STUDIES ON THE BIOLOGY AND ECOLOGY OF *AMBLYOMMA HEBRAEUM* KOCH, 1844 AND OTHER TICK SPECIES (IXODIDAE) OF THE EASTERN CAPE.

by

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A THESIS PRESENTED TO RHODES UNIVERSITY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY.

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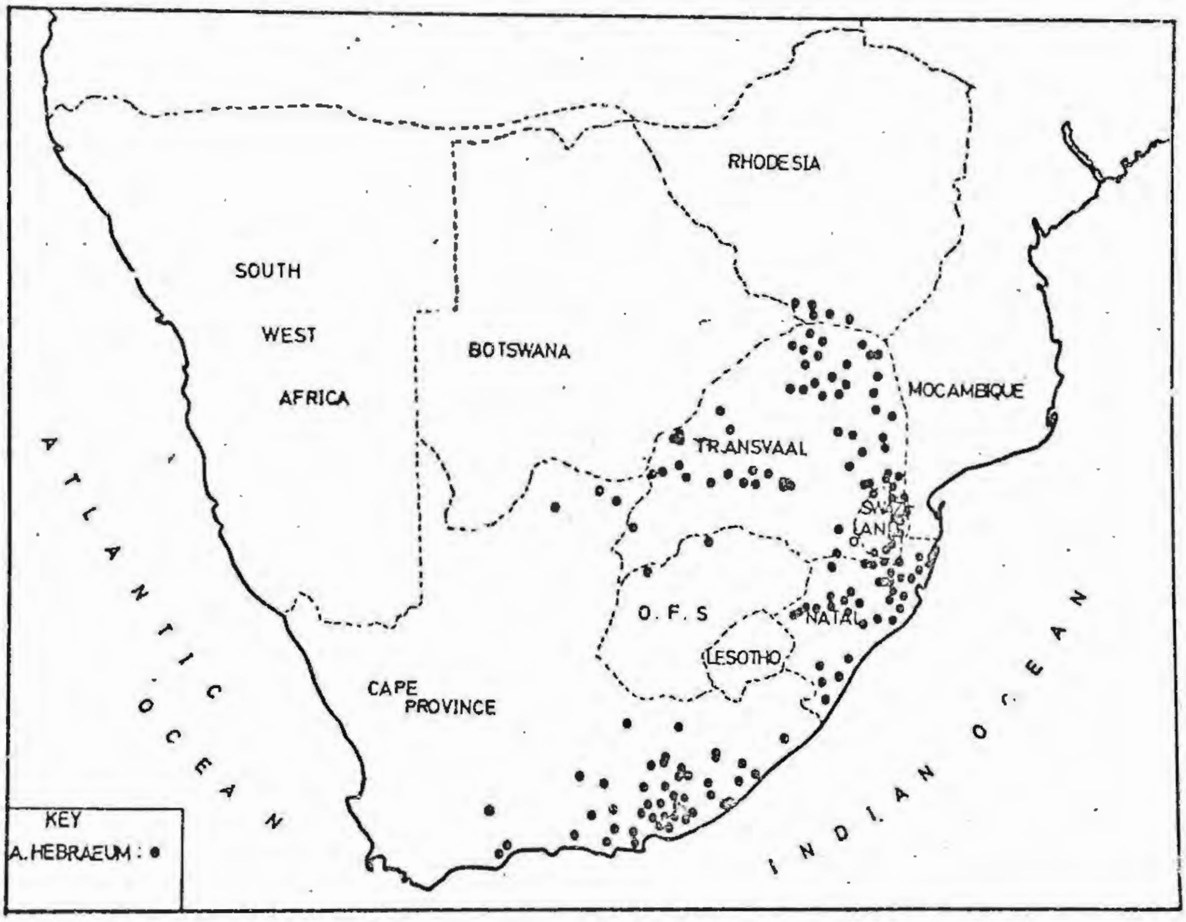
December, 1974.

FRONTISPIECE

The distribution of <u>Amblyomma</u> <u>hebraeum</u> Koch in southern Africa, based on the records of Theiler (1948).



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Acknowledgements.

I wish to thank the following for their assistance during this investigation.

Professor G.B. Whitehead, of Rhodes University, for advice and encouragement throughout the investigation, and for constructive criticism of the manuscript.

Professor D.R. Arthur, of London University King's College, for his considerable assistance during the initial stages of the investigation.

Dr J.G.H. Londt, of Rhodes University, for useful discussion and comments on the work.

Mr L.A. Capitini, of Trenton, New Jersey, in collaboration with whom the work on spermatogenesis was done.

Dr D.J. van Schalkwyk and Professor B.R. Allanson, of Rhodes University, for advice on statistical methods.

From the Tick Research Unit of Rhodes University, Mr M.M. Knight, for his considerable technical assistance. Miss C. Crowe, for the preparation of the majority of the figures and for criticism of the manuscript. Mrs A. Holland, for advice and discussion.

Mr R. Cross, of Rhodes University, for his assistance with the electron microscope.

Mr J.C. Greig, of the Department of Nature Conservation, for his assistance with the host survey.

Dr A. Jacot-Guillarmod, of Rhodes University, for identifying the plant material collected at Paardekraal Farm.

Mr F.D. Ford, of Paardekraal Farm, for allowing me to work on his Farm, and for providing the experimental cattle, together with many other deeds of kindness. I would also like to thank his sons, Anthony and Geoffery, for their assistance in collecting hosts.

Mr E. Knight, of Beaconsfield Farm, for allowing me to use the facilities at his farm to rear ticks, while the Research Station of the Tick Research Unit was under construction.

Mr G. Walsh of Bucklands Farm, for furnishing information on heartwater mortalities in Angora goats.

Lastly, I would like to thank the organizations which have contributed funds to the Tick Research Unit, making it possible to undertake this investigation.

1. Introduction.

Tick borne diseases of livestock are among the most important factors which have retarded economic development in many parts of Africa. Modification of the environment due to the expansion of agriculture into previously undeveloped areas, together with the introduction of livestock, has disturbed the natural balance which existed between ticks and indigenous hosts. Many tick species have adapted to domestic stock, and in some instances have spread over large areas which were previously uninfested. A number of tick species which are parasitic on domestic stock, eg. Amblyomma hebraeum Koch, 1844, Boophilus decoloratus (Koch, 1844), Rhipicephalus evertsi Neumann, 1897 and Rhipicephalus appendiculatus Neumann, 1901, are vectors of pathogenic micro-organisms. Unlike indigenous hosts however, domestic stock have no innate immunity to tick-borne diseases.

In order to control tick-borne diseases in domestic stock, it is most expedient to control the tick vectors. The normal method of tick control in current use is the 'dipping' of domestic stock with acaricides. In South Africa this has effectively reduced tick populations to low levels in most parts of the country, and appears to have eradicated individual species from certain areas (Stampa, 1969a). Dipping, however, has serious limitations, as tick populations are able to develop resistance to acaricides (Whitehead, 1973). It is therefore necessary to investigate alternative methods of tick control.

In a recent review on current worldwide research on the control of ticks, Drummond (1970) drew attention to progress which has recently been made in controlling ticks by methods such as pasture spelling (rotation of cattle in pastures), alteration of the environment and the selection of tick resistant breeds of cattle. These approaches present possible alternatives to dipping, but require as a basis, a sound understanding of tick biology and ecology. Unfortunately in South Africa, as observed by Londt (1973), there is a paucity of quantitative biological and ecological data on economically important tick species.

The bont tick, A. hebraeum, at present represents one of the most serious tick problems in South Africa, and for this reason was chosen as the subject of this thesis. A. hebraeum occurs throughout south-eastern Africa and transmits Cowdria (Rickettsia) ruminatum which causes 'heartwater' fever in ruminants. If untreated, heartwater can be fatal in sheep, goats and cattle. The animals most susceptible to the disease are Merino sheep and Angora goats, (Alexander, 1931). Heartwater is a particularly serious problem in the Eastern Cape Province of South Africa, where Merino sheep and Angora goats play an important part in livestock farming. The prevalence of heartwater has prevented the introduction of Angora goats into large, potentially productive areas of the province. In other areas, where heartwater mortality rates of up to 30% per annum have recently been recorded in flocks of goats (Walsh, personal communication), the continued production of mohair is threatened. Throughout the Eastern Cape Province, stock losses due to heartwater, dipping costs and the costs of innoculation, and treatment of infected stock, pose a serious threat to the profitability of stock farming.

The heartwater problem has arisen as a result of the shortcomings of the presently practised method of controlling A. hebraeum by dipping. The aims of this investigation are to accumulate information which in the short term,could lead to a more efficient use of acaricides in the control of A. hebraeum, and in the long term, provide a basis on which to develop alternative methods of control.

The thesis is divided into four sections. Section one covers the biology of A. hebraeum and includes information on the life cycle under controlled laboratory conditions, the rate of feeding, mating behaviour and spermatogenesis. Section two deals with the non-parasitic stages of A. hebraeum, or that part of the life cycle which occurs off the host. Data are given on the distribution of larvae in different habitats, and the seasonal activity of all stages of the life cycle in relation to macroclimatic conditions. In addition, the survival and development of the non-parasitic stages have been studied in relation to temperature and atmospheric humidity. Section three covers the parasitic stages of *A. hebraeum*. The results of a host survey are given, together with data on the responses of laboratory hosts to repeated infestations of the tick. In the last section (four), information is given on the biology and ecology of species other than *A. hebraeum*, which were collected during the field surveys. The results in section four provide a useful comparison with the results in earlier sections on *A. hebraeum*.

SECTION ONE

THE BIOLOGY OF *AMBLYOMMA HEBRAEUM* KOCH

2. The biology of *Amblyomma hebraeum*.

2.1. Introduction

This chapter is comprised of two papers, covering the biology of *A. hebraeum*.

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J. ent. Soc. sth. Afr. 1974
Vol. 37, No. 2, pp. 357–367

The life cycle of *Amblyomma hebraeum* Koch, 1844 (Acarina: Ixodidae)

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Quantitative data are given on the preovipostion, oviposition, incubation and premoult periods of *Amblyomma hebraeum* Koch maintained in darkness at 26°C and 90% RH; the duration of feeding in all stages on laboratory hosts and the onset of pharate development in engorged larvae and nymphs were also examined. Sexual maturation, mating capacity and longevity of parasitic males and mate-seeking in relation to engorgement in females have been studied.

INTRODUCTION

The life cycle of the bont tick, *Amblyomma hebraeum* Koch, was studied by Lounsbury (1899), Nuttall (1915–16) and Theiler (1943). Unfortunately, none of the authors related their observations to environmental factors, except in the most general terms, and the data in respect of specific developmental periods showed wide variations. The present investigation was prompted by a need for more quantitative information and covers the life cycle of *A. hebraeum* under controlled laboratory conditions.

MATERIALS AND METHODS

Ticks were originally obtained from cattle at Gulu Farm, East London. Parasitic stages were fed on caged laboratory hosts, maintained in the field station of the Tick Research Unit of Rhodes University. Each cage housing a single host stood over a water bath, or in the case of cattle, a metal tray into which detached ticks dropped. Larvae were fed on shaved areas on the backs of Himalayan Giant rabbits. Nymphs were fed on the ears of rabbits and Merino sheep. Adults were fed on the ears of rabbits, or the tail or belly of Guernsey calves. Males were allowed to feed on the host for at least 4 days before females were released in their vicinity.

Engorged ticks which dropped from the host were removed daily and maintained in a dark incubator at 26°C and approximately 90% relative humidity (RH). Eggs were either counted daily or else weekly yields were removed and weighed. Daily examination of engorged larvae, nymphs and adult females was undertaken to determine the duration of the nymphal and adult premoult periods, the preoviposition period and oviposition period. Newly emerged ticks were kept in the incubator for at least 10 days before being placed on hosts.

To assess the progress of development of the pharate nymph, batches of 20 larvae were removed daily from a rabbit during the feeding period and a sample of 100 detached larvae was collected from the water tray. These were weighed immediately and then cleared for 1–3 hours in lactic acid. Engorged nymphs did not clear well, and to assess the progress of development of the pharate adult, nymphs were dissected. On days 1–7 of the adult premoult period, 10 nymphs were dissected daily, while on days 8–10, 20 nymphs were dissected each day. Before dissection nymphs were injected with a fixative consisting of 7 ml 40% formaldehyde, 5 ml glacial acetic acid and 100 ml 70% alcohol and were left in 70% alcohol for 24 hours.

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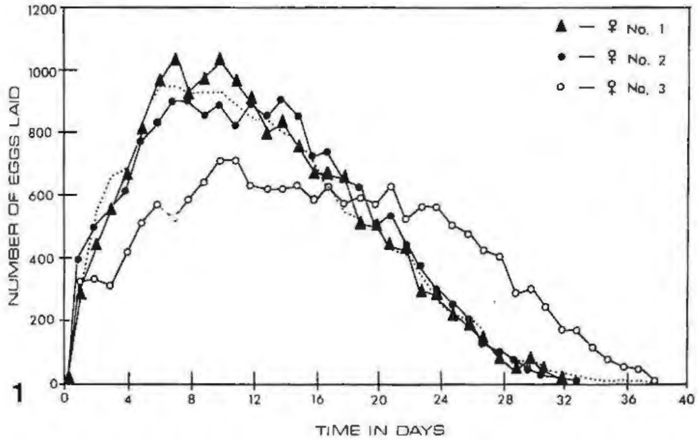

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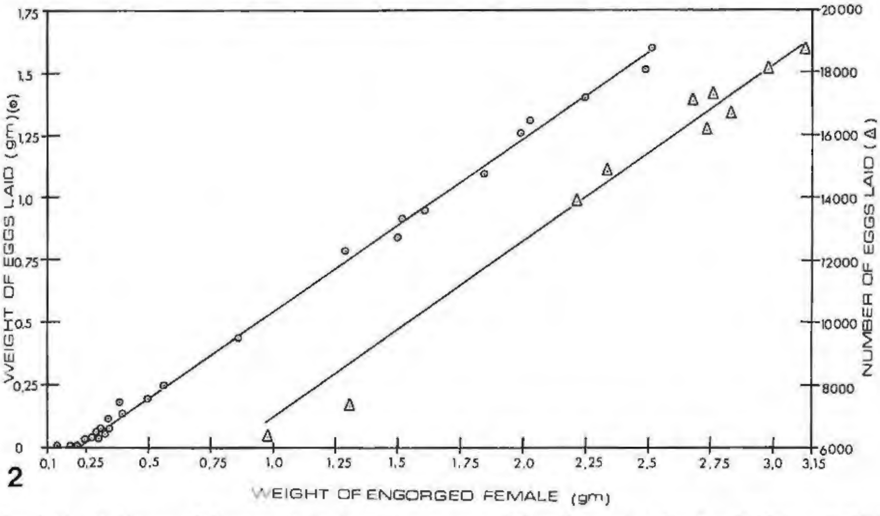


Figs 1–2. *Amblyomma hebraeum*. 1. Oviposition curves of females maintained at 26°C and 90% RH in continuous darkness. . . ., mean curve for 8 females. 2. The relationship between engorged weight of females and the weight and number of eggs produced.

RESULTS

Preoviposition

In 27 engorged and partially engorged females (removed from the host before complete engorgement) which weighed more than 0,325 g, the preoviposition period lasted 10–14 days (mean 11,1 days). While in three partially engorged females weighing less than 0,325 g, the duration of the preoviposition period was 15, 16 and 17 days.

Oviposition

From 8 females the numbers of eggs produced per day were counted (fig. 1). In two females there was a sharp rise to a peak of egg production on the 6th day of oviposition, while in three females the peak was on the 7th day, and in the remaining three on the 10th, 11th and 14th days. The egg production curve is characterized by a period of several days when production is maintained at a high level, after which production decreases and laying ceases between the 30th and 38th day. Since the ticks were all maintained under the same experimental conditions, the relative peaks of egg production are probably due to individual variation. In the case of those ticks having lower initial peaks of production (e.g. tick No. 3, fig. 1), this was compensated for by extended periods of laying and the production of larger numbers of eggs per day in the later stages.

Snow & Arthur (1966) showed that the number of eggs laid by female ticks is a function of the weight of imbibed nutrients less the quantity needed for metabolic purposes other than egg production. To test the validity of this in respect of *A. hebraeum*, the weight of eggs produced by each of 26 partially engorged and fully engorged females was plotted against body weight. The results (fig. 2) show a linear relationship between weight of female ticks above 0,2 g and weight of eggs produced. A similar relationship (fig. 2) was found to exist between the numbers of eggs laid and the weights of 10 engorged females. In other words, the greater the weight of the female, the more eggs will be deposited. The total number of eggs laid by fully engorged females varied from 6 366 to 18 765 (mean 14 711).

Incubation

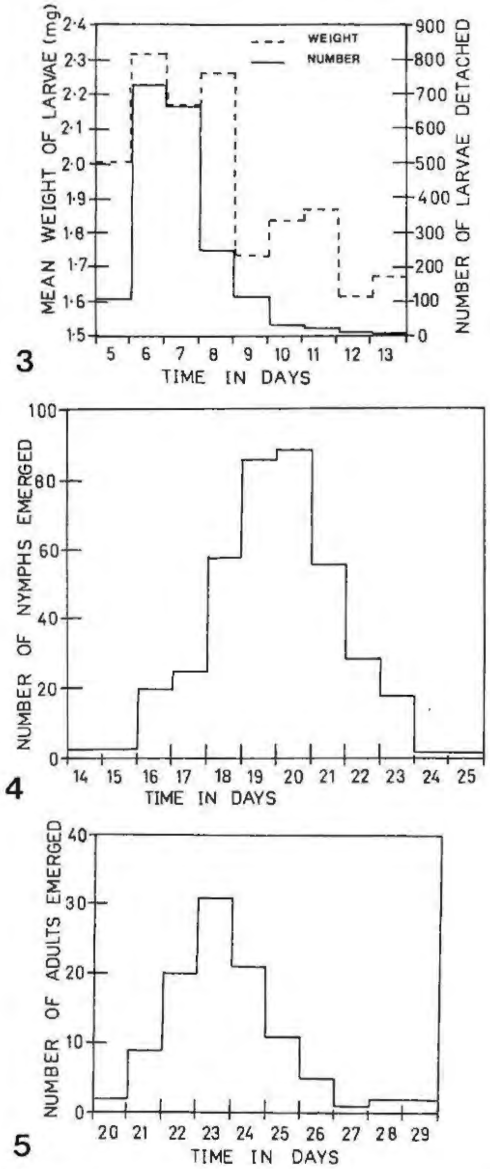
The incubation period of eggs taken from any single day's production was 54–61 days.

Larval stage

Larvae placed on rabbits which had not previously been infested, fed for 4–15 days with the majority detaching satiated on the 6th, 7th and 8th days. An example of such a "drop off" curve is shown in fig. 3, and in this case all larvae had completed feeding by the 13th day. The mean weight per batch of engorged larvae varied between hosts and on individual rabbits was higher in summer than in winter (Norval, in preparation) and ranged from 1,30 to 2,45 mg. In 16 out of 22 batches examined, the mean weights of larvae detaching within 4–8 days were heavier than those detaching within 9–15 days. An example is shown in fig. 3; here the mean weight of ticks recovered each day was in excess of 2,0 mg on days 5–8, while on days 9–11 it was 1,7–1,9 mg and decreased to 1,6–1,7 mg on days 12 and 13.

Once detached from the host, larvae were active for 2–3 days, and presumably in the field this is when they search for moulting sites.

In fully engorged larvae which had been detached from the host for 0–24 hours, the development of the pharate nymph was well advanced. Viewed ventrally, the coxae of the first three pairs of rudimentary nymphal legs and the entire 4th pair of



Figs 3–5. *Amblyomma hebraeum*. 3. Histogram of detachment of engorged larvae from a rabbit in January 1973, and the mean weight of detached larvae on each day of the feeding period. 4 & 5. Histograms of nymphal and adult premoult periods, at 26°C and 90% RH in continuous darkness.

legs could be seen through the larval cuticle. Dissection of engorged larvae revealed that the legs of the pharate nymph developed within the structure of the larval legs, before the larval leg musculature had disappeared. This suggests that histolysis of larval leg musculature and histogenesis of nymphal legs occur simultaneously and this is reflected in a gradual decline in the walking activity of engorged larvae. The 4th pair of legs of the pharate nymph was visible on the 4th day of larval feeding in 20% of larvae, in 35% of larvae on the 5th day of feeding and in 50% and 60% of larvae on the 6th and 7th days of feeding respectively. The development of the pharate nymph depends on the quantity of nutrient imbibed by the larva rather than the time spent feeding. Irrespective of when they were removed from the host, all larvae of more than 1 mg in weight showed pharate characters, while these were absent in all but 5% of larvae below this weight.

The nymphal premoult period lasted 14–25 days (mean, 19,5 days) (fig. 4).

Nymphal stage

Nymphs took up to 36 hours to attach while confined in muslin bags on the ears of rabbits, while all attached within 12 hours when confined on the ears of sheep. On rabbits which had not previously been infested, nymphs fed for 5–13 days and the mean engorged weight was 43 mg. On previously uninfested sheep, maintained under the same conditions, nymphs fed for 6–9 days and the mean engorged weight was 62 mg. As in the previous stage, the mean weight per batch of engorged nymphs also varied between individual hosts of the same species, and on the same host engorged nymphs were heavier in summer than in winter (Norval, in preparation). The mean weight per batch ranged from 19,8 to 65,9 mg. In summer conditions, nymphs engorged in 4–9 days on the ears of sheep, with the majority detaching satiated on the 5th, 6th and 7th days (fig. 6).

Arthur & Snow (1966) showed that two size groups of nymphs exist in *Hyalomma anatolicum anatolicum* (Koch) and reflect potential sexuality. Nymphs which produce males are smaller in size than those which produce females. To test this relationship in *A. hebraeum*, a batch of 163 engorged nymphs were weighed and maintained individually in an incubator. 65 nymphs moulted into males and 98 into females. The mean weight of male nymphs was 51,2 mg and of female nymphs was 64,2 mg, and the difference between the groups was highly significant ($p = < 0{,}001$).

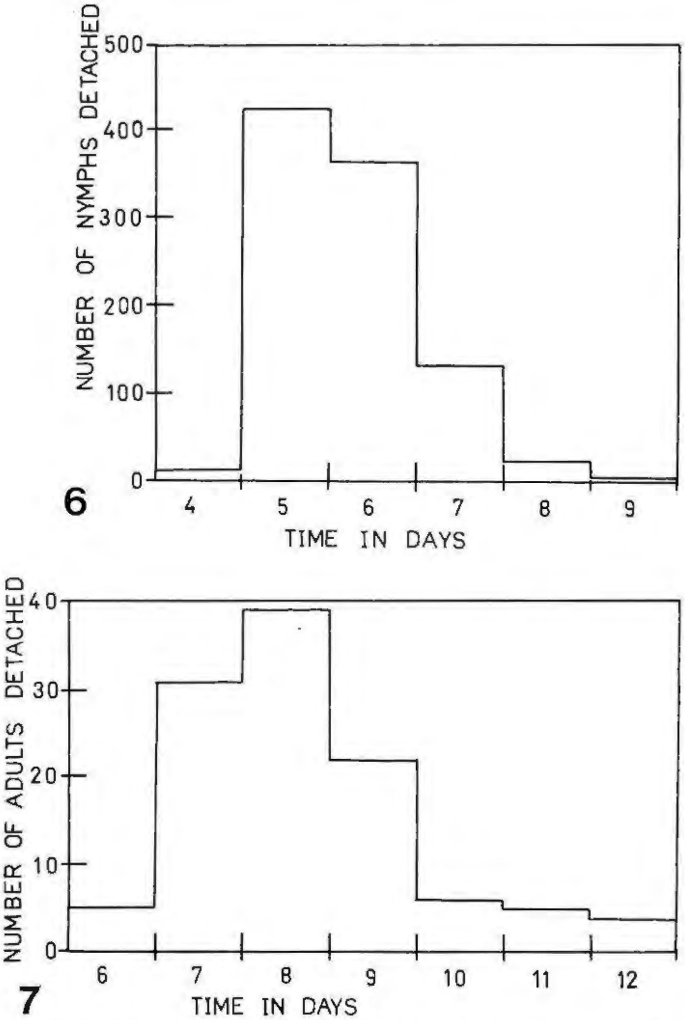
Engorged nymphs were active for 5–7 days after detaching from the host. Unlike the previous stage the limbs of the pharate adult were not observed until the nymphs had ceased to walk. By dissection of engorged nymphs it was found that the legs of the pharate adult were discernible in 10% of nymphs on the 7th day after detachment, in 30% of nymphs on the 8th day, in 90% of nymphs on the 9th day and in 100% of nymphs on the 10th day. The legs of the pharate adult developed within the structure of the nymphal legs, and unlike the previous stage, it appeared that histolysis of the nymphal leg musculature was complete at the onset of histogenesis of the adult leg.

The adult premoult period lasted 20–29 days (mean 23,4 days) (fig. 5).

Adult stage

To determine the behaviour of adults on the host, a series of experiments was undertaken in which adults were placed on the ears of rabbits and on the tail and belly of a calf. These are summarized in Tables 1 and 2.

Female ticks placed on the host in the absence of males failed to attach (Tables 1 and 2, treatment 1), while males attached readily in the absence of females (Tables 1 and 2, treatment 2). When both sexes were placed simultaneously on the host, the majority of males and a few females attached (Table 2, treatments 3 and 4). None of the attached females was paired with a male, the position necessary for copulation, and all failed to engorge. When females were placed on the host with males which had been attached for 1–2 days, all failed to attach (Table 1, treatment 3). Similarly, if females were held adjacent (venter to venter) to newly attached males, there was no attachment (Table 1, treatment 4; Table 2, treatment 5). However, when held adjacent to males



Figs 6–7. *Amblyomma hebraeum*. 6. Histogram of detachment of engorged nymphs from sheep in January 1973. 7. Histogram of detachment of engorged adult females from Guernsey calves in January and February 1973.

which had been attached for 7 days, females attached immediately (Table 1, treatment 5; Table 2, treatment 6). Females placed 2–3 cm from males which had fed for 7 days, were able to locate the male and attach within a few minutes (Table 1, treatment 6; Table 2, treatment 7). The length of time required by individual males to feed before becoming sexually mature, varied from 4 to 6 days.

TABLE 1. The attachment of males and females of *Amblyomma hebraeum* on the ears of rabbits.

Treatment	No. ticks attached at:			
	start		24 hours	
	♂	♀	♂	♀
(1) 10 ♀ in ear bag	—	0	—	0
(2) 10 ♂ in ear bag	0	—	9	—
(3) 10 ♀ in ear bag with 10 ♂ attached 1–2 days previously	10	0	10	0
(4) 10 ♀ placed adjacent to 10 ♂ attached 1–2 days previously	10	0	10	0
(5) 10 ♀ placed adjacent to 10 ♂ attached 7 days previously	10	10	10	10
(6) 10 ♀ placed 2–3 cm from 10 ♂ attached 7 days previously	10	10	10	10

On the host, males of *A. hebraeum* generally did not wander far from the site of release and usually attached within a few minutes. Females on the other hand were very active and did not attach unless they encountered a sexually mature male. The attachment of females away from the male (Table 2, treatments 3 and 4) may have resulted from unnatural restriction on the host. Normally, when 2–5 cm away from a sexually mature male, the female stopped running and raised the first pair of legs in questing movements. The male responded by raising the body perpendicular to the surface of the host. This was followed by periodic active movements of the legs, which appeared to coincide with movements of the female. After remaining stationary for between a few seconds and 2 minutes, the female moved directly to the male, and on contact the pair embraced. The venter to venter orientation was achieved by complicated leg movements, after which the female attached and copulation proceeded.

With the exception of the genus *Ixodes*, spermatogenesis in males of all ticks of the family Ixodidae is completed on the host (Arthur, 1962). In *A. hebraeum* the completion of spermatogenesis is accompanied by physiological and behavioural changes, viz. the production of a sex pheromone and the response to the presence of a female. Although nothing is known about the site of production or the chemical nature of the pheromone, there is little doubt as to its existence, which is evident from the behaviour of the female in relation to the sexually mature male, and the existence of sex pheromones in other ixodid species (Gladney, 1971; Berger *et al.*, 1971). The response of the sexually mature male to the female appears to be mechanically elicited either by direct disturbance of the male or by disturbance of the hairs of the host in the vicinity of the male. After mechanical stimulation the male may remain in the perpendicular position for as long as half a minute, and will actively move the legs in response to further stimulation. Males will embrace any objects placed immediately adjacent to them, for example, the tip of one's finger, small pieces of wood, unfed males of *A. hebraeum* and even unfed females of *Hyalomma marginatum rufipes* Koch. It is clear that the male is incapable of discriminating between ticks and other objects or between tick species or sexes. This draws attention to the role of the sex pheromone in mating, and shows that mate selection rests solely with the female.

TABLE 2. The attachment of males and females of *Amblyomma hebraeum* on Guernsey calves.

Treatment	No. ticks attached at:													
	start		1 day		2 days		3 days		4 days		5 days		6 days	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
(1) 40 ♀ in tail bag . .	—	0	—	0	—	0	—	0	—	0	—	0	—	0
(2) 40 ♂ in tail bag . .	0	—	39	—	39	—	39	—	39	—	39	—	39	—
(3) 15 ♂ and 10 ♀ in tail bag	0	0	11	6	11	6	11	4	11	2	11	1	11	0
(4) 6 ♂ and 6 ♀ under sheet on belly . .	0	0	5	1	5	0	5	0	5	0	5	0	5	0
(5) 50 ♀ placed adjacent to 50 ♂ attached 1–2 days previously . .	50	0	50	0	50	0	50	0	50	0	50	0	50	0
(6) 30 ♀ placed adjacent to 30 ♂ attached 7 days previously . .	30	30	30	30	30	30	30	30	30	30	30	30	30	30
(7) 20 ♀ placed 2–3 cm from 20 ♂ attached 7 days previously . .	20	20	20	20	20	20	20	20	20	20	20	20	20	20

In the laboratory, unfed males and females which were maintained together in glass tubes for many months, never attempted to copulate, while sexually mature males, removed from a host, mated readily with unfed females. Placed in a glass petri dish, females were attracted to males and on contact, pairs embraced. Within 10 minutes males had applied their mouthparts to the female genital aperture and had secreted a clear liquid into the aperture. In a number of cases a single white spermatophore was seen in the genital aperture, approximately 20 minutes after the pair had embraced.

To determine the number of times that males of *A. hebraeum* are able to mate, 30 males were allowed to attach on the tail of a calf. After 6 days a female was allowed to embrace each male, and new females were introduced with the males, soon after all of the first batch had engorged. This was repeated until all the males had disappeared. The results showed that males remained attached for as long as 132 days and were able to mate a maximum of eight times. 50% of males mated five times and remained on the host for as long as 60 days. In no instances did males change their location on the host by more than a few millimeters, and this can probably be attributed to the detachment of the mouthparts during copulation and subsequent reattachment. The loss of males appeared to result from grooming by the host and natural mortality. As evidence for the latter, four of the 15 males lost between the 58th and 94th day were found dead while attached to the host. The eggs laid by all females in this experiment were viable.

Females of *A. hebraeum* fed for 6–12 days on the tails of calves, with peak numbers detaching on the 8th day of feeding (fig. 7). Of two females which remained attached on the ears of a rabbit for 13 and 15 days, neither showed any size increase. The mouthparts appeared to have passed through the cartilage of the pinna and the skin on the opposite side of the ear was ruptured.

DISCUSSION

A. hebraeum has an extremely long life cycle, which under laboratory conditions (non-parasitic stages maintained at 26°C and 90% RH) required 169–238 days for completion. Under the same conditions, *Boophilus decoloratus* (Koch) required 67–86 days (Londt, 1973), while *H. marginatum rufipes* required 111–146 days (Norval, unpublished). Arthur & Londt (1973) attribute the shorter life cycles of 1- and 2-host ticks to the higher temperatures experienced by the premoult stages which remain on the host than those experienced by the premoult stages in 3-host ticks which develop on the ground. Further they note that the blood meal is more rapidly digested and metabolised in 1- than in 3-host ticks. This results in a more rapid transition to the pharate state, which reduces the length of the life cycle, to the extent that the entire parasitic cycle in *B. decoloratus* requires only 21–23 days. Although the time spent feeding (17 days) is only slightly shorter than in *A. hebraeum* which spends approximately 22 days feeding.

In the non-parasitic premoult stages of 2- and 3-host ticks, a delay in the onset of pharate development is necessary, as engorged ticks must seek a suitable situation on the ground in which to moult. In *A. hebraeum* the rudimentary legs of the nymph appear before larval engorgement is complete. The early appearance of pharate characters in the larva and not in the nymph may suggest that this tick tends towards a 2-host condition, although in a true 2-host tick such as *H. marginatum rufipes* the engorged larva is immobile (Norval, unpublished). The premoult period in nymphs which is longer than in larvae, may be a result of a delay in the appearance of the pharate adult.

Within the family Ixodidae there are marked differences in the requirements for mating, between the subfamilies Ixodinae and Amblyomminae. In Ixodinae spermatogenesis in males is completed in the nymphal stage and adults are able to mate immediately after emergence, either on the host or on the ground (Arthur, 1962). In Amblyomminae spermatogenesis in male nymphs proceeds only as far as the formation of primary spermatocytes (Arthur, 1962). The process is completed in adult males only after the acquisition of a blood meal, and mating occurs exclusively on the host (Arthur, 1962).

Within the Amblyomminae, mating behaviour is of 2 basic types and it appears that species from the same genus can belong to either group. In the first group, which includes *Amblyomma maculatum* Koch (Gladney, 1971) and *A. hebraeum*, males make stable attachments on the host (i.e. make no subsequent migrations) and appear to emit a sex pheromone on completion of spermatogenesis. Males remain attached to the host for many months and are capable of fertilizing numerous females. Consequently there is an accumulation of *A. hebraeum* males on cattle, and females can be outnumbered by males in a ratio of 5 to 1 (Whitnall *et al.*, 1951). Females rarely attach in the absence of sexually mature males.

Included in the second group are *Amblyomma americanum* (L.) (Gladney & Drummond, 1970a; Berger *et al.*, 1971), *Dermacentor variabilis* (Say) (Berger *et al.*, 1971) and *Hyalomma excavatum* (Koch) (Rechav & Oppenheim, 1969). After an initial blood meal, males of these species detach their mouthparts and move to an attached female. In *A. americanum* and *D. variabilis* it has been shown that the female produces a sex pheromone (Berger *et al.*, 1971). Females make stable attachments in the absence of sexually mature males (Berger *et al.*, 1971; Rechav & Oppenheim, 1969; Gladney & Drummond, 1970a), but do not commence rapid engorgement until after copulation (Rechav & Oppenheim, 1969; Gladney & Drummond, 1971; Pappas & Oliver, 1972). As in the first group, males are able to mate with numerous females. In *A. americanum*, Gladney & Drummond (1970b) observed individual males to inseminate 18–37 females in 43–127 days.

The prolonged attachment of males on the host is of obvious importance in the survival of ticks, for it greatly increases the chances of fertilization of any female which encounters the host. Why mate-seeking is undertaken by the male in some species and by the female in other species is not understood. However, it is clear from observations made in this laboratory that migrations on the host by large ticks such as adults of *A. hebraeum* involve a definite danger of falling from the host. Attached males of *A. hebraeum* which were removed from the host seldom lived for longer than a week. It therefore appears to be of greater advantage for males rather than females to remain continuously attached, for if unfed females fall from the host they remain alive for long periods and are able to await another host.

ACKNOWLEDGEMENTS

I express my thanks to Professor Don R. Arthur for useful advice during the course of the investigation, to Dr G. B. Whitehead and Dr J. G. H. Londt for valuable comment concerning the manuscript and to Mr M. Knight for invaluable assistance.

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Manuscript received 11 March 1974.

C.T.P. LTD.

J. ent. Soc. sth. Afr. 1974
Vol. 37, No. 2, pp. 393–401

The rate of feeding, and spermatogenesis in *Amblyomma hebraeum* Koch, 1844 (Acarina: Ixodidae)

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Data are given on the rate of feeding and quantity of nutrient imbibed by all stages of *Amblyomma hebraeum* Koch. Growth of testes and the progress of spermatogenesis in the males has been studied in relation to feeding. The ultrastructure of primary spermatocytes has been examined.

INTRODUCTION

Data on the duration of attachment of larvae, nymphs and females of *Amblyomma hebraeum* Koch to the host were given by Lounsbury (1899), Nuttall (1915–16), Theiler (1943) and Norval (1974), and of males by Nuttall (1915–16) and Norval (1974). With the exception of males, attachment is of relatively short duration and seldom exceeds 2 weeks. Males remain attached to the host for many months and show no marked increase in size. This led Lounsbury (1899) to speculate that these ticks did not feed. However, Arthur (1962) stated that in males of all species of the Metastriata, a blood meal is required for the completion of spermatogenesis.

In this paper the rate of feeding and quantity of nutrient ingested in all parasitic stages is compared. The growth of testes and the progress of spermatogenesis at a cellular level has been studied in relation to the rate of feeding and the duration of attachment of the male. The ultrastructure of developing spermatocytes has been examined.

MATERIALS AND METHODS

The rate of feeding in parasitic stages was determined by weight increase as this has been shown to be a valid measure of the quantity of nutrient ingested (Sutton and Arthur 1962). Larvae were fed on the backs of Himalayan Giant rabbits, nymphs on the ears of Merino sheep and adult females (in association with males) on the tails of Guernsey calves, as described by Norval (1974). Males were fed on shaved areas on the backs of Himalayan Giant rabbits. Fibre-board collars were fitted around the necks of the rabbits to restrict grooming. Groups of 5 males were placed within gauze covered perspex rings, which were glued to the skin of the rabbits. Any males not attached after 12 hours were removed.

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Samples of approximately 60 larvae and 30 nymphs were removed from the hosts on each day of the feeding period. Larvae were weighed in groups of 20 and nymphs individually on a Cahn G-2 electrobalance. Adult males and females were weighed individually before attachment and after removal from the host. This was necessary as unfed ticks showed considerable variation in weight. Individual ticks were marked for identification by removing the tarsal segment from one of their legs (excluding the first pair). 10–20 ticks of each sex were removed from the hosts each day during the feeding period and weighed on a Sartorius single pan balance.

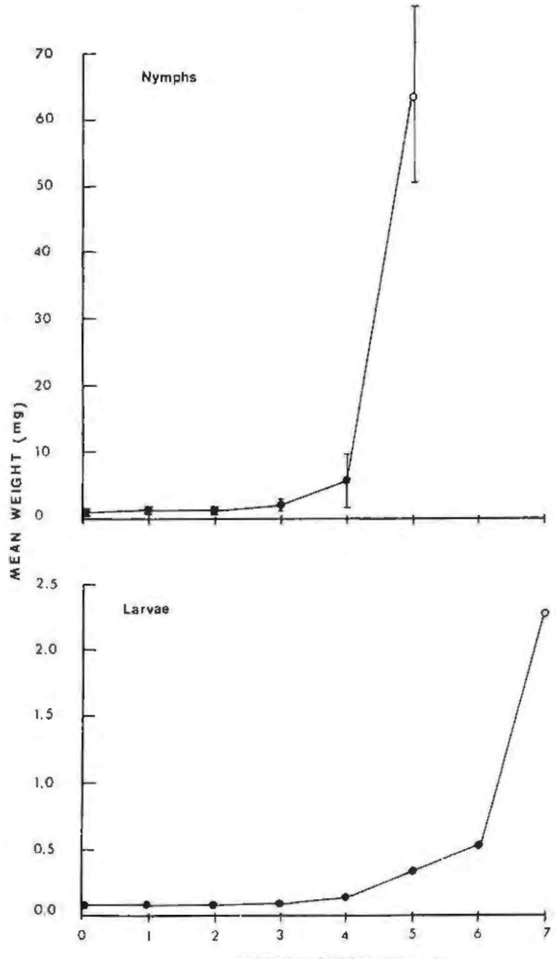


Fig. 1. The changes in weight of larvae and nymphs of *Amblyomma hebraeum* during feeding. The vertical lines represent standard deviation from the mean. ● = attached ticks removed from the host. ○ = engorged ticks which had detached from the host.

To determine dry weight of testes, males were dissected and the testes removed, then dried for 24 hours at 60°C and weighed. In preparation of light microscope sections, males were dissected in saline solution and the testes removed, then fixed in Heidenhain's "Susa" fixative. The tissues were embedded in paraffin wax and 6μ serial sections cut and then stained with Heidenhain's iron haematoxylin. In preparation of electron microscope sections, males were dissected in buffered gluteraldehyde. Testes were fixed in osmium tetroxide and embedded in araldite resin. 400 Å sections were cut, and stained with uranyl acetate and lead citrate. Sections were viewed with a Hitachi HU 11 B electron microscope.

RESULTS

Rate of feeding

The feeding curves of larvae and nymphs (fig. 1) were characterized by an initial period of slow weight increase, lasting 3 days in larvae and 2 days in nymphs. This was followed by a period of more rapid weight increase, again lasting 3 days in larvae and 2 days in nymphs. The final period of extremely rapid engorgement, during which time the greater part of the blood meal was ingested, occurred during the 24 hours prior to detachment from the host. In fig. 1 the points representing the weights of detached larvae and nymphs were taken on the days when peak numbers of each stage detached from the host. Larvae increased in weight by 37,8 fold from 0,059 mg in the unfed state to 2,29 mg in the engorged state. Nymphs increased in weight by 102,4 fold from 0,62 mg in the unfed state to 64,13 mg in the engorged state. In nymphal feeding (fig. 1) it was found that the variability in individual weights was extremely small during the initial period of slow feeding. The variability increased during the period of more rapid feeding and was greatest in engorged ticks which had detached from the host.

The feeding curve of female ticks (fig. 2) was similar to those of larvae and nymphs. The initial period of slow feeding lasted 3 days and the period of more rapid feeding lasted 4 days. Females increased in weight by 103,7 fold from 24,43 mg in the unfed state to 2557,21 mg in the engorged state.

The feeding curve of male ticks (fig. 2) differed from the other stages of the life cycle, in that there was an initial decrease in weight during the first 2 days of attachment. This was followed by an increase in weight on the 3rd day of attachment, to be approximately 20% above the unfed weight. The weight then fluctuated about this level over the following 5 days of the experimental period.

Growth of testes

In unfed males (fig. 4) testes measured approximately 10 mm in length and 0,2 mm in diameter. 48 hours after attachment, testes were of the same diameter, but had lengthened to approximately 15,5 mm. 96 hours after attachment, testes had increased in diameter to 0,3 mm (fig. 5). Thereafter the testes showed no noticeable increase in size.

The growth of testes was reflected in an increase in the dry weight of testes relative to initial body weight (fig. 3). During the first 48 hours of attachment there was little increase in testes dry weight which varied from 0,3 to 0,8% of the initial body weight. 72 hours after attachment the testes dry weight had risen to 0,7–1,2% of the initial body weight. The testes dry weight continued to rise until 168 hours after attachment, when it stabilized at 1,85–2,1% of the initial body weight. The rapid growth of testes (fig. 3) occurred subsequent to an increase in body weight (fig. 2), indicating that the ingested nutrients were utilized in testes growth.

Spermatogenesis

The testes of unfed adults of *A. hebraeum* were covered by an epithelial tissue sheath containing primary spermatocytes within spermatocysts. Transverse sections of testes showed 8 spermatocysts arranged radially around a lumen, similar to those found in *Dermacentor occidentalis* Marx (Oliver and Brinton, 1972). The spermatocysts were continuous from the vasa deferentia-testis junction to the distal end of the testes. Through-

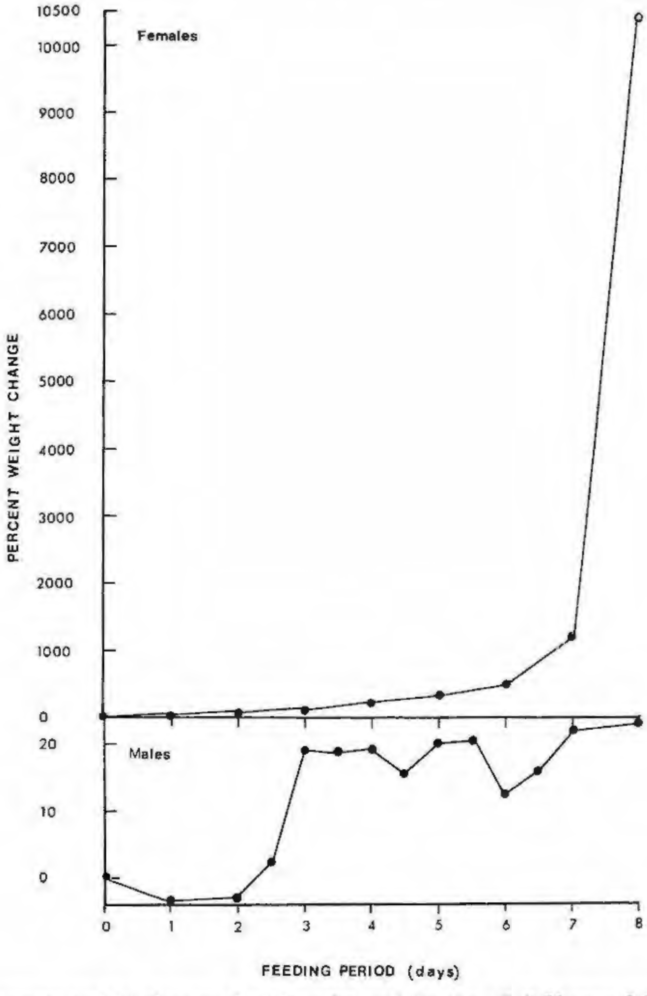


Fig. 2. The percent weight change of adult males and females of *Amblyomma hebraeum* during feeding. ● = attached ticks removed from the host. ○ = engorged ticks which had detached from the host.

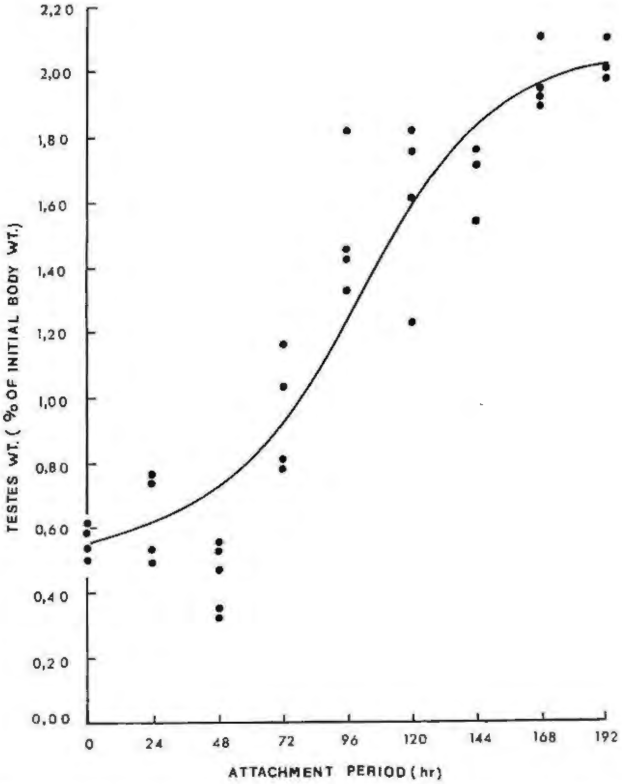


Fig. 3. *Amblyomma hebraeum.* The changes in testes dry weight (expressed as a percentage of initial body weight) in relation to the duration of attachment. Each point represents a single male.

out the 7 day experimental period, spermatogenesis proceeded in a wave-like manner with cells in the distal end of the testes maturing first.

In unfed males the nuclei of primary spermatocytes measured approximately 10μ in diameter and each contained a densely staining nucleolus.

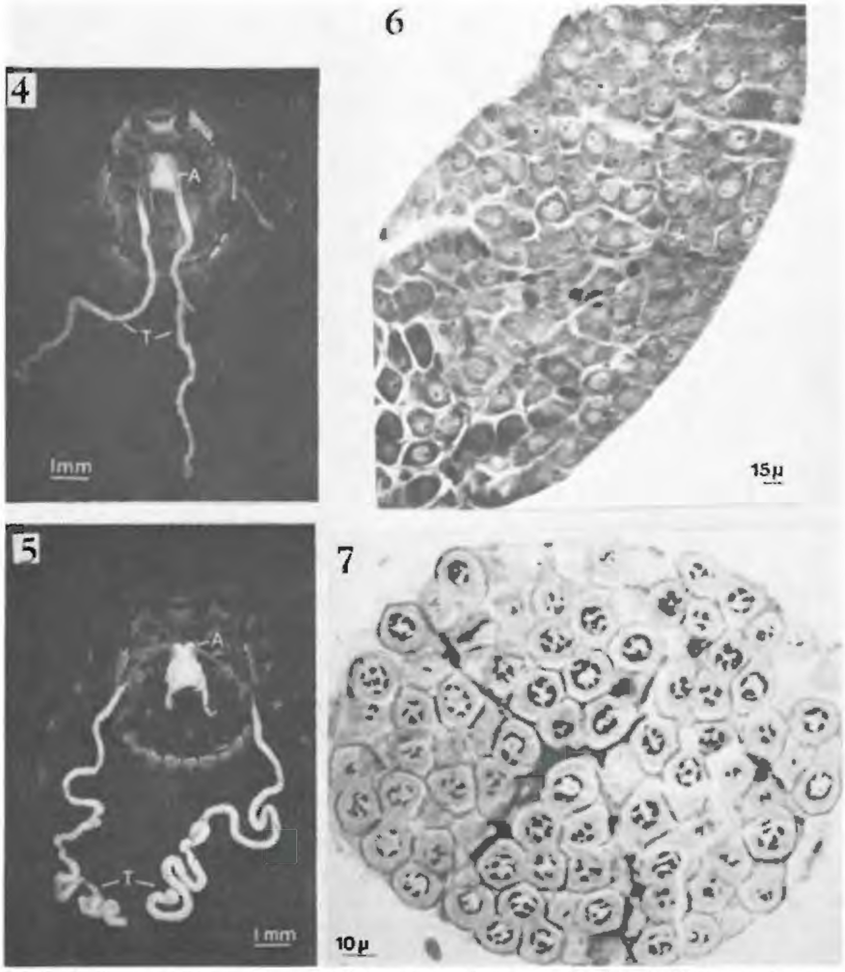
Twenty-four hours after attachment the nuclei of primary spermatocytes in the distal half of the testes had enlarged to approximately 13μ in diameter. Prominent nucleoli and large aggregations of chromatin were present in the nuclei.

After 48 hours, primary spermatocytes in the distal half of the testes were at prophase 1. Cells proximal to the vasa deferentia showed little change from those in the unfed state.

After 72 hours, the nuclei of primary spermatocytes in the proximal half of the testes had increased in size to approximately 15μ in diameter and many contained 2 nucleoli (fig. 6).

After 96 hours, cells in the distal half of the testes were beyond prophase 1 and all cells contained peripheral cisternae (fig. 7).

Small round cells, approximately 8μ in diameter, containing dense round nuclei, appeared in the distal half of the testes 132 hours after attachment. These cells appeared to be secondary spermatocytes (Arthur 1962). At this stage, aggregations of



Figs 4–7. *Amblyomma hebraeum.* 4 and 5. Dissections of males. 4. Unfed. 5. 96 hours after attachment. T = testes. A = accessory gland complex. 5 and 6. Light micrographs of cross sections of testes. 5. Proximal region of testes. 72 hours after attachment. Early primary spermatocytes with prominent nucleoli are present. 6. Distal region of testes, 96 hours after attachment. Cells are beyond prophase 1, and peripheral cisternae are visible around the margins of the cells.

chromatin began to appear in the nuclei of the primary spermatocytes in the proximal half of the testes.

After 156 hours, developing spermatids similar to those seen in *D. occidentalis* by Oliver and Brinton (1972) were found in the distal lumen of the testes. In the proximal region of the testes, cells had undergone prophase 1 and were similar to developing primary spermatocytes in the distal region at 96 hours (fig. 7).

Ultrastructure of primary spermatocytes

Electron micrographs of sections from the proximal half of the testes in males which had been attached for 132 hours revealed early primary spermatocytes, containing prominent nuclei, golgi complexes and peripheral cisternae (fig. 8). Cells were found in various stages of development. In some the nucleus contained a single dense nucleolus and aggregations of heterochromatin. In others the nuclei contained more dispersed quantities of heterochromatin and 2 irregular nucleoli, while in a few the nucleoli had dispersed.

