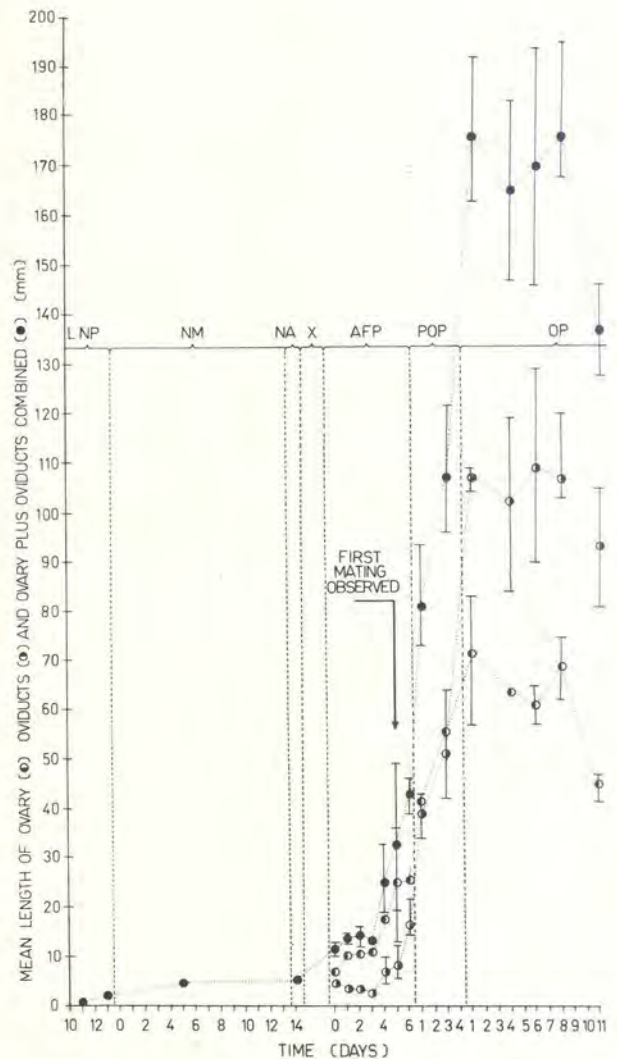


FIG. 16 Changes in mean length of female *Rhipicephalus e. evertsi* ovary, oviducts and ovary plus oviducts combined throughout larval/nymphal and adult phases. Vertical lines indicate range. Abbreviations as in Fig. 14

Female ticks that had dropped from the host on Day 7 after adult infestation of the calf were placed in the incubator (30 °C, 95% R.H.) and watched throughout their preoviposition and oviposition periods. Rapid development of the ovary continued throughout the preoviposition period and maximum lengths were recorded on Day 1 of the

oviposition period. The ovary length decreased gradually during egg production and females, dissected on Day 11 of their oviposition period, contained few unladen eggs. No further dissections were made after Day 11, although oviposition continued for a further 9–10 days. The combined lengths of both oviducts increased very rapidly during the preoviposition period and they were first seen to be packed with eggs on Day 1 of the oviposition period. The very marked increase in oviduct length shown between Day 3 of the preoviposition period and Day 1 of the oviposition period is caused by hypertrophy, while the gradual decrease in their length thereafter is probably due to the presence of fewer and fewer eggs. These observations parallel those described for *B. decoloratus* by Londt & Spickett (1976).

Females have a diploid chromosomal complement of 20 autosomes and 2 long x-chromosomes, and, as in *B. decoloratus*, no meiosis was ever noted in nymphs or adult ticks. Spermiphores were observed in their capsules within the seminal receptacle from Day 5 of the adult parasitic phase until Day 1 of the preoviposition period, when they were seen both in the capsules and in the oviducts. On Day 3 of the preoviposition period, a few spermiphores were found in the oviducts only, the capsules being empty. At no time were spermiphores seen in the ovary lumen although they may have been masked by the presence of the large developing ova. Londt & Spickett (1976) reported wax-like bodies in the seminal receptacles of *B. decoloratus* females and similar bodies were found in *R. e. evertsi*. During the oviposition period, these bodies often looked pink. Spermiphore capsules were found to be intact till Day 11 of the oviposition period (when the last females were dissected), but in some individuals the contents of the seminal receptacle appeared to have changed and become rather uniform and structureless. The receptacles of these individuals had apparently collapsed and no signs of spermiphore capsules were seen.

ACKNOWLEDGEMENTS

We wish to thank Miss J. B. Walker and Dr J. D. Bezuidenhout for their constructive criticism of the manuscript and Dr C. J. Howell, head of the Department of Entomology, Veterinary Research Institute, Onderstepoort, for permission to publish this work.

REFERENCES

ARTHUR, D. R., 1973. Host and tick relationships: A review. *Journal of Wildlife Diseases* 9, 74–84.
 ARTHUR, D. R. & LONDT, J. G. H., 1973. The parasitic cycle of *Boophilus decoloratus* (Koch, 1844) (Acarina: Ixodidae). *Journal of the Entomological Society of Southern Africa* 37, 87–116.
 BAKER, MAUREEN K. & DUCASSE, F. B. W., 1967. Tick infestation of livestock in Natal I. The predilection sites and seasonal variations of cattle ticks. *Journal of the South African Veterinary Medical Association* 38, 447–543.