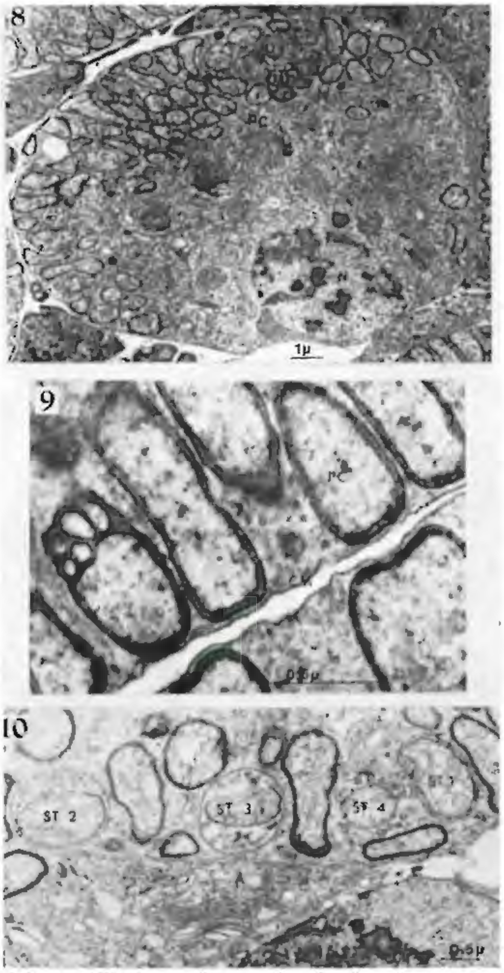
Up to 8 golgi complexes were found in single primary spermatocytes. Numerous double membrane peripheral cisternae were found in close proximity to the cell membrane (fig. 9). Although Oliver and Brinton (1972) found similar cisternae in *D. occidentalis*, — no details of their structure or function were given. In the more mature primary spermatocytes, single membrane structures containing a large vacuole, partially surrounded by microtubule-like structures, were found interspersed among the peripheral cisternae (fig. 10). Similar structures were found in the developing spermatid of the crane fly *Nephrotoma suturalis* Loew (Behnke and Forer, 1967). The large vacuole was thought to be a mitochondrion, and the microtubules were considered to be part of the developing flagellum of the spermatid. There is little evidence to support such a hypothesis in the case of *A. hebraeum*. However, there is evidence to suggest that the single membrane structures are derived from the peripheral cisternae. In fig. 10, adjacent to the double membrane peripheral cisterna is a structure (ST 1) resembling the peripheral cisterna but with 3 microtubules between the 2 membranes. In the structure, ST 2, the intermembrane space is enlarged and a greater number of microtubules are present. In the structure, ST 3, the membranes have almost completely separated and the inner membrane appears as a vacuole within a single membrane. Finally, in the structure, ST 4, the outer membrane is absent, leaving the vacuole surrounded by micro- tubules.

DISCUSSION

The rate of feeding and quantity of nutrient ingested relative to initial body weight in males of *A. hebraeum*, differed from that in other stages of the life cycle. The differences appear to be due to the fundamental differences in the morphology, attachment behaviour and nutritional requirement of males. Unlike other stages of the life cycle, males are unable to undergo cuticular distension during feeding, which limits the quantity of nutrient ingested. The long attachment period of males does not necessitate the ingestion of a large blood meal, as these ticks may feed intermittently. In males the nutritional requirements are limited to the requirements of spermatogenesis and metabolism during the attachment period.

It appears that the mechanism of spermatogenesis in males is initiated by feeding. In this investigation it was found that the onset of sexual responsiveness of males (Lounsbury, 1899 and Norval, 1974) coincided with the appearance of spermatids in the lumen of the testes.

Spermatogenesis in *A. hebraeum, Hyalomma anatolicum excavatum* Koch (Khalil, 1970), *D. occidentalis* (Oliver and Brinton, 1972) and *Dermacentor variabilis* (Say) (Homsher and Sonenshine, 1972) proceeds in a similar rate and manner. It should be noted, how-



Figs 8–10. *Amblyomma hebraeum.* Electron micrographs of early primary spermatocytes in proximal region of testes, 132 hours after attachment. 8. G = golgi complex. N = nucleus. PC = peripheral cisternae. SMS = single membrane structures. 9. CM = cell membrane. PC = peripheral cisterna. 10. For explaination of structures (ST) 1–4, see text.

ever, that the use of an unnatural host (rabbit) may have affected the rate of feeding and subsequent development of testes in *A. hebraeum.* The above workers relied in part on squash techniques using orcein stains to determine the progress of spermatogenesis, as this technique gives more conclusive results in respect of different meiotic stages, chromosome number, etc. than do sections. However, attempts to apply this technique to *A. hebraeum* were unsuccessful, as spermatocytes adhered to the epithelial sheath of the testes in such a manner that it was impossible to view individual spermatocytes.

Males of *A. hebraeum* are known to remain on the host for up to 132 days and mate a maximum of 8 times (Norval, 1974). Due to this long attachment period, a large accumulation of males is seen on hosts in the field. It was found in this investigation that unfed males possessed a full compliment of primary spermatocytes and no germinal tissue was present. It is therefore considered possible that topical application of a suitable chemosterilant to attached males, or irradiation of unattached males, could result in permanently sterile males. The consequential non-fertile matings might cause a decline in tick numbers.

ACKNOWLEDGEMENTS

The authors express sincere appreciation to Prof. G. B. Whitehead for his advice during the course of the study and for constructive criticism of the manuscript, and to Mr M. M. Knight for his technical assistance.

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Manuscript received 22 April 1974.

C.T.P. LTD.

SECTION TWO

THE NON-PARASITIC STAGES OF *AMBLYOMMA HEBRAEUM* KOCH

3. Studies on the ecology of the non-parasitic stages of *Amblyomma hebraeum*.

3.1 Introduction.

Our present knowledge of the ecology of *A. hebraeum* is based largely on qualitative observations. Distribution records of Theiler (1943; 1948; 1962), Jack (1942), Zumpt (1958), Affleck (1968) and Jooste (1969) show that *A. hebraeum* is essentially a South African tick. The species occurs in the north-eastern Transvaal, from where it extends westwards into the western Transvaal and eastern Botswana, northwards into the south of Rhodesia, and eastwards into Swaziland, southern Mocambique and Natal. The species has spread southward from Natal over the past 150 years. *A. hebraeum* was first recorded in the lower Albany district of the Eastern Cape, prior to 1835 (Lounsbury, 1899). By 1877 the species was common in the Albany district (Webb, 1898), and by 1899 had spread as far south as Humansdorp. The tick has since become established in the Mossel Bay and Oudtshoorn districts of the south-western Cape (Theiler, 1948).

The distribution records of *A. hebraeum* in South Africa, show that the species occurs in 'tall grassveld' where rainfall is in excess of 380 mm annually, provided bush or shrub coverage is adequate. On the basis of these observations, Theiler (1948) concluded that the most important factor limiting the survival of the species in South Africa is the nature of the vegetation cover, except in the west where increasing aridity is more important. These conclusions are supported by field observations in the Eastern Cape Province by Stampa *et al*. (1972).

Jooste (1967) suggested that *A. hebraeum* had not become established on the Rhodesian highveld, because of its inability to withstand conditions of high rainfall. This is supported by Affleck (1968), who found that although the species is not entirely absent from the highveld, it is restricted to areas of well-drained, planted pastures, which provide a drier environment than natural grassland.

It is widely recognised that the association of tick species with specific types of vegetation, relates to the suitability of the microclimatic conditions, created by the vegetation, for the survival of the non-parasitic stages of the ticks. In the Karoo regions of South Africa, Stampa (1959; 1969b) has shown that the microclimatic conditions necessary for the survival of *Ixodes rubicundus* Neumann, 1904 are created by the rank, unpalatable shrub *Rhus erosa*. In the Eastern Cape Province it has been shown that larvae of *Ixodes pilosus* Koch, 1844 (Kraft, 1961; Londt & Whitehead, 1972) and *Haemaphysalis silacea* Robinson, 1912 (Londt & Whitehead, 1972) are restricted to humid microhabitats in which there is a protective tree canopy. Unfortunately previous results on the distribution of larvae of *A. hebraeum* have been inconclusive. Kraft (1961) was unable to show any correlation between vegetation structure and the occurrence of larvae, due to the low numbers of larvae which she sampled. Londt and Whitehead (1972) found that larvae were associated with medium and tall protected vegetation, but the authors (personal communication) admit that it is possible that larvae could have been incorrectly identified, being easily confused with *Amblyomma marmoreum* Koch, 1844.

No quantitative data are available on the seasonal activity of *A. hebraeum*. Lounsbury (1899) stated that in the Eastern Cape, "mature ticks appear to be most abundant during the late summer and autumn months but are to be found all the year through" and that "it is inferred that larval ticks are most common in midsummer". Baker and Ducasse (1968) found that in Natal, adult ticks were active between December and mid-February, nymphs between March and mid-September and larvae between February and mid-May.

In this Chapter an attempt has been made to elucidate the factors regulating the distribution and seasonal activity of the non-parasitic stages of *A. hebraeum* in the Eastern Cape Province. Quantitative data are given on the distribution of larvae in relation to vegetation and microclimate, and on the seasonal activity of all developmental stages in relation to macroclimatic conditions.

3.2 The survey area.

Paardekraal Farm, situated approximately 15 km SE of Grahamstown and owned by Mr F.D. Ford, was selected for study as it was known to be heavily infested with A. hebraeum and has been used previously in experiments on the control of A. hebraeum with acaricides (Whitnall et al., 1951). 'Biekwes' Camp, situated in the Kowie River valley, was selected as the survey area. This camp is notorious for heavy infestations of A. hebraeum (Ford, personal communication), and the well defined habitats which occur in the river valley make it ideal for comparative ecological studies.

The survey area consists of 3 major components:-

(1) River banks.

The river banks supported a narrow band of marginal riverine vegetation (habitat 1). This consisted of a canopy of dense, low growing trees, above a ground cover of leaf litter and scattered herbs, shrubs and climbers (Fig. 1). The slightly alkaline soil (pH 7,3) was composed of a fine sediment, and had a high humus content.

The following are the plant species found most commonly in marginal riverine vegetation:-

SHRUBS AND TREES

Acacia karroo
Rhus (2 species)
Maytenus heterophylla
Noltea africana
Fagara capensis
Salix mucronata
Scutia indica
Pappea capensis
Pavetta sp.
Lycium campanulatum
Lycium ferocissimum
Croton rivularis
Xeromphis rudis
Tephrosia grandiflora

Abutilon sonneratianum
Allophylus decipiens
Plumbago auriculata
Grewia occidentalis
Nesaea sp. (exotic)

HERBS

Asystasia stenosiphon
Rhinacanthus gracilis
Peristrophe cernua
Hypoestes sp.
Cotula sp.
Centella coriacea
Crassula lineolata
Cyperus usitatus
Galenia sp.
Drosanthemum hispidum
Commelina benghalensis
Commelina africana

CLIMBERS

Jasminum angulare
Mikania scandens
Asparagus racemosus
Senecio angulatus
Plumbago auriculata
Grewia occidentalis

GRASSES (on margins, in sunny positions)

Cynodon dactylon
Stenotaphrum secundatum
Panicum deustum
Paspalum dilatatum

Fig. 1.
Marginal riverine vegetation.

(2) River flood plain flats, merging into gently rising ground.

The dominant plant species was *A. karroo*, in the form of low growing trees, above a ground flora comprised mainly of grasses (Fig. 2). This type of vegetation, described as Acacia grassland (habitat 2a), had in parts been artificially modified by the removal of *A. karroo* trees, to form open grassland (habitat 2b; Fig. 3). The slightly acid soil of the flood plain (pH 6,8) was composed of fine to coarse sediments, and had a low humus content.

The following are the plant species found most commonly on the river flood plain:-

GRASSES

Digitaria sp.
Cynodon dactylon
Sporobolus fimbriatus
Panicum deustum

SHRUBS AND TREES

Lycium (2 species)
Maytenus heterophylla
Abutilon sp.
Salix mucronata
Acacia karroo
Plumbago auriculata
Azima tetracantha
Rhus (2 species)
Diospyros lycioides

BUSHES AND HERBS

Sida sp.
Sutera sp.
Galenia secunda
Hypoestes verticillaris
Hypoestes aristata
Chlorophytum sp.
Asparagus (2 species)
Ricinus sp. (exotic)
Nesaea sp. (exotic)
Datura sp. (exotic)

Fig. 2.

Acacia grassland.

Fig. 3.

Open grassland (foreground).

(3) Steeply rising slopes bordering on the river valley.

The vegetation was mostly typical Fish River Bush (habitat 3a), which consisted mainly of exceptionally dense, spiny or succulent evergreen plants. These produced little leaf litter, and there was little or no undergrowth. The Fish River Bush was traversed by game paths (habitat 3b), some of which were bordered by short grass and herbs. Many gulleys or minor tributaries (habitat 3c) arose from the valley slopes. Here the vegetation was similar to marginal riverine vegetation, with a canopy of low growing deciduous trees and a ground cover of leaf litter and scattered shrubs and herbs. The soils of the valley slopes were acid (pH 4,8-6,3).

The following are the plant species found most commonly in Fish River Bush:-

SHRUBS AND DWARF TREES

Tarchonanthus camphoratus
Portulacaria afra
Carissa bispinosa
Euphorbia (several species)
Euclea undulata
Schotia afra
Grewia occidentalis
Scutia indica
Rhoicissus tridentata
Aloe ferox
Olea africana
Ehretia rigida
Phyllanthus sp.
Asparagus spp.
Cussonia spicata
Crassula spp.
Maytenus spp.

UNDERGROWTH

Sansevieria thyrsiflora
Dietes vegeta
Aster filifolius (mainly marginal)

Fig. 4.
Fish River Bush.

3.3 Microclimatic records.

One of the most serious problems encountered in previous ecological investigations in South Africa, was the accurate measurement of microclimatic relative humidities. Stampa (1959) and Kraft (1961) attempted to gain microclimatic information from thermohygrograph records, which, as seen in Table 3, can be misleading. Londt and Whitehead (1972) used cobalt thiocyanate paper indicators, placed in microhabitats. The drawback of this method was that indicator papers required two hours in which to equilibrate, and as a result reading could only be taken at times of day when conditions remained fairly constant, i.e. midday (11.00-13.00 hr) and early morning 03.00-05.00 hr). In this investigation the problem was overcome by using a Rotronic, Hygroskop BT, humidity measuring instrument, with a Rotronic air probe, type KF. With this instrumentation it was possible to obtain accurate and almost instantaneous relative humidity readings, and consequently comparative microclimatic data could be recorded in a number of habitats over a relatively short period of time. Microclimatic temperatures were measured with a mercury thermometer.

Microclimatic conditions were recorded in each habitat at given heights above ground level, and all data are given in terms of saturation deficit.[1] Saturation deficits recorded hourly over a 24 hour period (19/20 January, 1974) at heights of 0, 10 and 30 cm above ground level, at stations in marginal riverine vegetation (habitat 1), Acacia grassland (habitat 2a) and open grassland (habitat 2b), are given in Fig. 5. Day-time saturation deficits recorded at these stations, at heights of 0, 1, 5, 10, 20, 30, and 40 cm above ground level, on 7 occasions during the summer and autumn of 1973/74 are given in Table 1. Similar data for habitats in the Fish River Bush complex (habitats 3a-c) are given for 2 occasions in the autumn of 1974 (Table 2). In Table 3, microclimatic data and thermohygrograph readings are compared.

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[1] Saturation deficit is the difference between saturated vapour pressure and vapour pressure, and consequently represents the real 'drying power' of the air (Wharton, 1963; Londt, 1973). Saturation deficit is dependent on both temperature and relative humidity, and for this reason is useful for comparative purposes, particularly in respect of field data.

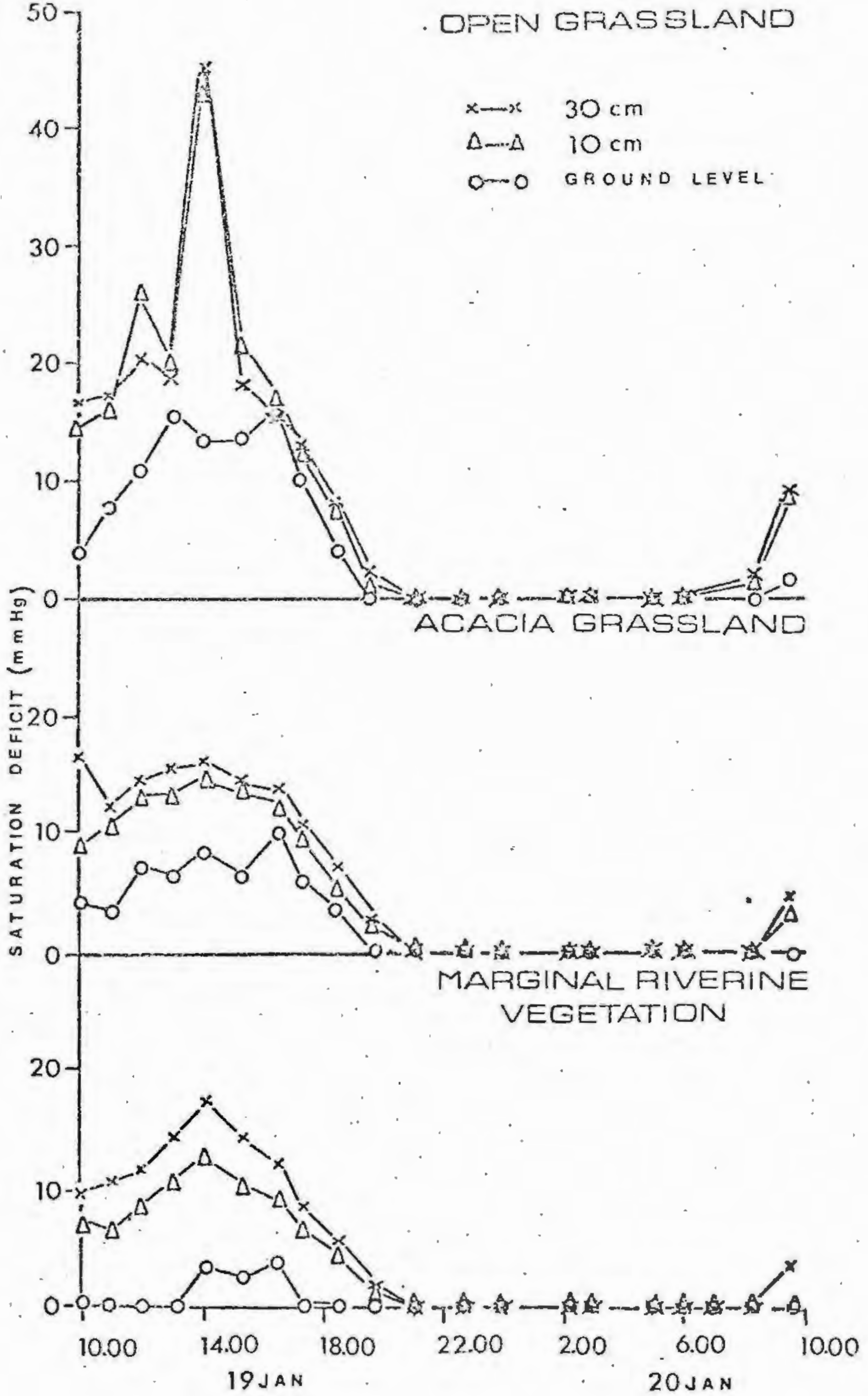


Fig. 5.

Fluctuations in saturation deficit recorded over 24 hours at different levels in the vegetation, in three habitats in the Kowie River valley, in summer, 1974.

Table 1.

Microclimatic conditions in the Kowie River valley, expressed as saturation deficits (mm Hg).

	29/12/73	4/1/74	10/1/74	19/2/74	14/3/74	10/5/74	15/5/74
	10.20 -	10.20 -	15.15 -	14.50 -	15.50 -	15.30 -	11.00 -
	11.00 hr	11.00 hr	15.45 hr	15.50 hr	16.10 hr	16.00 hr	11.20 hr
				Open grassland			
GL	36,7	61,6	32,5	3,4	1,8	0,0	0,0
1 cm	37,9	63,5	28,3	8,3	2,1	0,4	0,0
5 cm	35,4	54,2	26,3	13,5	3,9	0,9	0,0
10 cm	35,9	51,1	22,2	14,1	4,5	1,4	0,5
20 cm	34,9	45,1	15,3	14,3	5,5	5,4	2,2
30 cm	31,6	43,9	15,2	13,1	7,5	10,5	3,0
40 cm	30,7	42,7	14,0	12,8	7,6	10,9	4,3
				Acacia grassland			
GL	17,1	30,5	9,5	0,5	0,0	1,0	0,0
1 cm	17,4	32,0	9,8	3,6	0,9	1,3	0,0
5 cm	20,5	34,7	10,5	6,1	3,1	3,1	0,8
10 cm	21,1	34,0	10,9	7,2	3,9	3,6	2,2
20 cm	22,1	35,2	11,0	9,3	4,7	4,8	3,2
30 cm	22,7	34,4	11,0	10,6	5,1	4,4	3,1
40 cm	23,6	34,0	10,6	12,0	5,5	5,9	3,1
				Marginal riverine vegetation			
GL	11,5	15,7	13,5	1,8	0,0	0,0	0,0
1 cm	12,7	20,3	14,1	3,2	1,3	0,0	0,0
5 cm	14,8	24,6	13,8	7,8	2,7	1,4	0,0
10 cm	18,2	26,9	13,7	10,4	2,3	2,3	0,0
20 cm	20,7	29,9	13,1	13,1	3,3	3,4	1,0
30 cm	21,7	38,0	13,6	13,9	3,7	3,9	1,8
40 cm	22,5	33,6	13,4	13,7	4,5	4,2	1,5

KEY. GL, ground level; 1 cm, 5 cm etc., heights above ground level.

Table 2.

Microclimatic conditions in the Fish River Bush complex, expressed as saturation deficits (mm Hg).

	Fish River Bush		Game path		Gulley vegetation	
	10/5/74^{+}	15/5/74$^{\$}$	10/5/74^{+}	15/5/74$^{\$}$	10/5/74^{+}	15/5/74$^{\$}$
GL	17,8	2,9	5,0	0,8	4,4	0,0
1 cm	20,8	3,5	5,8	1,6	5,3	0,0
5 cm	20,8	4,3	7,8	2,8	8,3	0,3
10 cm	21,4	5,2	9,1	2,6	9,2	0,7
20 cm	20,2	5,4	11,4	2,8	9,6	1,6
30 cm	21,7	5,2	11,9	4,3	10,0	1,8
40 cm	21,4	5,1	12,9	3,8	11,5	2,0

KEY. GL, ground level; 1 cm, 5 cm etc., heights above ground level; +, 15.00-15.30 hr; \$, 10.20-11.00 hr.

Table 3.

Comparison of macroclimatic (thermohygrograph records) and microclimatic saturation deficits, recorded in Acacia grassland.

	10/1/74	19/2/74	14/3/74
	15.15 hr.	15.27 hr.	15.05 hr.
GL (p)	20,3	5,2	3,1
1 cm (p)	19,3	6,7	4,8
5 cm (p)	18,5	6,9	6,4
10 cm (p)	17,7	9,1	7,6
20 cm (th)	20,5	17,7	12,6
20 cm (p)	17,5	16,9	11,0

KEY. th, thermohygrograph readings; p, Rotronic air probe and thermometer readings.

3.4. Macrolimatic records.

Rainfall.

Rainfall was recorded by Mr F.D. Ford at the Paardekraal farmhouse, situated 4 km from the survey area. Weekly rainfall for the period 1971-1974 is given in Fig. 6. Monthly rainfall for the period 1958-1970 is given in Fig. 7.

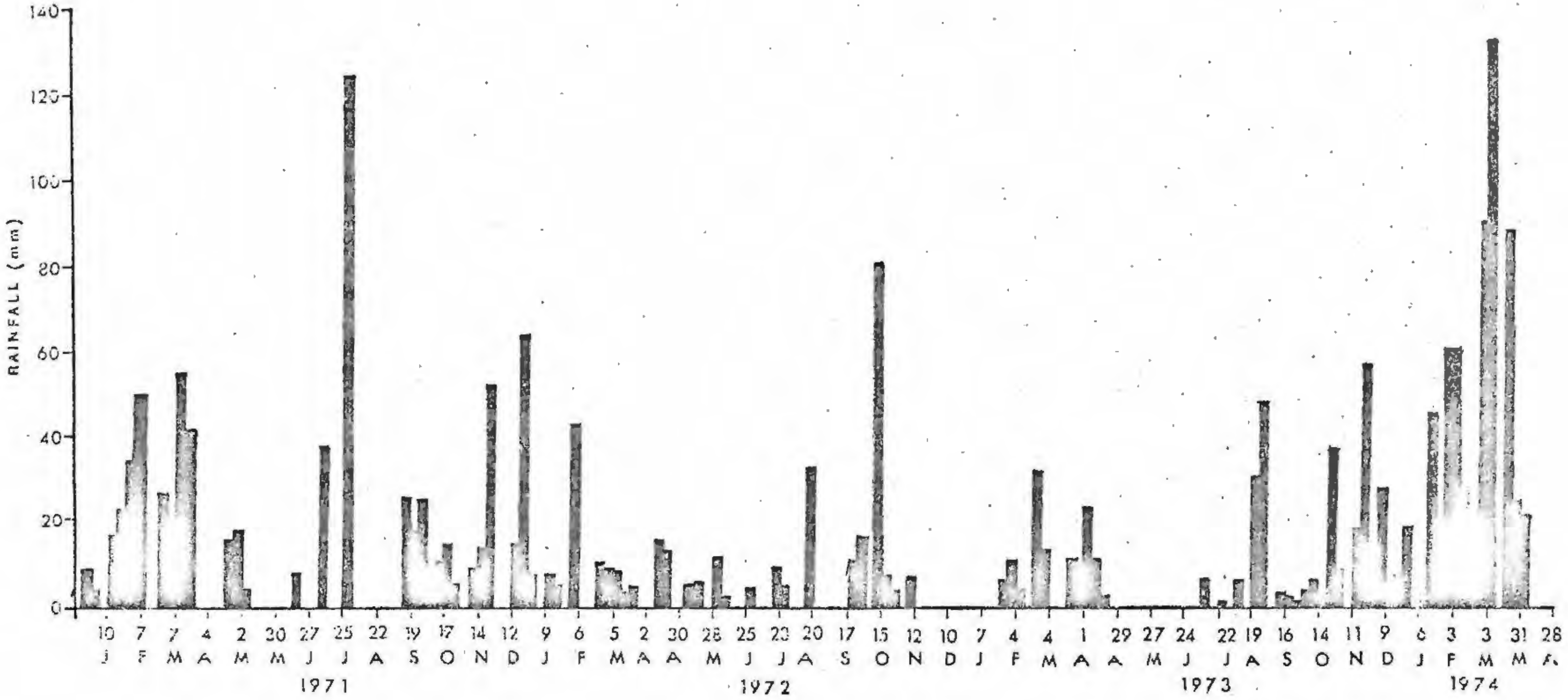


Fig. 6.

Weekly rainfall recorded at Paardekraal Farm for the period January, 1971 to April, 1974.

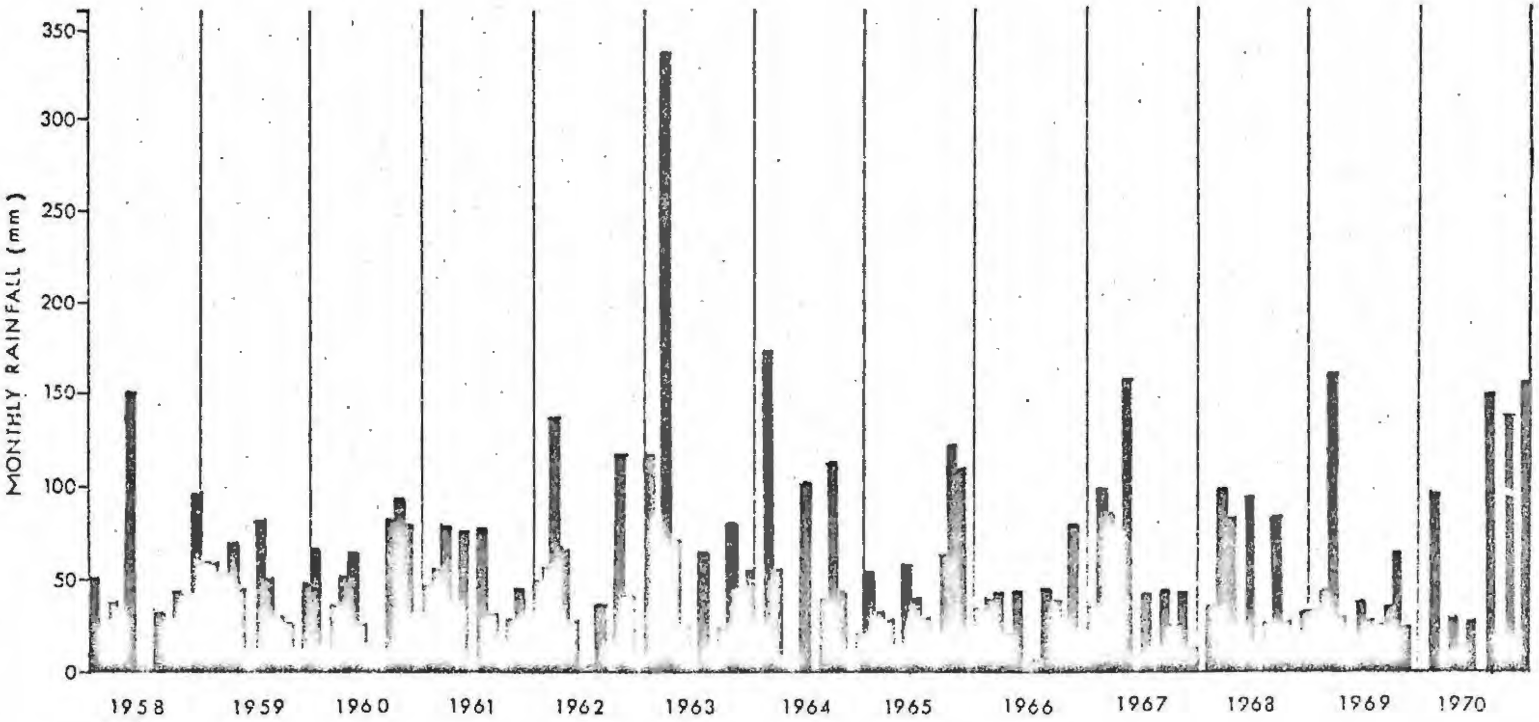


Fig. 7.

Monthly rainfall recorded at Paardekraal Farm for the period 1958 to 1970.

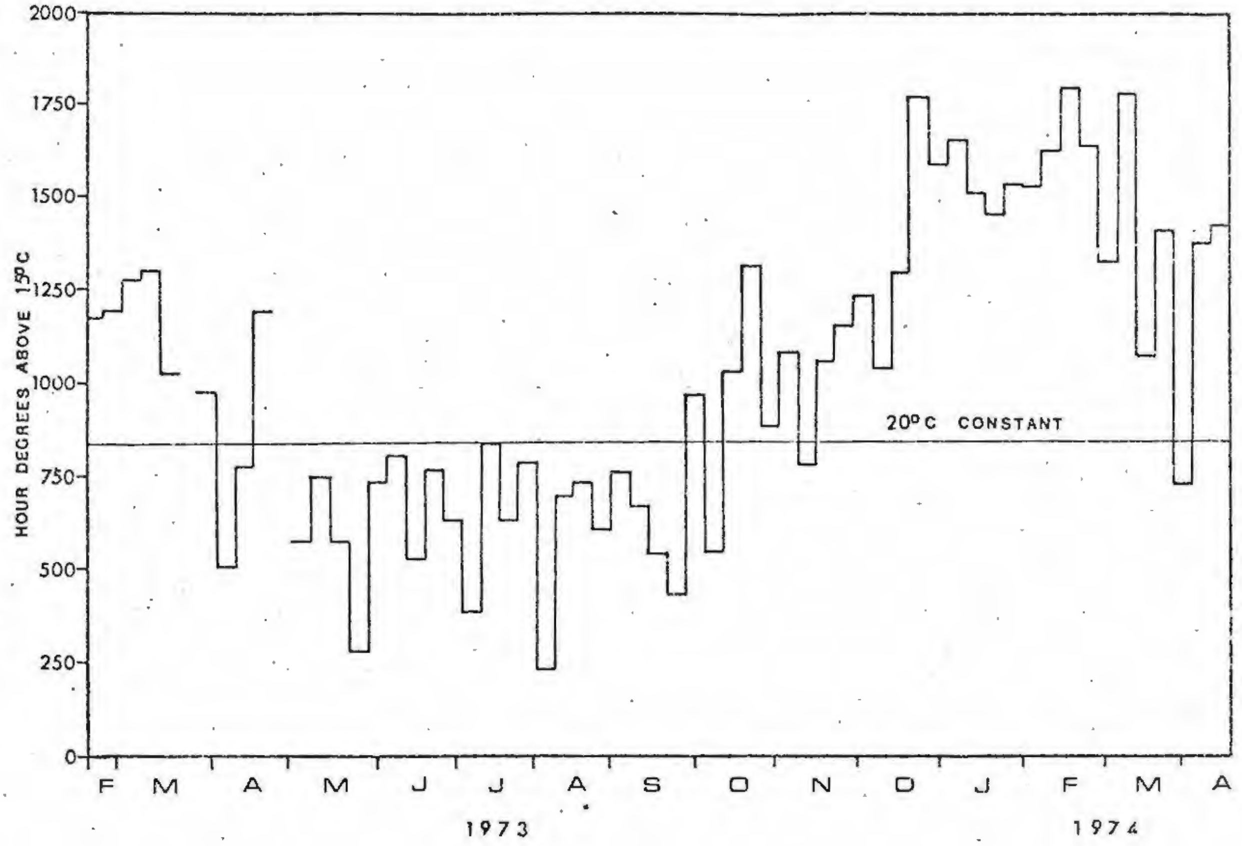


Fig. 8.

Hour degrees per week above 15°C, calculated from thermohygrograph records from the Kowie River valley.

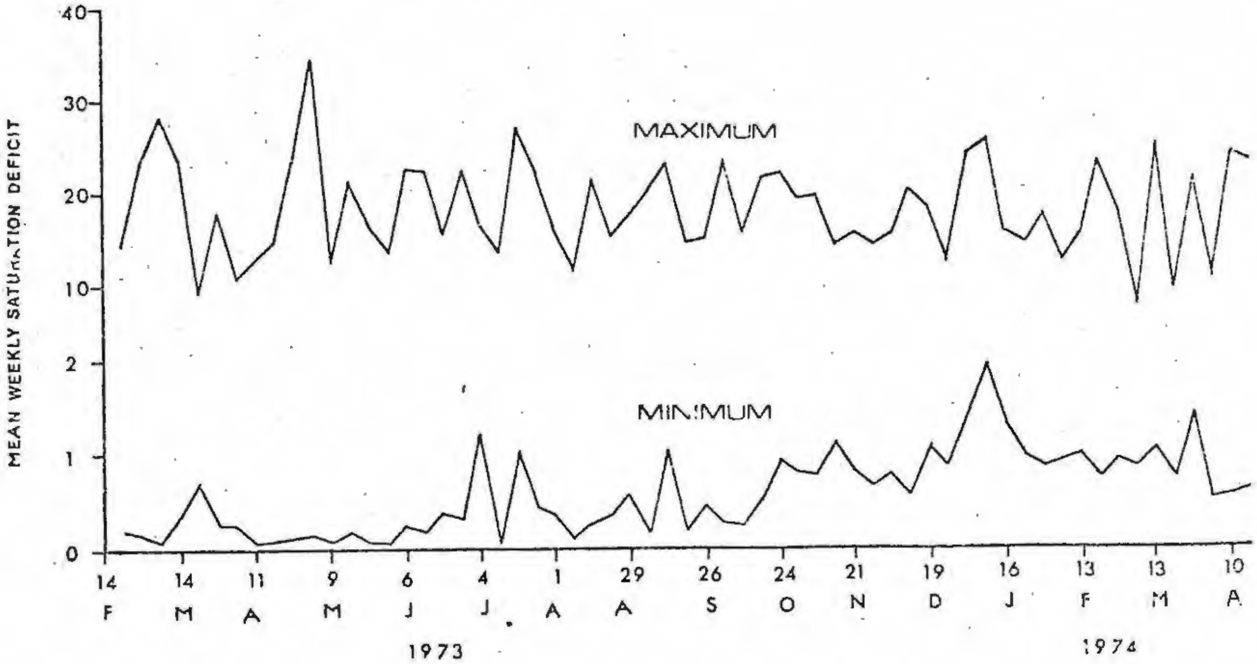


Fig. 9.

Mean weekly saturation deficits calculated from thermohygrograph records from the Kowie River valley.

Temperature and saturation deficit.

Continuous records of temperature and relative humidity were obtained using a thermohygrograph, which was housed in a Stevenson's screen, situated in Acacia grassland (habitat 2a). The number of hour degrees per week, recorded above 15°C, for the period February, 1973 to April, 1974, are given in Fig. 8. Mean weekly maximum and minimum saturation deficits, calculated from thermohygrograph records, are given for the same period (Fig. 9).

3.5. Sampling of ticks.

Larvae.

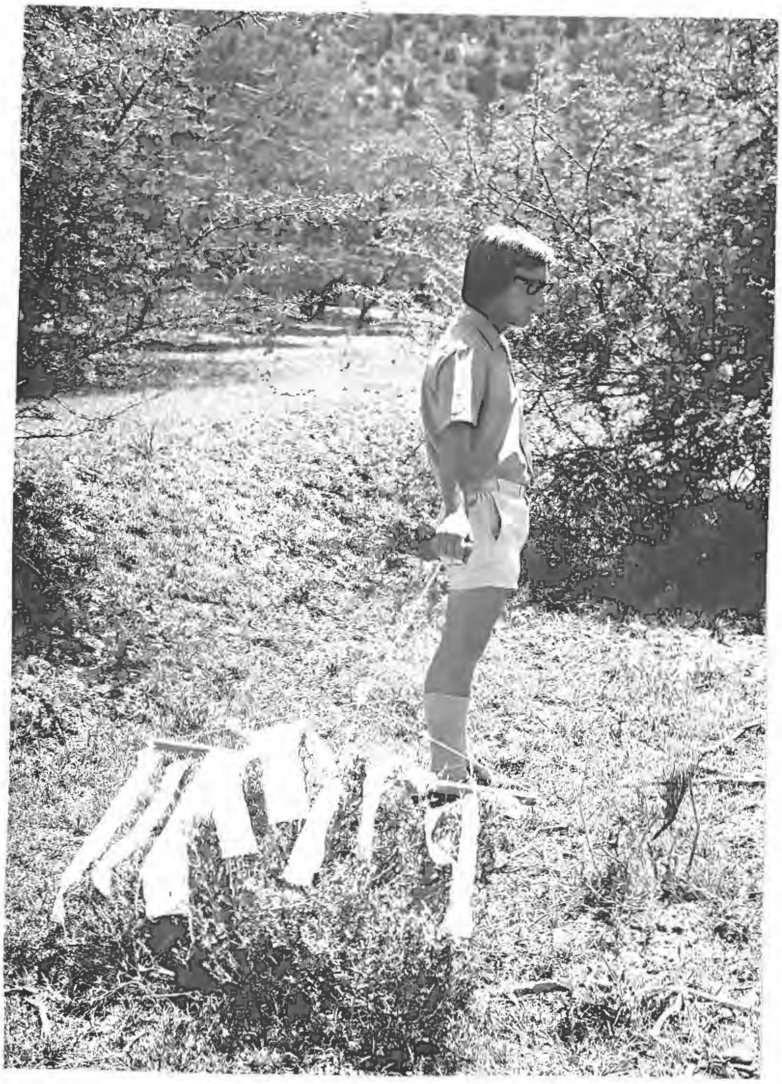
When in an active state, the larvae of most species of ixodid ticks climb to the tips of low-growing vegetation to await a passing host. It has been shown (Milne, 1943) that it is possible to sample these larvae quantitatively, by dragging a woollen fabric (which resembles the hair of the host) over the vegetation. By use of a standardized dragging technique, it is possible to determine both seasonal activity, and the distribution of larvae in relation to vegetation.

In this survey larvae were sampled using the apparatus described by Londt and Whitehead (1972), which consists of ten flannelette strips or 'tails', each measuring approximately 60 x 8 cm, attached at equal intervals down the length of a one meter broom handle. The apparatus is pulled over vegetation by means of a cord, attached to the broom handle (Fig. 10).

The sampling procedure was designed to fulfill the requirements set out by Milne (1943) for the comparison of tick populations in different habitats. A previously unsampled stretch of ground was used for each drag in each season. Each drag was over 50 m, whereafter ticks were removed from the tails and placed in 70% alcohol, to be examined later in the laboratory. Samples taken in each habitat consisted of two drags, taken between 10.00 and 13.00 hr. Flannelette tails were replaced after approximately 80 drags.

Fig. 10.

The dragging apparatus, used for sampling larvae.



Marginal riverine vegetation (habitat 1), Acacia grassland (habitat 2a) and open grassland (habitat 2b) were sampled at weekly intervals from April, 1973 to April, 1974. Fish River Bush was impenetrable and largely impossible to sample, except on the fringes. Habitats in the Fish River Bush complex (habitats 3a-c) were sampled only on 5 occasions during the above period.

Nymphs and adults.

Nymphal and adult ticks were not collected during dragging, and consequently no data are available on the distribution of these stages in relation to vegetation. It was possible, however, to determine seasonal activity from counts of the numbers of ticks attaching to cattle. Two Short-horn steers, which belonged to a herd of approximately 40 cattle kept in Biekwes Camp, were used for this purpose. The steers were not dipped from November, 1972 until January, 1974, but were examined for ticks at 1-3 weekly intervals, when the herd was mustered for dipping. Occasionally one or both of the steers were 'lost' in the thick bush for periods of up to 6 weeks, and hence not examined. For examination, each steer was cast, and then held on the ground by 4 or 5 farm labourers. Nymphs and females were removed at the request of Mr F.D. Ford, and males were counted _in situ_.

3.6. Identification of larvae and nymphs.

The immature stages of the genus _Amblyomma_ are notably difficult to identify. _A_. _hebraeum_ and _A_. _marmoreum_ were the only _Amblyomma_ species collected at Paardekraal Farm, and it was necessary at the outset to ensure that larvae and nymphs could be accurately identified. Descriptions of the morphology of the immature stages of _A_. _hebraeum_ are given by Arthur (1973) and of _A_. _marmoreum_ by Theiler and Salisbury (1959). Arthur (1973) based his descriptions on scanning electron microscope studies. In this investigation the scanning electron microscope was used to establish morphological differences between the two species, which were then used in the day to day identification of ticks under a light microscope.

Scanning electron microscopy.

Larvae and nymphs of _A_. _hebraeum_ and _A_. _marmoreum_ were obtained in the first instance from laboratory cultures, and later from the field, by dragging.[1] Ticks were killed in 70% alcohol, then dried in air and fixed

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[1] With the exception of nymphs of _A_. _hebraeum_.

to specimen stubs by "Sellotape" adhesive dissolved in chloroform. A layer of gold (100-150 Å) was evaporated onto the specimens in a Hitachi HUS 3B vacuum evaporator. The specimens were examined in a JEOL JSM U3 scanning electron microscope. Comparative micrographs of the capitulum and scutum of larvae (Fig. 11) and nymphs (Fig. 12) are given.

Larvae.

The following characters, based on light microscope and scanning electron microscope studies, were used to distinguish A. hebraeum from A. marmoreum:-

(1) General appearance. A. marmoreum larvae tend to be larger and more rounded than A. hebraeum larvae, but on both points there is some degree of overlap. In freshly collected specimens which have been kept in 70% alcohol for less than a week, the scutum of A. hebraeum is orange in colour and the eyes are black, whereas the scutum of A. marmoreum is light yellow in colour and the eyes are brownish yellow.

(2) Shape of scutum. In A. marmoreum the posterior margin of the scutum is broadly rounded, whereas in A. hebraeum there is a tendency towards a V-shape.

(3) Cervical grooves. In A. hebraeum the cervical grooves are short and straight, and extend to the level of the anterior margins of the eyes. In A. marmoreum the cervical grooves are longer, extending past the level of the anterior margins of the eyes, and are slightly sinosus.

(4) Shape of eyes. In A. hebraeum the eyes are slightly convex, whereas in A. marmoreum they are flush with the scutum.

(5) The body setae. In A. marmoreum the body setae are extremely short and often difficult to see under the light microscope, whereas in A. hebraeum the setae are longer and easily seen under the light microscope.

Nymphs.

It was easier to distinguish nymphs of A. hebraeum from nymphs of A. marmoreum, than was the case with larvae. The following characters, based on light microscope and scanning electron microscope studies, were used for this purpose:-

(1) General appearance. Nymphs of A. marmoreum tend to be larger, more rounded and darker in colour, than nymphs of A. hebraeum.

(2) Shape of scutum. As in larvae.

(3) Punctation of scutum. In A. hebraeum, large, deep punctations are restricted to the lateral fields, whereas in A. marmoreum large punctations occur in the lateral and cervical fields.

(4) Shape of eyes. In A. marmoreum the eyes are flush with the scutum and are almost circular in shape, whereas in A. hebraeum the eyes are convex and elongate, extending inwards, parallel to the postero-lateral margins of the scutum.

(5) The body setae. As in larvae.

Accuracy of identification.

Two simple experiments were conducted to test the accuracy of identification of larvae and nymphs. In the first experiment, a sample of 80 larvae was collected in the field by dragging. Forty nine larvae were identified under the light microscope as A. marmoreum and 31 as A. hebraeum. The two 'species' were separated, and reared through the larval and nymphal stages on rabbits (as in Chapter 2). Twelve of the A. marmoreum group and 8 of the A. hebraeum group reached the adult stage. All were found to have been identified correctly.[1]

The second experiment involved 26 engorged nymphs, which had been removed from a tortoise collected in the field. Nineteen of the nymphs were identified as A. marmoreum and 7 as A. hebraeum. The two 'species' were separated, and allowed to moult in the laboratory. It was found that in all cases the initial identification had been correct.

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[1] Adults of A. hebraeum and A. marmoreum are markedly different.

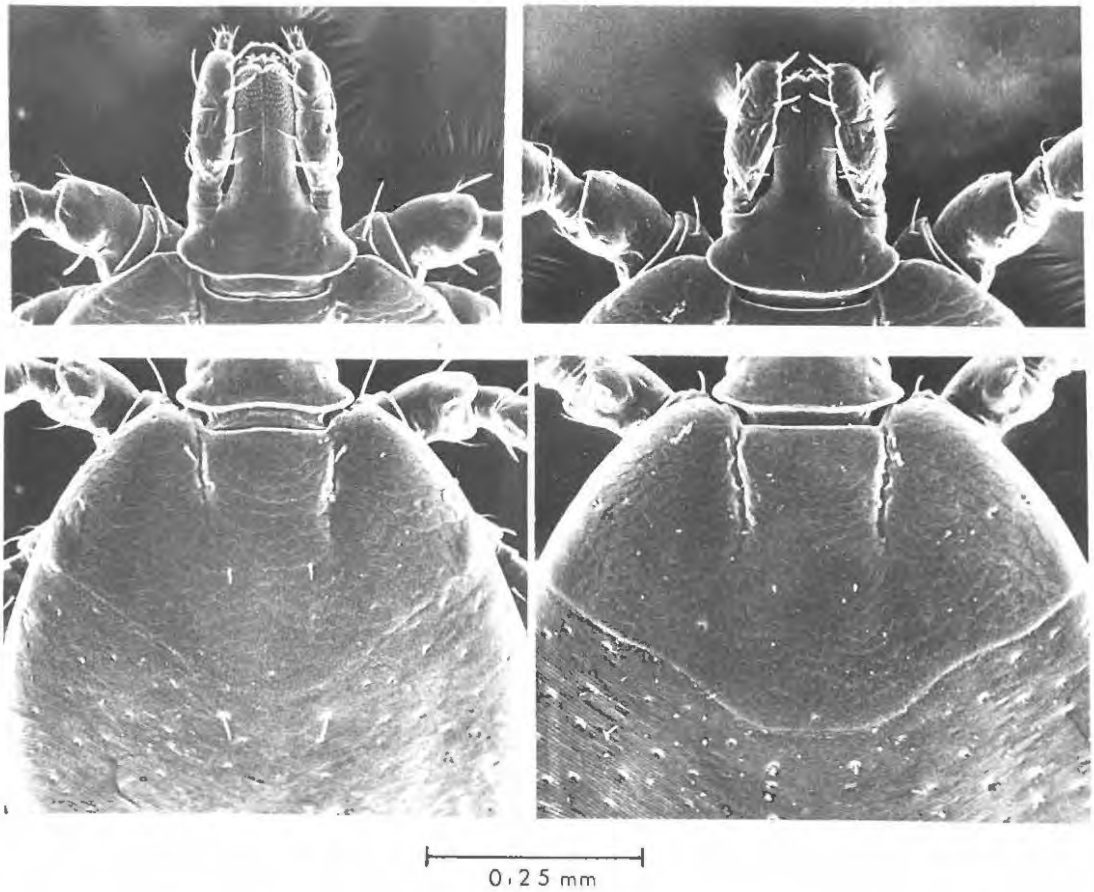

Fig. 11.

Scanning electron micrographs of dorsal capitulum and scutum of larva of *Amblyomma hebraeum* (left) and larva of *Amblyomma marmoreum* (right).

3.7. The distribution of larvae in relation to vegetation.

The total numbers of larvae collected on 48 occasions in open grassland, Acacia grassland and marginal riverine vegetation are given in Table 4. The results show that the majority of larvae were collected in Acacia grassland, and that the numbers of larvae collected in open grassland and marginal riverine vegetation were negligible. In the Fish River Bush complex, a total of 5 larvae were collected (5 occasions) on the grass covered verges of game paths. No larvae were collected in typical Fish River Bush or in the vegetation of the gulleys.

Table 4.

The total numbers of larvae of Amblyomma hebraeum, collected in habitats in the Kowie River valley, on 48 occasions, from April 1973 to April 1974.

	Open grassland (Fig. 3)	Acacia grassland (Fig. 2)	Marginal riverine vegetation (Fig. 1)
Total No. larvae	10	911	12
% of larvae	1,1	97,6	1,3

3.8. The distribution of larvae in relation to microclimatic conditions.

Microclimatic conditions recorded in habitats at Paardekraal Farm were similar to those recorded in comparable habitats in the Port Alfred district by Londt and Whitehead (1972). Maximum daily saturation deficits, calculated from thermohygrograph records, normally occurred between 12.00 and 14.00 hours and varied between 0,9 and 66,7 mm Hg. Minimum daily saturation deficits normally occurred between 03.00 and 06.00 hours and usually approached 0 mm Hg. Saturation deficits recorded in microhabitats in open grassland, Acacia grassland and marginal riverine vegetation, in January, 1974, showed similar daily fluctuations (Fig. 5). Day-time saturation deficits recorded in these habitats on 7 occasions in the summer and autumn of 1973/4 (Table 1) followed the same pattern as in Fig. 9, with lowest values occurring in the leaf litter zone of marginal riverine vegetation and highest values occurring in open grassland. Above ground level, saturation deficits recorded in Acacia grassland were similar to those recorded in marginal riverine vegetation.

In Acacia grassland and marginal riverine vegetation, lowest saturation deficits were recorded in microhabitats at ground level, and saturation deficits increased with increasing height above the ground. In open grassland, saturation deficits were highest at ground level in hot, dry midsummer conditions, when the soil was dry and the herbaceous ground cover was sparse. Lowest saturation deficits were recorded at ground level in open grassland, when the soil was wet (as in Fig. 9) and/or when there was a substantial herbaceous ground cover to protect the soil from direct exposure to the sun.

In the hot, dry conditions of midsummer, the magnitudes of difference between saturation deficits recorded in microhabitats both at different levels in the vegetation and in different habitats, were exceptionally large (Table 1). These differences, however, decreased as the height and density of the herbaceous ground cover increased, following the heavy rains of late summer (Fig. 6). In late summer and autumn, day-time saturation deficits recorded at ground level in open grassland, Acacia grassland and marginal riverine vegetation seldom exceeded zero. The soil in each of these habitats remained continually moist, and in marginal riverine vegetation, was water-logged for much of the time.