BAKER, MAUREEN K. & DUCASSE, F. B. W., 1968. Tick infestation of livestock in Natal. The role played by goats as reservoirs of the economically important cattle ticks. *Journal of the South African Veterinary Medical Association* 39, 55–59.
 BEDFORD, G. A. H. & GRAF, H., 1935. Ticks, tick-borne diseases and their eradication in South Africa. II. The transmitters of East Coast fever and redwater in cattle. *Farming in South Africa* 10, 14–17, 20.
 BROWN, A. W. A., 1968. Insecticide resistance comes of age. *Bulletin of the Entomological Society of America* 14, 23–27.
 DUCASSE, F. B. W., 1969. The distribution of ticks on the host. In: *The biology and control of ticks in Southern Africa*. Symposium held at Rhodes University, Grahamstown, 1–3 July 1969. pp 43–50.
 GEAR, J., 1954. The rickettsial diseases of Southern Africa. A review of recent studies. *South African Journal of Clinical Science* 5, 158–175.
 GRAY, W. J., 1961. *Rhipicephalus evertsi*: Notes on free-living phases. *Bulletin of Epizootic Diseases in Africa* 9, 25–27.
 HOOGSTRAAL, H., 1956. African Ixodoidea. I. Ticks of the Sudan. *Department of the Navy, Bureau of Medicine and Surgery, Washington D.C.* 1101 pp.
 JOOSTE, KATE F., 1966. A two-year study of the seasonal occurrence of adult ticks on a herd of red poll cows. *Rhodesian Agricultural Journal* 63, 97–99.
 LONDT, J. G. H., 1974. The preoviposition period of *Boophilus decoloratus* (Koch, 1844) (Acarina: Ixodidae). *Journal of the Entomological Society of Southern Africa* 37, 405–412.
 LONDT, J. G. H., 1977. Oviposition and incubation in *Boophilus decoloratus* (Koch, 1844) (Acarina: Ixodidae). *Onderstepoort Journal of Veterinary Research* 44, 13–20.
 LONDT, J. G. H. & ARTHUR, D. R., 1975. The structure and parasitic life cycle of *Boophilus microplus* (Canestrini, 1888) in South Africa (Acarina: Ixodidae). *Journal of the Entomological Society of Southern Africa* 38, 321–340.
 LONDT, J. G. H. & SPICKETT, A. M., 1976. Gonad development and gametogenesis in *Boophilus decoloratus* (Koch, 1844) (Acarina: Metastriata: Ixodidae). *Onderstepoort Journal of Veterinary Research* 43, 79–96.
 MOREAU, R. E., 1933. The food of the Redbilled Oxpecker, *Buphagus erythrorhynchus* (Stanley). *Bulletin of Entomological Research* 24, 325–335.
 NEITZ, W. O., 1956. Classification, transmission, and biology of piroplasms of domestic animals. *Annals of the New York Academy of Science* 64, 56–111.
 NEITZ, W. O., 1958. *Rhipicephalus* tick toxicosis in cattle: Its possible aggravating effects on certain diseases. *Journal of the South African Veterinary Medical Association* 29, 39–50.
 NORVAL, R. A. I., 1974. The life cycle of *Amblyomma hebraeum* Koch, 1844 (Acarina: Ixodidae). *Journal of the Entomological Society of Southern Africa* 37, 357–367.
 PAL, R. & KALRA, R. L., 1965. Insecticide resistance. A review of developments in 1960–1963. World Health Organization, Vector Control, 51 pp.
 SHAW, R. D. & STONES, L. C., 1966. The problem of resistance in cattle tick control. *Proceedings of the 1st International Congress of Parasitology*, (Rome, September 21–26, 1964) 2, 1050–1052.
 THEILER, GERTRUD, 1950. Zoological survey of the Union of South Africa. Tick survey. Part V. Distribution of *Rhipicephalus evertsi*, the red tick. *Onderstepoort Journal of Veterinary Science and Animal Industry* 24, 33–36.
 THOMAS, A. D., 1962. Ticks, their habits and behaviour in Nature. *Journal of the South African Veterinary Medical Association* 33, 163–179.
 WHITEHEAD, G. B. & BAKER, J. A. F., 1960. Toxaphene resistance in the red tick, *Rhipicephalus evertsi* Neumann in South Africa. *Veterinary Record* 72, 566.
 WHITEHEAD, G. B. & BAKER, J. A. F., 1961. Acaricide resistance in the red tick, *Rhipicephalus evertsi* Neumann. *Bulletin of Entomological Research* 51, 755–764.
 WILSON, S. G., 1953. A survey of the distribution of the tick vectors of East Coast fever in East and Central Africa. *Proceedings of the 15th International Veterinary Congress*, (Stockholm, August 9–15) 1, 287–290.