Day-time saturation deficits recorded in the Fish River Bush complex (Table 2), show that microhabitats in typical Fish River Bush were exceptionally dry, due to the lack of leaf litter and undergrowth. Saturation deficits recorded in microhabitats on the grass-covered verges of game paths were considerably lower, and were lowest in the leaf litter zone of gulley vegetation.

As a result of the change in the pattern of macroclimatic conditions, from the extreme of drought in midsummer (1973/74) to floods in late summer

(1974), it is only possible to draw general conclusions from the data presented in this section. The results in Table 4 show that larvae were largely absent from:- (a) Open grassland, in which day-time saturation deficits during midsummer reached exceptionally high levels (+ 60 mm Hg at ground level). (b) Marginal riverine vegetation, in which day-time saturation deficits in the leaf litter zone were consistently low (maximum 15,7 mm Hg, during midsummer). Larvae were present in Acacia grassland, in which day-time saturation deficits recorded at ground level rose to 30,5 mm Hg during midsummer, but remained close to 0 mm Hg during late summer and autumn. The major difference between Acacia grassland and marginal riverine vegetation, lay in the presence of the leaf litter zone and absence of grass cover in the latter. The leaf litter zone protected the surface layers of the soil from rapid drying, and consequently the soil remained wet or water-logged for long periods.

The results obtained in the Fish River Bush complex, although less conclusive, showed similar trends. Larvae were absent from:- (a) Typical Fish River Bush, in which high day-time saturation deficits were recorded. (b) Gulley vegetation, in which there was a leaf litter zone. Larvae were present along the grass covered verges of game paths, where day-time saturation deficits in the microclimate were moderately low.

3.9. Seasonal activity of larvae.

A histogram of the seasonal abundance of larvae collected in Acacia grassland, is given in Fig. 13. In plotting the histogram the results of each 3 consecutive weekly samples have been summed, to allow comparison of a larger number of ticks and to reduce the effects of variation in tick behaviour, caused by changing daily weather conditions (Milne, 1943). Larval activity remained at a low level during late summer, autumn and early winter. There was a slight increase in activity in mid-July, followed by a marked increase in activity towards the end of September. Larval activity then remained at a high level until mid-January, with a clear peak of activity in November/December.

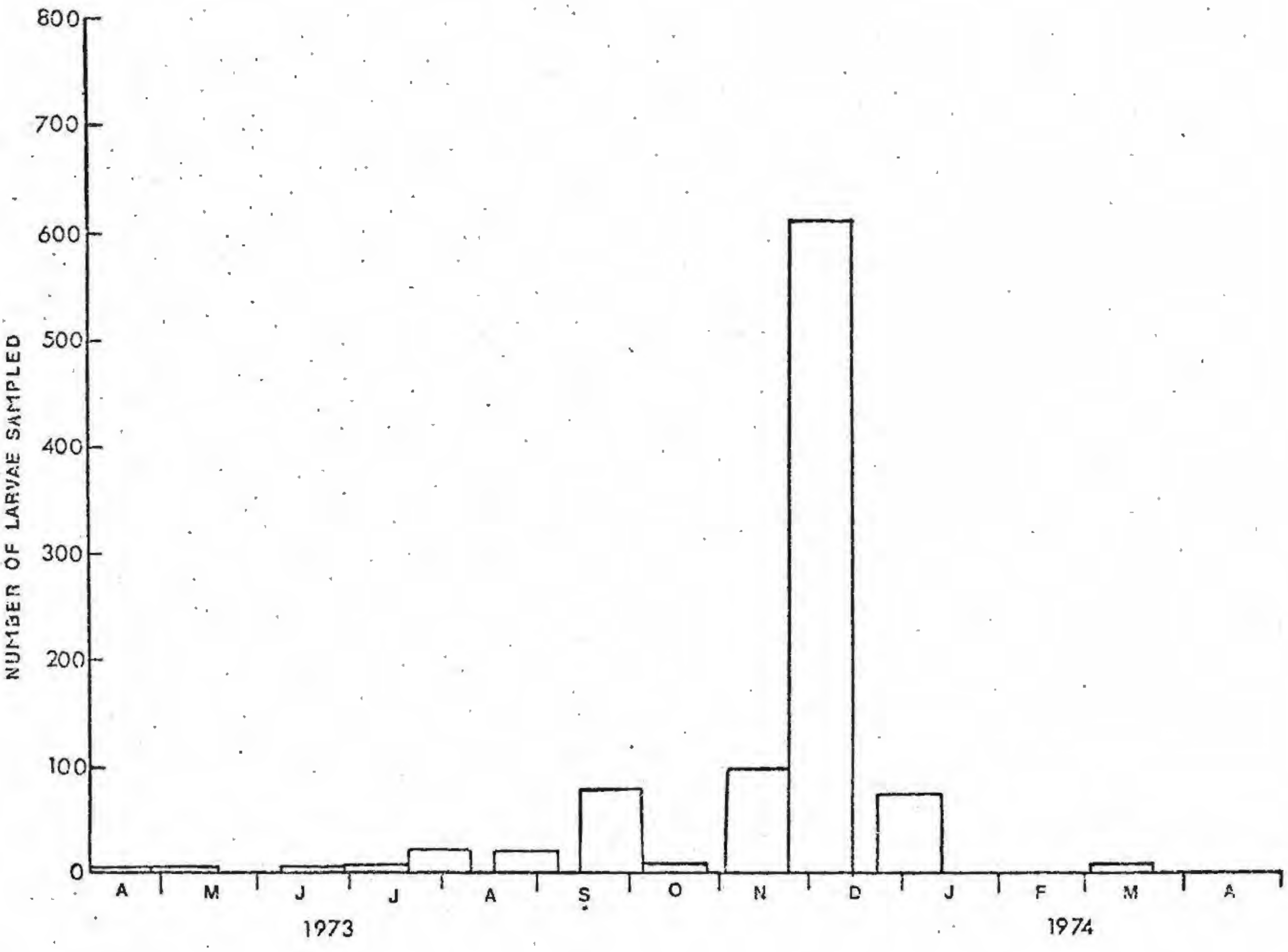

Fig. 13.

Histogram of seasonal activity of larvae of Amblyomma hebraeum, sampled by the drag method in Acacia grassland habitat in the Kowie River valley.

Relationship of seasonal activity with macroclimatic conditions.

(a) Temperature.

There was no direct correlation between temperature (hour degrees per week) (Fig. 8) and the onset of larval activity (Fig. 13). Larval activity was low during the cool months, between May and August, and then increased in late September, despite the continuing low temperatures. Activity then remained at a high level during the warmer months of spring and early summer. There was a decline in larval activity during the period of intense heat of late December and early January, whereafter, activity was negligible for the rest of summer.

(b) Rainfall.

There was no direct correlation between larval activity (Fig. 13) and weekly rainfall (Fig. 6). It was seen, however, that with the exception of one dry week in March, there was no larval activity during the heavy rains of late summer (mid-January until April).

(c) Saturation deficit.

There were no clear seasonal differences in mean weekly maximum saturation deficits (Fig. 9), which ranged from 7,9 to 35,4 mm Hg. Mean weekly minimum saturation deficits were lowest (0,0-0,6 mm Hg) in autumn and early winter, and highest in summer (0,8-2,0 mm Hg). During the early part of summer, in which larval activity was greatest (Fig. 13), mean weekly minimum saturation deficits remained below 1,0 mm Hg. Larval activity ceased in mid-January, when mean weekly minimum saturation deficits rose to 2,0 mm Hg.

Conclusions.

The onset of larval activity was not linked directly with either a rise in temperature or with rainfall. This indicates that larvae became active soon after hatching, irrespective of weather conditions, and that the main factors which determine seasonal activity are:- (a) The seasonal occurrence of engorged female ticks (3.11), and (b) the rate of oviposition and egg development in relation to climatic conditions (4.5).

The importance of tree cover in the survival of larvae is appreciated, when the summer peak of activity is considered in relation to summer microclimatic conditions. Summer rainfall in the Eastern Cape is often low (Fig. 7), resulting in little growth of herbaceous vegetation. Under these conditions, the differences in microclimate between tree covered and open habitats are large, and during the day saturation deficits can differ by almost 30 mm Hg (Table 3). Londt and Whitehead (1972) stated that larvae of ixodid ticks did not generally occur in microhabitats in which midday saturation deficits exceeded 10 mm Hg. During this investigation, saturation deficits exceeded 10 mm Hg in all microhabitats during the extremely dry conditions of midsummer. It is likely that these conditions resulted in a high mortality of larvae, causing the rapid decline in activity over this period. The low numbers of larvae collected during the humid conditions of late summer may therefore have been incidental. The survival of larvae in relation to temperature and saturation deficit, under laboratory and field conditions, is discussed in detail in Chapter 4 (4.7).

It is seen that the macroclimatic data (thermohygrograph records) (Fig. 9) bear little relationship to the microclimatic data (Table 1), in respect of seasonal trends. This can be attributed to the fact that the thermohygrograph was located in a Stevenson's screen, above the level of the herbaceous vegetation (see Table 3). This emphasizes the importance of the modifying influence of the herbaceous vegetation on the microclimatic conditions likely to be encountered by the non-parasitic stages of ticks.

3.10. Seasonal activity of nymphs.

The seasonal occurrence of nymphs on two undipped Short-horn steers is given in Fig. 14. The steers were largely free of nymphs from November, 1972 until the end of July, 1973. There was a slight increase in nymphal infestation in August, 1973, followed by a marked rise in

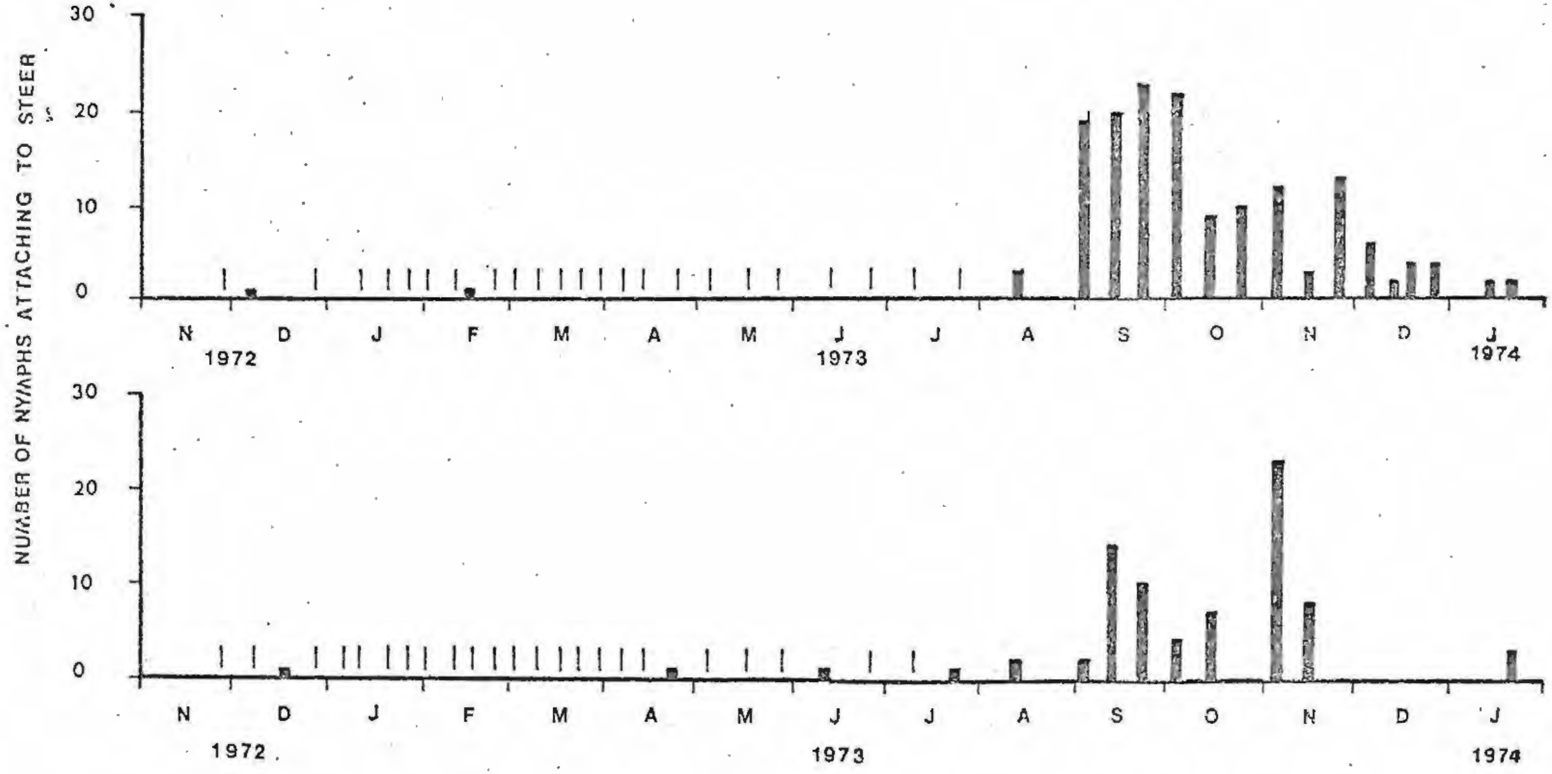

Fig. 14.

The numbers of nymphs of <u>Amblyomma</u> <u>hebraeum</u> attaching to steer No. 1 (above) and steer No. 2 (below). Narrow vertical lines indicate occasions on which no nymphs were recorded.

September. On steer No. 1, peak levels of infestation occurred over September and the first week of October. Then followed a sharp decline in nymphal numbers in mid-October, and a secondary rise in November. There was a gradual decline in nymphal numbers from the end of November until January. Infestations on steer No. 2 showed similar trends, but the September peak was lower than the November peak.

Factors regulating the seasonal activity of nymphs.

The seasonal activity peak of nymphs follows approximately one year after the activity peak of larvae (3.9). As the nymphal premoult period lasts only about 2 months in late summer conditions (4.6), it can be concluded that the unfed nymphs spend winter in a state of behavioural diapause or quiescence. Seasonally regulated quiescence in the unfed stages has been reported in a number of ixodid species (reviews by Balashov (1968) and Belozerov (1971)). Semtner and Hair (1973) found that over-wintering adults of <u>Amblyomma</u> <u>americanum</u> (L.) became active in early summer in response to the combined effects of increasing temperature and daylength, and high relative humidity. The authors expressed the opinion that increasing temperatures were important in initiating early seasonal activity, and later in the summer the level of activity was more dependent upon relative humidity. Similar results have been obtained in respect of other species. Macleod (1936) has shown a significant correlation between the activity of <u>Ixodes</u> <u>ricinus</u> L. and temperature. Lees and Milne (1951) showed that vertical migration (i.e. activity) of <u>I. ricinus</u> was correlated with body water content. Other workers (Belozerov, 1966; Balashov, 1968) report that activity in nymphs of <u>I. ricinus</u> is controlled by photoperiod for 5-6 months after moulting.

During the period of nymphal activity in <u>A. hebraeum</u> it was observed that nymphs were most abundant during the humid conditions which followed heavy falls of rain (Fig. 6). Rainfall was not, however, the sole factor which initiated or regulated nymphal activity, and as in other species it appeared that daylength and temperature may have also been involved.

The correlations between nymphal activity and temperature, daylength and rainfall (humidity), were tested both individually and in combination by means of a multiple linear regression. Milne (1948/9) reported that the level of tick (I. ricinus) infestation increased as young hosts increased in age (hence size). As nymphal activity, in this investigation, was measured by the numbers of nymphs attaching to steers (which were approximately 6 months old at the start of the sampling period), it was necessary to include an additional linear variable in the analysis, which related to the effects of monthly increases in the size of steers on the levels of infestation. The equation for the regression[1] was therefore, $Y = a_o + a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4$. Y was the number of ticks per sample, x_1 was the rainfall (mm) in the two weeks preceeding the sample, x_2 was the temperature (total hour degrees in the week of the sample), x_3 was the daylength on the day of the sample and x_4 the monthly linear host age factor (i.e. January, 1; February, 2; March, 3 etc.). The results for steer No. 1 (Table 5) show that between January and July, 1973 when nymphs were in a state of quiescence, there were no significant correlations between nymphal activity and the individual variables or between nymphal activity and the combined variables (multiple correlation coefficient). Between August, 1973 and January, 1974 there were significant negative correlations between nymphal activity and temperature, daylength and the linear host age factor, and a significant multiple correlation coefficient. Over the entire sample period from January, 1973 until January, 1974, there was a significant negative correlation between nymphal activity and temperature, and a significant positive correlation between nymphal activity and the linear host age factor, and also a significant multiple correlation coefficient.

The significance of the multiple correlation coefficient for the spring and summer period suggests that nymphal activity was regulated by the combined effects of temperature, daylength and rainfall. The negative

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[1] A Model 9810A, Hewlett-Packard Calculator was used for the analysis.

correlations between nymphal activity and increasing temperature, daylength and rainfall do not, however, conform to the trends established in A. americanum and I. ricinus (see earlier) or even adults of A. hebraeum (3.11). It appears that the negative correlations arise as a result of a factor which was not accounted for in the regression. Qualitative evidence obtained at Paardekraal Farm suggests that this factor may have been the depletion of the population of nymphs. In the survey area (Biekwes Camp), where cattle had been maintained continuously for a number of years, peak infestations of nymphs occurred in September, and then the levels of infestation declined gradually until January (disregarding week to week fluctuations) (Fig. 14). However in camps which had been 'spared' (i.e. maintained free of domestic stock) for periods of 6 months to one year, the situation was different. Cattle introduced into spared camps on 15th November and 6th December, 1973, became heavily infested with nymphs for periods of 3-6 weeks, before a decline in the level of infestation was observed. This suggests that nymphs which become active in spring, remain active over the summer months until a host is encountered. Initially the density of nymphs in the environment is high, but decreases as the number of nymphs which attach to hosts increases. The probability of a host-nymph encounter (and consequently the level of host infestation) therefore decreases progressively over the summer months. If the depletion of the nymphal population is taken into account, it becomes clear that the negative correlations are incidental, and consequently the significance of the multiple correlation coefficient is misleading. There is evidence however (3.11; 3.12), to show that nymphal activity is regulated by temperature, daylength and rainfall.

In experiments with I. ricinus, Milne (1945) found that delayed stocking "did not give rise to any appreciable prolongation of the female tick activity into the normal summer off-season". This was caused by a change in tick behaviour during the midsummer months; a feature which did not apparently occur in nymphs of A. hebraeum.

Table 5.

The correlation coefficients (r) between nymphal activity (numbers of nymphs attaching to a steer) and rainfall, temperature, daylength and a linear host age factor (see text). Also multiple correlation coefficients between nymphal activity and the above variables.

	Jan. '73-Jul. '73	Aug. '73-Jan. '74	Jan. '73-Jan. '74
Activity-rainfall	-0,106	-0,283	0,162
Activity-temp.	0,296	-0,769 **	-0,349 *
Activity-daylength	0,227	-0,529 *	0,119
Activity-host age factor	-0,194	-0,634 **	0,513 **
Multiple correlation coefficient	0,336	0,779 *	0,607 **

KEY. Significance of correlation; * ($p < 0,05$); ** ($p < 0,01$).

3.11. Seasonal activity of adult ticks.

The seasonal occurrence of adult male and female ticks on steer No. 1 is given in Fig. 15 and on steer No. 2 in Fig. 16. An accumulation of males, resulting from prolonged periods of attachment (Chapter 2), was observed on both steers. Ticks of both sexes were present on the steers in all seasons of the year, but there were definite seasonal fluctuations in the levels of tick activity. On steer No. 1, there was a rapid build-up of males from the start of the sample period in November, 1972, until the end of January, 1973. The numbers of males declined through February and March and then rose for a second time in April. This was followed by a decline in numbers in the first half of May and then a slight rise in late May. Thereafter there was a gradual decline in activity through the winter months. From the beginning of September, 1973

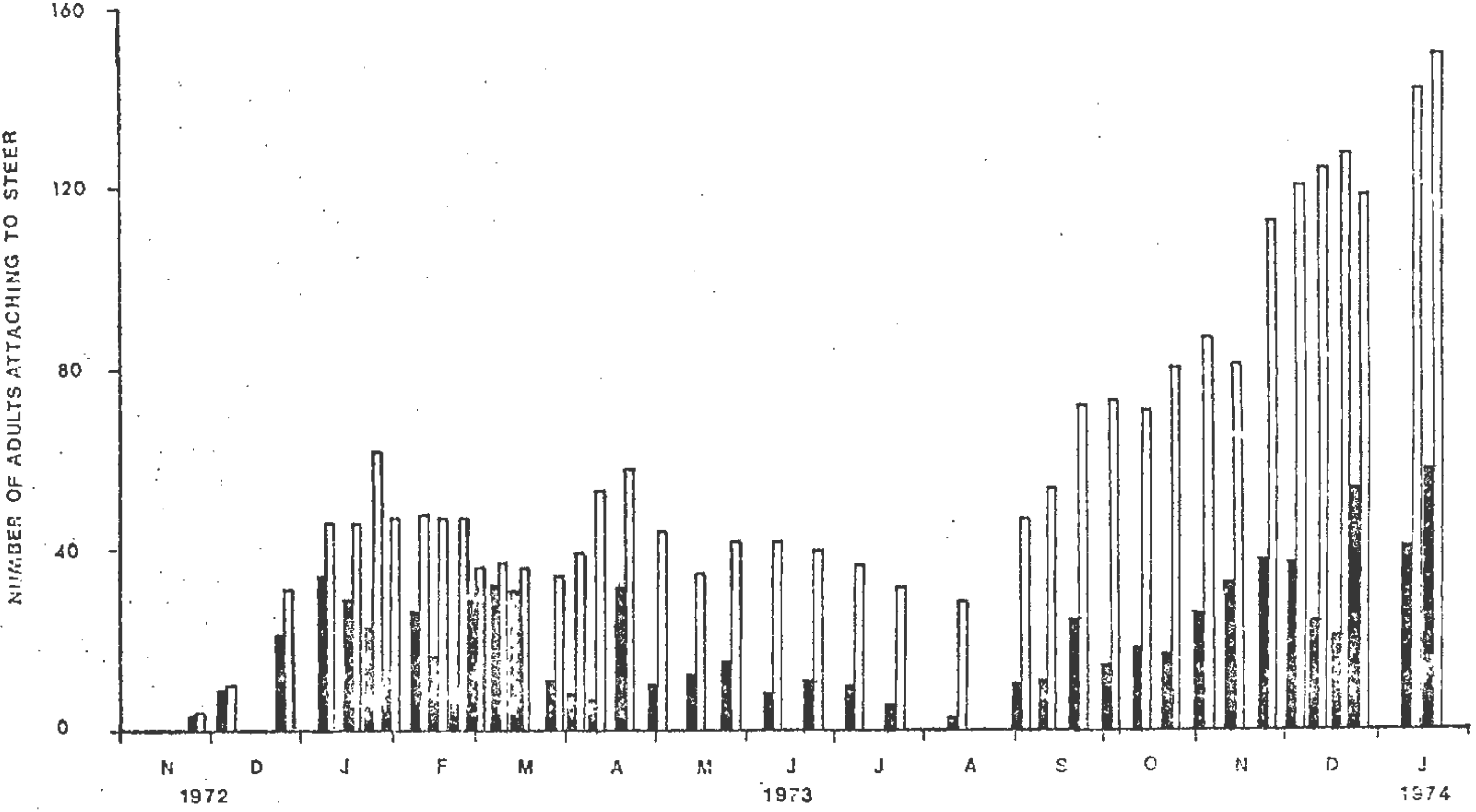

Fig. 15.

The numbers of adult males (unshaded) and females (shaded) of <u>Amblyomma hebraeum</u> infesting steer No. 1. Males remained continuously attached for long periods, and consequently the same individuals were counted on more than one occasion.

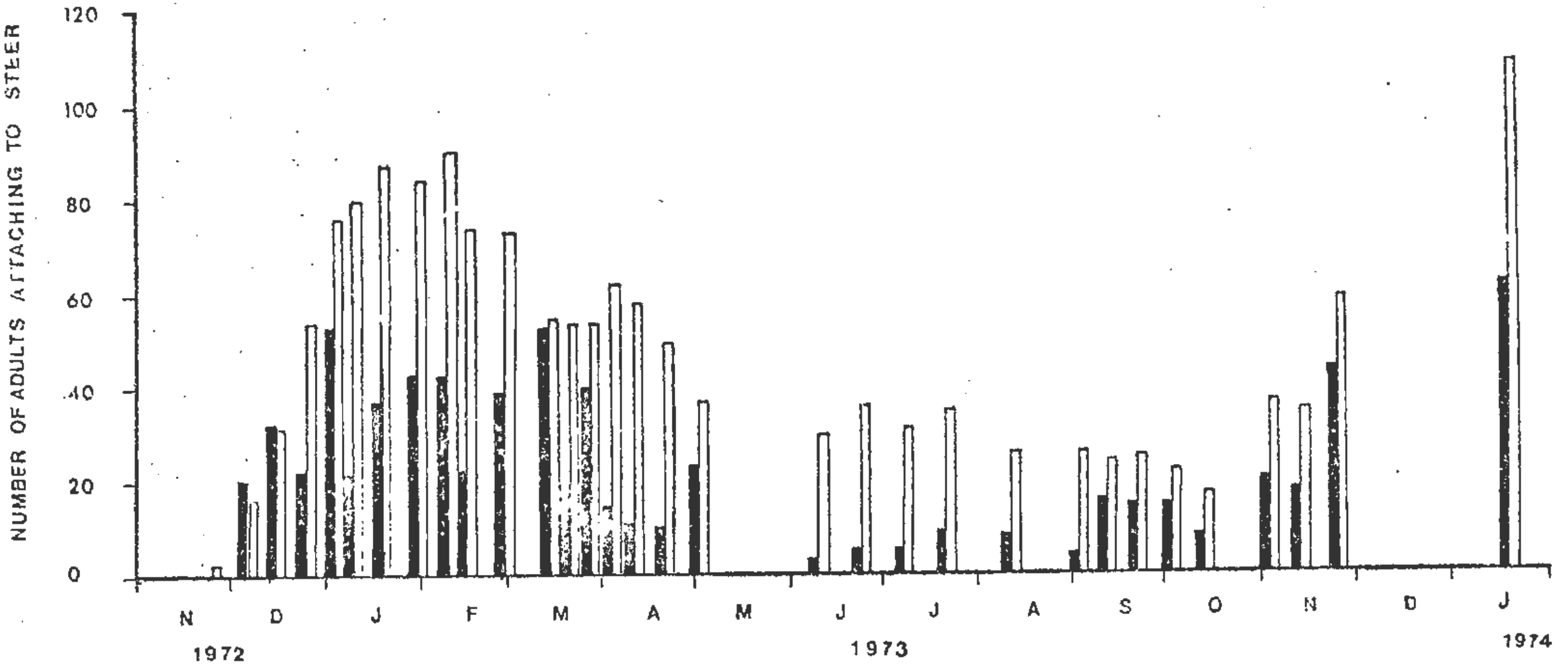

Fig. 16.

The numbers of adult males (unshaded) and females (shaded) of <u>Amblyomma hebraeum</u> infesting steer No. 2. Males remained continuously attached for long periods, and consequently the same individuals were counted on more than one occasion.

until the end of the sample period in January 1974, there was a steady accumulation of males on the steer. The seasonal incidence of female ticks on steer No. 1, showed similar general trends. In the summer of 1972/3, however, female numbers reached a peak in early January (i.e. 3 weeks earlier than the male peak). Then followed a decline in female numbers through late January and February. In March, when male numbers were low, there was a second rapid rise in female numbers, bringing the sex ratio to the level of almost 1:1. Female numbers declined through mid-March and early April, and then rose for a third time towards the end of April. The seasonal incidence of male and female ticks on steer No. 2 was similar to that on steer No. 1, but the actual numbers of ticks differed considerably.

Factors regulating the seasonal activity of adult ticks.

The seasonal activity peak of adult ticks follows approximately one year after the activity peak of nymphs (3.10). As the adult premoult period lasts only about two months in late summer conditions (4.6), it can be concluded that as with nymphs (3.10), unfed adult ticks spend the winter months in a state of quiescence. The spring rise in adult tick activity (Figs 15 and 16) coincided with the spring rise in nymphal activity (Fig. 14), indicating that the same factors were responsible for initiating activity in nymphs and adult ticks.

The correlations between adult female tick activity and temperature, daylength and rainfall were tested both individually and in combination by means of a multiple linear regression, as previously described for nymphs (3.10). The results in respect of steer No. 1 (Table 6) show that between January and July, 1973 there were significant positive correlations between adult female tick activity and temperature and daylength, and a significant negative correlation between adult female tick activity and the linear host age factor. The multiple correlation coefficient was also significant. Between August, 1973 and January 1974 there was a significant multiple correlation coefficient and significant positive correlations between adult female tick activity and temperature, daylength, rainfall and the linear host age factor. Over the entire survey period, from January, 1973 until January, 1974 there were significant positive correlations between adult female tick activity and temperature, daylength and rainfall and a significant multiple correlation coefficient.

These results show that both individually and in combination, temperature, daylength and rainfall had a direct influence on adult female tick activity in all seasons of the year. The values of the correlation coefficients (r) suggest that over the entire survey period, daylength had the greatest influence on activity, followed by temperature and rainfall respectively. It is also evident that rainfall was more important in summer than in autumn and winter, while the reverse was true with temperature. The significance of the correlation between female tick activity and daylength remained constant throughout the year. The negative correlation between female tick activity and the linear host age factor, for the period January to July, 1973, resulted from the winter decline in tick activity.

Table 6.

The correlation coefficients (r) between adult female tick activity (numbers of females attaching to a steer) and rainfall, temperature, daylength and a linear host age factor (see text). Also multiple correlation coefficients between adult female tick activity and the above variables.

	Jan. '73-Jul. '73	Aug. '73-Jan. '74	Jan. '73-Jan. '74
Activity-rainfall	0,105	0,587 *	0,355 *
Activity-temp.	0,786 **	0,551 *	0,676 **
Activity-daylength	0,781 **	0,734 **	0,706 **
Activity-host age factor	-0,772 **	0,818 **	-0,007
Multiple correlation coefficient	0,817 **	0,842 **	0,782 **

KEY. Significance of correlation; * $(p < 0{,}05)$, ** $(p < 0{,}01)$.

There was no evidence of a depletion of the population of adult ticks, which were active over the midsummer months. The depletion of the nymphal population (3.10) and not the adult population, appears to result from a response to shorter daylength in nymphs; this results in an earlier (spring) activity peak in nymphs and consequently a depletion of the population over the midsummer months, as discussed in section 3.12. It is also possible that as nymphs have a wider host range than adult ticks (Chapter 5), the nymphal population becomes depleted more rapidly than the adult population, as the probability of nymphs finding a suitable host is higher. The evidence (3.12), however, indicates that the former is more important.

It was not possible to perform a statistical analysis on the influences of environmental factors on the activity of adult male ticks, as the number of males attached to a host did not reflect tick activity in the days immediately preceeding the tick count. In general, however, it can be stated that the response of male ticks to environmental factors was similar to the response of female ticks.

3.12. Discussion

Londt and Whitehead (1972) expressed the opinion that one of the most important factors delimiting the distribution of unfed larval ticks is the effect of microclimatic conditions on the development of the egg stage. Habitats which favour egg development being likely to be habitats in which larvae occur. Lewis (1970) has shown that larvae are able to migrate over considerable distances under the influence of wind. Londt and Whitehead (1972), however, observed that air current speeds were negligible in habitats in which larvae were found to occur in the Eastern Cape, and therefore concluded that there was little horizontal migration of larvae. The results obtained in this investigation support the opinions of Londt and Whitehead (1972). At Paardekraal Farm it was observed that eggs of A. hebraeum did not develop in the water-logged soil fo marginal riverine vegetation (4.5). As a result larvae were largely absent from this habitat, despite the fact that microclimatic conditions above ground level were similar to those in Acacia grassland where larvae were abundant. The scarcity of larvae in open grassland in 1973/74 probably resulted from the mortality of eggs laid in this habitat during the dry conditions of the previous summer (Fig. 6).

The life cycles of ixodid ticks can be either uninterrupted (i.e. not synchronized with annual seasons) or synchronized through diapause with seasonal climatic changes (Balashov, 1968). According to Balashov (1968) uninterrupted life cycles are typical of tropical and burrow inhabiting species. The lengths of both types of life cycle are determined by locality and climatic conditions. The longest life cycles have been recorded in ticks which occur in the far Northern latitudes. In Karelian (ASSR) the life cycles of Ixodes persculatus (Schulze, 1930) and I. ricinus may require as long as 6 years for completion (Balashov, 1968). By contrast Trink von Think (1962) (cited by Theiler, 1969) reported that the life cycle of B. microplus may require only 1½ to 2 months for completion in the tropical conditions of Vietnam. Under the temperate conditions of South Africa, Theiler (1969) states that "the three host ticks probably average one generation in a year; the two-host and one-host ticks could, theoretically, average more". The life cycle of A. hebraeum in the Eastern Cape Province requires three years for completion, and is therefore an exception to this generalization. The results obtained in this investigation show that larvae of A. hebraeum are active in the first summer of the life cycle, nymphs in the second summer and adult males and females in the third summer.

The life cycle of A. hebraeum is partly uninterrupted and partly synchronized with seasonal climatic changes. Field data (4.5) have shown that larvae become active soon after hatching. The low level of larval activity recorded during the autumn and winter months, was a direct result of the long, temperature dependent incubation period of the eggs (4.5). The annual occurrence of larvae during the spring and summer months is ensured, because the activity of adult females is regulated by climatic conditions, and occurs during the midsummer months. As the rates of oviposition (4.4) and egg incubation are temperature dependent, it can be expected that winter temperatures will influence the timing of the larval activity peak, i.e. the peak will occur early in summer after a warm winter and later in summer after a cold winter. The duration of the larval activity peak can be expected to be influenced by (a) seasonal climatic conditions which determine the survival of larvae (4.7) and (b) the availability of hosts, which affects the rate of depletion of the larval population. It is thought that the rapid decline in larval activity in the survey area during late December, 1973 and early January, 1974 was caused by larval mortality, resulting from the exceptionally dry conditions which were recorded at this time of year.

The activity of nymphal and adult ticks is synchronized with seasonal climatic conditions. After a period of quiescence, lasting from late summer until spring, nymphs and adults become active in response to increasing temperature, daylength and humidity (rainfall). By means of a multiple linear regression (Table 6) it was shown that daylength was probably the most important factor in determining the level of adult tick activity. It is possible, however, that the influences of temperature and humidity were underestimated, as gross macroclimatic data, rather than microclimatic data were used in the analysis. Unfortunately in the case of nymphs, statistical analysis (Table 5) was of limited value due to the over-riding effects of the depletion of the population.

The observations of Baker and Ducasse (1968) that in the Natal thornveld (altitude 300-900 m) adults of A. hebraeum are active in midsummer, larvae in late summer and autumn and nymphs from autumn through winter until spring, suggests that under the warm sub-tropical conditions of Natal, the life cycle is completed in one year. It is assumed that eggs laid in midsummer are able to hatch before the onset of winter. Why the nymphs do not enter a prolonged state of quiescence in winter is of interest. The major differences between the winter climatic conditions of the low lying areas of Natal and the Eastern Cape, are that in Natal temperatures are generally higher, and rainfall (hence humidity) is lower. Low temperatures do not, however, appear to be the main factor responsible for nymphal quiescence in the Eastern Cape, as warm spells which could initiate nymphal activity are not uncommon during winter (Fig. 8). As nymphs are active during dry winter conditions in Natal, it can also be concluded that quiescence is not caused by low humidities. The remaining factor is daylength. On the shortest day of the year the daylength at Port Elizabeth (Eastern Cape) is 10 hours 13 minutes, and at Durban (Natal) is 11 hours 4 minutes. In the Eastern Cape the daylength remains below 11 hours from the end of April until mid-August. As the rise in nymphal activity at Paardekraal Farm began in mid-August, it can be concluded that the critical daylength required for nymphal activity is approximately 11 hours. As the daylength in Natal never falls below 11 hours, there is no prolonged quiescence and therefore there is winter activity. The absence of an autumn (March-April) peak of activity in the Eastern Cape, when the daylength is longer than 11 hours, results from the age effect (6.6) whereby nymphs can not be stimulated to activity for approximately three months after moulting (as is the case with unfed adults - 6.9).

Although there was a simultaneous spring rise in nymphal and adult tick activity at Paardekraal Farm, peak adult activity occurred approximately 4 months later than peak nymphal activity. This suggests that the mean critical daylength required for adult activity is longer than the mean critical daylength required for nymphal activity. This hypothesis is supported by the fact that in Natal, peak adult activity occurs in midsummer and peak nymphal activity occurs in winter. It seems logical that A. hebraeum, which originates from sub-tropical summer rainfall areas, should restrict adult activity to the midsummer months, as this would guarantee that the egg stage would occur in late summer and autumn. This is the time of year most suited to egg development, because (a) the soil should have a high water content (after the summer rains), which is necessary for egg development (4.5). (b) The herbaceous ground cover is generally most dense, giving maximum protection to the surface layers of the soil and so increasing the chances of egg survival (4.5). (c) The air temperatures are sufficiently high to ensure that the eggs hatch before the onset of cold winter conditions, when egg development is reduced to an extremely slow rate and egg mortality rises (4.5).

A response to shorter daylength in nymphal than in adult ticks, would, in the Eastern Cape, result in a larger proportion of the nymphal population encountering hosts in early summer. This would result in a marked depletion of the nymphal population by midsummer, but not of the adult population, as was observed at Paardekraal Farm.

Belozerov (1966) and Balashov (1968) report that activity in nymphs of I. ricinus is only controlled by photoperiod for 5-6 months after moulting. The presence of adults of A. hebraeum in low numbers on steers during the winter months, indicates a similar photoperiod response i.e. those adult ticks which do not encounter hosts during the summer months remain active during winter, irrespective of daylength. The termination of the photoperiod response at the end of summer would be advantageous, as there is little likelihood that the ticks could survive until the following summer (4.7).

While it has been established that daylength is probably the most important individual factor controlling nymphal and adult tick activity, it must be stressed that overall it is the combined influences of temperature, daylength and rainfall, which determine the level of activity.

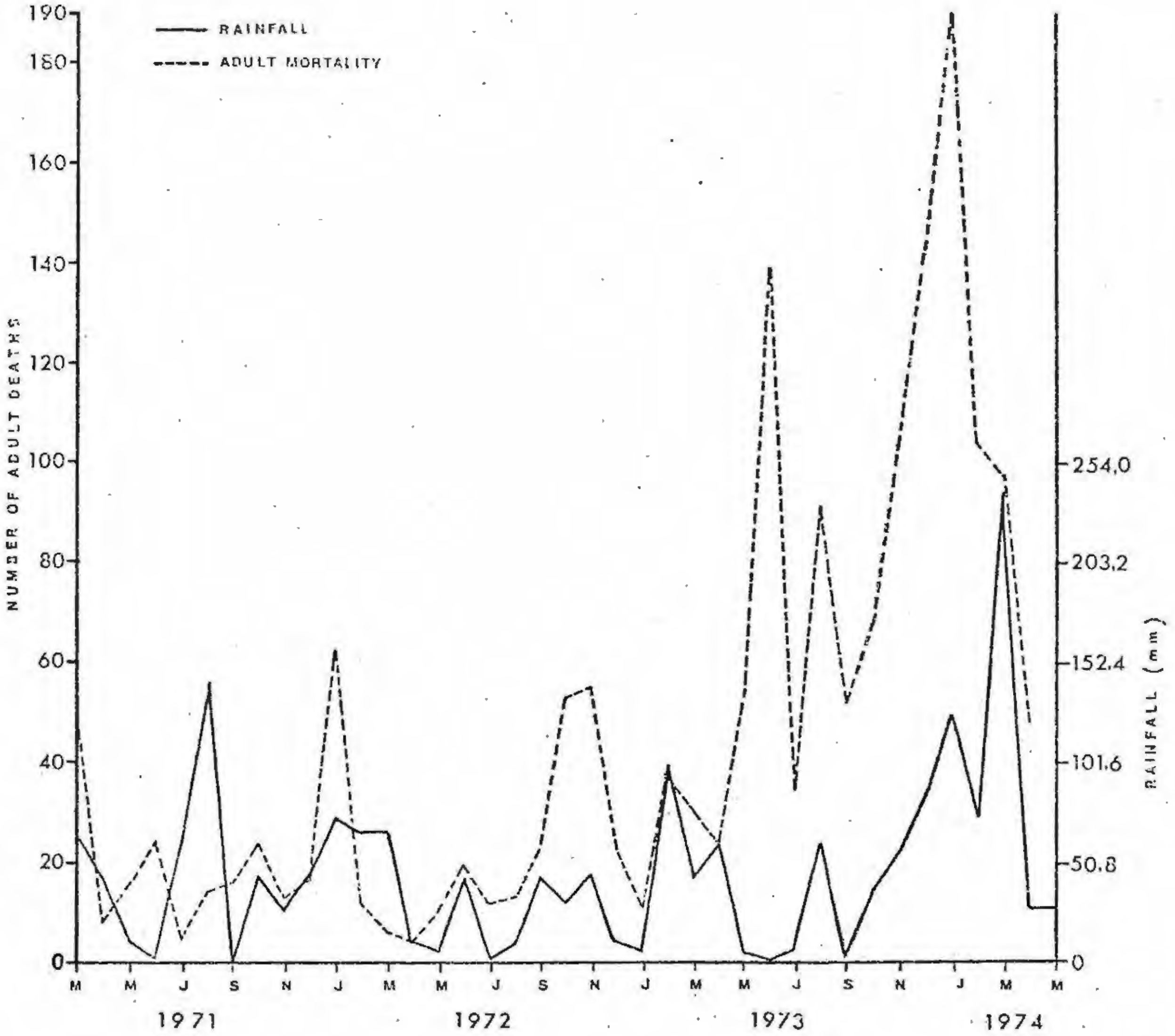

Fig. 17.

The relationship between heartwater mortality in adult Angora goats and rainfall, at Bucklands Farm (near Grahamstown), for the period March, 1971 until May, 1974. The data were kindly supplied by Mr G. Walsh.

This is clearly shown by data collected by Mr G. Walsh of Bucklands Farm, on the relationship between heartwater mortality[1] in adult Angora goats and monthly rainfall, for the period March, 1971 to May, 1974, (Fig. 17). Over the entire period there was a significant correlation (r=0,392) between monthly rainfall and goat mortality. If each year (1st April-31st March) is considered individually, however, it is seen that in 1971/2, when 573 mm of rain was recorded and in 1973/4 when 751 mm of rain was recorded, the correlations (r=0,058 and r=0,379 respectively) were not significant. In 1972/3 when only 343 mm of rain was recorded, the correlation (r=0,627) was significant. This shows that the importance of rainfall in tick activity increases in dry conditions. While there was no rise in heartwater mortality during the heavy winter rains of 1971, there was a sharp rise in mortality during the dry winter conditions of 1973. It seems likely that in these instances, temperature was more important than rainfall. In all three years of observation, peak heartwater mortality occurred during the spring and summer months, presumably as a result of the tick photoperiod response. The peaks, however, were timed to coincide with the rainfall peaks.

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[1] The number of heartwater mortalities is an indication of the level of activity of nymphal and adult ticks.

4. Survival and development of the non-parasitic stages of *Amblyomma hebraeum* in relation to temperature and atmospheric humidity.

4.1. Introduction.

It has been shown in the previous chapter that the life cycle of *A. hebraeum* requires three years for completion in the Eastern Cape Province. The parasitic phase in female ticks lasts for approximately 22 days (Chapter 2) or 2% of the duration of the life cycle. The remaining 98% of the duration of the life cycle is occupied by the non-parasitic stages. In a study on the ecology of *A. hebraeum*, it is therefore necessary to consider the influences of abiotic factors on the non-parasitic stages. The most important factors affecting the survival and development of most terrestrial arthropods, including ticks, are temperature and humidity (or saturation deficit).

The only southern African tick species for which comprehensive data exists on the survival and development of the non-parasitic stages in laboratory and field conditions, is the one-host tick, *B. decoloratus* (Londt, 1973). In the case of *A. hebraeum* our knowledge is scant. Lounsbury (1899) observed that the durations of the preoviposition, oviposition, incubation and nymphal premoult periods increased at low temperatures. Theiler (1943) reported that unfed larvae were able to survive for 7 months, unfed nymphs for 6 months and unfed adults for 7-20 months, but unfortunately the author made no reference to abiotic factors. Kraft (1961) observed that in the field, eggs did not develop in open habitats, but did develop in shaded habitats. In a more detailed study Londt and Whitehead (1972) showed that in larvae, the equilibrium humidity (below which water was lost rapidly) was approximately 70% RH at 26°C (i.e. 7,53 mm Hg saturation deficit). It was also shown that the critical temperature (above which larvae lost water rapidly) lay between 40 and 45°C. Londt and Whitehead (1972) demonstrated that larvae were able to drink free water, and consequently larvae which had access to free water were able to survive for considerably longer periods than larvae which did not have access to free water.

In this investigation the survival and rate of development (where applicable) of all non-parasitic stages i.e. egg stage, unfed larvae, engorged larvae, unfed nymphs, engorged nymphs, unfed adults and engorged females (preoviposition and oviposition periods), were recorded in laboratory and field conditions. The laboratory and field data are compared, and the significance of the results are discussed in relation to the distribution and seasonal activity of A. hebraeum in the field (Chapter 3).

4.2. Materials and methods.

Experimental ticks were obtained from a laboratory culture, in which the non-parasitic stages were maintained in darkness in an incubator at 26°C and approximately 90% RH. Larvae were reared on Himalayan giant rabbits, nymphs on Merino sheep and adults on Guernsey calves, as described in Chapter 2. In all experiments ticks were maintained in glass tubes, in which the open ends were covered with gauze to prevent the escape of the ticks. In laboratory experiments ticks were placed in glass humidity chambers which were kept in darkness in incubators, set at constant temperatures. Different relative humidities were obtained using potassium hydroxide solutions of different concentrations (Peterson, 1953). The relative humidity levels were checked periodically using cobalt thiocyanate paper indicators in the manner discussed by Solomon (1957). Each developmental stage was tested in the following conditions of temperature and relative humidity:-

	40% RH	70% RH	90% RH
15°C	"	"	"
20°C	"	"	"
26°C	"	"	"
30°C	"	"	"
35°C	"	"	"

In field experiments, tubes of ticks were placed in a Stevenson's screen, which was kept outside the field station of the Tick Research Unit of Rhodes University. Continuous records of temperature and relative humidity in the Stevenson's screen were obtained using a thermohygrograph.

4.3. Preoviposition period.

The preoviposition period is the interval which elapses between the detachment of an engorged female and the first appearance of eggs. A number of authors (Hunter & Hooker, 1907; Graybill, 1911; Legg, 1930; Macleod, 1935a; Arthur, 1951; Hitchcock, 1955; Sweatman, 1967; Sardey & Rao, 1971; Londt, 1973; Branagan, 1973) have shown that the duration of the preoviposition period in ixodid ticks is temperature dependent. There are, however, differing reports on the influence of humidity on the duration of the period. In certain species i.e. *I. ricinus* (Macleod, 1935a), *Ixodes hexagonus* Leach (Arthur, 1951), *A. americanum* (Lancaster & Macmillan, 1955) and *Rhipicephalus sanguineus* Latreille (Sweatman, 1967), there is evidence of a correlation between the duration of the period and relative humidity, while in other species i.e. *D. variabilis* (Smith *et al*., 1946), *Boophilus microplus* (Canestrini) (Hitchcock, 1955), *Hyalomma aegyptum* (L.) (Sweatman, 1968), *R. appendiculatus* (Branagan, 1973) and *B. decoloratus* (Londt, 1973), no significant correlations were recorded.

Laboratory studies.

Within 24 hours of detachment, engorged females were placed in humidity chambers in an incubator, and then examined daily to determine the length of the preoviposition period. Three females were tested in each of the fifteen different combinations of temperature and relative humidity given above.

The results (Fig. 18) show that the duration of the preoviposition period was temperature dependent. The period was shortest at 30°C and increased at both higher and lower temperatures. The critical temperature, below which development became extremely slow, lay between 15 and 20°C.

Within the temperature range 20-30°C, there was no apparent correlation between the duration of the preoviposition period and humidity. At 15 and 35°C, however, the duration of the period increased with decreasing relative humidity (i.e. increasing saturation deficit). There were no mortalities in ticks maintained at 20, 26 and 30°C. At 35°C two ticks in 70% RH and one tick in 40% RH died before laying eggs. At 15°C all three ticks maintained in 40% RH died after approximately 2½ months, all showing marked signs of desiccation.

Field studies.

Field studies on the preoviposition period are discussed in the following section (4.4), in conjunction with studies on the oviposition period.

Conclusions.

By comparison with other ixodid species tested, the preoviposition period in A. hebraeum is exceptionally long. This was most noticeable at 15°C, where the preoviposition period ranged from 120 to 194 days, as opposed, for example, to approximately 30 days in B. decoloratus (Londt, 1973) and R. sanguineus (Sweatman, 1967), and approximately 20 days in I. ricinus (Macleod, 1935a).

The finding in A. hebraeum that low humidities increase the duration of the preoviposition period at low and high temperatures, is exactly the opposite of the finding of Sweatman (1967), that humidity only influences the duration of the preoviposition period of R. sanguineus between 20 and 30°C, when increasing humidity increases the duration of the period. In I. hexagonus (Arthur, 1951), I. ricinus (Macleod, 1935a) and A. americanum (Lancaster & Macmillan, 1955) the trends were similar to those recorded in A. hebraeum. The results in respect of I. ricinus and A. americanum, however, need to be repeated.

The deaths of females maintained at 15°C and 40% RH, are thought to have been caused by desiccation during the exceptionally long preoviposition period.

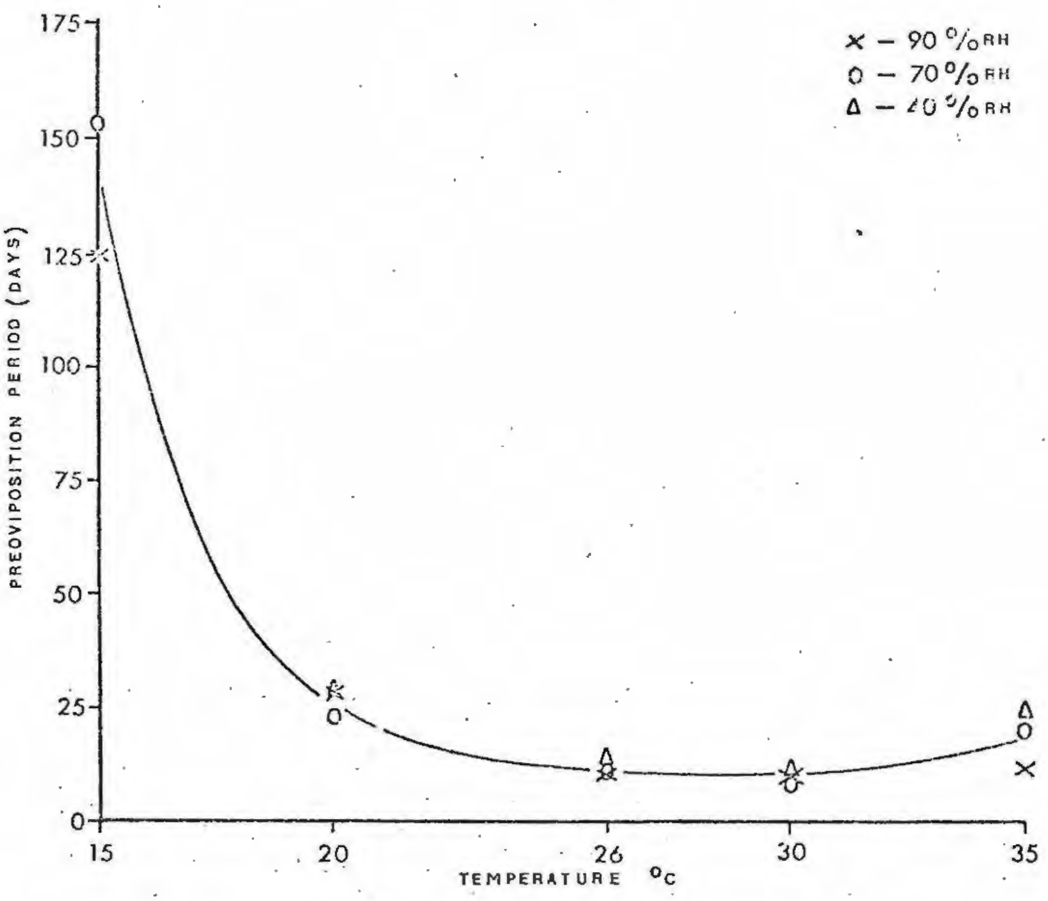

Fig. 18.

Amblyomma hebraeum. The duration of the preoviposition period in conditions of constant temperature and relative humidity. Each point is the mean value for three ticks.

4.4. Oviposition period.

The duration of the oviposition period in a number of ixodid tick species e.g. B. annulatus (Hunter & Hooker, 1907; Graybill, 1911), B. microplus (Legg, 1930; Hitchcock, 1955), B. decoloratus (Londt, 1973), H. anatolicum anatolicum (Snow & Arthur, 1966), I. hexagonus (Arthur, 1951), I. ricinus (Macleod, 1935a), R. sanguineus (Sweatman, 1967) and R. appendiculatus (Branagan, 1973) has been shown to be temperature dependent. In A. americanum, D. variabilis (Sonenshine & Tigner, 1969), B. decoloratus (Londt, 1973), B. microplus (Hitchcock, 1955), H. aegyptum (Sweatman, 1968), R. appendiculatus (Branagan, 1973), I. hexagonus (Arthur, 1951), and I. ricinus (Macleod, 1935a), atmospheric humidity had no observed effect on the duration of the period. In A. americanum (Lancaster & Macmillan, 1955), H. anatolicum anatolicum (Snow & Arthur, 1966) and R. sanguineus (Sweatman, 1967), on the other hand, humidity was shown to influence the duration of the period. Other factors which have been found to be important are photoperiod (Belozerov & Kvikto, 1965, cited by Theiler (1969)), the number of eggs laid (Graybill, 1911; Drummond & Whetstone, 1970; Londt, 1973) and the initial engorged weight of female ticks (Graybill, 1911; Londt, 1973). Snow and Arthur (1966) found that in H. anatolicum anatolicum the conditions experienced during the preoviposition period, did not affect the duration of the oviposition period.

The initial engorged weight of female ticks is, in conditions of constant temperature and relative humidity, the most important factor which determines the number or weight of eggs produced (Chapter 2). With the exceptions of I. ricinus (Macleod, 1935a) and I. hexagonus (Arthur, 1951), atmospheric humidity has not been found to influence the number of eggs produced. Temperature has been shown to determine the total numbers of eggs laid by females of B. microplus (Hitchcock, 1955), B. decoloratus (Londt, 1973) and R. sanguineus (Sweatman, 1967).

Laboratory studies.

Female ticks which had been maintained through the preoviposition period (4.3) in the given combinations of temperature and relative humidity (4.2) were maintained in the same conditions through the oviposition period. From the onset of laying, egg batches were removed daily from individual females, and immediately weighed on a Sartorius single pan balance.

The egg laying curves of individual females are given in Figs 19-23. From these curves it is clear that the rate of oviposition in _A. hebraeum_ is temperature dependent. At 90% RH the oviposition periods were longest at 15°C (190-199 days). The periods were considerably shorter (58-62 days) at 20°C, and shortest at 26 and 30°C (25-46 days). At 35°C the oviposition periods ranged from 5 to 30 days. The short duration of oviposition at this temperature did not, however, result from a rapid rate of egg laying, but a decline in egg production.

Between 20 and 30°C the egg production curves at 40, 70 and 90% RH, followed the general pattern described in Chapter 2 (with the exception of tick No. 3 at 26°C and 40% RH, which died before egg laying was completed). At 15°C and 90% RH, peak levels of egg production were reached on about the 25th day of the oviposition period. In females No. 2 and 3 egg production was maintained near the peak level until about day 80, after which there was a decline in daily egg production. In female No. 1, in which there was a high initial peak, the daily egg production began to decline after the 25th day. At 15°C and 70% RH the numbers of eggs produced were considerably lower than at 90% RH, and consequently the oviposition periods were shorter (15-72 days). No eggs were produced at 15°C and 40% RH, as all three females died during the preoviposition period (4.3). At 35°C the patterns of egg laying at all three humidities showed considerable variations, and it was clear that egg laying was adversely affected by this high temperature.

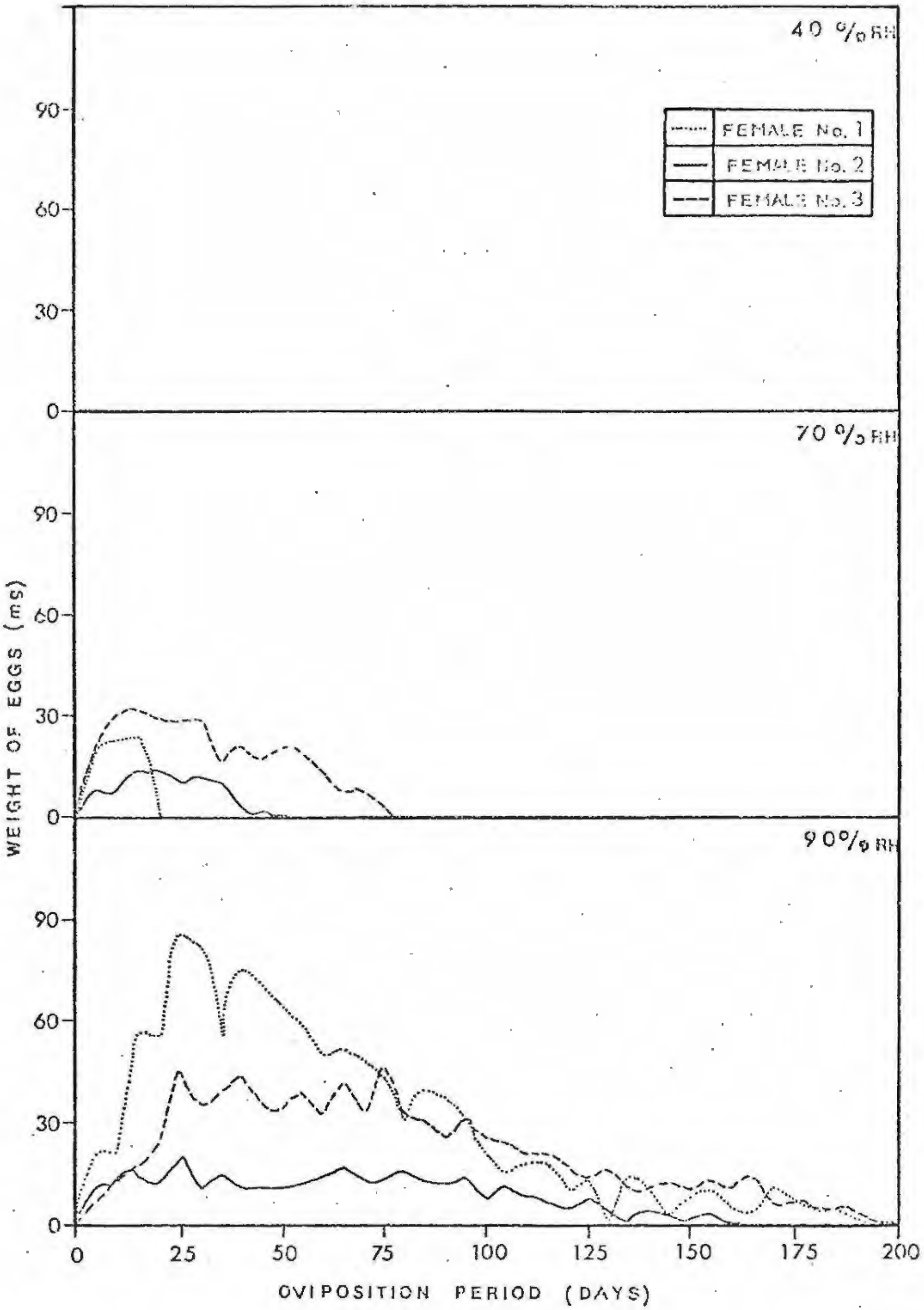

Fig. 19.

Oviposition curves of females of <u>Amblyomma hebraeum</u> maintained at 15°C and 40, 70 and 90% RH. The curves represent the weight of eggs laid by individual females over 5-day periods. No eggs were laid at 40% RH.

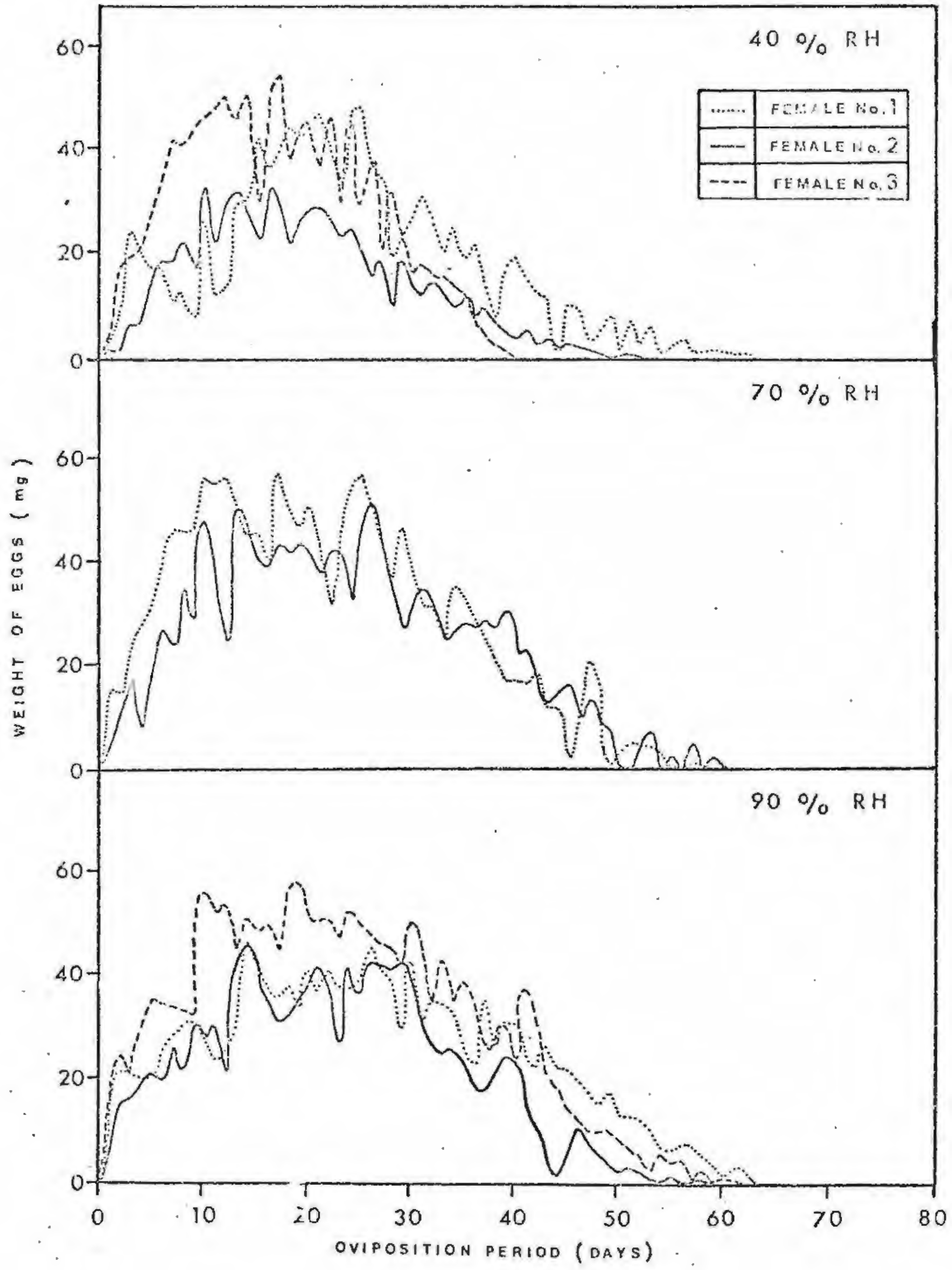

Fig. 20.

Oviposition curves of females of Amblyomma hebraeum maintained at 20°C and 40, 70 and 90% RH. The curves represent the weight of eggs laid by individual females over 24-hour periods.

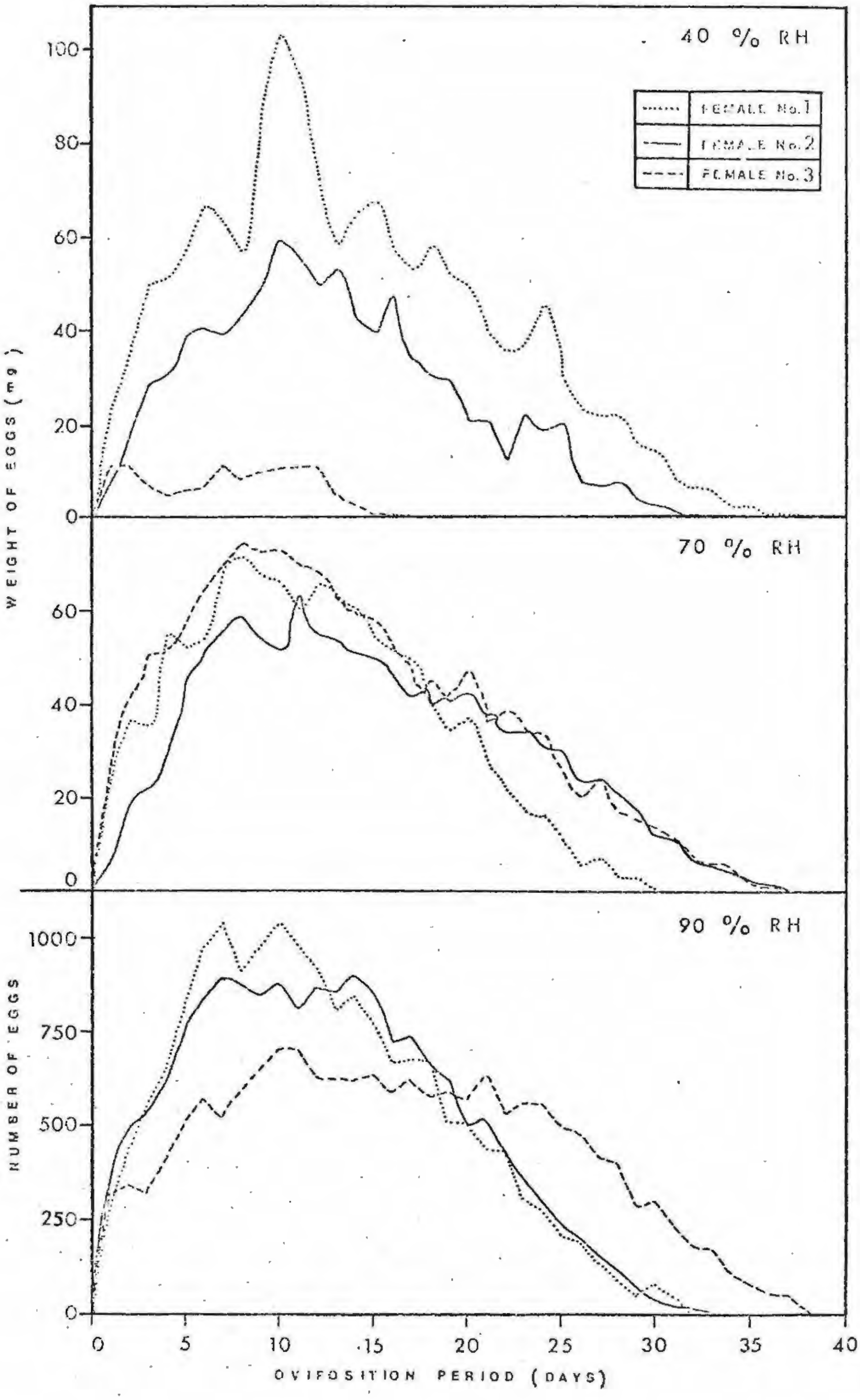

Fig. 21.

Oviposition curves of females of <u>Amblyomma hebraeum</u> maintained at 26°C and 40, 70 and 90% RH. The curves represent the weight (40% RH and 70% RH) or number (90% RH) of eggs laid by individual females over 24-hour periods.

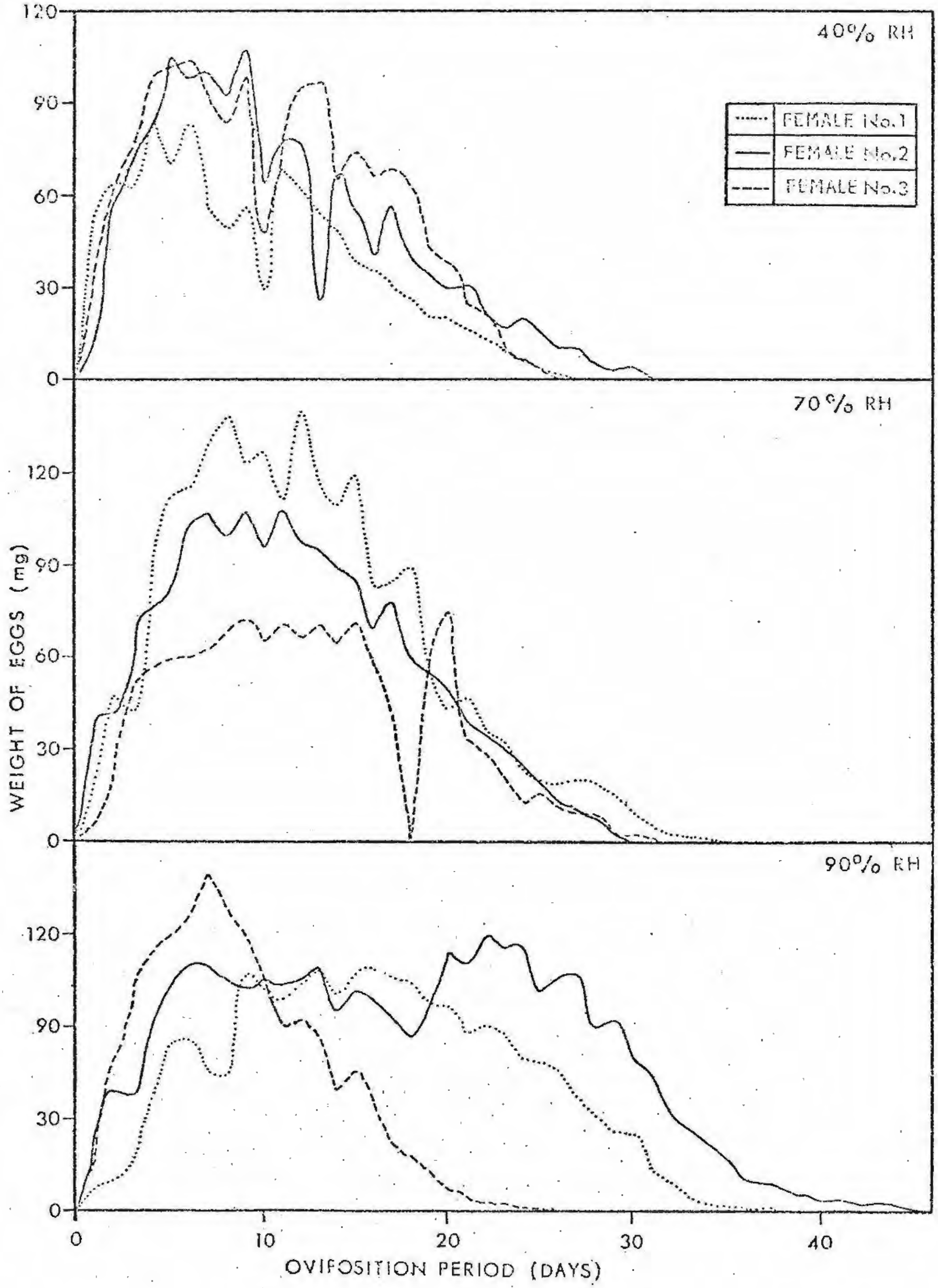

Fig. 22.

Oviposition curves of females of Amblyomma hebraeum maintained at 30°C and 40, 70 and 90% RH. The curves represent the weight of eggs laid by individual females over 24-hour periods.

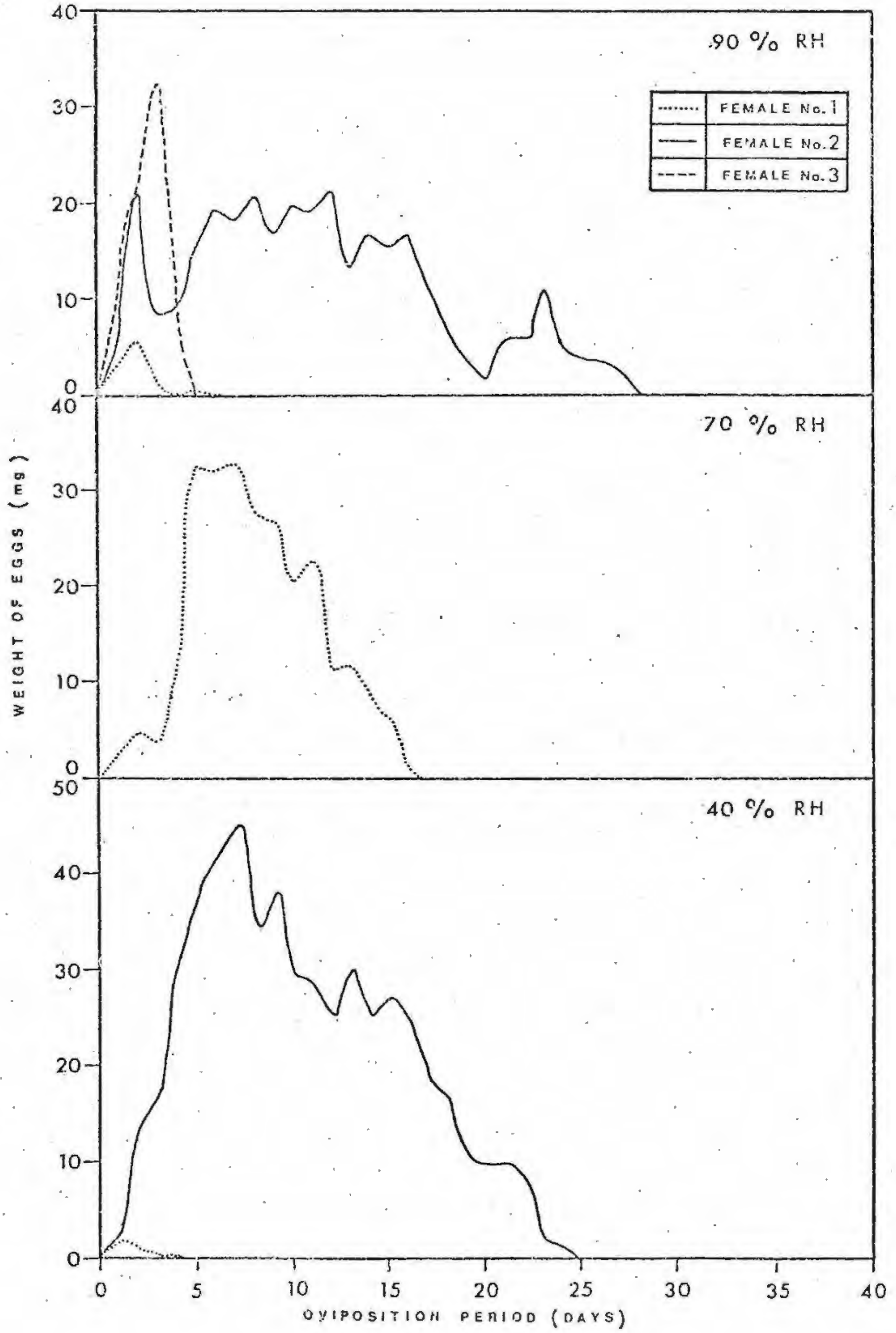

Fig. 23.

Oviposition curves of females of Amblyomma hebraeum maintained at 35°C and 40, 70 and 90% RH. The curves represent the weight of eggs laid by individual females over 24-hour periods. Two females at 70% RH and one female at 40% RH failed to lay eggs.

Table 7

The weight of eggs (mg) produced per mg ♀ weight under different conditions of constant temperature and relative humidity.

No.	Engorged Wt. ♀ (mg)	Weight eggs (mg)	Weight eggs (mg) per mg ♀ weight
15°C/40% RH			
1	2415,6	0,0	0,00
2	2069,3	0,0	0,00
3	1571,6	0,0	0,00
15°C/70% RH			
1	2465,8	67,5	0,03
2	1804,6	84,0	0,05
3	1806,9	291,9	0,16
15°C/90% RH			
1	3237,4	1219,5	0,38
2	1637,2	317,6	0,19
3	2297,1	781,7	0,34
20°C/40% RH			
1	2516,4	1148,4	0,46
2	1664,5	721,3	0,43
3	2937,2	1161,6	0,40
20°C/70% RH			
1	2902,1	1699,5	0,59
2	2690,3	1461,3	0,54
20°C/90% RH			
1	2758,6	1569,5	0,57
2	2254,5	1283,4	0,57
3	3408,3	1818,3	0,53
26°C/40% RH			
1	2708,8	1530,4	0,56
2	1931,0	886,2	0,46
3	1441,8	116,2	0,05
26°C/70% RH			
1	1852,8	1155,2	0,62
2	2028,6	1182,8	0,58
3	2185,9	1422,8	0,65

Table 7 continued.

No.	Engorged Wt. ♀ (mg)	Weight eggs (mg)	Weight eggs (mg) per mg ♀ weight
26°C/90% RH			
1*	1750,0	1100,0	0,63
2	1900,0	1262,5	0,66
3	2425,0	1600,0	0,66
30°C/40% RH			
1	1888,7	1064,2	0,56
2	2521,4	1425,8	0,57
3	2644,2	1556,3	0,59
30°C/70% RH			
1	3565,4	2143,8	0,60
2	2832,5	1783,5	0,63
3	2067,9	1249,0	0,60
30°C/90% RH			
1	3069,8	1627,9	0,53
2	4057,7	2237,2	0,55
3	1884,9	1136,0	0,60
35°C/40% RH			
1	2072,3	2,4	0,00
2	2984,1	533,4	0,18
3	3102,5	0,0	0,00
35°C/70% RH			
1	1761,8	258,5	0,15
2	2435,6	0,0	0,00
3	3154,9	0,0	0,00
35°C/90% RH			
1	2192,3	9,8	0,00
2	1672,9	315,7	0,19
3	2342,7	73,3	0,03

* Not the same ticks as given in Fig. 21.

In addition to the duration of the oviposition period, the egg production capacity was directly influenced by temperature. In Table 7 it is seen that the weight of eggs produced per mg of female weight, in constant relative humidities, decreased at temperatures above and below 26°C. The lowest levels of egg production occurring at 15 and 35°C.

At temperatures below 35°C, the egg production capacity of female ticks (Table 7) tended to decrease with decreasing relative humidity, and was lowest at low temperatures and low relative humidities. It was initially thought that this effect may have resulted directly from water loss from the eggs during the period (0-24 hours) before the eggs were weighed. It was found, however, that there was no significant difference[+] in the mean weights of eggs laid at either 40, 70 or 90% RH over a 24 hour period.

Under conditions of constant temperature and relative humidity (Figs 19-23) it was apparent that the duration of the oviposition period was influenced by the weight (or number) of eggs laid, and possibly also by the initial weight of engorged females (given in Table 7). Unfortunately the numbers of ticks tested under each set of conditions were not sufficiently large to facilitate statistical treatment. In each set of conditions the patterns of egg laying of individual ticks showed a wide variability (as described in Chapter 2), and consequently a large number of ticks would have to be tested to confirm either trend.

Field studies.

Three engorged female ticks were placed in the Stevenson's screen on 13th February, 1973. Egg laying commenced after 32-34 days. The weight of eggs produced per day was temperature dependent and the minimum

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[+] At constant relative humidities the weights of eggs laid by individual females showed considerable variability. At different relative humidities the differences in the weights of eggs resulting from desiccation were less than the variability in the weights of eggs laid by different females.

temperatures required for egg laying were 15-17°C. All three females died within three weeks of the start of oviposition, indicating that microclimatic conditions in the Stevenson's screen were unsatisfactory for egg laying. The high temperatures (up to 38°C) which were recorded during the preoviposition periods were probably the most important factor. Later field experiments (4.5) involving oviposition, were conducted under more natural conditions at Paardekraal Farm.

Conclusions.

Within the lethal limits of temperature the duration of the oviposition period in A. hebraeum, as in other ixodid species, decreased with increasing temperature. The upper lethal limit for oviposition lay between 30 and 35°C. The critical temperature, below which egg laying became extremely slow, lay between 15 and 20°C. There was no apparent decrease in the duration of the oviposition period between 26 and 30°C. This conforms with the results obtained for other species i.e. H. anatolicum anatolicum (Snow & Arthur, 1966), H. aegyptum (Sweatman, 1968) and B. decoloratus (Londt, 1973), where it was observed that the oviposition period reaches a minimum length at a certain temperature value, and then shows no further decrease at higher, sub-lethal temperatures. Londt (1973) suggests that once a specific temperature has been reached "it becomes physically or physiologically impossible for the female ticks to further increase the rate at which eggs are produced". It has also been suggested by Londt (1973) that as the quantity of eggs produced is a function of the engorged weight of the female, the duration of the oviposition period in ticks producing eggs at the maximum possible rate would be a function of the engorged weight of the female. Such a relationship does appear to exist in A. hebraeum, but is overshadowed by the variation in the maximum rates of egg production attained by individual females maintained in the same controlled conditions.

At temperatures exceeding 20°C the pattern of oviposition in A. hebraeum, i.e. with a period of several days during which egg production is maintained at a high level, is not typical of the normal pattern of egg production in ixodid ticks. In other species, e.g. *Ixodes canisuga* (Johnson) (Smith, 1972), *I. hexagonus* (Arthur, 1951), *B. microplus* (Hitchcock, 1955), *B. decoloratus* (Londt, 1973), *R. sanguineus* (Sweatman, 1967), *R. appendiculatus* (Branagan, 1973), *Amblyomma tuberculatum* Marx (Conney & Hays, 1972), *A. maculatum* (Drummond & Whetstone, 1970), *A. americanum*, *D. variabilis* (Sonenshine & Tigner, 1969), *H. anatolicum anatolicum* (Snow & Arthur, 1966) and *H. aegyptum* (Sweatman, 1968), there is a sharp rise to a peak of egg production a few days after laying has begun and then a progressive decrease in egg production until laying ceases. The total numbers of eggs produced by females of *A. hebraeum* (up to 18 765) are, with the exception of *A. maculatum* (Drummond & Whetstone, 1970), considerably larger than the numbers given for the above species. As the maximum rate of egg production in *A. hebraeum* is limited (see previous paragraph), it follows that in order to lay a large number of eggs, the rate of egg production must remain at or near the maximum level for many days. In other species which lay fewer eggs, the ratio of maximum daily egg production to the total number of eggs produced tends to be higher than in *A. hebraeum*, and consequently the majority of eggs are laid over a shorter period of time. As a result the numbers of eggs produced per day decrease rapidly after the initial peak. At sub-optimum temperatures, where the maximum rate of egg production is reduced, the oviposition curves in *I. hexagonus* (Arthur, 1951), *B. decoloratus* (Londt, 1973), *H. anatolicum anatolicum* (Snow & Arthur, 1966) *H. aegyptum* (Sweatman, 1968) and *R. sanguineus* (Sweatman, 1967) resemble those of *A. hebraeum* at optimum temperatures.

Sutherst (1969) reported the use of covariant analysis to compare the effects of extrinsic factors on oviposition in female ticks of different weights. Drummond & Whetstone (1970) showed, however, that covarient analysis was unnecessary if an index of conversion efficiency, i.e.

weight of eggs/weight of female tick, was used. In this investigation it was found (Table 7) that the egg production capacity or conversion efficiency of females of A. hebraeum was greatest at 26°C and decreased with either increasing or decreasing temperatures. Similar results have been obtained in respect of R. sanguineus (Sweatman, 1967) and less conclusively in B. microplus (Hitchcock, 1955). In B. decoloratus, Londt (1973) found that there was a linear increase in egg productivity with increasing temperature.

With the exception of I. ricinus (Macleod, 1935a) and I. hexagonus (Arthur, 1951) atmospheric humidity has been found to have no influence on egg production capacity in ixodid ticks. In A. hebraeum there was a definite correlation between humidity and egg production capacity at constant temperature (Table 7). As in I. ricinus and I. hexagonus the egg production capacity increased with increasing humidity.

Except at 35°C, where egg laying was directly inhibited by temperature, the egg production capacity was determined by the combined effects of temperature and relative humidity. Between 15 and 26°C the egg production capacity increased with both increasing temperature and relative humidity, and then decreases slightly between 26 and 30°C with increased temperature and decreasing relative humidity. There was no direct correlation between egg production capacity and saturation deficit. This was due to the overriding effect of temperature, as pointed out by Londt (1973). For example, at 15°C and 90% RH both the saturation deficit and the egg production capacity was low, while at 26°C and 90% RH the saturation deficit was low and the egg production capacity was high, as was the case at 26°C and 40% RH when the saturation deficit was high. It is evident from this observation that the egg production capacity was directly related to the duration of the preoviposition and oviposition periods. At low temperatures (15°C) and low relative humidities female ticks lose water over long periods of time. Consequently the egg production capacity is reduced and in very dry conditions (i.e. 40% RH) female ticks die of desiccation before any eggs are laid (4.3). As the duration of the developmental periods decrease the relative amount of water lost prior to the deposition of eggs decreases, and consequently more eggs are produced. The optimum temperatures for egg laying were 26 and 30°C. The slightly lower egg production capacity at 30°C may have resulted from the higher saturation deficits which occur at this temperature.

The similarity in the effect of humidity on the egg laying capacity of _A_. _hebraeum_ with ticks of the genus _Ixodes_, which are extremely sensitive to desiccation (Lees, 1946), arises as a result of the extremely long preoviposition and oviposition periods in _A_. _hebraeum_ (as discussed above).

4.5. Incubation period.

In previous studies (Hunter & Hooker, 1907; Graybill, 1911; Legg, 1930; Macleod, 1935a; Arthur, 1951; Hitchcock, 1955; Londt, 1973; Branagan, 1973) it has been shown that low temperatures increase the duration of the incubation period in ixodid ticks. In none of the above studies, however, was humidity found to affect the duration of the period. Both temperature (Hunter & Hooker, 1907; Graybill, 1911; Legg, 1930; Macleod, 1935a; Smith _et al_. 1946; Arthur, 1951; Hitchcock, 1955; Gothe, 1967; Londt, 1973) and humidity (Graybill, 1911; Legg, 1930; Macleod, 1935a; Smith _et al_., 1946; Arthur, 1951; Hitchcock, 1955; Lancaster & Macmillan, 1955; Sonenshine & Tigner, 1969; Londt, 1973; Branagan, 1973) have been shown to affect the hatching of eggs.

Laboratory studies.

To test the duration of the incubation period and the percent hatch of eggs in relation to temperature and saturation deficit, daily egg yields (500-1 000 eggs) were removed from ovipositing females, which were maintained in darkness at 26°C and 90% RH. The egg clusters were placed in glass tubes sealed with nylon gauze, and then maintained in each of the 15 different temperature and humidity regimes (4.2).

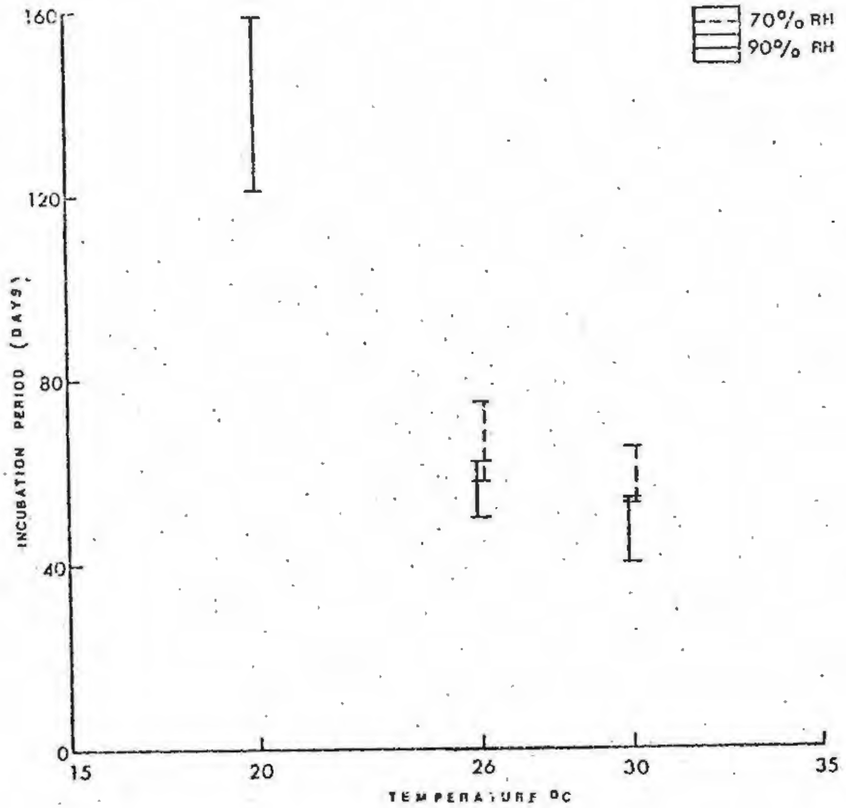

Fig. 24.

Amblyomma hebraeum. The duration of the incubation period in conditions of constant temperature and relative humidity. Vertical lines represent the period of time over which eggs hatched.

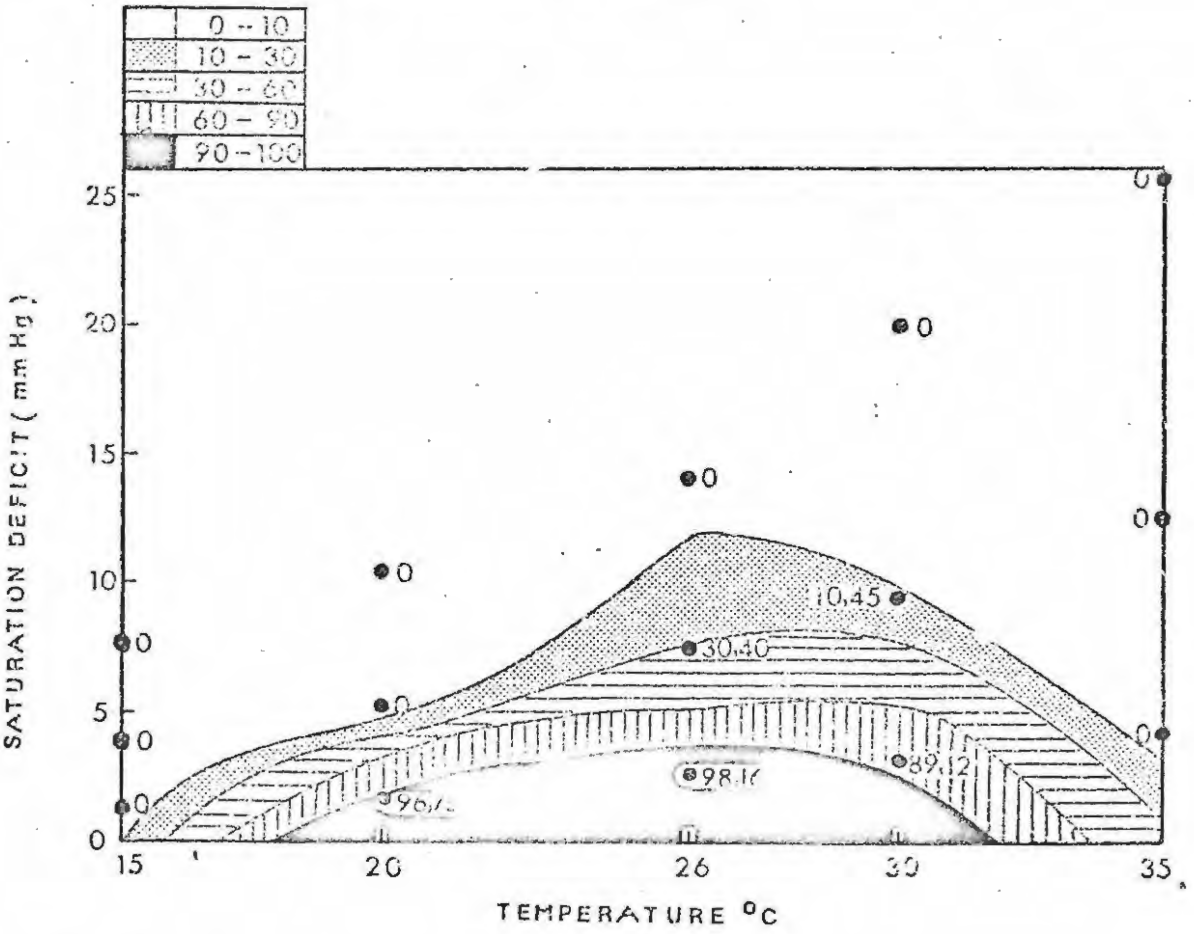

Fig. 25.

A contour diagram showing the relationships existing between temperature, saturation deficit and percent hatch of eggs of Amblyomma hebraeum.

Daily examination of eggs was undertaken to determine the duration of the incubation period. Approximately two weeks after the last hatch, larvae and unhatched eggs were placed in 70% alcohol and counted to determine the percent hatch. Data for each regime are based on five replicates. Experimental clusters of eggs were only taken during the first two weeks of the oviposition period, to eliminate any discrepancies which might arise as a result of a decline in fertility towards the end of the oviposition period (Hitchcock, 1955; Londt, 1973).

Data on the duration of the incubation period are given in Fig. 24. At 90% RH eggs only hatched in the temperature range 20-30°C. The incubation period at 20°C ranged from 121 to 159 days, at 26°C from 50 to 62 days and at 30°C from 40 to 54 days. At 70% RH, eggs only hatched in the temperature range 26-30°C. The incubation period at 26°C ranged from 58 to 76 days, and at 30°C from 53 to 65 days. These results show that the duration of the incubation period increased both at low temperatures and at low humidities.

The relationship between temperature, saturation deficit and percent hatch has been illustrated by means of a contour diagram[1] (Fig. 25). In the temperature range 20-30°C high percent hatches only occurred at low saturation deficits ($>$5 mm Hg). At saturation deficits ranging from 5 to 10 mm Hg, low percent hatches were recorded at 26 and 30°C, while eggs did not hatch at any other temperature. No eggs hatched at saturation deficits higher than 10 mm Hg.

Field studies.

On five occasions during 1973 tubes containing clusters of eggs laid by females which had completed oviposition in the laboratory (26°C and 90% RH),

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[1] The use of contour diagrams in illustrating the relationship between temperature, saturation deficit and a third variable is discussed by Londt (1973). The author points out that saturation deficit is temperature dependent and consequently multi-variant analyses can not be used in assessing such relationships.

were placed in the Stevenson's screen. In no instances did any of the eggs hatch, and within 2 to 5 weeks it became obvious that the majority of eggs had collapsed as a result of desiccation. It was therefore decided to conduct further experiments under more realistic conditions at Paardekraal Farm.

Engorged females were allowed to oviposite naturally in three habitats (open grassland, Acacia grassland and marginal riverine vegetation) in the Kowie River valley. In each habitat ticks were confined in cylindrical, gauze covered cages (diameter 15 cm), similar to those described by Semtner et al. (1973). Four engorged females were placed in each cage on 29th December, 1973. In Acacia grassland and marginal riverine vegetation it was observed that within 24 hours the ticks had buried themselves 2-3 cm under the surface of the soil. In open grassland, however, the ticks were found to be dead on the surface of the soil. This can probably be attributed to the exceptionally high ground-level temperatures (maximum 44°C) which were recorded during this period. A second batch of engorged females placed in open grassland on 10th January, 1974, successfully burrowed into the soil and layed eggs.

Unfortunately, as the ticks were buried beneath the ground, it was impossible to record the durations of the preoviposition, oviposition and incubation periods. It was possible, however, to record the approximate duration of the entire prehatch period, and the survival of engorged females and eggs. On 19th June, 1974, larvae were first observed on the gauze roof of the cage in open grassland. It was then decided to investigate the state of development of eggs in all of the cages. To do this the soil, to a depth of 10 cm, was removed from beneath each cage, placed in a plastic bag, and returned to the laboratory for examination. Two female ticks together with their respective egg masses were recovered from the cage in open grassland. An estimated 10-20% of the larvae had hatched, while the majority of eggs were in the final stages of development, i.e. contained large white spots which are indicative of an accumulation of guanine in the rectal sac of the developing larva (Londt, 1973). Four female ticks together with egg clusters were recovered from the cage in Acacia grassland. None of these eggs had hatched and one female tick was still in the process of laying. The eggs ranged in development from nearly transparent newly laid eggs to well developed eggs in which there were conspicuous white spots. No female ticks or egg clusters were recovered from the cage in marginal riverine vegetation.

Conclusions.

As in other ixodid species, the duration of the incubation period in A. hebraeum increases with decreasing temperature. Unlike other species, however, the duration of the period also increases with decreasing humidity. As in other species both temperature and humidity influence the survival of eggs. The relationship between temperature, saturation deficit and percent hatch (Fig. 25) is similar to the relationship between these variables and the egg production capacity of engorged females[1] (Table 7). In other words, as the temperature decreases the survival limits in terms of humidity also decrease, due to the increase in the length of time over which water is lost from the eggs. Londt (1973) drew similar conclusions from his studies on the survival of the eggs of B. decoloratus. Londt's conclusions were supported by the finding that, unlike larvae (Londt & Whitehead, 1972), eggs "do not have the capacity to take up water vapour to any marked degree from the atmosphere". It is therefore reasonable to assume that at low temperatures the factor limiting the survival of eggs is the limited water content of the eggs. This is supported by the observation that in eggs of A. hebraeum maintained at 15°C and 90% RH, white spots, indicative of development, were observed after 12 months incubation. By 15 months, however, all of the eggs had collapsed through desiccation and no further development was observed.

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[1] The data on egg production capacity was not illustrated by means of a contour diagram, as there were insufficient replicates in each regime to obtain realistic mean values.

At 90% RH the minimum temperature at which eggs hatched was 20°C in B. decoloratus (Londt, 1973), 16,6°C in B. microplus (Hitchcock, 1955), 15°C in I. hexagonus (Arthur, 1951) and 17-23°C in I. ricinus (Macleod, 1935a). Apart from B. decoloratus, therefore, the minimum temperatures required for egg survival in other ixodid species, are lower than those required in A. hebraeum. This is probably due to the shorter incubation periods of these species i.e. at 20°C the incubation period is approximately 32 days in I. ricinus (Macleod, 1935a), 58 days in I. hexagonus (Arthur, 1951) and 41 days in B. microplus (temperature 21,6°C) (Hitchcock, 1955), as opposed to 121-159 days in A. hebraeum. In B. decoloratus (Londt, 1973), B. microplus (Hitchcock, 1955) and I. ricinus (Macleod, 1935a), it was observed that as in A. hebraeum, hatching at low temperatures occurred only in high humidities.

Eggs of A. hebraeum maintained at 35°C showed no development, indicating the upper lethal temperature limit lay between 30 and 35°C.

In field conditions at Paardekraal Farm the prehatch period lasted approximately six months in open grassland. In Acacia grassland development was slower, no eggs having hatched within 7 months. The longer developmental period in Acacia grassland was almost certainly due to the lower temperatures which occur in this shaded habitat.

For survival, the eggs of A. hebraeum rely on the high humidity in the damp surface layers of the soil. For this reason it can be expected that under 'normal' summer conditions eggs would not survive in open grassland, where, during periods of low rainfall the surface layers of the soil become extremely dry, and in the absence of a good cover of grass the temperatures at the surface of the soil often rise above 40°C. The rainfall records in Fig. 7 show that high rainfall during late summer and autumn is an infrequent occurrence in the Eastern Cape. Consequently the results obtained during the exceptionally wet conditions of January-June, 1974 (Fig. 6), can be considered unusual. During drier conditions, as recorded in 1973 (Fig. 6) for example, it can be expected that eggs will only survive in shaded habitats, where, by comparison with open habitats, the soil temperatures will remain low and the soil humidity high.

The field results show that engorged female ticks and/or eggs did not survive in the water-logged soils of marginal riverine vegetation. This is in agreement with the findings of Sutherst (1971), that while engorged females and eggs of _B_. _microplus_ are able to withstand short periods of flooding, prolonged periods of water immersion are fatal.

4.6. Nymphal and adult premoult periods.

As with other developmental periods, the durations of the nymphal and adult premoult periods in ixodid ticks have been shown to be temperature dependent (Arthur, 1951; Macleod, 1934; Branagan, 1973). Macleod (1934) found that the durations of the nymphal and adult premoult periods in _I_. _ricinus_, increased with decreasing humidity. Branagan (1973), however, observed that differing levels of humidity exerted no discernible influence on the durations of the premoult periods in _R_. _appendiculatus_.

Laboratory studies.

To determine the durations of the nymphal and adult premoult periods, batches of 40-70 engorged larvae and 15-40 engorged nymphs were placed in each of the 15 temperature and humidity regimes (4.2) and examined daily. Tick mortalities in each regime were also recorded.

The effect of temperature on the durations of the nymphal (Fig. 26a) and adult (Fig. 26b) premoult periods, was the same as in the preoviposition, oviposition and incubation periods, where there was a sharp increase in the duration of the periods between 20 and 15°C. The minimum duration of the premoult periods occurred at 30°C, and within the limits set by humidity, moulting occurred at all temperatures within the range 15-35°C. Humidity did not exert any significant influence on the durations of the premoult periods. At all temperatures the adult premoult period was of longer duration than the nymphal premoult period; this was probably due to the delayed development of the pharate adult (as discussed in Chapter 2).

Contour diagrams of percent survival during the nymphal and adult premoult periods are given in Figs 27a and 27b respectively. During the nymphal premoult period, percent mortality increased with decreasing temperature and increasing saturation deficit. The lowest percent mortalities occurred in the temperature range 26-35°C, when saturation deficits were less than 10 mm Hg. The pattern of survival during the adult premoult period was more complex. At both high (30-35°C) and low (15-20°C) temperatures, the percent mortality increased with decreasing saturation deficit. At 15°C the percent mortality also increased at high saturation deficits. Between 20 and 35°C, mortalities of less than 20% were recorded in the saturation deficit ranges 5-25 mm Hg. Below 5 mm Hg, a mortality of less than 20% was only recorded at 26°C.

Field studies.

The durations of the nymphal and adult premoult periods in the Stevenson's screen were recorded during late summer and winter conditions. The results (Table 8) show that the number of hour degrees required for moulting was larger in winter than in summer conditions. Mortality during the adult premoult period was also higher in winter than in summer conditions.

Conclusions.

The durations of the nymphal and adult premoult periods in A. hebraeum are considerably longer than in other studied ixodid species. At 15°C, for example, the duration of the nymphal premoult period in I.hexagonus is approximately 60 days and about half this length in D. variabilis (Arthur, 1951), as opposed to approximately 185 days in A. hebraeum.

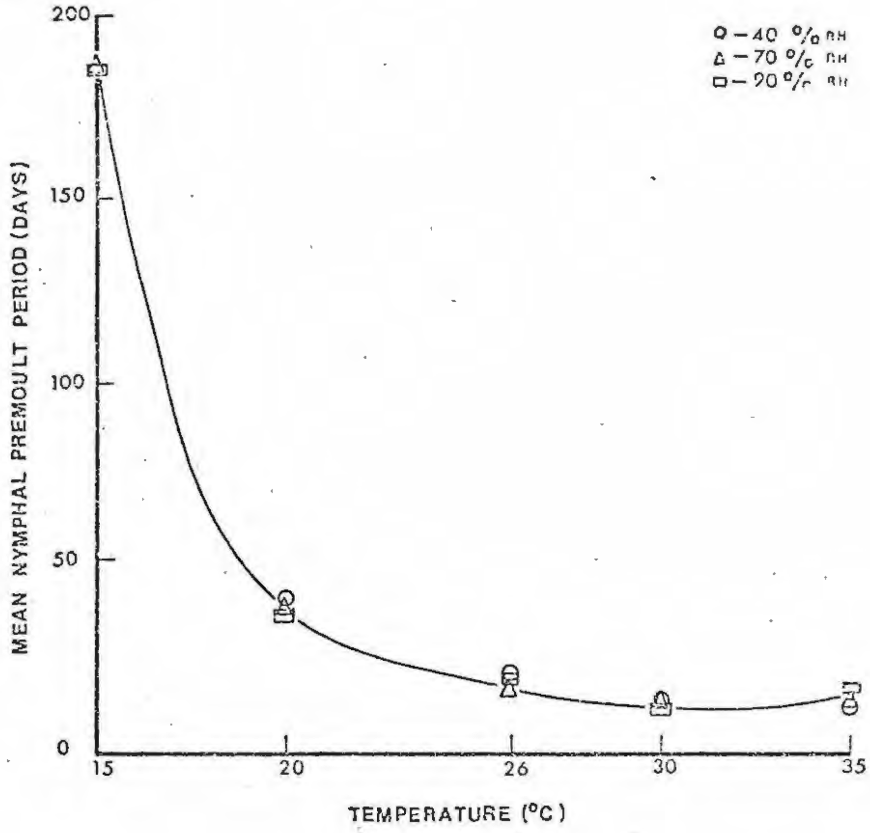
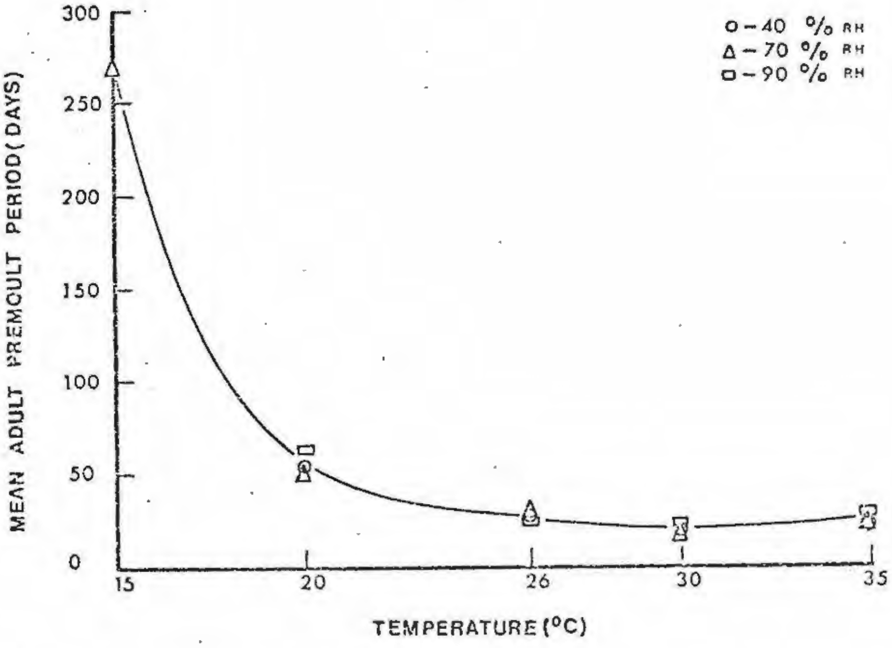


Fig. 26.

(a) Amblyomma hebraeum. The duration of the nymphal premoult period in conditions of constant temperature and relative humidity.



(b) Amblyomma hebraeum. The duration of the adult premoult period in conditions of constant temperature and relative humidity.

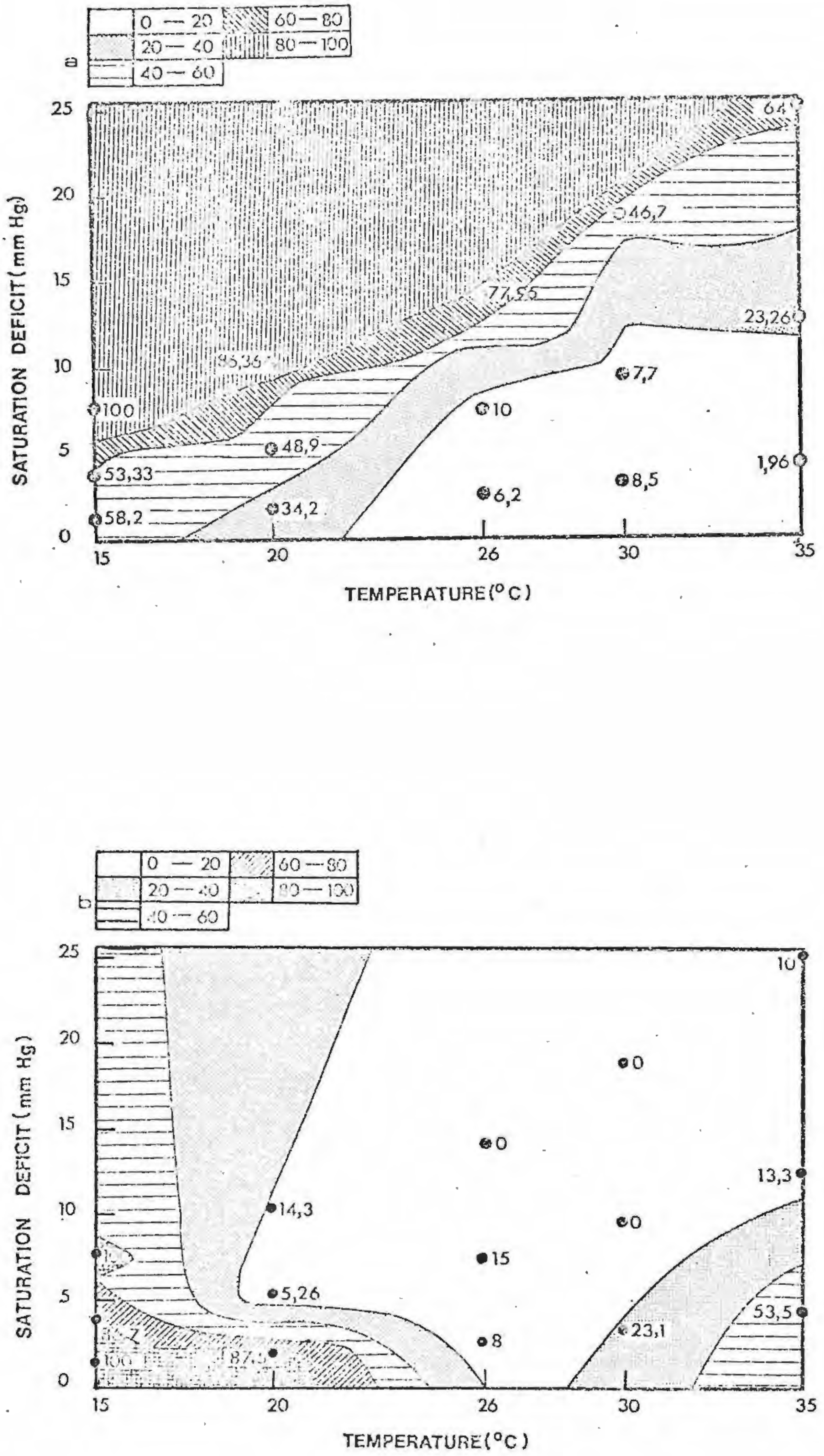


Fig. 27.

Amblyomma hebraeum. Contour diagrams showing the relationships existing between temperature, saturation deficit and percent mortality during (a) the nymphal premoult period and (b) the adult premoult period.

Table 8.

The duration of the premoult periods of Amblyomma hebraeum in fluctuating conditions in a Stevenson's screen. The total numbers of hour degrees above 15°C are given for the mean premoult periods.

Date of detachment of engorged ticks	Mean premoult period (days)	Percent mortality	Total No. hour degrees
Nymphal premoult period			
27/3/73	61,5	43,8	14 851
17/7/73	93,5	50,0	18 988
Adult premoult period			
7/2/73	56,5	23,8	15 614
10/7/73	114,0	57,1	21 864

The pattern of mortality during the nymphal premoult period was similar to that during the incubation period, i.e. at constant temperature mortality increased with increasing saturation deficit, and mortality increased with decreasing temperature. As in the egg stage (4.5) the latter is thought to have resulted from the longer period of time over which water was lost at low temperatures than at high temperatures. Unlike egg development, the development of nymphs and adults occurred successfully at 35°C. There was a significant change in the pattern of survival from the nymphal premoult to the adult premoult period. At temperatures above and below 26°C, the ability of engorged nymphs to survive in humid conditions decreased rapidly. The highest levels of survival occurred in warm dry conditions. At 15°C, 100% mortality occurred in both humid and dry conditions. Mortality in dry conditions is thought to have been caused by desiccation, as in the incubation and nymphal premoult periods. The reason for the mortality of ticks in humid conditions at 15°C and other temperatures is not understood.

4.7. Survival of unfed ticks.

There are numerous reports in the literature on the longevity of ixodid ticks in laboratory and field conditions (reviews by Knulle, 1966 and Balashov, 1961). With the exception of the work of Macleod (1935b) and Feldman-Muhsam (1947), however, there are no comprehensive comparative studies on the longevity of different developmental stages of ixodid tick species under various conditions of controlled temperature and relative humidity. Feldman-Muhsam (1947) considered that relative humidity was more important in the survival of larvae and nymphs of Hyalomma savignyi Gerv. than temperature, but did not consider her results in terms of saturation deficit; a more realistic measure of the "drying power" of the air. Macleod (1935b) found that in I. ricinus longevity was a function of saturation deficit, only within a limited temperature range.

Laboratory studies.

Newly emerged ticks, obtained from the laboratory culture, were placed in glass tubes and examined at weekly intervals until a mortality of 50% was recorded. In each set of conditions (4.2) this was replicated 5 times with larval ticks (100-300 per tube) and 3 times with nymphal (30-50 per tube) and adult ticks (20 per tube). The lower numbers of nymphs and adults were necessitated by the lower numbers of these stages which were available.

Contour diagrams of the mean longevity (to 50% mortality) of larvae, nymphs and adult ticks, in relation to temperature and saturation deficit, are given in Figs 28a, 28b and 28c respectively. The results in Fig. 28a show that larvae were extremely sensitive to desiccation. At saturation deficits greater than approximately 11 mm Hg, larvae did not survive for longer than one week. The longest survival periods occurred in the lowest saturation deficits, and longevity decreased rapidly as saturation deficit increased. The near parallel distribution of the lines of equal survival, indicate that within the range tested, temperature had little influence on the longevity of larvae. There may, however, have been a slight tendency for longevity to decrease at low temperatures (15°C).

Unlike the previous stage, the longevity of unfed nymphs (Fig. 28b) was clearly influenced by temperature. The longevity of nymphs was greatest in low to moderate saturation deficits (2-7 mm Hg) in cool conditions (15-26°C). At temperatures above 26°C, longevity decreased rapidly with increasing temperature. The longevity of adult ticks (Fig. 28c) was also influenced by temperature, but unlike nymphs, adults survived for the longest periods at a high temperature (30°C). At 30°C the maximum longevity of adult ticks occurred at a saturation deficit of 9,5 mm Hg; from this point longevity decreased with both increasing and decreasing temperature and saturation deficit.

Field studies.

Tubes of newly emerged ticks (as described above) were placed in the Stevenson's screen, and examined at weekly intervals until a mortality of 50% was recorded.

Table 9.

The mean longevity in weeks of unfed larvae, nymphs and adults of _Amblyomma hebraeum_ in fluctuating conditions in a Stevenson's screen.

Date of introduction into screen	Mean longevity (weeks)
Larvae	
21/2/73 1/8/73	21,8 21,8
Nymphs	
31/1/73 19/9/73	63,0 +56 *
Adults	
14/2/73 27/8/73	32,0 46,0

* Observations on the ticks were terminated at the time of writing.

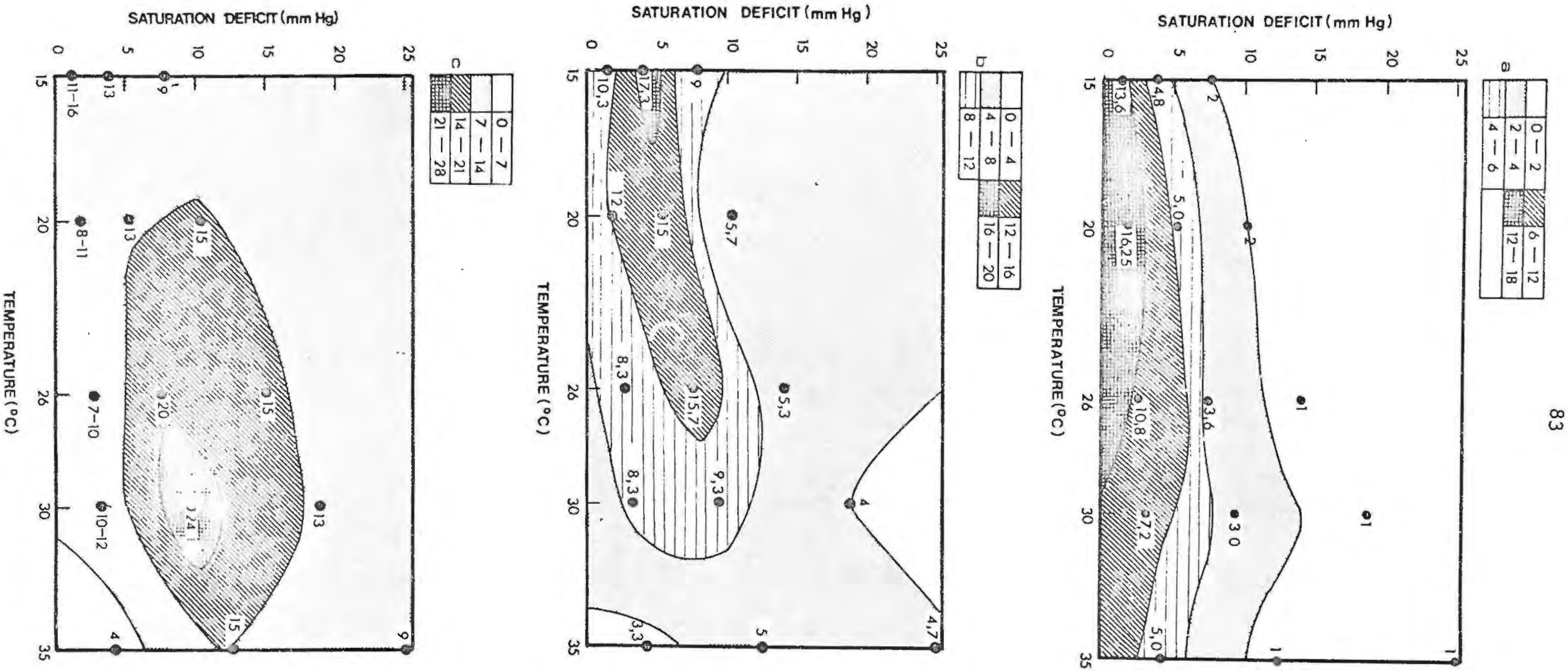


Fig. 28.

Amblyomma hebraeum. Contour diagrams showing the relationships existing between temperature, saturation deficit and the survival of (a) unfed larvae (b) unfed nymphs and (c) unfed adult ticks. The data points (●) represent the duration of survival, in weeks, to 50% mortality.

The results (Table 9) show that for all developmental stages, longevity in natural fluctuating conditions was greater than the maximum longevity in controlled laboratory conditions (Fig. 28). There was no difference in the longevity of larvae in spring/summer and autumn/winter conditions. Batches of nymphs placed in the Stevenson's screen in January and September, 1973, both survived for well over a year. The longevity of adult ticks, placed in the Stevenson's screen towards the end of summer, was considerably shorter than the longevity of adults placed in the screen in spring.

Conclusions.

The results in Fig. 28 show that saturation deficit is a more meaningful parameter than relative humidity in the evaluation of tick survival patterns. It is seen in Fig. 28a that at constant relative humidity the decrease in the longevity of larvae at high temperature, was not a direct temperature effect, but related to increased saturation deficit. The pattern of survival in larvae of _A_. _hebraeum_, in which temperature had no significant influence on longevity, is similar to the patterns of survival in larvae and nymphs of _H_. _savignyi_ (Feldman-Muhsam, 1947). In nymphs and adults of _A_. _hebraeum_, however, temperature had a considerable influence on longevity; this is probably of considerable ecological importance and is discussed in section 4.8.

It is clear from a comparison of the laboratory and field data, that unfed ticks are better equipped to survive in naturally fluctuating conditions than in controlled laboratory conditions. It has been shown by a number of authors (Lees, 1946, 1947, 1948; Browning, 1954; Knulle, 1966; Hafez _et_ _al_., 1971; McEnroe, 1971; Sauer & Hair, 1971; Londt & Whitehead, 1972) that above the 'equilibrium humidity', ticks are able to absorb moisture from the atmosphere. Consequently water lost during dry midday conditions can be replaced during the more humid conditions which normally occur at night. The larvae of _B_. _microplus_ (Wilkinson, 1953; Schuntner & Tatchell, 1970), _B_. _decoloratus_, _A_. _hebraeum_, _R_. _evertsi_ and R. appendiculatus (Londt & Whitehead, 1972), have also been shown to drink free water. Under favourable climatic conditions it is therefore probable that one of the factors most likely to limit the longevity of unfed ticks is the quantity of stored nutrients. Cook (1973) working on Ornithodoros concanensis (Cooley & Kohls) showed that food reserves were depleted more rapidly in ticks which were subjected to repeated desiccation and rehydration, than in ticks which were maintained in constantly high humidities, above the equilibrium humidity. On this basis the author suggested that ticks which are maintained in constant high humidities should survive for longer periods, than ticks maintained in fluctuating conditions. In A. hebraeum the opposite result was observed, for which, with our available knowledge, no adequate explanation can be given.

4.8. Discussion

By comparison with other ixodid species (see earlier) the developmental periods of A. hebraeum are exceptionally long, particularly at low temperatures. With the exception of the nymphal and adult moulting, normal development did not occur at 35°C. In the temperature range 15-30°C, the developmental periods of all stages[1] were shortest at 30°C, and then increased in length exponentially with decreasing temperature (Table 10). At 30 and 26°C the sum of the mean developmental periods was in the region of 4-5 months. At 20°C the figure was approximately 11 months, and at 15°C (excluding the incubation period) was approximately 25 months.

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[1] The mean oviposition period was slightly longer at 26°C than at 30°C. This was, however, caused by factors other than temperature (4.4).

Table 10.

The mean developmental periods of <u>Amblyomma</u> <u>hebraeum</u> at different temperatures, in a relative humidity of 90%.

Developmental period	15°C	20°C	26°C	30°C	35°C
Preoviposition	123,7	27,7	11,0	9,3	13,0
Oviposition	190,0	61,0	34,3	36,3	12,0
Egg incubation'	-	140,0	56,0	47,0	-
Nymphal premoult	185,5	36,8	19,5	14,1	17,3
Adult premoult	*268,0	63,5	23,4	19,7	23,1
Totals (days)	766,7	329,0	144,2	126,4	65,4

' Median values.

- Eggs did not hatch.

* Data obtained in 70% RH.

Londt (1973) pointed out that in assessing the effects of temperature and humidity on any stage in the life cycle of a tick, it is important to distinguish between tolerance ranges and preferenda. With regard to the effect of temperature on the developing stages of <u>A</u>. <u>hebraeum</u>, it has been shown that both the tolerance ranges and preferenda change throughout the life cycle. At 35°C both oviposition and egg development were inhibited, while moulting of larvae and nymphs occurred normally. The optimum temperatures for oviposition and egg development were 20-30°C, and for larval and nymphal moulting, 26-35°C and 20-35°C respectively. Below the optimum temperature there was an increase in mortality in eggs and engorged larvae and nymphs, and a decline in the egg production capacity of female ticks. These were not direct temperature effects however, but occurred as a result of prolongation of the developmental periods, i.e. the ticks were subjected to desiccation for longer periods. The results of Lees (1946), Sauer and Hair (1971) and Londt (1973) show that developing stages of ixodid ticks, i.e. eggs, engorged larvae, engorged nymphs and engorged females, unlike the active unfed stages, do not have the ability to take up moisture from the atmosphere.

Consequently, even in conditions of fairly low saturation deficit there is a gradual depletion in the body water-store. In this investigation it was shown that as the size increases, i.e. from egg to engorged larva, the ability to survive in dry conditions at high temperatures or in humid conditions at low temperatures increases. This is probably due to the larger water-store and smaller surface area/volume ratio (i.e. proportionately smaller area over which water can be lost) in the larger stages.

As a result of the exceptionally long developmental periods of A. hebraeum at low temperatures, and the concomitant humidity effects, it can be concluded that low temperatures are important in limiting the distribution of the species. The longest developmental periods occur in the egg stage. This fact, together with the small size of eggs, makes the egg stage the most susceptible to desiccation of all developmental stages. Suitable microclimatic conditions for the survival of eggs are therefore necessary for the establishment of A. hebraeum. The required microclimatic conditions are found in the humid surface layers of the soil in well drained, shaded habitats. Unshaded habitats in which high soil temperatures and dry conditions occur, are generally unsuitable for egg development. To ensure the survival of eggs, the activity peak of female ticks occurs in midsummer, when conditions are most likely to favour oviposition and egg development (3.12). Engorged larvae and nymphs are able to develop over a considerably wider range of temperature and saturation deficit, than are eggs. As a result these stages should have less restricted habitat requirements than eggs, and should be able to moult during the dry seasons of the year. Engorged nymphs in fact have a preference for dry conditions, and mortality increases in humid conditions.

Macleod (1934) showed that the development of I. ricinus did not follow the 'thermal-constant theory', which is based on the assumption that each hour degree has a fixed developmental value. Likewise the 'thermal-constant theory' does not apply in respect of A. hebraeum. It is seen in Fig. 29 that during the nymphal and adult premoult periods, the number of hour degrees required for moulting was lowest at 26 and 30°C, and increased at higher and lower temperatures. Between 20 and 15°C there was a sharp decrease in the efficiency of heat utilization, i.e. a marked increase in the number of hour degree required for moulting. It is a result of this decrease in efficiency of heat utilization, that the durations of the developmental periods increase exponentially with decreasing temperature. Were the 'thermal-constant theory' to apply over the entire temperature range, the development curve would be a hyperbola. The laboratory data on moulting are supported by the field data (Table 8), which show that the number of hour degrees required for moulting were considerably larger in winter than in summer. In order to predict the duration of development in fluctuating temperatures, it would therefore be necessary to calculate the developmental value for hour degrees at each temperature.

The unfed stages of A. hebraeum are adapted to survive for long periods in conditions of naturally fluctuating temperature and saturation deficit. Nymphs survived for approximately three times as long as larvae, and nearly twice as long as adults (Table 9). The ability of nymphs and adults to survive for long periods is of ecological importance, as these ticks may spend up to 10 months in a state of quiescence (3.10; 3.11). Larvae, on the other hand, become active soon after hatching, and consequently it is less important to survive for long periods. In the sub-tropical summer rainfall areas, from where A. hebraeum originates (3.1), nymphs are active in winter and adults in summer (Baker & Ducasse, 1968). For this reason the preferred temperatures for nymphal survival are lower than the preferred temperatures for adult survival. Unlike larvae, nymphs and adults are adapted to survive in fairly dry conditions, and longevity decreases in conditions of constant low saturation deficit.

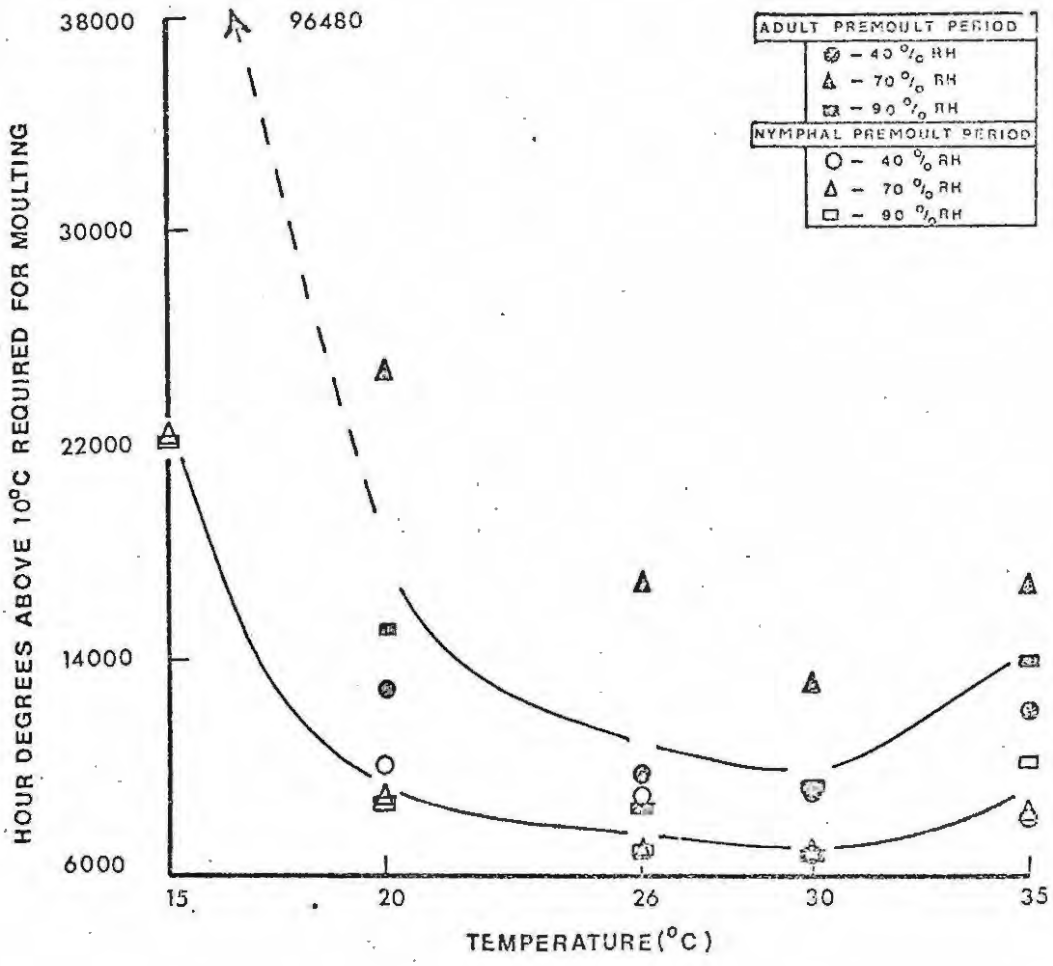

Fig. 29.

The relationship between temperature and the number of hour degrees above 10°C required for moulting during the nymphal and adult premoult periods.

SECTION THREE

THE PARASITIC STAGES OF *AMBLYOMMA HEBRAEUM* KOCH

5. Host survey.

5.1. Introduction.

The factors which influence the distribution and seasonal activity of the non-parasitic stages of A. hebraeum have been discussed in Chapters 3 and 4. This chapter deals with the influences of host specificity and host availability on the distribution and abundance of the species. Lists of hosts on which A. hebraeum has been found are given by Zumpt (1958), Theiler (1962) and Baker and Keep (1970). The findings of these authors show that all stages of the life cycle can occur on a wide range of hosts, including reptiles, birds and mammals. Large mammals, mainly artiodactyls, provide the greatest number of hosts of adult ticks. The range of hosts of immature ticks is somewhat wider, including numerous species of large and small mammals and birds, and one reptile species. Unfortunately the records of Theiler (1962) and Baker and Keep (1970) do not refer to the quantitative occurrence of the ticks on any of the host species. This information is vital from an ecological point of view, as it is necessary to establish the relative importance of each host species. It is only on consideration of the distributions of the major hosts of A. hebraeum, within the climatic and vegetation regions in which the non-parasitic stages of the tick can survive (Chapter 3), that an explanation can be given for the present distribution of A. hebraeum and the influence of domestic stock on its abundance and spread.

In this chapter data are given on the quantitative seasonal occurrence of ixodid ticks on indigenous hosts at Paardekraal Farm. Data on the occurrence of A. hebraeum on domestic hosts at Paardekraal Farm, and on indigenous hosts at other localities in the Eastern Cape are also given. The data in respect of species other than A. hebraeum are discussed in Chapter 7.

5.2. Collection of hosts.

Hosts collected at Paardekraal Farm were captured, shot or in the case of snakes, killed with a stick. Tortoises were captured by hand, small rodents were captured in 'Sherman' traps and small carnivores in 'spring-door' cage traps. Other hosts were shot, either with an air-rifle or fire-arm, depending upon the size of the host. With the exception of tortoises, the captured hosts were killed in the laboratory before being examined for ticks. Where possible all hosts which had been killed in the field were also examined for ticks in the laboratory. Small mammals, birds and reptiles were placed in sealed plastic bags immediately after collection, to prevent the escape of ticks. In the case of larger hosts (Bushbuck, Duiker, Lynx and Jackal) a preliminary examination was made in the field. If the animals were lightly infested the ticks were removed in the field; if the animals were heavily infested the skins were removed and placed in plastic bags for examination in the laboratory. The sampling of hosts was not entirely random due to the nature of the sampling methods. An attempt was, however, made to collect representatives of the species which occur most commonly at Paardekraal Farm.

Samples of ticks collected from hosts at localities other than Paardekraal Farm were brought in to the Tick Research Unit by farmers and Nature Conservation officials.

5.3. Host specificity.

Quantitative records of the occurrence of <u>A</u>. <u>hebraeum</u> on hosts collected at Paardekraal Farm are given in Table 11. The records show that adult ticks, unlike larvae and nymphs, were not found on any indigenous hosts. Significant numbers of nymphs ($>$ 5 ticks per host) were recorded on Mountain tortoises (Chelonia) and Duiker (Artiodactyla). Light infestations of nymphs ($<$ 5 ticks per host) were recorded on species belonging to the following orders: Galliformes, Ciconiiformes, Coraciiformes, Passeriformes, Artiodactyla (Bushbuck) and Carnivora. Significant numbers of larvae were found on Guineafowl (Galliformes), Duiker (Artiodactyla) and Lynx (Carnivora). Light infestations of larvae were found on species belonging to the following orders: Ciconiiformes, Columbiformes, Lagomorpha and Carnivora (Jackal). Large numbers of both adults and nymphs of A. hebraeum were recorded on cattle at Paardekraal Farm (Chapter 3; Figs 14, 15 and 16). No quantitative records were obtained on the occurrence of larvae on cattle, but observations made in the early summer months of 1973 indicated that the numbers were high. On one occasion over 50 engorged and semi-engorged larvae were counted on the head of a steer. The numbers of all stages of the life cycle which occurred on sheep and goats were lower. On 10 Merino sheep examined on 11th September, 1973, only 1 nymph of A. hebraeum was found, while on 10 Angora goats examined on 26th October, 1973 a total of only 4 nymphs and 6 larvae were found. According to Mr F.D. Ford, adults do occur on sheep and goats, but only rarely. The results in Table 12 show that larvae and nymphs of A. hebraeum also occur in low numbers on domestic dogs.

The occurrence of A. hebraeum on indigenous hosts collected at localities other than Paardekraal Farm is given in Table 13. The records are significant in that adults were found on Kudu on a number of farms, and with the exception of one record from an Ant-bear, these were the only hosts on which adults occurred. In the Thomas Bains Nature Reserve adults were found on Zebra and Gemsbok. These species do not normally occur in the Eastern Cape (Roberts, 1951). Nevertheless the records confirm the trends, apparent in the host lists of Zumpt (1958), Theiler (1962) and Baker and Keep (1970), that infestation by adults is restricted by host size rather than any taxonomic grouping.

5.4. Host and habitat relationships.

The occurrence of larvae and nymphs of A. hebraeum on hosts at Paardekraal Farm (Table 11) was not restricted to any taxonomic or size group of hosts. The determining factor lay rather in the habitat preferences and feeding habits of the hosts in relation to the occurrence of ticks (3.7). Nymphs were not found on aquatic or carnivorous reptiles, but occurred in significant numbers on the herbivorous Mountain tortoises, which were frequently observed feeding in Acacia grassland. Among birds, larvae and nymphs did not occur on tree dwelling species, but were found on ground feeders i.e. Crowned guineafowl (Galliformes), Hadeda ibis (Ciconiiformes), Cape turtle dove (Columbiformes), Cape glossy starling and Cape raven (Passeriformes). Among mammals, burrow dwelling rodents and small carnivores, primates and Dassies (Hyracoidea) which inhabit barren, rocky areas, were not infested. Larvae and/or nymphs were found on Hares (Lagomorpha), Duiker and Bushbuck (Artiodactyla) and the larger carnivores (Lynx and Black-backed jackal). These animals are likely to have encountered the ticks while grazing (Lagomorpha and Artiodactyla) or hunting (Carnivora). The heaviest infestations occurred on Duiker, which are known to browse on low shrubs in grassland habitats (Wilson, 1966).

5.5. Seasonal occurrence.

The seasonal occurrence of larvae and nymphs of A. hebraeum on indigenous hosts collected at Paardekraal Farm (Table 11) confirms the results of Chapter 3 (3.8-9). Both stages were recorded on hosts between May and January. In the case of nymphs, the comprehensive records from Mountain tortoises (host Nos 1-10) and Duiker (host Nos 103-111) indicated a clear peak of activity in September/October.

5.6. Discussion.

The restriction of adults of A. hebraeum to large mammals appears to be primarily a function of the size of the host, this is similar to observations made by Milne (1948/9) in respect of I. ricinus. This author could offer no explanation for the scarcity of adult ticks on small hosts, having shown that self-deticking by small hosts was only of minor importance.

Similarly no explanation can be offered for the absence of A. hebraeum from small hosts, in particular the smaller artiodactyl species. The presence of adults on Kudu (Tragelaphus strepsiceros) but absence from Bushbuck (Tragelaphus scriptus) presents the most notable enigma.

Milne (1948/9) found that in general, small hosts had light infestations of all stages of the life cycle of I. ricinus, and large hosts had heavy infestations. The explanation given was that animals which cover the most ground (in contact with the appropriate vegetation) will become the most heavily infested. Hence, in small animals the small body size and generally short distances travelled in search of food etc. result in lower infestations than in larger more mobile animals. Exceptions to the 'size rule' were found to be hosts which live in specialized habitats i.e. moles, and do not normally come into contact with the appropriate vegetation. Similar trends in respect of the immature stages of A. hebraeum were observed at Paardekraal Farm, where heaviest infestations were recorded on cattle, followed by Duiker, Mountain tortoise, Lynx, Black-backed jackal, Crowned guineafowl, Hadeda ibis, sheep and goats. The incidence and number of ticks on small mammals and birds was considerably lower. In addition to host size, 'contact with the appropriate vegetation' is an important factor in the Eastern Cape (5.4), due to the heterogeneous nature of the vegetation.

It is impossible on the basis of the available data, to give an accurate assessment of the relative importance of indigenous and domestic hosts in the survival and abundance of A. hebraeum on farms in the Eastern Cape. It is clear, however, that Kudu are the only commonly occurring indigenous animals which act as hosts to adult ticks. As Kudu only occur in large numbers in the dense bush in the valleys of the major rivers, and in certain coastal forest regions of the Eastern Cape Province (Greig, personal communication), it can be concluded that over the greater part of the Province, the existence of A. hebraeum is linked with the presence of cattle. On farms where Kudu occur, these animals are normally considerably outnumbered by cattle, and from observations made by farmers, it appears that cattle become more heavily infested with adults than is the case with Kudu. The conclusion drawn from these observations is that, with the exception of a few farms (mainly in the Fish River valley) where Kudu are particularly abundant, this host is only of minor importance in maintaining large populations of A. hebraeum.

The results from Paardekraal Farm (Table 11) show that, with the exception of Duiker and possibly Bushbuck (which were not sampled during the months of tick activity), the numbers of nymphs found on indigenous hosts were considerably lower than on cattle. Although no data are available on the density of Duiker and Bushbuck on farms in the Eastern Cape, it seems unlikely that the numbers of these antelope ever approach or exceed the numbers of domestic stock. Indeed observations made on the density of unfed nymphs in spared camps at Paardekraal Farm (3.10) showed that indigenous animals were not the main hosts for nymphs of A. hebraeum. It was only under conditions of high density stocking with cattle that the majority of unfed nymphs obtained hosts. Although similar data are not available for larvae, the results of the host survey (Table 11) indicate that larvae have similar host requirements to those of nymphs, and are therefore also likely to be primarily parasites of cattle.

Prior to human settlement, A. hebraeum was absent from the Eastern Cape Province (3.1), despite the fact that the climate and vegetation are suited to the survival of the tick (Chapter 3). The limiting factor must therefore have been a lack of suitable hosts, particularly for the adult stage. It is well known that in the early nineteenth century the diversity of large mammal species in the Eastern Cape bore little comparison with the rich fauna of the sub-tropical grass and bushveld of the eastern Transvaal, from where A. hebraeum has spread. The records of an early inhabitant of the Eastern Cape Province (Black, 1901) show, however, that

Cape buffalo (*Syncerus caffer*) and Kudu, both of which are hosts of adults of *A. hebraeum* (Theiler, 1962), occurred in the dense bush of the river valleys. Other likely hosts of adult ticks which are known to have occurred in the Eastern Cape are Black wildebeest (*Connochaetes gnou*) and Red hartebeest (*Alcelaphus buselaphus*)(Hewitt, 1931). Although hosts for adult ticks were available, it is possible that host migrations or a low density of hosts in the environment (8.2) prevented the establishment of *A. hebraeum*. It is also conceivable that *A. hebraeum* was present in the Eastern Cape prior to the extensive hunting which occurred in the area in the late eighteenth and early nineteenth century, but disappeared after the decimation of the larger game species and then reappeared when early settlers introduced domestic stock into the area. Migratory birds are clearly important in the transportation of the immature stages of *A. hebraeum* (Table 11). Whether or not the tick becomes established in areas to which the immature ticks are transported, will depend on the climate, vegetation and availability of hosts.

Table 11.

The occurrence of ixodid ticks on indigenous hosts collected on Paardekraal Farm.

Species	Common name	Date	Host No.	Infestation
CHELONIA				
Geochelone pardalis ^{x}	Mountain tortoise	6/4/73	1	A. marmoreum ♂3: ♀1: N3: L27
		21/9/73	2	A. marmoreum ♂36: ♀7: N244: L48 A. hebraeum N14
		30/9/73	3	A. marmoreum ♂16: ♀7: N25: L2 A. hebraeum N3
		3/10/73	4	A. marmoreum ♂32: ♀3: N12: L16 A. hebraeum N2
		18/10/73	5	A. marmoreum ♂28: ♀5: N117 A. hebraeum N1
		23/11/73	6	A. marmoreum ♂63: ♀26: N67
		10/1/74	7	A. marmoreum ♂38: ♀3: N4
		15/2/74	8	A. marmoreum ♂15: ♀3: N1: L3
		15/3/74	9	A. marmoreum ♂71: ♀5: N1: L25
		19/4/74	10	A. marmoreum ♂52: ♀6: N8: L521
Pelomedusa subrufa ^{x}	Water turtle	31/10/73	11	-

Table 11 continued.

SQUAMATA				
Bitis arietans	Puff adder	22/3/73	12	*A. marmoreum* ♂5
Dispholidus typhus	Boomslang	7/12/73	13	*A. marmoreum* N24
Psammophis crucifer [x]	Cross-marked snake	18/1/74	14	-
		14/5/74	15	-
Varanus albigularis	Rock leguvaan	29/11/73	16	*A. marmoreum* ♂1: ♀1: N16 *A. exornatum* ♂19: ♀4: N4: L2
GALLIFORMES				
Numida meleagris	Crowned guinea-fowl	30/8/73	17	*A. hebraeum* L8 *H. marginatum rufipes* L3
		1/9/73	18	*A. hebraeum* N1: L8 *A. marmoreum* L2 *H. silacea* N4
		7/5/74	19	*A. hebraeum* N1 *A. marmoreum* L2
Pternistis afer	Red-necked frankolin	19/10/73	20	-
CICONIIFORMES				
Hagedashia hagedash	Hadeda ibis	23/7/73	21	*A. marmoreum* N1
		7/9/73	22	*A. hebraeum* N1: L2 *H. silacea* N22: L17

Table 11 continued.

CHARADRIIFORMES				
Stephanibyx coronatus	Crowned plover	1/9/73	23	-
ANSERIFORMES				
	Egyptian goose	20/5/74	24	-
COLUMBIFORMES				
Turtur chalcospilos	Emerald-spotted wood dove	27/4/73	25	-
		30/9/73	26	-
		20/1/74	27	-
Streptopelia capicola	Cape turtle dove	12/7/73	28	-
		27/11/73	29	-
		30/11/73	30	-
		30/11/73	31	-
		13/12/73	32	-
		13/12/73	33	A. hebraeum L1
		15/3/74	34	A. marmoreum L1
		12/4/74	35	-
		19/4/74	36	-
COLIIFORMES				
Colius striatus	Speckled mousebird	8/6/73	37	-
		1/9/73	38	-
Urocolius indicus	Red-faced mousebird	10/12/73	39	-
		13/12/73	40	-
CORACIIFORMES				
Lophoceros flavirostris	Crowned hornbill	11/10/73	41	A. marmoreum N1
PICIFORMES				
Dendropicos fuscescens	Cardinal woodpecker	8/6/73	42	-
Campethera notata	Knysna woodpecker	11/10/73	43	-

Table 11 continued.

PASSERIFORMES				
Zosterops pallidus	Cape white-eye	23/3/73	44	-
Andropadus importunus	Sombre bulbul	13/4/73	45	-
		20/7/73	46	-
		27/7/73	47	-
		11/10/73	48	-
		9/11/73	49	-
		13/12/73	50	-
Pycnonotus barbatus	Black-eyed bulbul	13/4/73	51	-
		20/4/73	52	*H. silacea* L1
		13/12/73	53	-
Lamprocolius nitens	Cape glossy starling	1/6/73	54	*H. marginatum rufipes* N1
		12/7/73	55	*H. marginatum rufipes* L3
		12/7/73	56	*A. hebraeum* N1
		9/8/73	57	-
		9/8/73	58	-
		6/9/73	59	*H. silacea* N1
		11/10/73	60	-
		11/10/73	61	-
		31/10/73	62	-
		1/11/73	63	-
		9/11/73	64	-
		30/11/73	65	-
		15/3/74	66	-
		15/5/74	67	*H. marginatum rufipes* N1
Onychognathus morio	Red-winged starling	28/11/74	68	-
Symplectes bicolor	Forest weaver	20/7/73	69	-
		8/9/73	70	-

Table 11 continued.

Arthus richardi	Richards pipit	3/9/73	71	-
Melaenoris pammelaina	Black flycatcher	8/9/73	72	-
Dryoscopus cubla	Puff-backed shrike	14/9/73	73	-
Apalis flavida	Yellow breasted apalis	28/9/73	74	-
Emberiza flaviventris	Golden breasted bunting	28/9/73	75	-
		12/10/73	76	A. marmoreum L1
		13/12/73	77	-
Turdus olivaceus	Cape thrush	30/9/74	78	-
Serinus scotops	Forest canary	3/10/73	79	-
Serinus Mozambicus	Yellow-eyed canary	13/2/73	80	-
		19/4/74	81	-
Dicrurus adsimilis	Fork-tailed drongo	15/11/73	82	-
		15/2/74	83	-
Corvultur albicollis	Cape raven	6/12/73	84	H. silacea N2 Haemaphysalis sp. ♂24: ♀32: N84: L178 A. hebraeum N1
Cossypha caffra	Cape robbin	10/12/73	85	-
Mirafra africana	Rufous-naped lark	15/3/74	86	H. marginatum rufipes N1 A. marmoreum L3
		10/5/74	87	H. marginatum rufipes N6: L1 H. silacea N2 A. marmoreum L3

Table 11 continued.

RODENTIA				
Praomys + (mastomys) natalensis	Multimammate mouse	20/7/73	88	-
		10/8/73	89	-
Aethomys + namaquensis	Namaqua rock mouse	3/8/73	90	H. silacea L3 Rhipicephalus sp. * L8 R. simus * N2
		21/9/73	91	-
Otomys + irroratus	Vlei rat	3/8/73	92	Rhipicephalus sp. * L8 R. simus * N1
		22/8/73	93	-
		22/8/73	94	-
Pedetes cafer	Spring hare	3/9/73	95	-
LAGOMORPHA				
Lepus sp.	Hare	9/5/73	96	H. marginatum rufipes * N181: L56 R. oculatus * N5: L174
		1/9/73	97	R. evertsi N95: L8
		16/10/73	98	R. oculatus * ♂4: ♀1: N19
		28/11/73	99	R. evertsi N12 R. oculatus ♂2
		7/5/74	100	H. marginatum rufipes N6: L2 H. silacea N5 R. oculatus N9: L1909 A. hebraeum L2

Table 11 continued.

				A. marmoreum L89
HYRACOIDEA				
Procavia capensis	Rock dassie	7/9/73	101	-
		19/9/73	102	*A. marmoreum* N2
ARTIODACTYLA				
Sylvicapra grimmia	Duiker	18/5/73	103	*H. silacea* ♂1: N47: L55 *H. marginatum rufipes* L2 *R. evertsi* N3
		7/9/73	104	*A. hebraeum* N32: L8 *H. silacea* ♂8: ♀2: N141: L8
		16/10/73	105	*A. hebraeum* N15 *H. silacea* ♂30: N437: L171
		15/12/73	106	*H. silacea* N1 *R. evertsi* N4: L47
		15/12/73	107	*A. hebraeum* N1 *H. silacea* N1
		21/5/74	108	*H. silacea* ♂13: ♀1: N300: L1826 *A. marmoreum* L50
		21/5/74	109	*H. silacea* ♂10: N593: L471 *I. pilosus* L1

Table 11 continued.

		21/5/74	110	H. silacea ♂34: ♀2: N899: L457 A. marmoreum L6 I. pilosus N1 R. evertsi N20: L30
		21/5/74	111	H. silacea ♂8: ♀1: N502: L932
Tragelaphus scriptus	Bushbuck	18/1/74	112	A. hebraeum N2 H. silacea ♂421: ♀42: N19: L15
		21/5/74	113	H. silacea ♂400: ♀34: N354: L2799 L2799 A. marmoreum N1: L13 I.pilosus L1
		21/5/74	114	H. silacea ♂515: ♀21: N345: L3645 A. marmoreum L1
		21/5/74	115	H. silacea ♂391: ♀19: N386: L2432 A. marmoreum L1
CARNIVORA				
Felis caracal	Lynx	6/6/72	116	A. hebraeum L7 A. marmoreum L1 I. pilosus N1 H. silacea N1 H. leachii leachii ♂51: ♀24

Table 11 continued.

		14/5/74	117	A. hebraeum L3 A. marmoreum L6 H. leachii leachii ♀1 I.pilosus N20: L101 H. silacea N54: L1043
Canis mesomelas	Black-backed jackal (2 individuals)	23/8/73	118 119	A. hebraeum N4 A. marmoreum N1 H. leachii leachii ♂72: ♀9 I. pilosus L2 Rhipicephalus sp. * ♂4: ♀2: N35: L3
		23/1/74	120	A. hebraeum L4 A. marmoreum N2 H. silacea L1
Cynictis ^{x} penicillata	Yellow mongoose	23/8/73	121	H. silacea ♂1 I. pilosus N1
		29/11/73	122	-
		PRIMATA		
Cercopithecus aethiops	Vervet monkey	22/8/73	123	-
		22/8/73	124	-
		20/5/74	125	-

KEY. L = larva(e); N = nymph(s); * = identified by Miss J.B. Walker (Onderstepoort Veterinary Research Institute); + = identified by Mr J.A. Ledger (South African Institute for Medical Research); x = identified by Mr J.C. Greig (Department of Nature Conservation).

Table 12.

The occurrence of ixodid ticks on a domestic dog at Paardekraal Farm.

Date	Infestation
15/5/73	*A. marmoreum*. L50
17/5/73	*A. marmoreum*. L29
1/9/73	*A. hebraeum*. L5
4/9/73	*H. leachii leachii*. ♂1 *I. pilosus*. N1 *H. silacea*. L16
11/9/73	*A. hebraeum*. L3 *H. leachii leachii*. ♂1 *I. pilosus*. ♀1 *H. silacea*. N1: L1
14/12/73	*A. hebraeum*. N1
22/3/74	*H. silacea*. N1: L82

KEY. L = larva(e); N = nymph(s).

Table 13.

The occurrence of _Amblyomma_ _hebraeum_ on indigenous hosts in the Fastern Cape Province.

No.	Species	Common name	Locality	Date	Infestation
CHELONIA					
1	_Geochelone pardalis_	Mountain tortoise	Sukses F.	?	N
TUBULIDENTATA					
2	_Orycteropus afer_	Ant-bear	Kenton-on-sea	9/10/72	♂
PERISSODACTYLA					
3	_Equus burchelli_	Zebra	Thomas Bains N.R.	9/8/72	♂ ♀
ARTIODACTYLA					
4	_Oryx gazella_	Gemsbok	Thomas Bains N.R.	25/8/72	♂
5			"	25/8/72	♂ ♀
6			"	25/8/72	♂ ♀
7	_Tragelaphus strepsiceros_	Kudu	Vaalkraans F.	June/72	♂
8			Grasslands F.	8/6/72	♂
9			"	16/6/72	♂
10			Bucklands F.	7/6/72	N
11			"	22/7/72	♂
12			Rusoord F.	6/6/72	N
13			Rockdale F.	23/6/72	♂
14			Picketts Bridge	?	♂
15	_Tragelaphus scriptus_	Bushbuck	The Lomonds (F.)	5/7/72	N
16			"	5/7/72	N
CARNIVORA					
17	_Canis mesomelas_	Black-backed jackal	Breakfast vlei	3/5/73	N

KEY. N = nymph(s). F = Farm. N.R. = Nature Reserve.

6. The interaction of *Amblyomma hebraeum* with laboratory hosts.

6.1. Introduction.

During the course of the investigation it was necessary to rear large numbers of ticks on laboratory hosts, to obtain a culture of ticks. As a result it was possible to obtain data on the responses of laboratory hosts to repeated infestations of *A. hebraeum*. The results obtained were unexpected, and consequently it has been necessary to review the literature on host-tick interactions to examine the results in perspective. The remainder of this introduction consists of a review paper, presented at the 'First National Congress of the Entomological Society of Southern Africa' (1974) (to be published in the Proceedings of the Congress).

Host-tick interactions: A review

by

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The interaction between ticks and vertebrate hosts is discussed in the light of our knowledge of tick feeding mechanisms and the host response to tick infestation.

INTRODUCTION

"One of the principles that has emerged from the study of host-parasite relationships is that a state of equilibrium is eventually reached, in which the parasite propagates without endangering the survival of the host species" (Wilkinson 1955). In tick-host systems the development of an equilibrium is dependent on both the tick feeding mechanism and the host response. In this paper an attempt has been made to clarify the basic principles involved in (a) innate and acquired host resistance to ticks, and (b) in host specificity in ticks.

THE TICK FEEDING MECHANISM

Attachment

Within the Ixodidae the pattern of attachment of different species within each genus is constant, except in the genus *Ixodes* (Moorhouse 1969). In some *Ixodes* species (e.g. *Ixodes ricinus*), mouthparts are deeply inserted into host tissues and are probably held *in situ* by transformed tissues (Arthur 1973a). In all other ixodid species, however, secure attachment results from the secretion of a salivary cement, which binds the mouthparts to the surrounding tissues. In the genera *Amblyomma*, *Hyalomma* and *Aponomma*, the long mouthparts are inserted deeply into the dermal tissues and there is little or no surface deposition of cement. In the genera *Dermacentor*, *Rhipicephalus*, *Boophilus* and some species of *Ixodes* (e.g. *Ixodes tasmani*) the deposition of cement is largely superficial and the tips of the mouthparts seldom extend below the level of the epidermis. In the genus *Haemaphysalis* the tips of the mouthparts only penetrate the outer epidermis and the cement is deposited almost entirely on the surface of the skin.

Formation of the lesion

After penetration, salivary secretions are injected into the dermal tissues, and this is followed by the formation of a lesion. The small focus of tissue destruction at the tip of the mouthparts, caused by tissue damage during penetration, "rapidly enlarges by necrosis of surrounding tissues, including muscle fibres and blood vessels" (Balashov 1968). Necrosis is usually preceded by an intense infiltration into the tissues, of polymorphonuclear neutrophil leucocytes (Tatchell & Moorhouse 1970). Feeding consists of alternately sucking fluids from the lesion, and injecting saliva into it (Balashov 1968).

There have been differing accounts amongst authors as to the role of salivary secretions in the formation of the lesion. Arthur (1973b) proposed that lysis of host tissues by salivary enzymes is important in feeding in *Hyalomma rufipes*. Support for this hypothesis is found in the presence of long channels, which extend from the apex of the mouthparts to the deeper corium and terminate in a 'pool' or terminal lesion. The invasion of neutrophils is first observed at the distal end of the lesion, and consequently it is thought that the channels are formed by the repetitive release of salivary lysins and withdrawal of lysed tissues. The combined necrotic effect of salivary enzymes and the host inflammatory response towards the end of the feeding period, make available large quantities of nutrient, which are required in the final stages of engorgement. The only other ixodid species in which there is evidence of strong lytic enzymes in the saliva is *Ixodes holocyclus* (Moorhouse 1971).

Tatchell & Moorhouse (1970) found that lesions were absent beneath the mouthparts of *Rhipicephalus sanguineus*, attached to dogs, in which a leukopenia had been induced by administration of nitrogen mustard. Capillaries situated near the mouthparts, however, were grossly dilated and haemorrhagic. Despite the absence of lesions, female ticks were able to engorge and lay eggs. The authors concluded that the feeding lesions arose as a result of the host inflammatory response, while haemorrhage was induced by substances present in the tick saliva. This is in agreement with the findings of Tatchell (1969) that powerful lytic enzymes are absent from the saliva of *Boophilus microplus*. The constituents which were present were shown to be weak enzymes and certain other substances, all of which are known to occur in tick haemolymph. The evidence suggests that the prime function of salivary secretion during feeding in *B. microplus* is ionic regulation. In a more recent investigation (Tatchell & Binnington 1971), a pharmacologically active substance isolated from the saliva of *B. microplus*, was found to cause an increase in capillary permeability after intradermal injection into a bovine host.

Differing opinions on the method of tick feeding have arisen as a result of the different methods of feeding of the different genera studied. Arthur (1973a) postulates that the method of feeding in ixodid ticks relates to the type of mouthparts and the method of attachment. Genera with deeply inserted mouthparts which are supported by cement are able to secrete lytic enzymes as circumfrential attachment is secure. Superficially attaching species, however, are unable to secrete powerful lytic enzymes, as this would imperil their attachment. "Accordingly such species must inflict tissue damage by more subtle specific means" (Arthur 1973a). Moorhouse (1971) reports that in *I. holocyclus*, in which there is no secretion of cement, feeding ticks burrow deeply into the host to achieve stable attachment.

HOST RESPONSE

Acquired and innate resistance to ticks has been widely reported, particularly in respect of *B. microplus*, parasitic on cattle. It is well established that European breeds of cattle (*Bos taurus*) are more susceptible to infestation than Zebu breeds (*Bos indicus*), and that within each breed a wide spectrum of resistance is found (Wilkinson 1955, Rick 1962, Roberts 1968). Roberts (1968) found that when previously uninfested cattle were infested with a constant, continuous, supply of larvae, there was an initial period of about eight days when the yield of engorged female ticks was high. This was followed by a decline to a fairly constant level, which could be high or low depending on the resistance status of the host. In previously exposed hosts there was no initial peak and each host immediately assumed its individual level of resistance. In all cattle it, therefore, appears that resistance is acquired, but Zebu breeds possess an inherited ability to achieve a more effective resistance than do European breeds (Hewetson, 1972).

Zebu and European breeds of cattle respond differently to bites of *B. microplus* (Rick 1962, Tatchell 1969 and Moorhouse and Tatchell 1969). In European breeds, an intense infiltration of neutrophils develops beneath the mouthparts of the larva, within a few hours of attachment. This is typical of an immediate allergic response to blood-sucking arthropods and results in increased availability of tissue fluids to the larva. In a few cases, cattle of European breeds obtain a high degree of resistance to *B.microplus*. Riek (1962) found that this was due to the development of a hypersensitivity, and Tatchell (1969) concluded that this condition was "merely the extreme of the spectrum of sensitivity found in European breeds of cattle".

In Zebu cattle, resistance (at least in part) appears to result from a lack of sensitivity to tick bites. There is no immediate tissue response, and Tatchell (1969) concluded that the high mortality of larvae during the first 24 hours of the parasitic phase was due to dehydration. This assumption is based on the fact that water (derived from tissue fluids) appears to be the prime requirement of newly attached larvae. Circumstantial evidence to support this hypothesis is that ticks developing on Zebu hosts show a marked tendency to occur in clusters, suggesting that the cumulative secretions of many ticks will create a more favourable environment for survival.

Tatchell (1969) regards the apparent absence of an initial response to tick antigens in Zebu cattle as a state of "adaptation tolerance", resulting from the long evolutionary association with *B. microplus*. Berenberg *et al* (1972) showed that the attraction of neutrophils to the site of tick attachment in rats, occurred subsequent to the fragmentation of a plasma complement (C5) after the interaction between C5 and tick saliva. It is, therefore, a non-immunological response, and it is possible that innate resistance in Zebu cattle is due to a higher threshold neutrophil chemotactic response than in European breeds of cattle.

Acquired resistance in both breeds of cattle appears to be immunological (Roberts 1968). Riek (1962) failed to detect any circulating antibodies using serological tests, but was able to show an increase in skin sensitivity (papular swelling) after repeated infestations of ticks or intradermal innoculation of larval extract. In Zebu cattle, epidermal walling off of larval mouthparts was also observed. This is a reaction usually associated with the host immunological response to metazoan parasites (Trager 1939a).

Acquired immunity has been observed in many artificial host-associations (Table 1). Trager (1939a) showed that after one infestation, guinea pigs and rabbits acquired an immunity to *Dermacentor variabilis*. This prevented most larvae in subsequent batches from engorging and resulted in a reduced intake of nutrients by nymphs and adults. In guinea pigs immunity was produced artificially by innoculation with tick extracts, or transferred passively by innoculation with serum from immune animals. The serum of immune rabbits showed specific complement fixation with a larval tick antigen (Trager 1939b). In sensitive guinea pigs a small haemorrhagic area developed beneath the mouthparts of engorging larvae. In immune animals, however, there was an intense infiltration of neutrophils, resulting in tissue necrosis. The epidermis showed thickening around the edges of the bite, and by the fourth day of feeding had grown below the necrotic area, effectively walling off the lesion. This caused some ticks to die *in situ*, and in others there was a reduction in the quantity of imbibed nutrients.

Our knowledge of natural host-associations (other than Zebu cattle and *B. microplus*) is limited. Moorhouse & Tatchell (1969) showed that as with Zebu cattle, there was little or no immediate tissue reaction to the bites of *Rhipicephalus appendiculatus* in Eland, Buffalo and Wildebeeste. Trager (1939a) observed that after one infestation, the Deer mouse (*Peromyscus leucopus*) showed no resistance to larvae of *D. variabilis*. After two or three infestations a partial resistance was acquired, but there was evidence to suggest that this was largely the result of grooming. Chabaud (1950) observed that *Rhipicephalus sanguineus* continued to feed successfully after repeated infestations on dogs.

DISCUSSION

The host response to tick infestation is manifested at two levels, firstly in a non-immunological tissue response and secondly in an acquired immunological response. The former results in localized tissue necrosis and consequently the release of tissue fluids; from this point of view it is beneficial to tick feeding. In natural hosts, the innate resistance to tick infestation arises, at least in part, from a lack of sensitivity (tissue response) to tick bites. In artificial systems it has been shown (Table 1) that acquired resistance can result in a partial or complete inhibition of tick feeding. In natural systems a complete resistance is not acquired; as yet little is known of the immunological regulating mechanisms in natural systems.

On the question of host specificity in ticks, Arthur (1962) observed that "species of British ticks having the longest and most heavily toothed digits have the widest host range", "whilst those with shorter digits and fewer teeth are limited to one group of hosts". These observations suggest that superficially attaching ticks are more susceptible to host resistance mechanisms, than ticks with long mouthparts which penetrate deeply into the dermis. This has been confirmed in laboratory studies. Riek (1959) found that, if previously uninfested guinea pigs or rabbits were infested with the superficially attaching, one-host tick, *B. microplus*, feeding was almost totally inhibited in the nymphal stage. In other superficially attaching genera (*Dermacentor* and *Rhipicephalus*) similar observations have been made after repeated infestations on the same hosts (Table 1). In the genus *Hyalomma* (long mouthparts) on the other hand, feeding is not always inhibited after repeated infestations (Table 1). Similarly in the genus *Amblyomma* (Norval unpublished), larvae have been fed repeatedly on individual rabbits for up to two years without any inhibition of feeding. In ticks with deeply penetrating mouthparts it is likely that the host resistance mechanism i.e. epidermal walling off of the mouthparts, is overcome by the secretion of lytic enzymes in the saliva. The secretion of lytic enzymes also overcomes the disadvantage, according to Moorhouse (1971), of the lesion occurring below the highly vascularized layers of the outer dermis. Host specificity is, therefore, directly related to the method of attachment and feeding in ticks. Those species which have long, deeply penetrating mouthparts are able to feed on a wide range of hosts, while those species which attach superficially and do not secrete lytic enzymes are restricted to a narrow range of hosts with which an equilibrium has developed.

ACKNOWLEDGMENTS

I wish to thank Professor G.B. Whitehead and Mr. A. Ribbink of Rhodes University for constructive criticism of the manuscript.

Table 1

Recorded host responses to repeated artificial infestations of ixodid ticks.

Author(s)	Host	Tick species	Host Response				
			Feeding not inhibited	Feeding partially inhibited	Feeding inhibited	Specific complement fixation with tick antigen	Encapsulation of mouthparts
Trager (1939a & b)	Guinea pig	D.variabilis	–	+	–	–	+
	Rabbit	"	–	+	–	+	*
Brumpt & Chabaud (1947)	"	H.excavatum	+	–	–	*	*
	"	H.dromedarii	+	–	–	*	*
	"	D.pictus	–	+	–	*	*
Chabaud (1950)	"	R.sanguineus	–	+	–	*	*
	Guinea pig	"	–	–	+	*	*
Pervomaisky & Maklygin (1959)	Rabbit	H.asiaticum asiaticum	–	+	–	*	*
Snow & Arthur (1966)	Guinea pig	H.anatolicum anatolicum	–	+	–	*	*
Musatov (1967)	Rabbit	R.bursa	–	+	–	*	*
	"	H.marginatum	–	+	–	*	*
	"	R.sanguineus	–	+	–	*	*
	"	H.asiaticum asiaticum	–	+	–	*	*
Emokpare (1969)	Rabbit	R.sanguineus	–	+	–	+	*
	"	H.anatolicum excavatum	–	+	–	+	*

Key: D, Dermacentor; R, Rhipicephalus; H, Hyalomma; +, positive response; –, negative response; *, not tested.

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6.2. Experimental infestations.

The ticks were obtained from a laboratory culture, which was maintained in darkness in an incubator at 26°C and approximately 90%RH. Caged laboratory hosts, maintained in the field station of the Tick Research Unit of Rhodes University, were infested with known numbers of ticks at intervals of 2-4 weeks over periods ranging from 7 to 23 months. After each infestation, engorged ticks which had detached from the host were collected daily (08.00-09.30 hours) from trays which were placed beneath each host (see Chapter 2). Engorged ticks were brought to the laboratory, counted and then weighed on a Sartorius single pan balance. It was then possible to calculate for each infestation, (a) the tick yield i.e. the percentage of ticks which engorged to completion, (b) the mean engorged weight and (c) the mean engorgement period. Continuous records of temperature and relative humidity at the field station were obtained using a thermohygrograph.

Larval feeding.

Larvae were fed on Himalayan giant rabbits. To facilitate attachment, the ticks were released onto a shaved area (approximately 40 sq. cm.) on the back of each rabbit, and then confined to the rabbit for 24 hours under a square of fine gauze, which was stuck to the skin with adhesive tape. Each rabbit was infested with a standard dose of 1 000 - 3 000 larvae. A total of six different rabbits were used in a series of experiments, conducted between March, 1972 and February, 1974. Prior to the first infestation, none of the rabbits had been subjected to any tick infestation. At the start of the experiments, rabbits No. 1-3 were approximately six months old and rabbits No. 4-6 were 2 months old. Larvae used in experiments ranged in age from 2 to 15 weeks. Where possible, rabbits in the experimental series were all infested on the same day, with larvae originating from the same female tick. This allowed a valid comparison of the attachment and feeding (engorgement) capacity of larvae on different hosts at any time of year, by eliminating any possible effects of age of ticks on these factors. Larvae of different ages were used at each infestation, to ensure that any progressive seasonal changes in the feeding capacity could not be attributed to the physiological state (i.e. age) of the ticks.

Nymphal feeding.

Nymphs were fed on the ears of Merino sheep and Himalayan giant rabbits. Approximately 40 nymphs were placed on each ear, and then confined to the ear for 24 hours in a muslin ear-bag. A series of experiments involving 2 sheep and 3 rabbits was conducted between April, 1972 and November, 1973. Nymphs used in the experiments ranged in age from 3 to 36 weeks, and for reasons discussed previously, hosts were infested, where possible, on the same day with nymphs of a similar age. Nymphs of different ages were used at each infestation.

Adult female feeding.

Adult female ticks were fed on the tails of Guernsey calves. To allow attachment, females were placed adjacent to sexually mature males, as described in Chapter 2. A series of experiments involving 6 calves was conducted between April, 1972 and April, 1974. Female ticks used in the experiments ranged in age from 2 to 20 weeks. Batches of 5-40 females (depending on the number of attached males) were placed on the calves at intervals of approximately 2 weeks.

6.3. Larval yield.

The term 'tick yield' as used by Roberts (1968) refers to the proportion of ticks in an experimental infestation which engorge to completion. It must be stressed that the term only applies to experimental infestations, in which the ticks are artificially placed on the host. Experimental tick yields may be influenced by the effects of meteorological conditions on the behaviour of the ticks, the physiological state of the ticks as determined by age or other factors, the influence of grooming by the host and possibly other factors relating to the suitability of the host.

Host variability.

The rabbits tested showed a wide range in susceptibility to larval infestation, as reflected in the mean larval yields (Table 14), which ranged from 11,4 (rabbit No. 3) to 552,3 (rabbit No. 1). The differences in larval yield were found to be due largely to the grooming behaviour of individual rabbits. Those rabbits from which the lowest yields were recorded were observed to spend the longest time grooming. In rabbits No. 2 and 3, from which the yields were exceptionally low, it was observed that tick bites caused localized swelling of the skin and considerable irritation. In rabbits which were fitted with fibre-board collars (Chapter 2) the yields of larvae were exceptionally high, normally exceeding 1 500 per infestation.

Table 14.

The mean numbers of engorged larvae of <u>Amblyomma hebraeum</u> recovered from rabbits, after initial infestations of approximately 2 000 unfed larvae.

Rabbit No.	Sex*	No. infestations	Total No. engorged larvae	Mean No. per infestation
1	♂	39	21 541	552,3
2	♂	13	725	55,8
3	♀	14	160	11,4
4	♀	20	1 963	98,2
5	♀	18	7 091	393,9
6	♀	11	3 372	306,5

*, refers to rabbits.

Fluctuations in larval yield.

The fluctuations in larval yield from the six rabbits tested are given in Fig. 30. The yield curves for each rabbit have been smoothed according to the method of Roberts (1968). The smoothed value for each

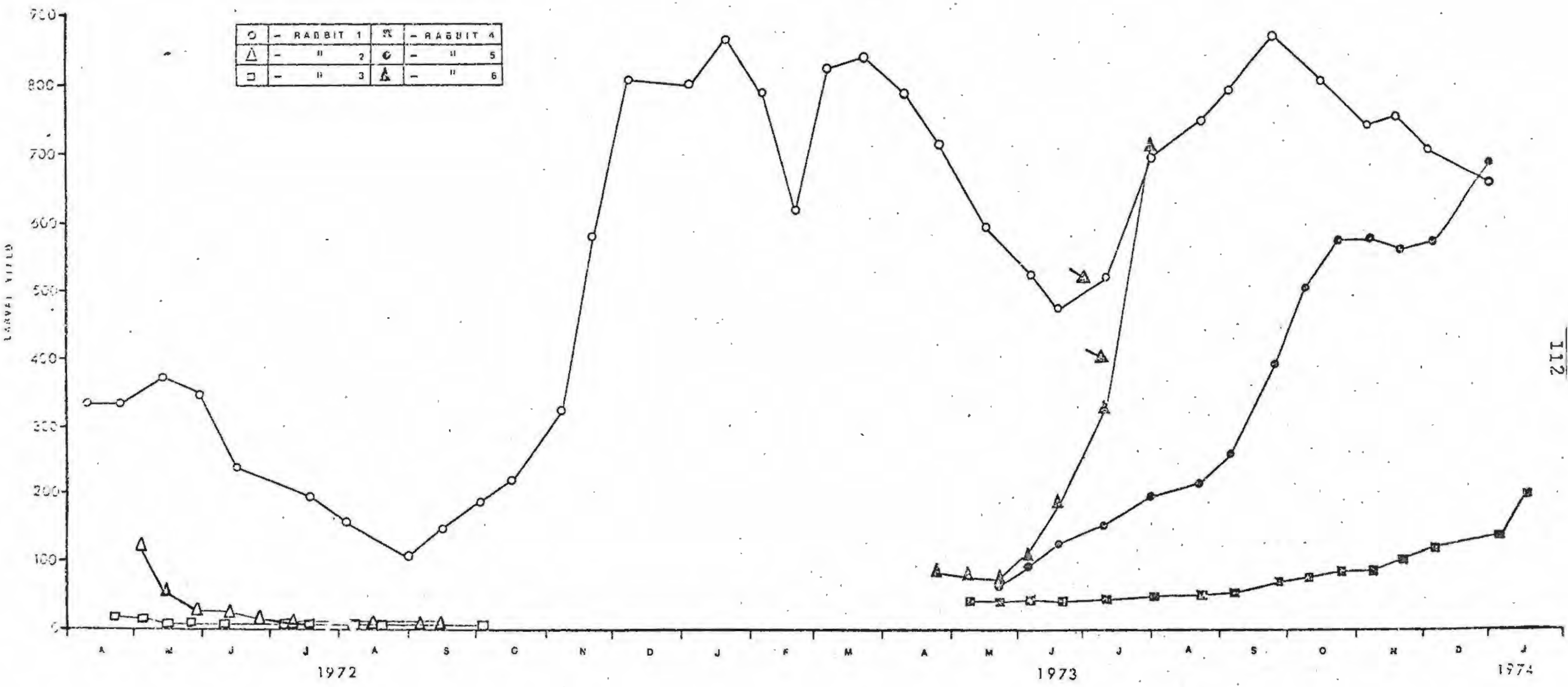

Fig. 30.

Seasonal fluctuations in the yield of engorged larvae from experimental rabbits (see text). Arrows indicate the onset of illness in rabbits.

point (infestation), r, was calculated as follows: $r = [(p/2)+q+r+s+(t/2)]/4$, where q and p were the points preceeding r, and s and t were the points following r.

There were clear seasonal fluctuations in the yield of larvae from rabbit No. 1, which was repeatedly infested between April, 1972 and February, 1974. The trends in respect of rabbits No. 4-6 were similar, although not as clear, due to the shorter periods of time over which these hosts were infested. In the case of rabbits No. 2 and 3, seasonal fluctuations were largely obscured by the low levels of the tick yield. In rabbits No. 1, 4 and 5 the larval yield per infestation showed a significant correlation with temperature (hour degrees during the week of infestation) (Table 15). The highest larval yields were recorded during warm summer conditions.

Table 15.

The correlation between larval yield and temperature.

Rabbit No.	Degrees of freedom	r	p
1	37	0,39	< 0,05*
2	11	0,13	> 0,05
3	12	0,09	> 0,05
4	18	0,60	< 0,01**
5	16	0,53	< 0,05*
6	9	0,39	> 0,05

KEY. r = correlation coefficient. p = probability level. *, correlation significant, **, correlation highly significant.

The most likely cause of the correlation between temperature and larval yield, was that the attachment behaviour of larvae was dependent on ambient temperature. Evidence to support this hypothesis is that low temperatures (less than approximately 20°C), were observed to inhibit the activity of larvae, both on and off the host. No marked increase in grooming was observed during the summer months, hence, if higher percentages of larvae attached to the rabbits in summer than in winter, the yields of larvae would be higher in the summer. Under field conditions larvae are only likely to be active within a specific temperature range; consequently the fluctuations in larval yield in the laboratory can be attributed to the artificial method of infestation.

In addition to temperature, larval yields were influenced by host stress factors (i.e. illness), which resulted in a decrease in grooming. In rabbits Nos 1 and 6, there was a sharp increase in the yield of larvae after the onset of illness (Fig. 30). In both cases the low values of the correlation coefficients (r) (Table 15), between temperature and larval yield, can be attributed to the influence of host stress factors.

There was no evidence that the attachment behaviour of larvae was influenced by the age of the ticks. It was apparent however, that the yield of larvae increased as rabbits increased in age, presumably due to a decrease in grooming in old rabbits.

6.4. Larval engorged weight.

The mean engorged weight of larvae at each infestation, varied slightly between rabbits, but in all rabbits showed similar seasonal fluctuations (Fig. 31). Unlike the seasonal fluctuations in yield (6.3), the fluctuations in engorged weight were not directly correlated with temperature. In 1972 the engorged weights of larvae which fed on rabbits No. 1, 2 and 3, showed a steady decline from March until June-August, and then remained at a low level until early October. The temperatures recorded in the field station (Fig. 32), declined rapidly from April until mid-August, and then rose sharply from late August. There was thus a delay of approximately two months between the rise in spring temperatures and the rise in larval engorged weights. In 1973

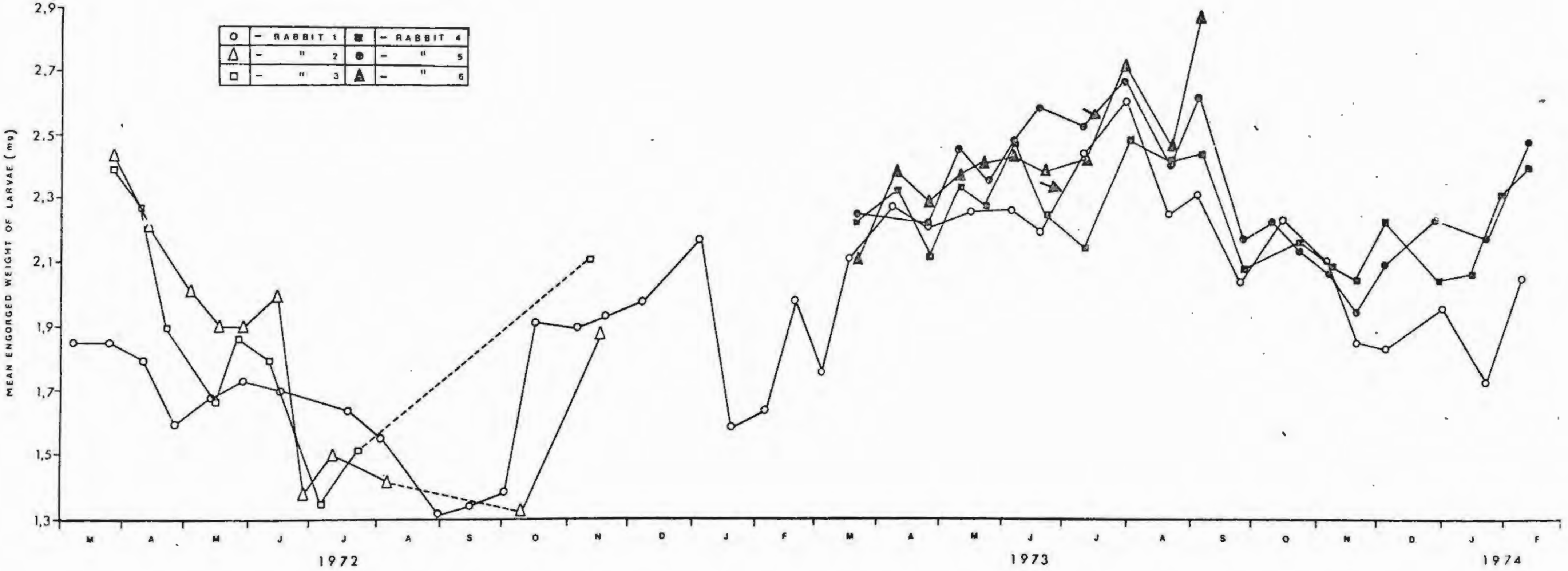

Fig. 31.

Seasonal fluctuations in the mean engorged weight (mg) per batch of larvae, fed on experimental rabbits. Arrows indicate the onset of illness in rabbits.

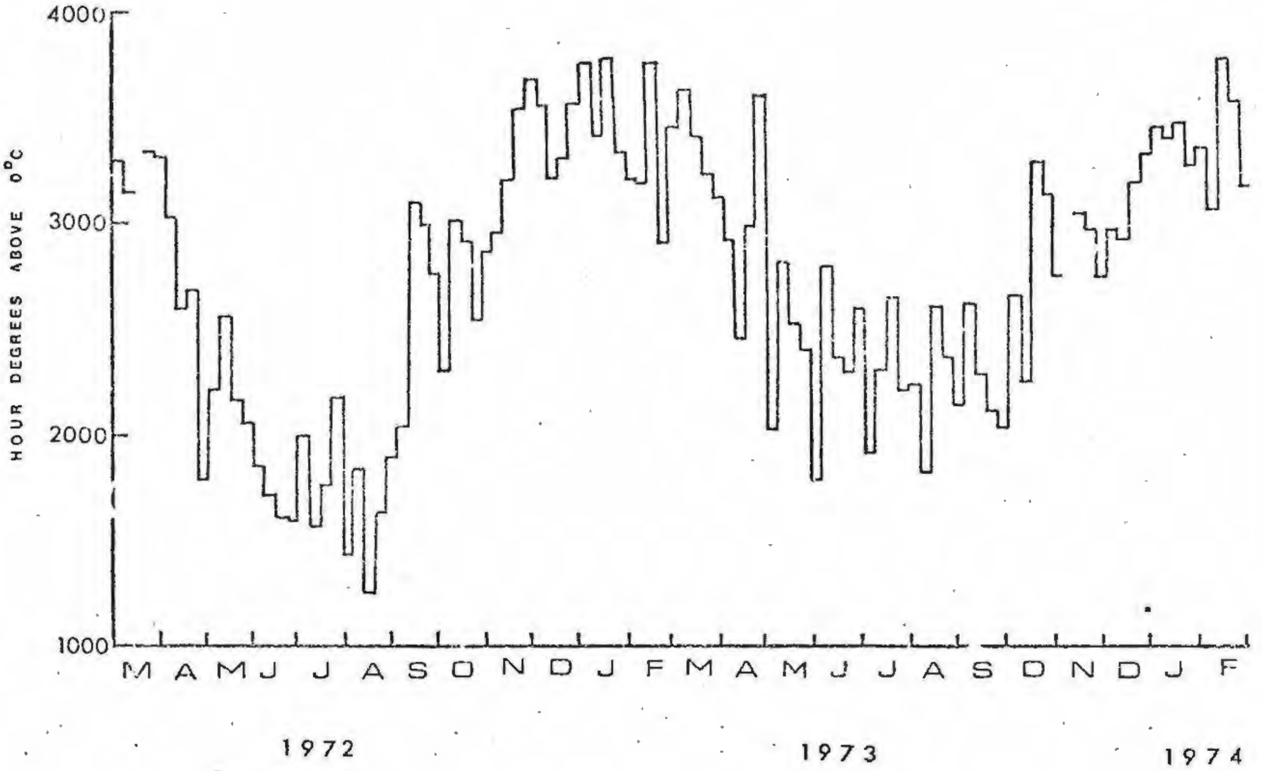

Fig. 32.

Hour degrees per week above 0°C, calculated from thermohygrograph records from the field station of the Tick Research Unit of Rhodes University.

the engorged weights of larvae which fed on rabbits No. 1, 4, 5 and 6 increased from March until July, despite the onset of winter. The engorged weights then decreased gradually until the end of December, 1973, and began to rise in January, 1974. The rise in spring temperatures in 1973 began in late October; again approximately two months before the rise in engorged weight.

The observation that temperature had no direct effect on the feeding capacity of larvae was confirmed in an experiment conducted in the laboratory in January/February 1974, when two rabbits which had been maintained in the field station, were placed in a constant temperature room (15°C). The rabbits were infested with larvae three times over a period of one month, and the mean weights were recorded. Despite the low temperatures the engorged weights continued to rise, as was the case with larvae which were fed on rabbits in the field station. It can therefore be concluded that seasonal fluctuations in the engorged weights (or feeding capacity) of larvae were induced by seasonal changes in the rabbits.

The results in Fig. 31 suggest that the reduction in the feeding capacity of larvae was caused by changes in the physiology of the rabbits, which arose from low temperature acclimatization. In 1972 the rapid decline in temperature between March and June, was followed closely by a decline in larval engorged weight, indicating rapid low temperature acclimatization in the rabbits. During the same months in 1973, the temperatures declined slowly, and there were no sustained periods of extreme cold (less than 2 000 hour degrees per week). As a result there was no low temperature acclimatization in the rabbits, and the engorged weight of larvae continued to rise. There was a decline in engorged weights between August and November, but the weights did not reach the low levels which were recorded in the colder winter of 1972. The time lag between the rise in spring temperatures and the rise in larval engorged weights, shows that rabbits required approximately two months of increased temperature to acclimatize to summer conditions. It is also clear, from the experiment conducted in the constant temperature room, that 15°C (constant) over a period of one month was insufficient to induce low temperature acclimatization in the rabbits.

It is difficult to speculate on the nature of the factors which cause seasonal fluctuations in the larval feeding capacity, as no detailed studies have been made on the feeding mechanism in the genus Amblyomma. If the feeding mechanism in A. hebraeum, however, conforms to the pattern established in ticks with long mouthparts (i.e. by secretion of lytic enzymes), it can be expected that seasonal changes in the chemical composition of the dermis will affect the feeding capacity. For example, if the ticks rely primarily on protein degrading enzymes for tissue destruction, deposition of large quantities of lipid in the dermis, may result in a decrease in the availability of ingestable nutrients. The role of the host tissue response in the feeding of A. hebraeum is not known. It was observed, however, that the mean weight of larvae increased when the rabbits became ill (Fig. 31). This could have resulted from an increase in the intensity of the tissue response, making greater quantities of ingestable nutrient available. Circumstantial evidence to support this hypothesis, is that larvae which fed on rabbits showing the greatest sensitivity to tick infestation (6.3), engorged to the heaviest weights. As discussed in the introduction (6.1), there was no evidence of an acquired immunity in the rabbits having any effect on larval feeding.

6.5. Larval engorgement period.

The mean engorgement periods of infestations of larvae on rabbits (Fig. 33), ranged from 6,4 to 11,5 days. The fluctuations from all rabbits were similar, with the longest engorgement periods occurring in early summer, and autumn or early winter. There was no correlation between the fluctuations in seasonal temperature and the mean engorgement period.

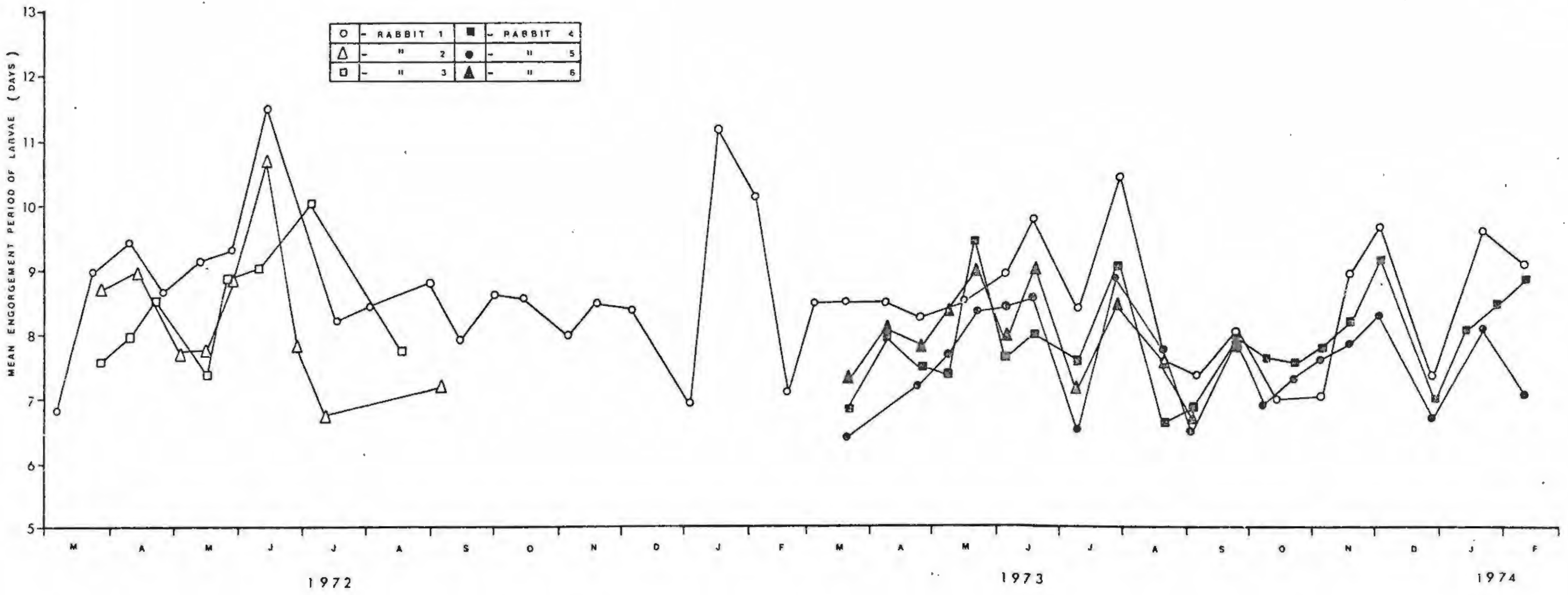

Fig. 33.

Seasonal fluctuations in the mean engorgement period (days) per batch of larvae, fed on experimental rabbits.

Sweatman (1970) has shown that the rate of engorgement of ixodid ticks is a function of the skin temperature of the host. Unfortunately skin temperatures were not recorded during these experiments. It was observed, however, that the rabbits moulted (i.e. shed hair) during the hot months of early summer. As the effect of moulting is to lower the skin temperature, this would account for the increase in the mean engorgement period at this time of year. In both 1972 and 1973 there were increases in the mean engorgement periods of larvae during the cold spells (less than approximately 1 800 hour degrees per week above $0^{\circ}C$) which occurred during the months of autumn and early winter. The initial increases in the mean larval engorgement period in early winter, were followed by decreases in the engorgement period during the cold months of late winter. These results suggest that after an initial lowering of the skin temperature in early winter, the rabbits adapted to the cold conditions by increasing the density of the fur. The skin temperatures would then be higher in late winter than in early winter, despite the lower ambient temperatures.

6.6. Nymphal yield.

The attachment behaviour of nymphs, unlike larvae, was influenced by age. In batches of nymphs under the age of 3 months, the percentage attachment after a 24 hour confinement period on the ears of sheep was low (normally less than 50%). In nymphs which exceeded 3 months in age, the percentage attachment was invariably higher than 50%, and in nymphs which exceeded 6 months in age, the percentage attachment normally approached 100%. The percentage attachment of nymphs of the same age was always higher on sheep than on rabbits. As a result of the age effect it was impossible to determine any seasonal trends in the yield of nymphs from rabbits or sheep.

6.7. Nymphal engorged weight.

Nymphs fed on rabbits.

Nymphs were fed repeatedly on the ears of 3 rabbits, between April, 1972 and January, 1973. The numbers of nymphs which engorged to completion were low, as a result of the grooming activities of the rabbits. The results (Table 16) nevertheless show that, as with larvae, the engorged weight of nymphs decreased between April and August/September, and then increased between October/November and December/January. Proportionately the decrease in the mean engorged weight between April and August/September, was considerably larger in nymphs than in larvae. The results indicate that the same host factors were responsible for the seasonal fluctuations in the feeding capacity of larvae and nymphs.

Table 16.

The mean engorged weight of nymphs of Amblyomma hebraeum which were fed repeatedly on three rabbits between April, 1972 and January, 1973.

Month	Mean engorged weight (mg)	Standard deviation	Number of ticks
April	42,68	14,04	33
May	29,98	13,70	65
June/July	12,81	10,36	15
August/September	9,19	8,70	7
October/November	13,97	13,47	7
December/January	29,60	16,45	5

Nymphs fed on sheep.

The mean engorged weights of successive batches of nymphs which were fed on the ears of sheep between May, 1972 and November, 1973, are given in Fig. 34. The engorged weights declined rapidly between May and June, 1972, and then remained at a low level until the end of October. From November, 1972, until November, 1973 the engorged weights remained at a high level.

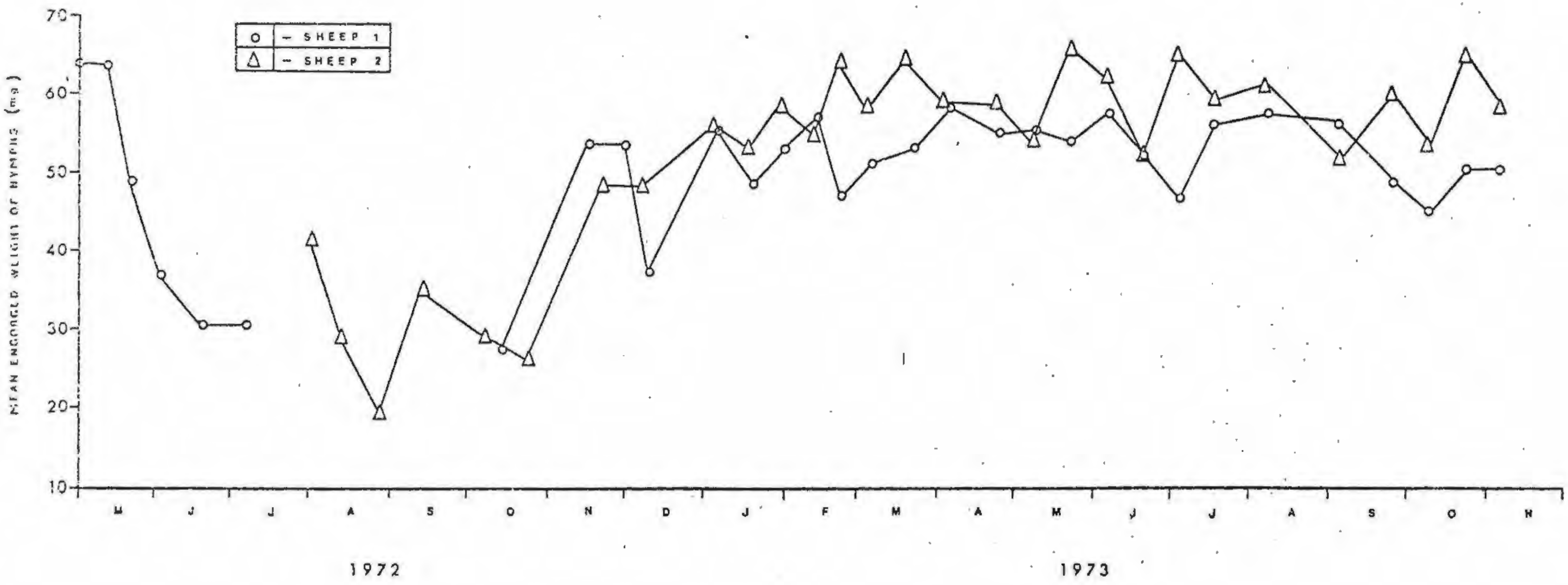

Fig. 34.

Seasonal fluctuations in the mean engorged weight (mg) per batch of nymphs, fed on the ears of experimental sheep.

The results (Fig. 34) show that the fluctuations in nymphal engorged weight in 1972, followed the same pattern as the fluctuations in larval engorged weight (6.4). This was not the case in 1973, however, when no decline in the nymphal engorged weight was recorded. On the basis of the results obtained during the cold winter of 1972 (Fig. 32), it can be concluded that the same factor, i.e. low temperature acclimatization in the host (6.4), was responsible for reducing the feeding capacity in larvae and nymphs on rabbits and in nymphs on sheep. The most likely explanation for the difference between the engorged weight curves of larvae (Fig. 31) and nymphs (Fig. 34) during the mild winter of 1973 (Fig. 32), is that sheep require lower temperatures than rabbits to initiate low temperature acclimatization. The results in Fig. 34 show that as with rabbits, sheep were unable to acquire a resistance to infestations of A. hebraeum.

6.8. Nymphal engorgement period.

The mean engorgement periods of infestations of nymphs on the ears of sheep (Fig. 35), ranged from 5,2 to 20,5 days. The large fluctuations in the engorgement periods were directly associated with the shearing of sheep. Immediately after shearing the engorgement periods increased sharply from the normal of 5-10 days to as much as 20,5 days, and then remained longer than normal for approximately two months. The increases in the engorgement periods resulted from a lowering of the skin temperature of the ears of sheep after shearing. Blaxter et al. (1959) found that below 25-27°C the ear temperature in closely shorn sheep remained 1-2°C above the ambient temperature, while in unshorn sheep the ear temperature remained at 36-38°C, irrespective of the ambient temperature.

In the periods between shearing, the weekly fluctuations in the mean engorgement period were similar in nymphs fed on both sheep, but there were no clear seasonal trends.

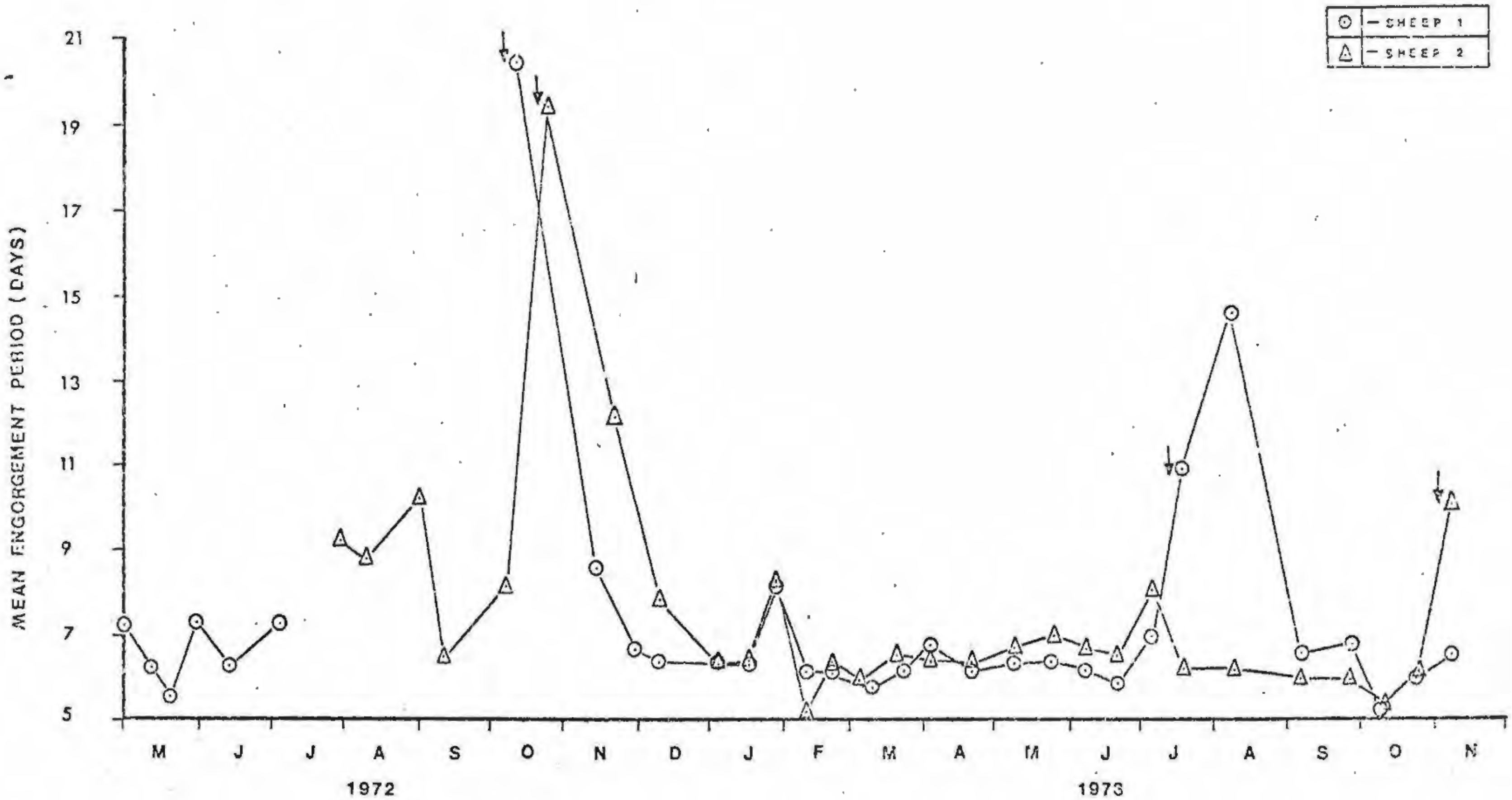

Fig. 35.

Seasonal fluctuations in the mean engorgement period (days) per batch of nymphs, fed on the ears of experimental sheep. Arrows indicate the shearing of the sheep.

6.9. Feeding in adult ticks.

The attachment behaviour of adult males and females of A. hebraeum on Guernsey calves has been described in Chapter 2. In both sexes the attachment behaviour was clearly influenced by age of ticks. Newly moulted males (i.e. under the age of two months) could seldom be induced to attach. Newly moulted females showed little response to sexually mature males (as described in Chapter 2) and often failed to attach.

Fully engorged females ranged in weight from 0,8 to 4,0 g. Despite the wide variations in engorged weight, there were no clear seasonal changes in the feeding capacity of female ticks. The cause of the variation in the engorged weights, was found to lie in the wide range in weights of unfed ticks, which were used to infest the calves. Small unfed females gave rise to small engorged females and large unfed females gave rise to large engorged females. This is in agreement with the results of Snow and Arthur (1966), in respect of H. anatolicum anatolicum. Small unfed females developed from small nymphs, which had fed on rabbits or sheep during the winter and spring of 1972 (6.7). In a sample of 30 ticks, the correlation between the weights of engorged nymphs and the weights of newly emerged females was highly significant (r=0,998).

No marked seasonal fluctuations in the engorgement periods of female ticks were observed during the course of the investigation. Similar observations, concerning the duration of the parasitic cycle of B.decoloratus on Guernsey calves, were made by Arthur and Londt (1973).

6.10. Discussion.

As stated in the introduction (6.1), laboratory hosts are unable to acquire a resistance to A. hebraeum. This undoubtedly relates to the morphology of the mouthparts, method of attachment and feeding mechanism in A. hebraeum (6.1). On the basis of the laboratory data, it can be expected that A. hebraeum will be catholic in choice of hosts. In the case of larvae and nymphs this is confirmed by the results of Chapter 5, where it was shown that the incidence of ticks on hosts was determined largely or wholly by the behaviour and habitat preferences of the hosts in relation to the distribution of the ticks. The restriction of adult ticks to large mammals (5.3), arises as a result of the behaviour of the ticks rather than the inability of the ticks to feed on small hosts (in Chapter 2 it was shown that males could feed successfully when artificially induced to attach to rabbits).

The results in this Chapter show the extent of the influence of host factors on tick feeding. There were differences in the feeding capacity of ticks, both on different host species (6.7) and on different individuals within a single host species (6,4; 6,7). The dependence of tick feeding on the physiological state of the host was shown by the seasonal fluctuations in the engorged weight of ticks, in response to changes in the host physiology as a result of low temperature acclimatization. The actual skin temperature of the host determined the rate of feeding, but not the engorged weight. This was shown in the experiment involving sheep Nos 1 and 2, where it was observed that the progressive seasonal changes in engorged weight (Fig. 34) were not influenced by fluctuations in the length of the engorgement period (Fig. 35). In the host survey (Table 11) it was observed that nymphs of A. hebraeum parasitized both homiotherms and poikilotherms. The rate of feeding in the latter can be expected to be influenced by ambient temperature (Sweatman, 1970), as was the case of nymphs feeding on the ears of closely shorn sheep.

Seasonal fluctuations in engorged weight were recorded in ticks fed on both rabbits and sheep. As low temperature acclimatization must occur in other mammalian hosts, one can expect similar results from other hosts. Consequently the timing of the activity peaks of larvae and nymphs could be important from the point of view of feeding. The extent of engorgement of the immature stages of A. hebraeum could have significant ecological implications, as it has been shown (6.9) that the weight of the unfed female is a function of the weight of the engorged nymph, and that the engorged weight of the female is a function of the weight of the unfed female (6.9). As the number of eggs produced by engorged females is a function of the engorged weight (Chapter 2), the number of eggs produced is directly related to the engorged weight of the nymph, which itself is probably determined by the engorged weight of the larva. As ticks rely on large numbers of eggs for survival (i.e. to counteract the high level of mortality during the life cycle), any reduction in egg productivity will influence the abundance of the tick. In the Eastern Cape, where nymphs are active in spring (3.10), the effects of low temperature acclimatization in the host may be important. The same may be true in Natal, where nymphs are active in winter (Baker & Ducasse, 1968). The mild winter conditions in this sub-tropical area, however, are unlikely to have the same effect on the host physiology as the temperate winters of the Eastern Cape. It would be interesting to compare the sizes of unfed or engorged females, collected in both areas. The engorgement of larvae and adult female ticks is unlikely to be affected by low temperature acclimatization, as the activity peaks of these stages occur in mid- and late summer, in both the Eastern Cape (3.7; 3.11) and Natal (Baker & Ducasse, 1968).

The observations in Chapter 3, that nymphs and adult ticks (3.12) enter an age determined period of inactivity after moulting, were confirmed by the results in this Chapter. Nymphs and adult ticks which had been maintained in darkness in an incubator for longer than three months, became active in response to human breath. Larvae became active immediately after the tanning process in the cuticle was completed.

SECTION FOUR

THE BIOLOGY AND ECOLOGY OF TICK SPECIES OTHER THAN *AMBLYOMMA HEBRAEUM* KOCH

7. Notes on the biology and ecology of ixodid tick species, other than Amblyomma hebraeum.

7.1. Introduction.

During the course of the field studies at Paardekraal Farm, information was obtained on the habitat preferences, seasonal activity and hosts of a number of ixodid species other than A. hebraeum. This chapter deals with the data concerning these species, which are:- Ixodes pilosus Koch, 1844; Haemaphysalis silacea, 1912; Haemaphysalis leachii leachii (Audouin, 1827); R. evertsi; Rhipicephalus simus Koch, 1844; Rhipicephalus oculatus Neumann, 1901; Hyalomma marginatum rufipes (Koch, 1844); Aponomma exornatum (Koch, 1844); A. marmoreum; B. decoloratus. Some of these species are primarily or exclusively parasites of indigenous animals, e.g. H. silacea, some species are primarily parasites of domestic animals, e.g. B. decoloratus, while other species, e.g. R. simus, are only dependent on domestic animals in the adult stage. A comparison of the seasonal activity, and host and habitat requirements of these species, yields further insight into the factors controlling the survival and abundance of ixodid ticks. In some instances useful comparisons can be made with A. hebraeum.

Apart from A. hebraeum, the most commonly occurring tick species in the Kowie River valley were H. silacea and A. marmoreum. The data in respect of these two species are presented in the form of papers, copies of which have been submitted for publication in the Journal of Parasitology. In the case of I. pilosus the biological data are presented in the form of a paper, published in the Journal of the Entomological Society of southern Africa.

7.2

Studies on the ecology of Haemaphysalis silacea Robinson, 1912 (Acarina: Ixodidae)

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ABSTRACT:

Haemaphysalis silacea Robinson is established only in the Eastern Cape Province of South Africa, in localized areas of Fish River Bush in the river valleys and in the coastal bush complex. In a study area in the Kowie River valley, it was shown that the distribution of larvae in the environment is limited principally by microclimatic conditions. The humid leaf litter zone in the dense vegetation on the river banks and along minor tributaries is the focus of the larval population. Nymphs occur in highest numbers in drier microhabitats on the wooded, river flood plain. Larvae are active during the humid conditions of autumn and early winter, nymphs during late winter and spring and adults during the hot, dry summer months. The main hosts of H. silacea are artiodactyls, which occur in high numbers in the dense Fish River Bush. The host/tick interaction occurs as a result of the daily movements and feeding habits of the hosts.

Haemaphysalis silacea Robinson is one of the least known of the haemaphysalid ticks of the Ethiopian Region and differs widely from other African species in its taxonomic associations (Hoogstraal, 1963). The species is established only in the Eastern Cape Province of South Africa, where it occurs in localized areas of xerophytic Fish River Bush in the hot, dry river valleys, and in the sub-tropical and deciduous bush complex along the coast (Theiler, 1945). H. silacea does occur on domestic stock, but has not, as yet, been implicated in disease transmission.

Little information is available on the ecological associations of H. silacea with the river valley and coastal bush complexes, or with natural hosts. Londt and Whitehead (1972) found, in coastal areas, that larvae occurred predominantly in habitats in which there was a complete canopy of bush or trees and a short herbaceous ground cover. Saturation deficits in these habitats generally remained low. Larvae were active during the cool months between April and October. Theiler (1945) lists domestic hosts of *H. silacea* as sheep, goats and cattle and indigenous hosts as Lynx (*Felis caracal*) and Bushbuck (*Tragelaphus scriptus*). In a later publication (Theiler, 1962), Hadeda ibis (*Hagedashia hagedash*), Guinea-fowl (*Numida meleagris*), hare (?), mongoose (?), White-tailed mongoose (*Ichneumia albicauda*), Blue duiker (*Cephalophus monticola*) and Bushbuck, are listed as hosts of immatures. Duiker (*Sylvicapra grimmia*), Nyala Bushbuck (*Tragelaphus angasi*), Kudu (*Tragelaphus strepsiceros*) and Bushbuck, are listed as hosts of adults.

This paper deals with the ecology of *H. silacea* in a study area in the Kowie River valley, 15 km SE of Grahamstown. Information is given on habitat preferences and seasonal activity of larvae and nymphs; the effect of changing microclimatic conditions on the distribution of larvae in the environment; the quantitative seasonal occurrence of all developmental stages on indigenous hosts. From this data it has been possible to show the interaction of *H. silacea* with its natural hosts within a specific habitat complex and the effects of this interaction on the geographical distribution of the species.

THE SURVEY AREA

The survey area, on Paardekraal Farm, consisted of 3 major components. (1) River banks. These supported a dense band of marginal riverine vegetation (habitat 1), composed of at least 10 species of low growing trees. There was a ground cover of leaf litter, and patches of shrubs and herbs (predominantly *Peristrophe cernua*) in the most shaded areas. (2) River flood plains, merging into gently rising ground. The dominant plant species was *Acacia karroo*, in the form of low growing trees above a ground flora of grass and scattered herbs. Part of the Acacia grassland (habitat 2a) had been artificially modified, by removal of A. karroo trees, to form open grassland (habitat 2b). (3) Steeply rising slopes bordering on the river valley. The vegetation was mostly typical Fish River Bush (habitat 3a), which consisted mainly of exceptionally dense, spiny or succulent evergreen plants. These produced little leaf litter, and there was little or no undergrowth. The Fish River Bush was traversed by game paths (habitat 3b), some of which were bordered by short grass and herbs. Many gulleys (habitat 3c) or minor tributaries arose from the valley slopes. Here the vegetation was similar to marginal riverine vegetation, with a canopy of low growing deciduous trees and a ground cover of leaf litter and scattered shrubs and herbs.

MATERIALS AND METHODS

Larvae and nymphs were collected using the dragging apparatus described by Londt & Whitehead (1972). A previously unsampled stretch of ground was used for each drag in each season. Samples taken in each habitat consisted of 2 drags, each of 50 m, taken between 10.00 and 13.00 hr. Marginal riverine vegetation (1), Acacia grassland (2a) and open grassland (2b) were sampled at weekly intervals from April 1973 to April 1974. Habitats in the Fish River Bush complex (3a-c) were sampled on 5 occasions during this period.

Rainfall was recorded at the Paardekraal farmhouse, situated 4 km from the survey area. Continuous records of temperature and relative humidity were obtained using a thermohygrograph, which was maintained in a Stevenson's screen, situated in Acacia grassland. Microclimatic relative humidities were measured with a Rotronic, Hygroskop BT, humidity measuring instrument, using a Rotronic air probe, type KF. Microclimatic temperatures were measured with a mercury thermometer. Microclimatic conditions were recorded in each habitat at heights of 0, 1, 5, 10, 20, 30 and 40 cm above ground level, either hourly over 24 hours or during the day between 10.20 and 16.10 hours.

RESULTS

Habitat preference

The total numbers of larvae and nymphs collected on 48 occasions in open grassland, Acacia grassland and marginal riverine vegetation are given in Table 1. Highest numbers of larvae were collected in marginal riverine vegetation,while highest numbers of nymphs were collected in Acacia grassland. The numbers of both stages collected in open grassland were extremely low. In the Fish River Bush complex (Table 2), larvae were largely absent from game paths and typical Fish River Bush. However, larvae were present in large numbers in the vegetation of the gulleys.

Recent ecological studies in South Africa (Stampa, 1959; Kraft, 1961; Londt & Whitehead, 1972) have shown that specific microclimatic conditions are necessary for the survival of individual ixodid species, and that these conditions are determined largely by the vegetation structure of the habitat. Microclimatic conditions recorded in habitats at Paardekraal Farm were similar to those recorded in comparable habitats by Londt and Whitehead (1972). Maximum daily saturation deficits, calculated from thermohygrograph records, normally occurred between 12.00 and 14.00 hours and varied between 0,9 and 66,7 mm Hg. Minimum daily saturation deficits normally occurred between 03.00 and 06.00 hours and usually approached 0 mm Hg. Saturation deficits recorded in microhabitats in open grassland, Acacia grassland and marginal riverine vegetation showed similar daily fluctuations (Fig. 1). Day-time saturation deficits recorded in these habitats on 7 occasions in the summer and autumn of 1973/74 followed the same pattern as in Fig. 1, with lowest values occurring in the leaf litter zone of marginal riverine vegetation and highest values occurring in open grassland. The magnitudes of difference between the 3 habitats decreased as the height and density of the herbaceous ground cover increased, following the heavy rains of late summer (Fig. 2). In late summer and autumn, day-time saturation deficits recorded at ground level in all 3

Table 1.

The total numbers of larvae and nymphs of <u>Haemaphysalis silacea</u>, collected in habitats in the Kowie River valley, on 48 occasions, from April 1973 to April 1974.

	Open grassland	Acacia grassland	Marginal riverine veg.
Total No. larvae	37	460	1973
% of larvae	1,5	18,6	79,9
Total No. nymphs	3	39	19
% of nymphs	4,9	63,9	31,1

Table 2.

The numbers of larvae of <u>Haemaphysalis silacea</u>, collected in habitats on the slopes of the Kowie River valley, on 5 occasions.

Date	Fish River Bush	Game Path	Gulley vegetation
21/3/73	0	0	-
8/9/73	0	0	-
10/4/74	1	9	30
19/4/74	0	3	116
20/4/74	0	1	102

KEY. -, habitat not sampled.

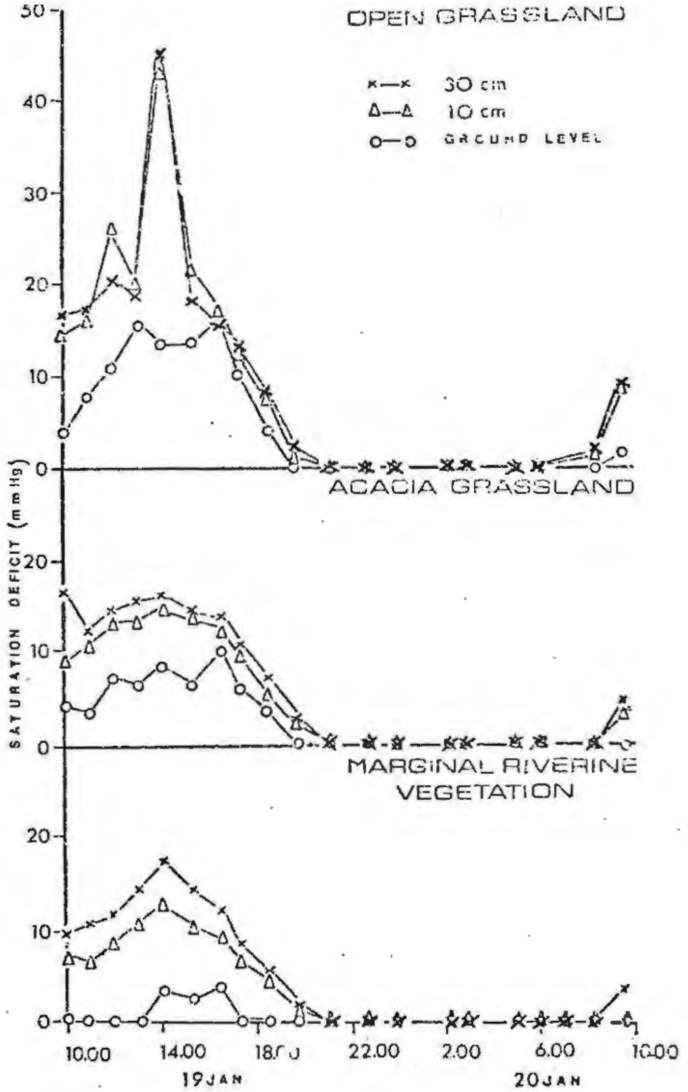

Fig. 1.

Fluctuations in saturation deficit recorded over 24 hours at different levels in the vegetation, in three habitats in the Kowie River valley, in summer, 1974.

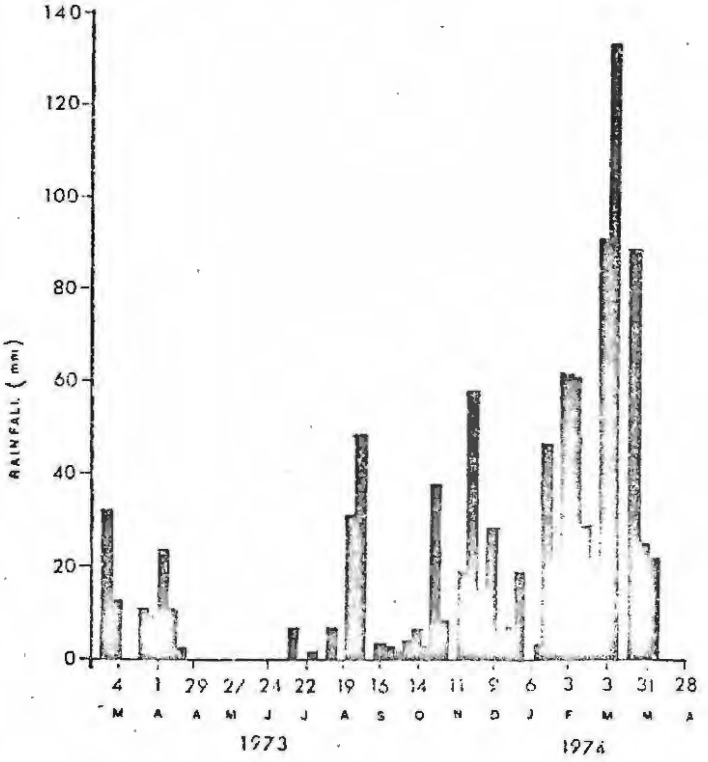

Fig. 2.

Weekly rainfall recorded at Paardekraal Farm.

habitats seldom exceeded zero. Day-time saturation deficits were recorded on 2 occasions in the Fish River Bush complex in autumn, 1974. Typical Fish River Bush was exceptionally dry, due to the lack of leaf litter and undergrowth. Saturation deficits were considerably lower on the verges of game paths, and were lowest in the leaf litter zone of gulley vegetation. These results show that larvae occurred in lowest numbers in the least humid microhabitats and in highest numbers in the most humid microhabitats. The latter were found in the protected leaf litter zones of decaying vegetable matter. The utilization of similar microhabitats has been recorded in Ixodes ricinus in Britain (Milne, 1952) and in Ixodes rubicundus in South Africa (Stampa, 1959).

Seasonal activity

Histograms of seasonal activity of larvae and nymphs are given in Fig. 3. In plotting the histograms, results of each 3 consecutive weekly samples have been summed, to allow comparison of a larger number of ticks and to reduce the effects of variation in tick behaviour, caused by changing daily weather conditions (Milne, 1943). For larvae, results are given for open grassland, Acacia grassland and marginal riverine vegetation. As the number of nymphs collected in all cases was low, the results for the 3 habitats have been summed.

Larvae were active from the start of the survey in April (autumn), 1973 until August, with a peak of activity in April and May. The decline in larval activity from the end of May, coincided with a decrease in the height and density of the herbaceous ground cover, caused by a lack of rain (Fig. 2). Larval activity was low in spring and early summer, and negligible in mid-summer, but increased in the humid conditions of late summer.

As winter conditions became drier (Fig. 2), there was a significant alteration in the distribution of larvae in the environment (Fig. 3). By the end of June, larvae were absent from open grassland. In July the

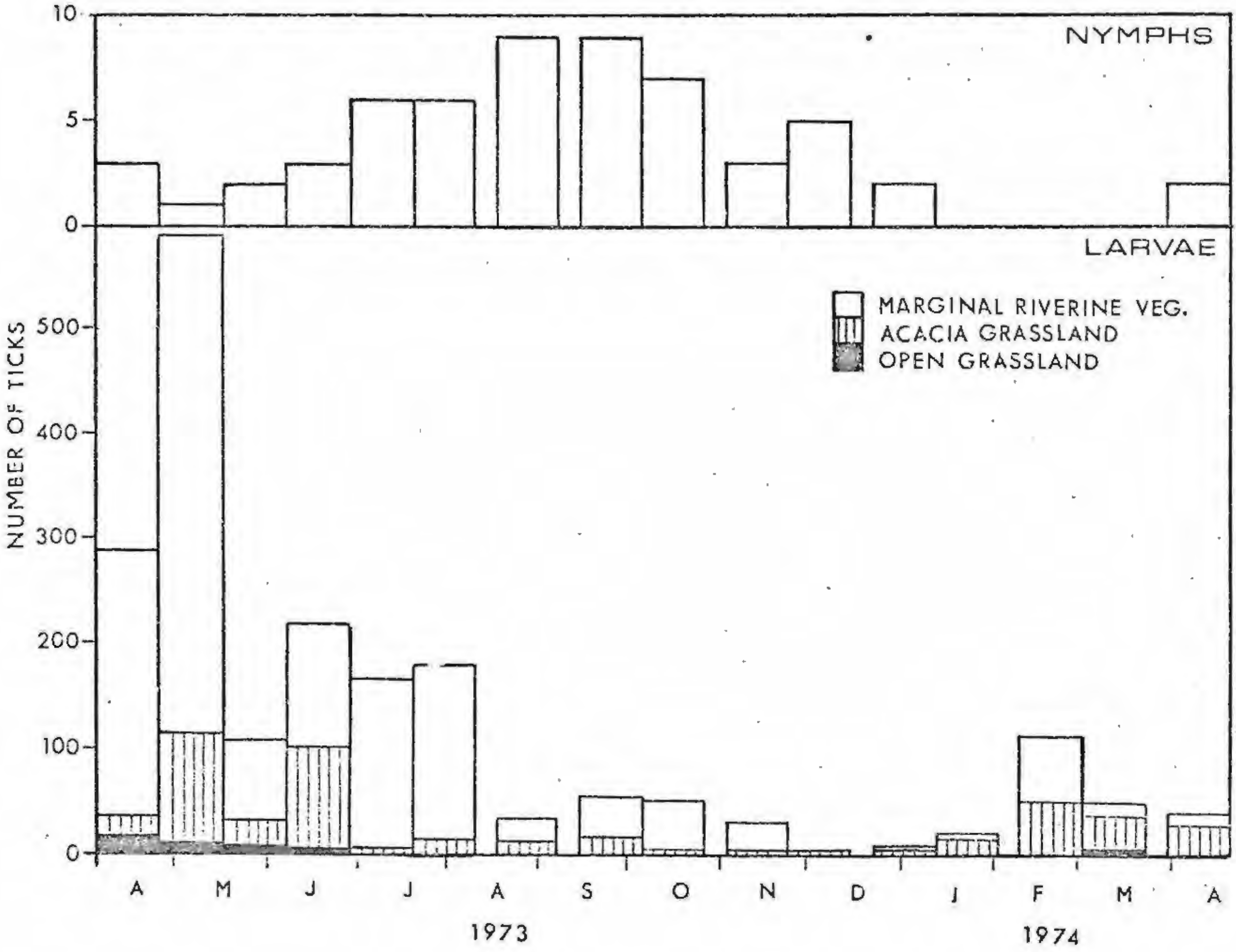

Fig. 3.

Histograms of seasonal activity of larvae and nymphs of *Haemaphysalis silacea*, sampled by the drag method.

numbers of larvae active in Acacia grassland relative to marginal riverine vegetation, were considerably lower than in May and June. This trend continued until November/December, when larvae became absent from Acacia grassland. The situation was reversed, however, during the more humid conditions of late summer.

The decline in larval numbers in marginal riverine vegetation in early March, was due to the flooding of this habitat by the swollen Kowie River. Most of the leaf litter and presumably a large number of the larvae were washed downstream.

Despite the low numbers of nymphs caught by the drag method, a clear trend of seasonal activity was discernible. There was an increase in nymphal activity from April, until a peak of activity in August/September. Activity then decreased, and there was no activity of nymphs from January until April. Peak nymphal activity followed approximately 4 months after peak larval activity.

Host relationships

The occurrence of H. silacea on hosts collected on Paardekraal Farm is given in Table 3. The highest incidence occurred on Artiodactyla, followed by Carnivora and Ciconiiformes. A low incidence occurred on Galliformes, Passeriformes, Rodentia and Lagomorpha.

Quantitative records of the seasonal occurrence of H. silacea on individual hosts are given in Table 4. Adults were restricted to artiodactyls, with the exception of 1 male which was removed from a Yellow mongoose. Immature ticks occurred on a wide range of hosts, but were found in highest numbers on artiodactyls. The numbers which occurred on other hosts were generally low, with the exception of a Lynx (Table 4, No. 25) and to a lesser extent a Hadeda ibis (Table 4, No. 2.).

The relative numbers of each developmental stage found on artiodactyls at different times of year (Table 4), indicate definite trends of seasonal activity which agree with those in Fig. 3. Immature ticks were present in largest numbers between May and October, while adults appeared to be more numerous in the summer months. Immature ticks occurred in considerably higher numbers in the humid conditions of autumn 1974, than in the drier autumn of 1973 (Fig. 2).

The numbers of ticks removed from hosts, collected at different localities on Paardekraal Farm, show the localized distribution of H.silacea. Duiker (Table 4, Nos 12 & 13) which were collected in open grassland, approximately 3 km from the river valley, had considerably lower infestations than Duiker (Table 4, Nos 9-11, 14-17) collected in the river valley. As Duiker have small home ranges (Wilson, 1966) it is concluded that the former were not in contact with the main population of H. silacea. Similar results were obtained in respect of Lynx (Table 4, Nos 24 & 25), Hadeda ibis (Table 4, No. 2 and an uninfested individual, collected 23/7/73) and domestic stock.

The Duiker (Table 4, Nos 14-17) and Bushbuck (Table 4, Nos 19-21), collected in the river valley on 21st May, 1974, showed marked differences in levels of infestation by different stages of H. silacea. On individual Bushbuck numbers of larvae were in excess of 2 400, while numbers of nymphs were less than 400. On 3 of the 4 Duiker examined, numbers of larvae were less than 1 000 per host and numbers of nymphs in excess of 500. On the 4th Duiker there were 1 826 larvae and 300 nymphs. These differences appear to arise as a result of the different feeding habits and habitat preferences of the 2 species of antelope, in relation to the habitat preferences of the ticks. Wilson and Child (1964) found that Bushbuck were browsers and "were restricted to areas with riparian scrub and dense cover along water courses". In the study area dense cover was provided by the Fish River Bush, while the marginal riverine and gulley habitats (the foci of the larval population) were extensively used as well-covered access routes into the Fish River Bush and along the river. It was also noted in these habitats that the herb, P. cernua, was extensively grazed and that large patches of the herb were invariably associated with high numbers of larvae. Wilson (1966) found that Duiker were also essentially

Table 3.

The occurrence of *Haemaphysalis silacea* on hosts collected at Paardekraal Farm.

Order	No. species	No. individuals	No. species infested	% species infested	No. individuals infested	% individuals infested
Chelonia	2	11	0	0	0	0
Squamata	4	5	0	0	0	0
Galliformes	2	4	1	50	1	25
Ciconiiformes	1	2	1	100	1	50
Anseriformes	1	1	0	0	0	0
Charadriiformes	1	1	0	0	0	0
Columbiformes	2	12	0	0	0	0
Coliiformes	2	4	0	0	0	0
Coraciiformes	1	1	0	0	0	0
Piciformes	2	2	0	0	0	0
Passeriformes	19	44	4	21	4	9
Rodentia	4	8	1	25	1	13
Lagomorpha	1	5	1	100	1	20
Hyracoidea	1	2	0	0	0	0
Artiodactyla	2	13	2	100	13	100
Carnivora	3	7	3	100	4	57
Primate	1	3	0	0	0	0
Totals	49	125	13	27	25	20

Table 4.

Hosts of *Haemaphysalis silacea*, collected at Paardekraal Farm.

Order	Species	Common Name	Host No.	Date	Infestation
Galliformes	*Numida meleagris*	Crowned guinea-fowl	1	30/8/73	N 4
Ciconiiformes	*Hagedashia hagedash*	Hadeda ibis	2	7/9/73	N 22: L 17
Passeriformes	*Pycnonotus barbatus*	Black-eyed bulbul	3	20/4/73	L 1
	Lamprocolius nitens	Cape glossy starling	4	6/9/73	N 1
	Corvultur albicollis	Cape raven	5	6/12/73	N 2
	Mirafra africana	Rufous-naped lark	6	10/5/74	N 2
Rodentia	*Aethomys namaquensis*	Namaqua rock mouse	7	3/8/73	L 3
Lagomorpha	*Lepus spp.*	Hare	8	7/5/74	N 5
Artiodactyla	*Sylvicapra grimmia*	Duiker	9	18/5/73	♂ 1:N 47:L 55
			10	7/9/73	♂ 8: ♀ 2:N 141:L 8
			11	16/10/73	♂ 30:N 437:L 171
			12	15/12/73	N 1
			13	15/12/73	N 1
			14	21/5/74	♂ 13: ♀ 1:N 300: L 1826
			15	21/5/74	♂ 10:N 593:L 471
			16	21/5/74	♂ 34: ♀ 2:N 89: L 457
			17	21/5/74	♂ 8: ♀ 1:N 502:L 932
	Tragelaphus scriptus	Bushbuck	18	18/1/74	♂ 421: ♀ 42:N 19: L 15
			19	21/5/74	♂ 400: ♀ 34:N 354: L 2799
			20	21/5/74	♂ 515: ♀ 21: N 345: L 3645
			21	21/5/74	♂ 391: ♀ 19:N 385 L 2432
Carnivora	*Cynictis penicillata*	Yellow mongoose	22	23/8/73	♂ 1
	Canis mesomelas	Black-backed Jackal	23	23/1/74	L 1
	Felis caracal	Lynx	24	6/6/74	N 1
			25	14/5/74	N 54:L 1043

KEY. L, larva(e); N, nymph(s).

browsers, but were extremely adaptable, and were found in a wide range of habitats. The observation that Duiker frequently browse on low shrubs in grassland habitats (Wilson, 1966) could account for the high infestations with nymphs. The lack of uniformity in samples of H. silacea removed from Duiker suggests that, those individuals having home areas in more open habitats, have higher infestations of nymphs than larvae, and vice versa. The higher numbers of adults on Bushbuck than on Duiker, suggests that adults occur in the same habitats as larvae.

The majority of larvae and nymphs of H. silacea attached on the lower regions of the limbs of hosts. Highest numbers occurred immediately above the hooves on artiodactyls and on the paws of Lynx. Low numbers occurred on the upper regions of the limbs, the sternum, belly, groin and perianal region. Unpaired adult males occurred in aggregations on the lower and mid regions of the limbs, and to a lesser extent on the groin. Paired adult males and females and single females were almost entirely restricted to the belly, groin and perianal regions. These observations suggest that the majority of ticks of all stages gain access to the host from the ground. On the host males always outnumbered females. Records from Bushbuck show that in mid-summer (Table 4, No. 18) males outnumbered females in a ratio of 10 to 1. By the end of autumn (Table 4, Nos 19-21), on average, males outnumbered females in a ratio of 18 to 1. This suggests that males remain attached for long periods of time, as is the case in A. hebraeum in which similar sex ratios occur on the host (Lounsbury, 1899; Whitnall et al., 1951; Norval, 1974).

On Paardekraal Farm H. silacea also occurred on domestic hosts; immatures were found on dogs, and all stages occurred on sheep, goats and cattle.

H. silacea was recorded at 17 localities in the Eastern Cape, other than Paardekraal Farm. Adults were found on Bontebok (Damaliscus dorcas), adults and immatures on Bushbuck and Kudu and immatures on Duiker and Water mongoose (Atilax paludinosus). All localities were either in the coastal bush area, or along the valleys of the major river systems.

DISCUSSION

In the Kowie River valley, there is 1 generation of H. silacea per annum. Larvae are active during autumn and early winter, nymphs during late winter and spring and adults during summer. As the activity peaks of each stage follow in close sequence, it is reasonable to assume that there are no prolonged periods of diapause (Balashov, 1968) and that the numbers of each stage which are active are a reflection of the numbers present in the environment. The abundance of larvae in the humid leaf litter zone of marginal riverine and gulley vegetation suggests that this microhabitat is the most favourable for egg development (Londt & Whitehead, 1972). Subsequent to hatching, the distribution of larvae in the environment is limited principally by microclimatic conditions. During dry conditions larvae are largely restricted to the leaf litter zone, but are able to penetrate adjacent habitats during humid conditions. The height of the herbaceous ground cover has no direct influence on the distribution of larvae, which are able to climb on to hosts from the ground. The density of the ground cover, however, modifies the microclimate and, therefore, has an indirect influence on larval distribution. Nymphs are able to tolerate higher saturation deficits than larvae, and occur predominantly in Acacia grassland on the river flood plain. Adults occur in the same humid microhabitat as larvae; where they are able to survive the hot, dry mid-summer conditions.

The hosts of H. silacea have in common an association with the river valley system. The major hosts are artiodactyls, in particular Bushbuck. Other hosts, such as Hadeda ibis and Lynx may be of importance in the transportation of H. silacea to other areas.

The association of H. silacea with Fish River Bush in the river valleys of the Eastern Cape (Theiler, 1945) is indirect. The dense Fish

River Bush provides a habitat for a large number of artiodactyls, in particular Bushbuck. The focus of the tick population, on the other hand, is the marginal riverine and gulley vegetation. The host/tick interaction arises as a result of the daily movements and feeding habits of the hosts. A similar host/tick interaction occurs in the coastal bush complex. Here the vegetation structure is in parts similar to marginal riverine vegetation (Londt & Whitehead, 1972) and large populations of Bushbuck and Duiker are known to exist in these areas.

The absence of H. silacea from the grass and shrub covered plateau of the Eastern Cape, can be attributed to the absence of suitable microhabitats and an insufficient density of artiodactyl hosts. The absence of one or other component of the habitat/host complex required for the survival of H. silacea, has prevented its establishment in other areas. It is likely that the long dry periods experienced in the winter rainfall areas of the Western Cape or in the summer rainfall areas to the north are limiting factors. In the Eastern Cape, which is situated between the summer and winter rainfall belts, there is generally some precipitation in all seasons of the year.

ACKNOWLEDGEMENTS

I wish to thank Mr F.D. Ford of Paardekraal Farm for his help and co-operation, Professor G.B. Whitehead and Mr J.W. Webb of Rhodes University for constructive criticism of the manuscript, Mr J. Greig of the Nature Conservation Department for assistance in the host survey, and Miss C. Crowe and Mr M. Knight for technical assistance.

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7.3

Studies on the ecology of Amblyomma marmoreum Koch, 1844 (Acarina: Ixodidae)

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ABSTRACT:

In the Eastern Cape Province of South Africa, larvae and nymphs of Amblyomma marmoreum Koch occur in habitats in which there is a combination of tree cover and herbaceous ground cover. The immature stages of A. marmoreum are parasitic on reptiles, birds and mammals, while adult ticks occur only on reptiles. The most important hosts for all developmental stages are Mountain tortoises (Geochelone pardalis), and in the home areas of tortoises the density of ticks is high. Larvae are active in late summer and autumn. The rate of feeding is temperature dependent, and some larvae which attach on tortoises in late autumn do not complete feeding until the following spring. Nymphs which occur in the home area of a tortoise become active in response to CO_2 in early spring. Adult ticks, and nymphs which occur outside the home area of a tortoise, become active in summer in response to rising temperatures. In nymphs which feed in spring, and hence develop into adults in midsummer, the life cycle is completed in one year. In nymphs which feed in midsummer, the life cycle is completed in two years.

Reptiles are the major hosts of many African tick species of the genera Amblyomma and Aponomma. No quantitative ecological studies have, however, been made on any of these species and little is known of the interactions of the ticks with reptilian hosts. For this reason a study has been made on the ecology of the Tortoise tick, Amblyomma marmoreum Koch. The distribution records of Theiler and Salisbury (1959) and Theiler (1962) show that A. marmoreum occurs over the greater part of south-eastern Africa, and is most common in the Eastern Cape Province of South Africa. Information on the biology of the tick is limited to a few observations recorded by Lounsbury (1905).

This paper deals primarily with the ecology of A. marmoreum in a study area on Paardekraal Farm, 15 km SE of Grahamstown. Information is given on habitat preferences of larvae and nymphs, and the quantitative seasonal occurrence of all developmental stages on indigenous hosts. In addition a brief study has been made on the life cycle of A. marmoreum in the laboratory. From this data it has been possible to show the relationship of A. marmoreum with reptilian and non-reptilian hosts, and the relationship of seasonal activity, development and occurrence of the tick with the seasonal activity and behaviour of the major host. The relationship of A. marmoreum with domestic stock, and possible implication in disease transmission is also discussed.

MATERIALS AND METHODS

The survey area, situated in the Kowie River valley, consisted of 3 major components. (1) River banks. These supported a narrow band of dense, marginal riverine vegetation (habitat 1). (2) River flood plain. The dominant plant species was Acacia karroo, in the form of low growing trees above a ground flora of grass and scattered herbs. Part of the Acacia grassland (habitat 2a) had been artificially modified, by removal of A. karroo trees, to form open grassland (habitat 2b). (3) Steeply rising slopes bordering on the river valley. These were covered by typical Fish River Bush (habitat 3a), which was traversed by game paths (habitat 3b) and broken by gulleys or minor tributaries (habitat 3c). Detailed descriptions of the vegetation structure and microclimate of each habitat, are given in a previous paper (Norval, 1974a). Macroclimatic conditions for the survey period (rainfall and thermohygrograph records) are also given by Norval (1974a).

Larvae and nymphs were sampled by the drag method, as described by Norval (1974a). Marginal riverine vegetation (1), Acacia grassland (2a) and open grassland (2b) were sampled at weekly intervals from April, 1973 to April, 1974. Habitats in the Fish River Bush complex (3a-c) were sampled on 5 occasions during this period. Hosts were either captured or shot in the field, and then examined for ticks in the laboratory.

To rear A. marmoreum in the laboratory, larvae were obtained either from the field, by dragging, or from eggs laid by females which had fed on tortoises (Geochelone pardalis). Larvae and nymphs were fed on the ears of a sheep, as described by Norval (1974b). Tortoises captured in the field were maintained individually in metal cages, each of which stood above a water bath. Detached ticks were collected daily from the water baths. Non-parasitic stages were maintained in darkness in an incubator at 26°C and 90% relative humidity.

RESULTS

Life cycle

The preoviposition period lasted 12-15 days, and the oviposition period, approximately 30 days. Larvae began to hatch 37 days after the start of oviposition. The larval engorgement period was 6-12 days on the ears of a sheep. Larvae required up to 30 days to complete feeding on a tortoise collected in the field. The nymphal premoult period lasted 2-3 weeks, and nymphs engorged to completion in 8-20 days on the ears of a sheep. Nymphs required up to 51 days to complete feeding on tortoises. The adult premoult period lasted 3-4 weeks, and females took up to 60 days to complete feeding on tortoises. The majority of males remained continuously attached while tortoises were held in captivity. Sweatman (1970) has shown that the slower feeding rate of ticks on poikilotherms than on homiotherms is due to the lower body and hence skin temperatures of the former.

Habitat preference

The total numbers of larvae and nymphs collected on 48 occasions in open grassland, Acacia grassland and marginal riverine vegetation are given in Table 1. Larvae and nymphs showed similar habitat preferences, with largest numbers occurring in Acacia grassland. No nymphs were collected

Table 1.

The total numbers of larvae and nymphs of <u>Amblyomma marmoreum</u>, collected in habitats in the Kowie River valley, on 48 occasions from April 1973 to April 1974.

	Open Grassland	Acacia Grassland	Marginal Riverine veg.
Total No. larvae	16	301	132
% of larvae	3,6	67,0	29,4
Total No. nymphs	0	19	8
% of nymphs	0	70,4	29,6

in open grassland, and the number of larvae collected in this habitat was low. In marginal riverine vegetation, larvae were invariably collected on patches of herbaceous vegetation and were absent from areas with no ground cover.

In the Fish River Bush complex, a total of 4 larvae were collected (5 occasions) on the grass covered verges of game paths. No larvae were collected in typical Fish River Bush or in the vegetation of the gulleys.

In previous ecological studies in South Africa (Stampa, 1959; Kraft, 1961; Londt & Whitehead, 1972; Norval, 1974a) it has been shown that the non-parasitic stages of ixodid ticks require specific microclimatic conditions for survival, and that these conditions are determined largely by vegetation structure. In the Kowie River Valley, Norval (1974a) found that larvae of Haemaphysalis silacea Robinson were most abundant in the humid leaf litter zones of marginal riverine and gulley vegetation, while nymphs occurred in highest numbers in slightly less humid microhabitats in Acacia grassland. Larvae and nymphs of H. silacea were largely absent from the dry microhabitats of open grassland and Fish River Bush. The distribution of larvae and nymphs of A. marmoreum was similar with regard to dry conditions, but larvae were able to tolerate less humid microhabitats than larvae of H. silacea. The results show that a combination of tree cover and herbaceous ground cover are necessary for the survival of A. marmoreum.

Seasonal activity

Histograms of seasonal activity of larvae and nymphs, collected in Acacia grassland and marginal riverine vegetation are given in Fig. 1. In plotting the histograms, results of each 3 consecutive weekly samples from both habitats have been summed, to allow comparison of a larger number of ticks, and to reduce the effects of variation in tick behaviour, caused by changing daily weather conditions (Milne, 1943). Larvae showed greatest activity in late summer and autumn, from February until early June.

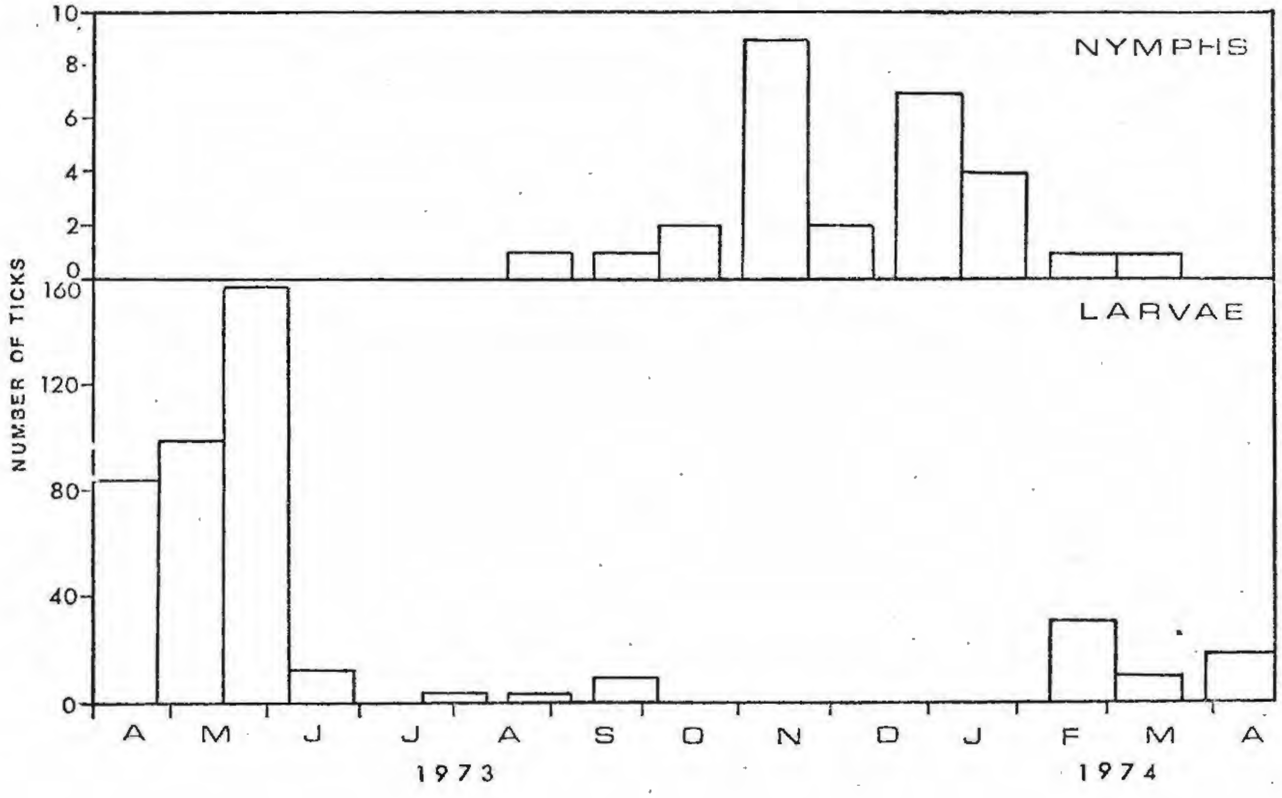

Fig. 1.

Histograms of seasonal activity of larvae and nymphs of *Amblyomma marmoreum*, sampled by the drag method.

Larval activity was low during winter, and there was no activity during the hot dry months of midsummer. Larvae reappeared in low numbers in late January. Nymphs were active during spring and summer, from August until March. Peak nymphal activity was recorded in midsummer, from November until the end of January.

Host relationships

A. marmoreum has frequently been confused with other *Amblyomma* species, belonging to the "*A. marmoreum*" group (Theiler & Salisbury, 1959). As a result, many of the pre-1959 host records of *A. marmoreum* are probably invalid. Theiler (1962) lists the following species as hosts of adult and immature ticks:- Squamata - *Gerrhosaurus validus*; *Varanus* sp.; *Varanus albigularis*; *Varanus niloticus*; *Python* spp.; *Python sebae*; *Dendroaspic* spp.; *Naja* spp.; *Naja nigricollis*; *Hemachatus hemachates*; *Bitis arietans*; Chelonia - *Kinixys belliana*; *Homopus femoralis*; *Geochelone pardalis*; *Psammobates* spp.; *Chersina angulata*. The following species are listed as hosts of immature ticks:- Insectivora - *Erinaceus frontalis*; *Elephantulus rupestris*; Lagomorpha - *Lepus saxatalis*; *Pronolagus* spp.; Galliformes - *Numida meleagris*. Theiler and Salisbury (1959) recorded adults on sheep (2 records) and oxen (1 record), and nymphs on turkeys.

The occurrence of *A. marmoreum* on hosts collected on Paardekraal Farm is given in Table 2. A high incidence of infestation occurred in Chelonia, Squamata, Coraciiformes and Carnivora, and a low incidence of infestation occurred in Galliformes, Ciconiiformes, Columbiformes, Passeriformes, Lagomorpha, Hyracoidea and Artiodactyla.

Quantitative records of the occurrence of *A. marmoreum* on individual hosts are given in Table 3. Adults were restricted to Reptilia, with highest numbers occurring on Mountain tortoises (*G. pardalis*). Nymphs occurred on a wide range of hosts, but were found in highest numbers on Reptilia. Larvae occurred on a similar host range, but in addition to

Table 2

The occurrence of *Amblyomma marmoreum* on hosts collected at Paardekraal Farm.

Order	No. species	No. individuals	No. species infested	% species infested	No. individuals infested	% individuals infested
Chelonia	2	11	1	50	10	91
Squamata	4	5	3	75	3	60
Galliformes	2	4	1	50	2	50
Ciconiiformes	1	2	1	100	1	50
Anseriformes	1	1	0	0	0	0
Charadriiformes	1	1	0	0	0	0
Columbiformes	2	12	1	50	1	8
Coliiformes	2	4	0	0	0	0
Coraciiformes	1	1	1	100	1	100
Piciformes	2	2	0	0	0	0
Passeriformes	19	44	2	11	3	7
Rodentia	4	8	0	0	0	0
Lagomorpha	1	5	1	100	1	20
Hyracoidea	1	2	1	100	1	50
Artiodactyla	2	13	2	100	5	38
Carnivora	3	7	2	67	4	57
Primata	1	3	0	0	0	0
Totals	49	125	16	33	32	26

Table 3

Hosts of *Amblyomma marmoreum*, collected at Paardekraal Farm.

Order	Species	Common Name	Host No.	Date	Infestation
Chelonia	*Geochelone pardalis*	Mountain tortoise	1	6/4/73	♂3: ♀1: N3: L27
			2	21/9/73	♂36: ♀7: N244:L48
			3	30/9/73	♂16: ♀7: N25: L2
			4	3/10/73	♂32: ♀3: N12: L16
			5	18/10/73	♂28: ♀5: N117
			6	23/11/73	♂63: ♀26: N67
			7	10/1/74	♂38: ♀3: N4
			8	15/2/74	♂15: ♀3: N1: L3
			9	15/3/74	♂71: ♀5: N1: L25
			10	19/4/74	♂52: ♀6: N8: L521
Squamata	*Bitis arietans*	Puff adder	11	22/3/73	♂5
	Dispholidus typhus	Boomslang	12	7/12/73	N24
	Varanus albigularis	Rock leguvaan	13	29/11/73	♂1: ♀1: N16
Galliformes	*Numida meleagris*	Crowned guinea-fowl	14	1/9/73	L2
			15	7/5/74	L2
Ciconiiformes	*Hagedashia hagedash*	Hadeda ibis	16	23/8/73	N1
Coraciiformes	*Lophoceros flavirostris*	Crowned hornbill	17	11/10/73	N1
Columbiformes	*Streptopelia capicola*	Cape turtle dove	18	15/3/74	L1
Passeriformes	*Emberiza flaviventris*	Golden-breasted bunting	19	12/10/73	L1
	Mirafra africana	Rufous-naped lark	20	15/3/74	L3
			21	10/5/74	L3
Lagomorpha	*Lepus* sp.	Hare	22	7/5/74	L89
Hyracoidea	*Procavia capensis*	Rock dassie	23	19/9/73	N2
Artiodactyla	*Sylvicapra grimmia*	Duiker	24	21/5/74	L50
			25	21/5/74	L6
	Tragelaphus scriptus	Bushbuck	26	21/5/74	N1: L13
			27	21/5/74	L1
			28	21/5/74	L1
Carnivora	*Canis mesomelas*	Black-backed jackal	29	23/8/73	N1
			30	23/1/74	N2
	Felis caracal	Lynx	31	6/6/72	L1
			32	14/5/74	L6

KEY. L, larva(e); N, nymph(s).

Reptilia, were found in high numbers on Duiker and a Hare.

It was found that the heaviest infestations of A. marmoreum occurred on the largest tortoises. In Fig. 2, the percentage infestation by each developmental stage is given for individual tortoises, to allow a comparison of the composition of infestations at different times of year. The results show that larvae first appeared on tortoises in February, and increased in number through March, to reach a peak in April (similar to Fig. 1). Tortoises entered a state of semi-hibernation (Hewitt, 1937) in autumn (April-June) and became active again in spring (September/October). Tortoises collected in September and early October, all had low numbers of larvae attached, despite the scarcity of larvae in the environment (Fig. 1). The majority of these larvae were approaching full engorgement, and it was concluded that they had attached the previous autumn. Sweatman (1970) reports that the temperature threshold for complete engorgement of Hyalomma aegyptum is 20°C. Fig. 3 shows that during winter, the total number of hour degrees per week remained below the level, equivalent to 20°C continuously. It can be expected that under these conditions the rate of engorgement was extremely slow, and in some cases required longer than the entire winter. Nymphs were present on tortoises in large numbers in early spring, when the tortoises became active. The numbers then declined through midsummer and were low by late summer and autumn. These results do not match the results obtained by the drag method (Fig. 1), where peak activity was recorded over the midsummer months. The percentage infestation of adult males and females on tortoises, increased from spring to reach a peak in midsummer and then declined through late summer and autumn.

On Paardekraal Farm, larvae of A. marmoreum were found on domestic dogs, and nymphs on cattle, sheep and goats. On 15th May, 1973, 50 larvae were removed from a dog, and 2 days later a further 29 larvae were removed from the same dog. Nymphs were frequently found on cattle during the spring and summer months, and infestations per animal ranged from 1 to 6 ticks. The numbers of nymphs occurring on sheep and goats were lower; approximately 1 nymph per 10 animals.

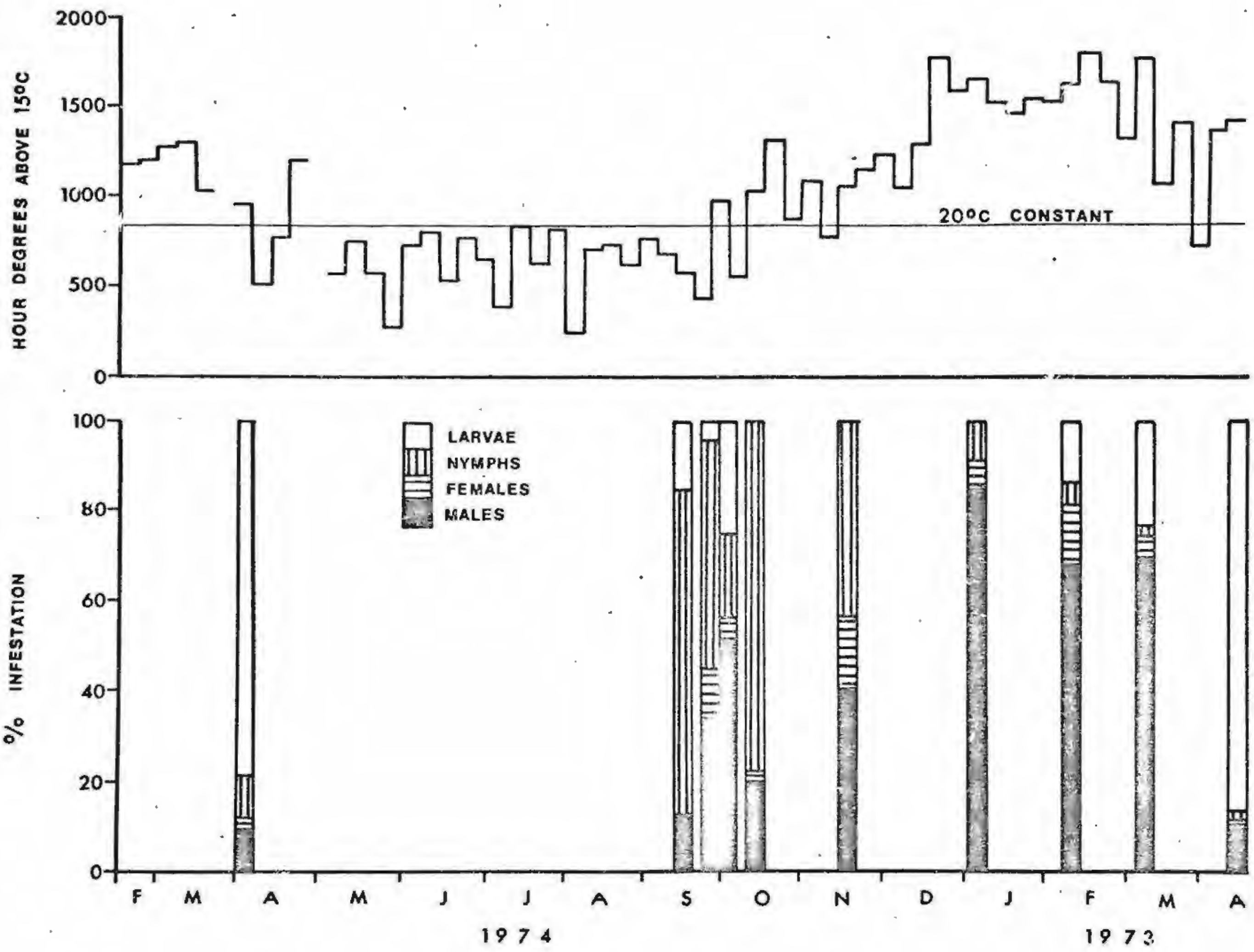

Fig. 2.

Hour degrees above 15°C, calculated from thermohygrograph records (above). The percentage infestation of Mountain tortoises (Geochelone pardalis) with larvae, nymphs and adult males and females of Amblyomma marmoreum (below).

At localities in the Eastern Cape, other than Paardekraal Farm, A. marmoreum was found on the following hosts:- G. pardalis, all stages; Orcteropus afer, nymphs; Hystrix africae, Canis mesomelas and Procavia capensis, larvae.

DISCUSSION

It is clear that the major hosts of A. marmoreum in the Eastern Cape are Mountain tortoises (G. pardalis), and that the ecology of the ticks is closely related to the seasonal activity and behaviour of the tortoises. Hewitt (1937) reports that tortoises have a pronounced "homing instinct" and "do not travel far from home". The same author states that tortoises "take up the same winter quarters year after year", and in tortoises kept in captivity it has been observed that individuals return to roughly the same spot each night (Paton, personal communication). From the point of view of tick ecology, the homing instinct of tortoises is of major importance, as it results in a concentration of ticks in a relatively small area in which there is a high probability of finding a host. This fact was demonstrated in the field during the summer of 1972/73, when a large female tortoise was observed on 6 occasions over a period of one month in an area of approximately 50 sq. m. A single drag of 50 m in this area (partly Acacia grassland and partly marginal riverine vegetation) on 22nd March, yielded 2 251 larvae, which is more than the total number of larvae collected over the entire survey period (Table 1) when drags were taken at random within each habitat.

In early summer the activity curve of nymphs collected by dragging (Fig. 1) followed the temperature curve (Fig. 2), as was the case with the case with the adult activity curve (Fig. 2). This indicates that under 'normal' circumstances, activity in nymphs and adults is stimulated by climatic conditions, notably by rising seasonal temperatures. Similar results have been obtained in respect of Ixodes ricinus L. in Britain

(MacLeod, 1936) and *Amblyomma americanum* (L.) in North America (Semtner & Hair, 1973). Nymphs of *A. marmoreum* which occur in the home area of a tortoise, must on the other hand, be stimulated to activity by host-induced factors (Balashov, 1968), to give the spring peak of activity seen on tortoises. In both *I. ricinus* (MacLeod, 1938) and *A. americanum* (Semtner & Hair, 1973) early spring infestations have also been observed on hosts, and it was suggested that ticks were stimulated by host body heat and CO_2. In the case of tortoises, the influence of body heat can be discounted. In regard to CO_2 it was found that nymphs of *A. marmoreum* were readily attracted to CO_2 traps (design by Wilson *et al*. (1972)), while adults and larvae were not. Further evidence for the attraction of nymphs by CO_2 is that the majority of nymphs attach on the head, neck and around the bases of the front legs of tortoises, while adults are more numerous around the bases of the hind legs and larvae are spread fairly evenly between the two areas. Nymphs may well have been attracted to tortoises during the winter months, as immediately after emergence in spring the tortoises were heavily infested and some of the nymphs were partially engorged.

It is apparent from the field data (in conjunction with observations made in the laboratory) that the life cycle of *A. marmoreum* is completed in either one or two years in the Eastern Cape. The one-year cycle is completed by ticks, which, as larvae, attach on a tortoise in late summer, and then detach in the home area of the tortoise and moult into nymphs during winter. The unfed nymphs are attracted to the tortoise and attach in late winter or spring, and then detach and moult into adults during early summer. Adults attach to the tortoise in midsummer, whereafter, the females detach and lay eggs. The eggs hatch during the later half of summer and autumn. The two-year cycle is completed by ticks, which, as larvae, attach either to a tortoise in late autumn (and do not complete feeding until the following spring) or to another host and moult outside the home area of a tortoise.

The former moult into nymphs in early summer, and the latter, as in the one-year cycle, moult during winter. The emergent nymphs in both cases become active in midsummer, and moult into adults during late summer. These adults are then active the following summer.

The host records show that the numbers of immature ticks which are likely to be carried out of the home areas of tortoises by other reptilian and non-reptilian hosts, are insignificant. The occasional host on which large infestations of larvae or nymphs were found, probably shared the same home area as a tortoise. Non-territorial or migratory hosts may be of ecological importance in the transportation of the immature stages of A. marmoreum to other areas. Adults of A. marmoreum showed a high degree of host specificity, and the only animals on which fully engorged females were found were tortoises. It seems unlikely that A. marmoreum will become established in areas from which tortoises are absent.

Domestic animals were shown to be only lightly infested by the immature stages of A. marmoreum, and played little part in the ecology of the tick. The only important disease of livestock in the Eastern Cape, which is known to be transmitted by ticks of the genus Amblyomma, is 'heartwater fever' (Neitz, 1956). Howell (1970) states that 'heartwater fever' is not transmitted by A. marmoreum, and this is supported by preliminary experiments carried out in this laboratory. It can, therefore, be concluded that A. marmoreum is of little or no importance to the farmer.

ACKNOWLEDGEMENTS

I wish to thank Mr F.D. Ford of Paardekraal Farm for his help and co-operation, Professor G.B. Whitehead and Mr J.W. Webb of Rhodes University for constructive criticism of the manuscript, Mr J. Greig of the Nature Conservation Department for assistance in the host survey, and Miss C. Crowe and Mr M. Knight for technical assistance.

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7.4. *Haemaphysalis leachii leachii*.

H. leachii leachii is primarily a parasite of carnivores and is common in most parts of Africa which receive more than 500 mm of rain per annum (Hoogstraal, 1956; Theiler, 1962). At Paardekraal Farm, *H. leachii leachii* was found on Lynx, Black-backed jackal (Table 11) and domestic dog (Table 12). One nymph was collected during dragging.

7.5. *Ixodes pilosus*.

I. pilosus occurs in the "sourveld" areas of South Africa, and in the Eastern Cape is confined to a narrow strip along the coast (Theiler, 1962). The rapid decline in abundance of *I. pilosus* away from the coast, was observed during this investigation. Heavy infestations of larvae, nymphs and adults of *I. pilosus* were recorded on Bushbuck and Duiker which were shot at the coast (Kasouga Farm) and at Woodlands Farm, 12 km inland. At Paardekraal Farm, 28 km inland, the incidence of *I. pilosus* on Bushbuck and Duiker was however low (Table 11), leaving little doubt that the species was only tenuously established on this farm. Kraft (1961) and Londt and Whitehead (1972) found, on coastal farms, that larvae of *I. pilosus* were restricted to humid, tree protected microhabitats. On the basis of these findings it seems likely that the absence of *I. pilosus* from inland areas results from the inability of the larvae to withstand the drier conditions which are encountered in these areas (Kraft, 1961). At Paardekraal Farm, only one nymph and one larva were collected during dragging.

The records of Theiler (1962) show that *I. pilosus* is restricted to mammalian hosts; the largest numbers of host species belonging to the orders Carnivora and Artiodactyla. Similar results were obtained in the host survey at Paardekraal Farm, where *I. pilosus* was recorded on Bushbuck, Duiker, Lynx, Black-backed jackal, Yellow mongoose (Table 11) and domestic dogs (Table 12). With the exception of one Lynx (Table 11, No. 117) infestations were light (one to two ticks per host). It seems likely that the heavily infested Lynx had migrated to Paardekraal Farm from the coastal area, shortly before collection.

J. ent. Soc. sth. Afr. 1974
Vol. 37, No. 1, pp. 129–133

Copulation and feeding in males of *Ixodes pilosus* Koch 1844 (Acarina: Ixodidae)

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In a sample of 29 males and 102 females of *Ixodes pilosus* Koch, removed from Bush Buck and Duiker, 51,7% of males were attached to the host. The remainder were in association with females; 24,1% in copula and 24,1% attached to females. Of the females, 90,2% were unpaired, 6,9% in copula, while 1% were parasitized by a single male and 2% were parasitized by 3 males. A large spermatophore sac protruded from the genital aperture in 5,9% of females, while in a number of others spermatophores were in various stages of deflation.

The attachment of males to engorging females has previously been observed in *Ixodes holocyclus* Neumann (Moorhouse, 1966). *I. pilosus* differs from *I. holocyclus* in that males remain attached to the female after full engorgement. Males of *I. pilosus* show no preferential sites of attachment and in some cases the mouthparts penetrate the lumen of the female gut.

INTRODUCTION

The genus *Ixodes* (Prostriata) differs from the genera of the Metastriata in that spermatogenesis is completed in the nymphal stage and males are able to copulate without a blood meal. This allows for copulation on the ground or on the host, and there is some doubt as to whether males actually feed (Arthur, 1962). Moorhouse (1966) observed that males of *Ixodes holocyclus* Neumann are parasitic upon engorging female ticks and suggests that the male "obtains at least the major part of its nutrition from this source". In *I. holocyclus* the chelicerae and hypostome of the male are fully inserted, and the ventral integument of the female is the most common site of attachment. The period of attachment varies from 25 minutes to longer than 6 hours. After detachment, wounds are left in the integument, from which haemolymph oozes. These later dry and leave permanent dark coloured scars.

In a sample of *Ixodes pilosus* Koch, removed from Bush Buck (*Tragelaphus scriptus sylvaticus* Sparrman) and Duiker (*Sylvicapra grimma burchelli* H. Smith), males were found either attached to the host or associated with females. The latter either in copula or parasitic on the female. In this paper it is shown that the coupling mechanism during copulation in *I. pilosus* is similar to that in other species of *Ixodes* (Arthur, 1962, Moorhouse, 1966). Unlike other ixodid ticks (Feldman-Muhsam and Borut, 1971), however, it appears that the entire spermatophore in *I. pilosus* is drawn into the receptaculum seminis after copulation. Homoparasitism in *I. pilosus* differs from *I. holocyclus* in that males remain attached to the female after full engorgement. Males of *I. pilosus* showed no preferential sites of attachment and in some instances the mouthparts penetrated the lumen of the female gut. As in *I. holocyclus*, homoparasitism is most common in females approaching full engorgement.

MATERIALS AND METHODS

Ticks collected from the hosts, shot in the Bathurst District of the Eastern Cape, in July 1973, were placed in 70% alcohol and later examined in the laboratory. Selected specimens were dried in air and fixed to specimen stubs with silver paint. Specimens were coated with gold in a Hitachi HUS 3B vacuum evaporator and examined in a JEOL JSM U3 scanning electron microscope.

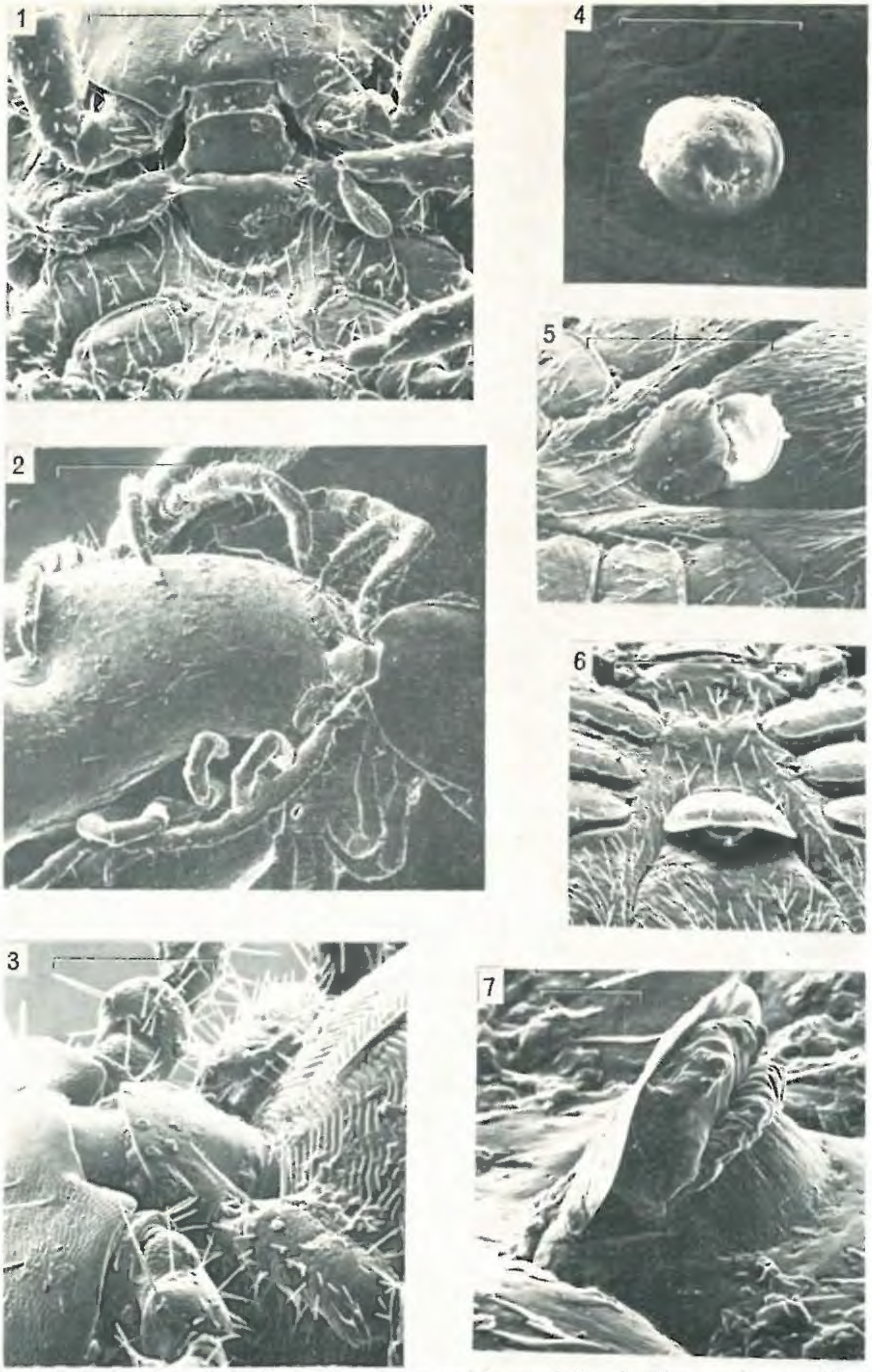
RESULTS

Of the total number of males in the sample (29), 51,7% were attached to the host. The remainder were in association with females. Of these, 24,1% were in copula and 24,1% were attached to females. Of the total number of females in the sample (102), 90,2% were unpaired, 6,9% were in copula, while 1% were parasitized by a single male and 2% were parasitized by 3 males.

During copulation (fig. 1) males insert the chelicerae and hypostome into the female genital aperture. The anterior lip of the female genital aperture is forced forwards and rests on the basis capitulli of the male. The palps of the male are splayed slightly forwards and rest on the female integument between coxae 3 and 4. The male mouthparts are held almost at right angles to the long axis of the body and appear to be entirely responsible for securing the male to the female.

Moorhouse (1966) states that after spermatophore transfer, the male *I. holocyclus* withdraws the mouthparts and leaves the female while the empty spermatophore sac is left protruding from the female genital aperture. In *I. pilosus* large bulbous spermatophore sacs (fig. 4), clearly visible under the light microscope, were present in 5,9% of females examined. A number of females possessed smaller sacs (fig. 5) which were often difficult to see and were therefore not counted. In some cases there appeared to be the remnants of a spermatophore sac protruding from the genital aperture (figs 6 and 7). These lay beneath the anterior lip of the genital aperture and could only be seen under the scanning electron microscope. It appears that there is a slow deflation of the spermatophore sac and that eventually the whole sac is drawn into the receptaculum seminis. As this process progresses the anterior lip of the genital aperture gradually returns to its normal position, covering the aperture.

In some instances males of *I. pilosus* were observed to parasitize engorging females. As seen in figs 2 and 3 the hypostome and chelicerae of the male penetrate the integument of the female to the level of the basis capitulli while the palps are splayed outwards. Males removed with forceps from the integument of the female left a circular hole of approximately 0,16 mm in diameter where the mouthparts had penetrated. To determine the depth of penetration, the cuticle was dissected from a female,which carried 3 parasitic males. One male was attached just anterior to the spiracle and the mouthparts were embedded in the fatty tissue which surrounds the trachae. The other 2 males were attached in the anal region, where the walls of the gut caeca adhere closely to the integument. In both cases the mouthparts had penetrated the lumen of the gut. Of the 7 homoparasitic males in the sample, 1 was attached dorsally, 2 ventrally and 4 laterally on the female idiosoma. This suggests that there is no preferential attachment site, and



Figs 1–7. *Ixodes pilosus*. 1. Male and female engaged in copulation. 2. Three males parasitic on engorging female. 3. Penetration of female integument by male. 4. Inflated spermatophore protruding from female genital aperture. 5. Partially deflated spermatophore protruding from female genital aperture. 6. Deflated spermatophore beneath anterior lip of female genital aperture. 7. Remnants of spermatophore protruding from female genital aperture. (Scale lines: 1, 4, 5, 6 = 0,5 mm, 2 = 1 mm, 3 = 0,25 mm, 7 = 0,1 mm).

the penetration of the gut is a matter of chance. No scars indicative of previous male attachments were found on females of *I. pilosus* that were examined, which differs from the observations on *I. holocyclus* (Moorhouse, 1966). A parasitized female which appeared to be fully engorged, detached naturally with 3 males remaining attached, within minutes of the host (Bush Buck) being killed.

The mean length of 92 unparasitized females was 2,50 mm (range 1,68–5, 54 mm) and of 7 females in copula was 2,72 mm (range 1,76–3,44 mm), while the lengths of the 3 parasitized ticks were 2,26 mm (1 parasitic male) and 4,21 and 9,56 mm (3 parasitic males). Of the 3 largest ticks in the sample, 2 were parasitized by 3 males each. This suggests that parasitism by males is most common on females approaching the fully engorged state. If this assumption is correct, the low percentage of parasitized females (2,94%) may be misleading, as the majority of females in the sample were in a partially engorged state.

DISCUSSION

Normally the empty ecto-spermatophore remains attached to the female genital aperture after copulation in ixodid ticks and the endo-spermatophore forms the capsule of spermiophores. This is ultimately found in the receptaculum seminis of the female (Feldman-Muhsam and Borut, 1971). It appears from the range of size of spermatophores protruding from the genital apertures of engorging females of *I. pilosus*, that the entire spermatophore is drawn into the receptaculum seminis.

Feeding in males of *Ixodes* remains an enigma, for Arthur (1962) states that no traces of fresh blood were found in the gut of *Ixodes* males. Moorhouse (1966) states that he never found males of *I. holocyclus* attached to the host, and concludes that the male feeds only on the haemolymph of the female. In *I. pilosus*, males were found attached to both the host and the engorging female and may therefore have alternative sources of food. It seems likely that many species of the genus *Ixodes* do not feed and the mouthparts function only in copulation. This could explain the sexual dimorphism of mouthparts, a feature restricted to this genus. Nuttall (1911) groups the various species of *Ixodes* as follows: 1. Species in which both sexes occur on the host. (*a*) Species in which the sexes are found in copula on the host. (*b*) Species in which the sexes attach near to one another on the host. 2. Species in which only the females occur on the host. 3. Species in which only the females are known.

Neither *I. holocyclus* nor *I. pilosus* fits into this scheme. In the former, males do not attach to the host, but are found both in copula with, and attached to, engorging females. In the latter, males are found attached to both host and female, and also in copula on the host. In *I. pilosus*, females outnumbered males by about 3:1 on the host, suggesting that mating may occur on the ground or on the host. This could explain the apparently stable attachments of males upon engorging females, as the former having fed, could detach on the ground and seek further unmated females.

ACKNOWLEDGEMENTS

I express my thanks to Mr L. G. Stirk of Woodlands Farm and Mr F. P. Ford of Kasouga Farm for allowing me to attend hunts on their farms, to Dr G. B. Whitehead and Dr J. G. H. Londt for valuable comment concerning the manuscript and Mr Robin Cross for his considerable assistance in the use of the scanning electron microscope.

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Manuscript received 1 October, 1973.

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7.6. Aponomma exornatum

The distribution of A. exornatum is the same as that of African Varanus lizards, which are the specific hosts of this tick (Theiler, 1945). At Paardekraal Farm, larvae, nymphs and adults of A. exornatum were found on a Rock leguvaan (Varanus albigularis). The species was neither collected during dragging nor observed on domestic animals.

7.7. Rhipicephalus simus.

The records of Hoogstraal (1956) and Theiler (1962) show that R. simus has a wide distribution in Africa. Adult ticks are parasitic on a variety of large and medium sized indigenous and domestic animals, and immature ticks are almost entirely restricted to burrowing rodents. At Paardekraal Farm, adult ticks were not recorded on indigenous hosts, but were observed on cattle during the summer months. Nymphs were recorded on two species of burrowing rodents (Table 11). Larvae and nymphs were not collected during dragging, but adult ticks were collected in CO_2 traps (design by Wilson et al., 1972). Adults were observed to emerge from rodent burrows within a few minutes of the release of CO_2.

7.8. Rhipicephalus oculatus.

R. oculatus is one of the lesser known rhipicephalids, and in many of the older records has been confused with Rhipicephalus pravus Donitz, 1910 (Theiler, 1962). The distribution records of Theiler (1962) show the species to be present in the drier regions of east, central and southern Africa. At Paardekraal Farm R. oculatus was recorded only on hares (Table 11); adults in spring and larvae in large numbers in autumn. R. oculatus was not collected during dragging.

7.9. Rhipicephalus evertsi.

The distribution and host records of Hoogstraal (1956) and Theiler

(1962) show that R. evertsi is widely distributed throughout the Ethiopian Region, where adult ticks are commonly found on wild antelopes, cattle, horses, sheep and goats. R. evertsi is a two-host tick, and the immature stages normally infest the same hosts as the adults. There are some exceptions however, e.g. hares, which are only infested by the immature stages. The predilection site of attachment of adult ticks is under the tail (i.e. the perianal area) and of the immature stages is the pinna and external meatus of the ear.

At Paardekraal Farm, adults of R. evertsi were recorded in the summer months on sheep, goats and cattle; the heaviest infestations occurring on cattle. In addition to these domestic hosts, the immature stages were recorded on indigenous hares and Duiker (Table 11). Larvae of R. evertsi were collected during dragging, but not in sufficient numbers to determine either habitat preferences or seasonal activity. Similar results were obtained by Londt and Whitehead (1972).

7.10. Hyalomma marginatum rufipes.

H. marginatum rufipes, the 'hairy hyalomma' occurs in many of the drier parts of Africa, and extends into the Middle-east and Russia (Hoogstraal, 1956 ; Theiler, 1962). The host records of Theiler (1962) show that the immature stages of this two-host tick occur on a large variety of birds, rodents and lagomorphs. Adult ticks are restricted to large mammals, mainly perissodactyls and large artiodactyls. Adult ticks are also found on domestic cattle, horses, sheep and goats (Hoogstraal, 1956).

On Paardekraal Farm, adult ticks were most abundant on cattle, but also occurred on sheep and goats. Immature ticks (Table 11) were recorded in low numbers on three species of ground feeding birds, and on one occasion two larvae were found on a Duiker. Heavy infestations of larvae and nymphs were recorded on hares. Adults were most abundant on cattle during the late summer months, and immatures were recorded on indigenous hosts during the winter months. A total of eleven larvae were collected during dragging.

7.11. Boophilus decoloratus.

The Blue tick, B. decoloratus, is distributed throughout most of the Ethiopian Region, barring arid areas (which receive less than 380 mm of rain per annum) and tropical forests (Hoogstraal, 1956; Theiler, 1962). B. decoloratus is a one-host tick, and occurs most commonly on cattle; indigenous hosts are mainly the larger antelope species (Hoogstraal, 1956; Theiler, 1962). At Paardekraal Farm, B. decoloratus was not recorded on any indigenous hosts, but did occur in fairly large numbers on cattle, particularly during humid conditions. Larvae were collected throughout the year by dragging, but the numbers were extremely low.

7.12. Discussion.

Paardekraal Farm (altitude, 180-400 m) is situated in the marginal area between the wet coastal lowlands (635-760 mm of rain per annum[1]) and the drier plateau (500-635 mm of rain per annum[1]) of the Eastern Cape Province. The vegetation is heterogeneous, ranging from open grassland to dense Fish River Bush. The extent of the grass cover varies from year to year, depending on the amount and seasonal distribution of rainfall, both of which vary considerably(Fig. 7). As a result of both the diversity of vegetation types and the climatic conditions, Paardekraal Farm supports a wide variety of ixodid tick species. These range from species which are normally associated with dry climates (e.g. H. marginatum rufipes) through to species which are restricted to areas of high rainfall (e.g. I. pilosus). The non-parasitic stages of some species, such as R. simus and H. silacea, survive in specialized,

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[1] According to the rainfall zones of Theiler (1948).

well defined microhabitats, while the non-parasitic stages of other species such as *B. decoloratus*, *A. hebraeum* and *A. marmoreum* are distributed more widely in the environment. As the latter are subjected to drier conditions, the all-seasonal rainfall of the region must be important in survival. In fact, the seasonal distribution of rainfall is probably one of the most important factors contributing to the rich variety of ticks (47 species, Arthur unpublished) which occur in the Eastern Cape Province. The numerous wooded river valleys of the Eastern Cape Province support a larger number of tick species than the drier open grassland habitats of the plateau, and probably provide the foci of most tick populations. The penetration of tick species into the more open habitats is probably determined by the extent of the grass cover, and seasonal rainfall, as was observed on a limited scale in the case of *H. silacea* (7.2). Paardekraal Farm being climatically and vegetationally transitional, supports a number of marginal tick populations, e.g. *I. pilosus*, in which the abundance of the species probably depends on seasonal weather conditions.

The availability of hosts is also an important factor in the occurrence of ticks at Paardekraal Farm. The presence of species such as *A. marmoreum*, *A. exornatum*, *H. silacea* and *R. oculatus* is directly linked with the presence of specific indigenous hosts. *B. decoloratus* on the other hand, is wholly dependent on cattle as hosts. Other species (*H. marginatum rufipes*, *R. evertsi* and *R. simus*) require domestic animals as hosts for the adult stage, but have alternative (*H. marginatum rufipes* and *R. evertsi*) or specific (*R. simus*) indigenous hosts for the immature stages. The larvae of tick species which have specific indigenous hosts (i.e. *A. exornatum*, *R. oculatus* and *R. simus*) were not collected during dragging, indicating that the restriction of these species to specific hosts was behavioural.

In other species which had a wider host range, larvae were collected during dragging. The species with the widest host range (immature stages) were *A. marmoreum*, *A. hebraeum*, *H. silacea* and *H. marginatum rufipes*. All but *H. silacea* were species with long mouthparts, confirming the earlier hypothesis (6.1) that ticks with long mouthparts are able to feed on the greatest number of hosts. *A. exornatum* has long mouthparts, but appears to be restricted, in all stages, by behaviour, to a specific host, as is the case with adults of *A. marmoreum*, *A. hebraeum* and *H. marginatum rufipes*. Whether or not *H. silacea* was able to feed successfully on all the hosts which were parasitized, is not known.

With the exception of *B. decoloratus*, in which the life cycle is uninterrupted, the adult activity peaks of all commonly occurring tick species at Paardekraal Farm (i.e. *R. oculatus*, *R. simus*, *R. evertsi*, *H. marginatum rufipes*, *A. marmoreum* and *H. silacea*) occurred during the spring and summer months. In species for which data are available (i.e. *R. oculatus*, *R. evertsi*, *H. marginatum rufipes*, *H. silacea* and *A. marmoreum*) (Table 11), larvae were found to be active in autumn or winter. As in *A. hebraeum* (3.12) it is likely that the summer activity peak of adults has evolved to ensure that eggs are laid in conditions best suited to egg development. The earlier larval activity peaks in the above species, than in *A. hebraeum*, result directly from shorter incubation periods. At 26°C and 90% RH the incubation period (to first hatch) is 50 days in *A. hebraeum* (4.5), as opposed to 37 days in *A. marmoreum* (7.3), 24 days in *R. evertsi* (Norval, 1971) and 26 days in *H. marginatum rufipes* (Norval, unpublished). By comparison with the long 3-year life cycle of *A. hebraeum* (3.12), the life cycles of other species which occurred at Paardekraal Farm, were considerably shorter. With the exception of *A. marmoreum*, in which the life cycle was completed in one or two years, the life cycles of all species appeared to be completed in one year (*R. oculatus*, *R. evertsi*, *H. marginatum rufipes* and *H. silacea*) or less (*B. decoloratus*). The short life cycles of the former result from the activity of the immature stages during the autumn and winter months.

8. Discussion.

8.1. Introduction.

Ticks are part of a biotic community, which includes the vegetational environment which supports the non-parasitic stages, the vertebrate hosts and disease-causing pathogens. The dynamic nature of the community relationships (based on our knowledge of I. ricinus) have been illustrated by an excellent mechanical analogue (Macleod, 1962) which shows the interdependence of the biotic components of the community and the influence of abiotic factors (i.e. climate) on the dynamics of the community as a whole. In this thesis the relationships of A. hebraeum with individual components of the biotic community, and the effects of abiotic factors on survival, development and activity, have been studied in isolation. In this Chapter the results of previous chapters have been brought together in an attempt to assess the factors affecting the distribution and abundance of A. hebraeum in southern Africa. Also discussed are adaptations which favour the survival of A. hebraeum, and the utilization of our available knowledge on the biology and ecology of A. hebraeum in improving the control of this tick.

8.2. Factors affecting the distribution and abundance of Amblyomma hebraeum in southern Africa.

(a) Latitude.

The duration of the life cycle of A. hebraeum in Natal is one year (Baker & Ducasse, 1968). Latitude becomes an important factor in the duration of the life cycle, south of approximately 32°S, where the daylength in winter falls below 11 hours. This is the critical daylength for nymphal activity (3.12), and in the Eastern Cape (32-34°S) nymphal activity ceases during the winter months (Fig. 14). This results in a prolongation of the life cycle by approximately one year. The life cycle in the Eastern Cape is prolonged by another year, through the influence of low autumn and winter temperatures on the incubation period of eggs (4.5). As with daylength, decreasing winter temperatures are, at least in part, a result of increasing latitude.

Theoretically, mortality in the non-parasitic stages should increase as the duration of the life cycle increases, due to (a) longer periods spent on the ground by unfed nymphal and adult ticks, and (b) the increase in mortality of eggs at low temperatures (4.5). The abundance of A. hebraeum in the Eastern Cape, despite the long life cycle, can probably be attributed to the all-seasonal rainfall which occurs in the region. This prevents the ground from becoming excessively dry during winter, thereby reducing egg mortality, and allows the over-wintering unfed ticks to replenish their water store. A. hebraeum is absent from the winter rainfall belt west of Humansdorp (34°S), as a result of the dry summer conditions (see Section C).

(b) Altitude.

Theiler (1948) states, "In the Parklands A. hebraeum survives up to 4-5000 ft. (1219-1524 m) or more, in the tall grasslands it tends to die out much sooner, the "middleveld" only going up to 3000-3500 ft. (919-1067 m) or frequently not even so high". Although no data are available on the survival of the developing stages of A. hebraeum in high lying areas, it is reasonable to assume that mortality (particularly in eggs) results from decreasing temperatures and the concomitant humidity effects (4.8). The ability of A. hebraeum to survive at higher altitudes in parklands than in grasslands, probably results from the more humid microclimatic conditions which occur in the former.[1]

(c) Vegetation and rainfall.

On the basis of the distribution of A. hebraeum, Theiler (1948) stated that "individually temperature, altitude, rainfall and soil

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[1] Although tall grassland and parkland receive the same amount of rainfall (635-760 mm per annum) (Theiler, 1948), the shaded habitats in parkland should remain humid for longer than the more open grassland habitats (see Section 3.8).

did not affect the tick directly, but they made themselves felt indirectly in so far as they influence the vegetation". This statement is in a broad sense correct, as it is the modifying influence of the vegetation which determines the microclimatic conditions in which the ticks must survive (3.8). At altitudes of less than approximately 1500 m, rainfall is probably the most important single factor which influences the growth of vegetation. The survival of A. hebraeum does not depend only on the total annual rainfall and the type of vegetation, however, but on the distribution of rainfall in relation to the seasonal activity of the tick. Specifically, the rainfall peak must coincide with the activity peak of adult female ticks, so that the eggs (which are the stage most susceptible to desiccation - sections 4.5 and 4.8) are laid when microclimatic conditions are most suitable for egg development (3.12; 4.8). As the activity peak of adult ticks is regulated by photoperiod (predominantly) (3.11) and occurs in the midsummer months, the species is absent from the winter rainfall belt of the Western Cape. West of Humansdorp, A. hebraeum only occurs on the fringes of the temperate evergreen forest around Mossel Bay (Theiler, 1948), which is marginally an all-seasonal rainfall area.

The restriction of A. hebraeum to the eastern part of the southern African sub-continent, has been shown by Theiler (1948, 1969) to be the result of decreasing rainfall in the west. In the presence of adequate tree or shrub coverage, A. hebraeum can survive in areas with a total summer rainfall of as little as 380 mm. In the absence of the modifying influence of tree cover, however, the species is absent from areas receiving as much as 760 mm per annum. This is clearly illustrated by the virtual absence of A. hebraeum from the Transkei (635-760 mm per annum - Theiler, 1948) in which tree cover is lacking except in small isolated areas.

The scarcity of A. hebraeum on the Rhodesian highveld, was thought by Jooste (1967) to be due to the high rainfall of the region (approximately

1000 mm per annum). It has been shown in this investigation that unfed nymphal and adult ticks (Figs 28b and c) and engorged nymphs (Fig. 27b) are adversely affected by continuous high humidity, and that engorged females and eggs are unable to survive in water-logged soils (4.5). These findings support the hypothesis of Jooste (1967), which was confirmed by Affleck (1968) who found that on the Rhodesian highveld A. hebraeum was associated with open, well drained habitats. This is the opposite of the findings in drier areas in South Africa, and emphasises the importance of vegetation in modifying microclimatic conditions, which ultimately affect the survival of ticks. From the above observations it can be concluded that the barrier preventing the northward spread of A. hebraeum, is probably the high rainfall of tropical Africa. The only area in South Africa, in which the absence of A. hebraeum can probably be attributed to high rainfall, is the evergreen temperate forest in the Knysna area, which receives more than 760 mm of rain per annum (Theiler, 1948).

(d) Host availability.

In a study on the spread of the American dog tick (D. variabilis) in the eastern USA, McEnroe (1974) observed that (a) dogs carried more ticks than indigenous hosts (fox and racoon), and (b) dogs in urbanized areas were more densely spaced than indigenous hosts would be in the same areas. As a result of these two factors, D. variabilis had spread into urbanized areas, which in the presence of indigenous hosts had not previously supported a tick population. It is therefore apparent that for an area to become infested with ticks, a certain 'host threshold' relating to the spacing and suitability of hosts must be exceeded. This is in principle similar to the 'vector threshold' in the transmission of certain diseases (Stampa, 1969a).

In A. hebraeum, in which the immature stages are catholic feeders and the adults are only found on large animals, it is most likely that the availability of hosts for adult ticks is the factor regulating the occurrence of the tick within the vegetational environment which supports the non-parasitic stages. In Chapter 5 (5.6) it has been shown how the absence of A. hebraeum from the Eastern Cape prior to human settlement was in all probability related to a low 'host threshold', and that the spread of A. hebraeum into the area occurred subsequent to the introduction of cattle. As cattle farming is at present practised throughout all but the extremely arid areas of southern Africa, it can be concluded that on a regional basis the distribution of A. hebraeum is limited by vegetation and rainfall. This is not the case at a local level however, where the availability of hosts and the efficiency of dipping must also be important. According to the results of McEnroe (1974), the 'host threshold' can be expected to rise when the suitability of the habitat for the survival of the non-parasitic stages decreases (i.e. in areas of low rainfall), to counter the increase in tick mortality. Conversely, as the density of bovine hosts increases the greater will be the utilization of the grass-cover, which is essential for the survival of the ticks. Eventually a point will be reached beyond which an increase in the density of bovine hosts will have a negative effect on the tick population level. Indeed, it is well known amongst farmers (Walsh, personal communication) that over-grazed farms have less of a tick problem than well managed farms. According to Macleod (1962), the equilibrium between ticks, their hosts and the environment which supports them, is maintained by disease pathogens (i.e. by regulating the number of hosts). In Macleod's opinion disease is "no more than a symptom of a time-lag in the continuing adjustments between the organism and the environment". According to this hypothesis the problem of tick-borne disease in domestic stock, stems from the high density at which domestic stock are maintained in the environment. The effect of acaricides is therefore to disrupt the natural equilibrium between ticks, their hosts and the environment. In principle dipping has the same effect on the tick population as a raising of the 'host threshold' or an increase in the spacing of the hosts.

(e) Parasites and predators.

Information on parasites and predators of ixodid ticks is scant (reviews by Wilkinson, 1970 and Londt, 1970). No specific references have been made to A. hebraeum, and during this investigation no information was obtained on parasitism or predation on A. hebraeum. In view of our lack of knowledge, it is impossible to speculate on the importance of parasites and predators in regulating populations of A. hebraeum. In general however, it appears that parasites and predators are only of minor importance with regard to ticks.

8.3. Adaptations which favour the survival of Amblyomma hebraeum.

A. hebraeum has a wide distribution throughout southern Africa, and occurs in areas receiving an annual rainfall of 370-1000 mm. In order to increase the chances of survival, particularly in the drier regions, the species has adapted in a number of ways. Perhaps the most obvious is the production of a large number of eggs, which may reach 18 500 per female (Chapter 2). As the number of eggs produced by a female tick is a function of the weight of imbibed nutrients, ticks which lay a large number of eggs must of necessity engorge to a large size. This generalization can be made as ticks of the family Ixodidae all produce eggs of a comparable size (Arthur, 1962). As the potential quantity of nutrient which a tick can imbibe is a function of the weight of the unfed tick (Snow & Arthur, 1966; Bassal & Hefnawy, 1972), it is necessary, as discussed in Section 6.10, that all stages of the life cycle be of a large size. The large size of A. hebraeum is seen, when the weights of the adult and immature stages are compared with those of H. marginatum rufipes and B. decoloratus (Table 17). The data in Table 17 show that in addition to being the largest tick in all its stages, A. hebraeum also had the greatest capacity to increase in weight. From the unfed larval stage to the engorged female the weight increase varied between 14 000 and 67 000 fold, as opposed to 20 000 to 47 000 fold in *H. marginatum rufipes*, and a mere 8 000 to 17 000 fold in *B. decoloratus*. As the limit in weight increase in *A. hebraeum* is set at approximately 67 000 fold, eggs of a relatively large size must be laid to ensure that female ticks have the potential to increase to the required weight. This results in a vicious circle, as the larger the eggs the fewer can be laid per unit weight of tick. An optimum size must therefore be reached where sufficient eggs are laid to maintain the population, without the detrimental effect of the female ticks becoming unnecessarily conspicuous (see below). In *A. hebraeum* the weight of engorged females normally ranged between 2 and 3 gm, with the heaviest recorded in this laboratory being 4,0 gm; this has been exceeded only by females of *A. marmoreum* which weigh up to 5,2 gm. The large size of *A. hebraeum*, by comparison with most other species of ticks, is also important from the point of view of water balance. Not only is there a smaller surface area to volume ratio (4.8), but in the developing stages which are not capable of taking up water (4.8), there is a large water store. The main disadvantage of increasing size is that ticks become increasingly susceptible to host deticking mechanisms. It is probably for this reason that adults of *A. hebraeum* have adapted to large hosts. *A. marmoreum*, which engorges to a larger size than *A. hebraeum*, feeds in the axillae of tortoises where the ability of the hosts to remove the ticks is negligible.

Table 17.

The weight in mg. of the stages of the life cycle of Boophilus decoloratus (Londt 1973), Hyalomma marginatum rufipes (Norval - unpublished data) and Amblyomma hebraeum. (+) mean weight; (-) no record; (x) weight of engorged female/mean weight of unfed larvae, corrected to the nearest thousand.

Stage	B. decoloratus	H. rufipes	A. hebraeum
Egg	0,05 +	-	0,10 +
Unfed larva	0,024 +	0,03 +	0,06 +
Engorged larva	0,25 +	0,85 +	1,0-3,2
Unfed nymph	0,16 +	0,42 +	0,80 +
Engorged nymph	1,90 +	10-50	15-100
Unfed adult	1,37 +	5-35	10-75
Engorged female	200-400	600-1400	850-4000
Min x	8 000	20 000	14 000
Max x	17 000	47 000	67 000

Among the adaptations in the behaviour and physiology of A. hebraeum which are important in survival, are mating behaviour and spermatogenesis (Chapter 2). Accumulations of males on the host, similar to those in A. hebraeum, were also observed in the 3-host ticks, H. silacea (7.2) and A. marmoreum (7.3), and to a lesser extent in the 2-host ticks R. evertsi and H. marginatum rufipes. There was however, no accumulation of males in the 1-host tick, B. decoloratus. These differences between 3-, 2- and 1-host ticks indicate that as the number of hosts increases, and hence the number of non-parasitic stages, the importance of adaptations which increase the chances of survival also increase, to counter mortality during the non-parasitic phase. It should be noted that 3-host ticks of the genus Ixodes e.g. I. pilosus (7.5) do not fit into the above scheme, as mating is able to occur off the host.

Other adaptations which favour the survival of A. hebraeum relate to seasonal activity and water balance. As discussed previously (3.12) peak adult activity occurs in midsummer, so that eggs are laid when conditions are best suited to egg development. Nymphs are active during winter or spring, depending on latitude (3.12). Both nymphal and adult ticks enter a period of quiescence before activity, which is initially age dependent (3.12; 6.6). Later activity is regulated by photoperiod (3.10-12). Temperature and humidity are, however, important modifying influences (3.10-12), and it is the response to these factors which ensures that ticks are active when conditions are best suited to survival. No studies have been made on the influences of temperature and humidity on the behaviour of individual nymphs and adults of _A. hebraeum_. The results obtained in respect of other ixodid species (Lees & Milne, 1951; Balashov, 1960; Semtner _et al_., 1971; Semtner & Hair, 1973) however, have shown that the activity patterns of ticks are influenced to a large extent by microclimatic temperature and humidity. In _A. americanum_ (Semtner & Hair, 1973), for example, adult ticks move from the humid ground level microhabitat to the tips of vegetation during warm humid conditions, but descend to ground level during hot dry conditions, and do not move off the ground during cold conditions. During the periods spent on the ground, ticks are able to replenish their water store by absorption of water from the humid atmosphere (Sauer & Hair, 1971). By deduction it appears that the behaviour of _A. hebraeum_ is similar, as the results in Figs 14-17 and Table 6 show that during dry conditions rainfall is important in activity, and in cool conditions high temperatures are important. In dry summer conditions, as in 1972/3, however, adult activity persists (Figs 15 and 16) as a result of the photoperiod and temperature responses; this is probably important in ensuring the continuity of the life cycle, despite adverse climatic conditions.

The absence of diapause in larvae is advantageous, as these ticks are extremely sensitive to adverse climatic conditions (Fig. 28a; Table 9), and consequently it is important to gain access to the host as soon as possible after hatching. Londt and Whitehead (1972) studied the orientation of larvae on vegetation, but unfortunately made no reference to daily migrations of larvae in relation to microclimatic conditions. These authors did however show that larvae are able to absorb moisture from the atmosphere and imbibe water through the mouthparts, both of which must be important in survival.

8.4. The application of available knowledge in the control of *Amblyomma hebraeum*.

Stampa (1969a) showed that, as with East Coast Fever (transmitted by *R. appendiculatus*), heartwater can be eradicated by reducing the tick vector population to an extremely low level, whereby the chances of a tick engorging on a carrier host in one stage and on a susceptible host in the next stage become zero. In order to reduce populations of *A. hebraeum* to a low level, it is necessary to carry out an efficient control programme. In this section the possible application of our knowledge of the ecology of *A. hebraeum* in improving the control of the tick is discussed.

(a) Improved farm management.

Theiler (1948) stated that in the Albany District "dipping as carried out (14 day period), is anything but conscientious and is quite inadequate". Unfortunately on many farms the pattern remains much the same today, and it is clear that this fact is in many ways responsible for the worsening heartwater problem. There has only been one report of resistance to acaricides in *A. hebraeum* (Whitehead, 1973), and consequently there is no urgent necessity to introduce new methods of tick control. The more realistic approach would be to improve farm management and perhaps to introduce integrated control programmes, with the aim of eliminating heartwater on a provincial or regional basis.

Our knowledge of (a) the seasonal activity of *A. hebraeum*, (b) the host requirements and (c) the habitat requirements, can be used to the advantage of the farmer. With the knowledge that in the Eastern

Cape, ticks of all stages of the life cycle are active in the spring and summer months (September-April), a programme of intensive (5-7 day interval) 'strategic' dipping could be introduced during this period. As adult ticks occur in low numbers on cattle during the winter months, 10-14 day interval dipping of cattle may also be necessary in winter. As sheep and goats carry mainly nymphs, however, there is no necessity to dip these animals during the winter months. Sheep and goats should be dipped most conscientiously during spring and early summer when nymphal activity reaches a peak.

With a knowledge of the habitat requirements of A. hebraeum (i.e. well-drained tree-covered areas), the farmer can, by rotation of his livestock within his pastures, reduce heartwater mortalities to a minumum. A proposed system of rotation for the Eastern Cape, based on the knowledge (a) that sheep and goats are more susceptible to heartwater than cattle (Alexander, 1931), (b) that heartwater transmission to sheep and goats is mainly by nymphal ticks, while in cattle it is by nymphal and adult ticks, and (c) that the nymphal population is rapidly depleted by heavy stocking, is as follows. In spring when nymphs are active, sheep and goats should be maintained in open pastures to avoid infestation. Cattle, on the other hand, should be maintained at high density in tree covered pastures and should be dipped regularly. This should deplete the nymphal population so that sheep and goats can be introduced into the pastures later in summer. During mid- and late summer cattle should be maintained in open pastures, to avoid infestation by adult ticks. Another advantage of restricting cattle to open habitats during this period, is that eggs laid by female ticks which detached in these habitats would have little chance of hatching.

Any newly acquired stock which is known to be sensitive to heartwater, should be maintained in open pastures until after innoculation (or 'blooding') if this method of heartwater prevention is practised.

On farms which specialize in sheep or goats, it would probably be advisable to maintain no cattle or horses, as in the absence of Kudu these animals are the only commonly occurring hosts of the adults of A. hebraeum in the Eastern Cape. Alternatively, on farms on which large numbers of both small stock and cattle are kept, the farms could be divided into separate units i.e. for sheep or goats and for cattle. If no transfer of stock between the sheep/goat and cattle areas occurred, the former should remain largely free of A. hebraeum. A number of engorged larvae and nymphs will be transported into the 'heartwater free' areas by birds etc. (Table 11), but the tick will never become established and the number of heartwater mortalities can be expected to be negligible.

(b) Integrated control.

The use of acaricides in dipping is directed against the parasitic stages of ticks. A number of other methods of 'biological' or chemical control have been successfully applied against the non-parasitic stages. The effectiveness of these methods varies, and it is usually when integrated with dipping that the most effective control is achieved.

One of the most commonly advocated methods of controlling the non-parasitic stages of ticks is through alteration of the environment (Milne, 1948; Stampa, 1959, 1969b; Clymer, et al., 1970; Hair & Howell, 1970; Hoch et al., 1971a, 1971b). Basically this involves removing certain types of vegetation, which provide the necessary microclimatic conditions for the survival of the ticks. The disadvantage of this method is that in the long term more damage may be done to the environment, than is justified for the eradication of a particular tick species. Milne (1948) and Stampa (1969b) have shown that alterations in the environment, necessary for the control of I. ricinus and I. rubicundus respectively, actually constitute pasture improvements. The results of this investigation (3.7) indicate that the removal of tree cover in grassland habitats should result in a large measure of control of A. hebraeum in South Africa. Whether or not tree clearing can be justified from an ecological or economic point of view, will probably vary from area to area. Less drastic measures, such as the mowing of long grass (Hair & Howell, 1970) or controlled burning (Hoch et al., 1972) may also be worth considering.

Area control with short-lived organophosphate insecticides applied to vegetation has been found to be fairly effective in controlling the non-parasitic stages of A. americanum (Clymer et al., 1970; Hair & Howell, 1970; Hoch et al., 1971a). This method has potential in the control of A. hebraeum, if insecticides are applied at the correct time of year, in areas where the tick is restricted to small patches of wooded habitat. The wide-spread application of insecticides, however, would probably be both impractical and uneconomical.

A number of Australian workers (Wilkinson, 1957, 1964; Wilkinson & Wilson, 1959; Hall & Wilkinson, 1960; Harley & Wilkinson, 1964, 1971; Harley, 1966; Wharton et al., 1969) advocate pasture 'spelling' (rotation of cattle in pastures) as a means of controlling B. microplus. Pasture spelling relies on the fact that in this 1-host tick, the non-parasitic larvae die within a few months in the absence of cattle. The method would not, however, be practical in the control of A. hebraeum, as (a) the non-parasitic stages of this tick are able to survive for well over a year (4.7), and (b) in the absence of cattle alternative hosts are available for larvae and nymphs (Table 11).

Another method of controlling B. microplus is the use of 'tick resistant' Zebu cattle (Wharton, 1967). As shown in laboratory studies (Chapter 6), however, mammalian hosts are unable to acquire a resistance to A. hebraeum, and consequently this method could not be used in the control of the tick.

(c) Other methods.

Drummond (1970) noted that methods such as genetic mechanisms, application of hormones and the sterile male technique, are possible future methods of controlling ticks. Indeed it has been shown (Chapter 2) that the sterile male technique could possibly be applied in the case of A. hebraeum, were a suitable sterilant available.

In conclusion it must be stated that for any new tick control measures to be applied, a good deal more research must be done. As stated in the introduction (Chapter 1), the aim of this investigation was to study the biology and ecology of A. hebraeum from a purely academic point of view, with the hope that the results obtained would form a basis for future more applied lines of research. It is clear that in the immediate future more research needs to be done on the distribution and seasonal activity of the non-parasitic stages in the field With a better understanding of the factors regulating the activity of nymphal and adult ticks, it may be possible to give an early warning of heartwater outbreaks, and so reduce the present high incidence of heartwater in sheep, goats and cattle.

9. Summary.

Quantitative data are given on the preoviposition, oviposition, incubation and premoult periods of A. hebraeum maintained in darkness at 26°C and 90% RH, together with data on the duration of feeding in all stages on laboratory hosts. The onset of the development of the pharate nymph was found to occur prior to the completion of larval feeding, while the onset of the development of the pharate adult occurred approximately eight days after the completion of nymphal feeding. The percent weight increase after feeding was shown to be considerably less in adult males, than in other stages of the life cycle. The growth of testes and spermatogenesis in males was shown to be initiated by feeding. Males became sexually mature approximately six days after attaching to the host. Sexually mature males produced a sex attractant pheremone, and were capable of mating with up to eight different females.

An ecological survey was carried out at Paardekraal Farm, 15 km SE of Grahamstown. Larvae were sampled by the drag method, in six different habitats. Microclimatic data were recorded in each habitat. The results showed that larvae were most abundant in well-drained, tree-protected habitats, in which there was a ground cover of grass. The main factor thought to influence the distribution of larvae, was the suitability of microclimatic conditions for the development of the egg stage.

The seasonal activity peak of larvae, determined by dragging, occurred in midsummer. There was no correlation between larval activity and either temperature or rainfall. Laboratory and field observations showed that larvae became active soon after hatching. The results indicated that the seasonal activity of larvae was determined by the seasonal activity of adult female ticks, and the rate of oviposition and egg development in relation to seasonal temperature.

The seasonal activity of nymphal and adult ticks was determined by counting the numbers of each stage attaching to two undipped Short-horn

steers. Both stages of the life cycle became active in spring. Peak nymphal activity occurred in spring and early summer, and peak adult activity in mid- and late summer. There were significant positive correlations between the numbers of adult ticks attaching to steers and daylength, temperature and rainfall. Daylength appeared to be the most important single factor regulating adult tick activity. The responses to temperature and rainfall (humidity), ensured that ticks were active when conditions were best suited for survival. In general, the responses to environmental factors were similar in nymphal and adult ticks. During midsummer, however, there was a sharp decline in the numbers of nymphs attaching to steers. There is evidence to suggest that this resulted from a depletion of the nymphal population, as a result of heavy stocking with cattle (which are the main hosts of nymphs). It appeared that the earlier activity peak in nymphs than in adult ticks resulted from a response to shorter daylength in nymphs.

As the peaks of nymphal and adult tick activity occurred approximately one year after the peaks of larval and nymphal activity respectively, it was concluded that unfed nymphs and unfed adults spent the winter in a state of quiescence. As a result of this fact, the life cycle of _A. hebraeum_ required three years for completion in the Eastern Cape. By contrast the results of Baker and Ducasse (1968) indicate that the life cycle is completed in one year in Natal, with adult ticks active in summer, larvae in autumn and nymphs in winter. The earlier larval activity peak in Natal is probably caused by the influence of higher temperatures on oviposition and egg development. The winter activity of nymphs on the other hand appears to result from the longer winter days in Natal. By deduction it appears that the critical daylength required for nymphal activity is approximately 11 hours. The absence of an autumn peak of nymphal or adult tick activity in the Eastern Cape, can be attributed to the fact that quiescence is initially age dependent.

Quantitative data are given on the survival and rate of development (where applicable) of all stages of the life cycle of A. hebraeum in laboratory and field conditions. In the laboratory, ticks were maintained in each of fifteen different permutations of temperature and relative humidity. In the field, ticks were maintained in a Stevenson's screen at the Field Station of the Tick Research Unit, and in cages in different habitats at Paardekraal Farm (engorged females and eggs). In all stages of the life cycle, development proceeded most rapidly at 30°C, and the durations of the developmental periods increased exponentially with decreasing temperature. Oviposition occurred successfully in the temperature range 15-30°C, egg incubation in the temperature range 20-30°C and larval and nymphal moulting in the temperature range 15-35°C. Among the developing stages (which were not capable of taking up moisture from the atmosphere), the egg stage required the most humid conditions to complete development. The ability of the developing stages to survive in dry conditions increased with increasing size. By contrast to eggs and engorged larvae, mortality in engorged nymphs increased in humidities approaching saturation. In all developing stages, mortality increased at low humidities as the temperature decreased, due to the longer periods of time over which water was lost. The weight of eggs produced per milligram weight of ovipositing female, was influenced by both temperature and atmospheric humidity. In the temperature range 15-35°C the longevity of unfed larvae was directly correlated with saturation deficit. This was not the case with unfed nymphal and adult ticks, however, where temperature was important. Unfed ticks, which were able to take up moisture from humid atmospheres, survived for considerably longer periods in naturally fluctuating conditions than in controlled laboratory conditions. Eggs on the other hand required continuous high humidities in the field to complete development. These conditions were found in the surface layers of the soil in shaded habitats, in which female ticks buried themselves after detaching from the host. Eggs and/or engorged female ticks did not survive in habitats where the soil was water-logged. The above results are discussed in relation to the distribution and seasonal activity of *A. hebraeum* in the field.

A host survey was carried out at Paardekraal Farm. Data are given on the quantitative seasonal occurrence of ixodid ticks on vertebrate hosts. Larvae and nymphs of *A. hebraeum* were found to be catholic feeders, and occurred on a wide variety of mammals and birds. Nymphs were also found to parasitize tortoises. Adult ticks were found to be restricted to large mammals, mainly of the family Bovidae. Records from Paardekraal Farm and other localities show that cattle and Kudu were the main hosts of adults of *A. hebraeum* in the Eastern Cape.

Data are given on the effects of repeated infestations of *A. hebraeum* on caged laboratory hosts. The yield of larvae from domestic rabbits was found to be influenced by grooming, and the effect of ambient temperature on the attachment behaviour of the ticks. Rabbits, sheep and cattle were unable to acquire a resistance to *A. hebraeum*, and it was proposed that this resulted from the method of feeding in the tick. It was shown, however, that the engorged weights of larvae and nymphs fed on rabbits and sheep respectively, showed definite seasonal fluctuations. There was evidence to suggest that the decline in engorged weights in winter arose from the effect on tick feeding of changes in the host physiology associated with low temperature acclimatization. The rate of feeding in both larvae and nymphs was found to be influenced by the skin temperature of the host.

Data on the distribution, seasonal activity and hosts of a number of ixodid tick species other than *A. hebraeum*, were obtained during the field surveys at Paardekraal Farm. These data are discussed and compared with the data on *A. hebraeum*.

The factors affecting the distribution and abundance of *A. hebraeum* in southern Africa are discussed in the light of our available knowledge. Also discussed are adaptations which favour the survival of *A. hebraeum*, and the application of our available knowledge in improving the control of the tick.

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