ECOLOGICAL STUDIES ON THE NON-PARASITIC LARVAL STAGES OF SOME TICK SPECIES IN THE EASTERN CAPE PROVINCE OF SOUTH AFRICA

(ACARINA : IXODIDAE)

by

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A THESIS PRESENTED TO RHODES UNIVERSITY FOR THE DEGREE
OF MASTER OF SCIENCE

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December 1970.

TABLE OF CONTENTS

ACKNOWLEDGMENTS

I wish to thank the following people for the assistance they rendered me during the period spent on the investigation reported in this thesis.

Dr. G.B. Whitehead and Prof. B.R. Allanson, of Rhodes University, for their advice, supervision and valuable criticism of the work and the preparation of the manuscript.

Miss. E.R. Norton, of Barville Park, and Mr. G. Reed, of Faithful Fountain, for allowing me access to their respective farms.

Mr. J.A.F. Baker, of Cooper and Nephews Ltd, East London, for supplying engorged adult ticks used in the rearing of larvae in the laboratory.

Miss. J.B. Walker and Dr. G. Theiler, of Onderstepoort, for giving of their time and help in the identification of larvae.

Mrs. M.F. Muggeridge for typing the final draft of this thesis.

I would also like to acknowledge the financial help given by the Sir Percy FitzPatrick award for 1970 and a grant given by the Department of Agricultural Technical Services.

1. INTRODUCTION

At a recent symposium on the biology and control of ticks in southern Africa, the following words were spoken by Professor B.C. Jansen, chief director of the Veterinary Research Institute at Onderstepoort.

> "Ticks have already been studied in our country and abroad. Progress in the field of taxonomy has probably been the most rapid and has culminated in a large number of papers and excellent monographs, but much more remains to be done. To produce an overall picture of the factors influencing the behaviour of the tick under natural conditions, studies have to be conducted on tick ecology and experimental physiology. We still have a lack of knowledge of host specificity, the selection of feeding sites on hosts and the nature of resistance to attacks by ticks. Because of the varied habits of different species of ticks, the first essential prerequisite is an adequate knowledge of their biology."
>
> (Jansen 1969)

The above words sum up the position of research on ticks in southern Africa at the present time.

The basic taxonoic work carried out at Onderstepoort by Dr. G. Theiler and her associates is of great importance in that it has led to an understanding of what species exist in the various regions of this country. Distributional information has, to some extent, been linked with macroclimatic conditions such as rainfall as well as to broad regional vegetational categories. Unfortunately the ecological problems associated with ticks and their control have not received much attention. During the last few decades, numerous chemical firms have been attempting to produce the perfect acaricidal compound. Although they have succeeded in maintaining tick populations at a fairly low level, the results of these years of work appear to be a population of acaricidal resistant ticks. Years ago, when the word 'resistant' had not entered the sphere of tick control, many workers were of the opinion that adequate control was possible using chemical acaricides. The brief history of what has transpired since those days (Whitnall 1969) shows just how wrong those early workers were.

In recent years it has become increasingly obvious that a thorough knowledge of tick ecology is an essential prerequisite for the development of effective 'biological' and 'chemical' control measures. By studying the ecology of ticks, improvements in dipping and spraying programmes might be made and ideas of possible biological control measures could emerge.

Workers in a few overseas countries, notably Australia and Britain, have produced a number of papers concerned with tick ecology. This fact is a source of embarrassment to southern African workers as these two countries have only a relatively few species of ixodid ticks which are of economic concern. The southern tip of the African continent has, on the other hand, many economically important tick species. These have received comparatively little attention.

The work reported in this thesis is basic biological information. This information should have been available years ago. The work consists, in part, of a distributional survey of the non-parasitic larval stages (those larvae which have not yet located a host) of the tick species on two coastal farms in the Port Alfred district. The species studied in this manner were Ixodes pilosus Koch, Haemaphysalis silacea Robinson, Amblyomma hebraeum Koch, Boophilus decoloratus Koch and Rhipicephalus evertsi Neumann. The survey was designed to reveal the types of vegetational situations occupied by these tick species. Greater attention was later given to a detailed study of these situations. Microclimatic relative humidities, temperatures and wind speeds (air currents) were measured in examples of the various vegetational situations. This type of information, it was believed, would lead to an understanding of the conditions which would, or would not, support larval ticks in the field.

The work reported in this thesis also includes laboratory investigations. The species dealt with in these studies included I. pilosus, A. hebraeum, B. decoloratus, R. evertsi, Rhipicephalus appendiculatus Neumann and Rhipicephalus simus Koch. Two main aspects were dealt with. The first concerned with the water relations of larval ticks. The ways in which larvae lose and take up water are important. This information could lead to a considerably greater understanding of why larvae live in the situations in which they are found. This type of work has been done by a number of previous workers but little appears to pertain to southern African tick species. The other aspect dealt with in the laboratory was the behaviour of larval ticks walking on vertically placed glass rods u (sim~~i~~lating grass stems). This investigation stemmed from the findings of the distributional survey and involved an investigation into the effects of vegetation height on the grass climbing behaviour of larvae. A brief study of the important stimuli involved in the orientation of larvae to the tips of glass rods was also undertaken. The stimuli considered were gravity, light and encounters with the tip of the rod. Previous workers have studied various aspects of this type of behaviour but as they appear to have conflicting opinions the brief study reported here, was done.

2. DISTRIBUTION OF LARVAL TICKS IN RELATION TO VEGETATIONAL COVER

Very little work has been done in South Africa on the distribution of ixodid tick larvae in relation to vegetational cover. Stampa (1959), working on the Karoo paralysis tick Ixodes rubicundus (Neumann), and Kraft (1961), working on various species of cattle tick (i.e. B. decoloratus, A. hebraeum, R. evertsi and I. pilosus.) in the Eastern Cape both demonstrated that the species studied were associated with definite vegetational situations. Stampa (1959) demonstrated that the shrub Rhus erosa created suitable environmental conditions for the development of I. rubicundus. Kraft (1961) was able to show that I. pilosus was "limited to situations with Complete Overhead Cover or Incomplete Overhead Cover", while the other three species were not found in such places. Kraft (1961) also suggests that sparse vegetation might be unfavourable for larval development. Stampa (1959, 1969) was of the opinion that the population density of I. rubicundus could be kept low by altering the nature of the vegetation. This type of suggestion is of great interest and importance as it offers the possibility of an alternative control measure. The distributional survey to be reported in this chapter was undertaken with the aim of relating the various species of tick larvae found on coastal farms with particular vegetational situations. It is my belief that a thorough knowledge of the conditions underwhich larvae live could lead to the development of some biological control measure, which may be used in conjunction with existing acaricidal control measures in an efficient 'integrated control' programme.

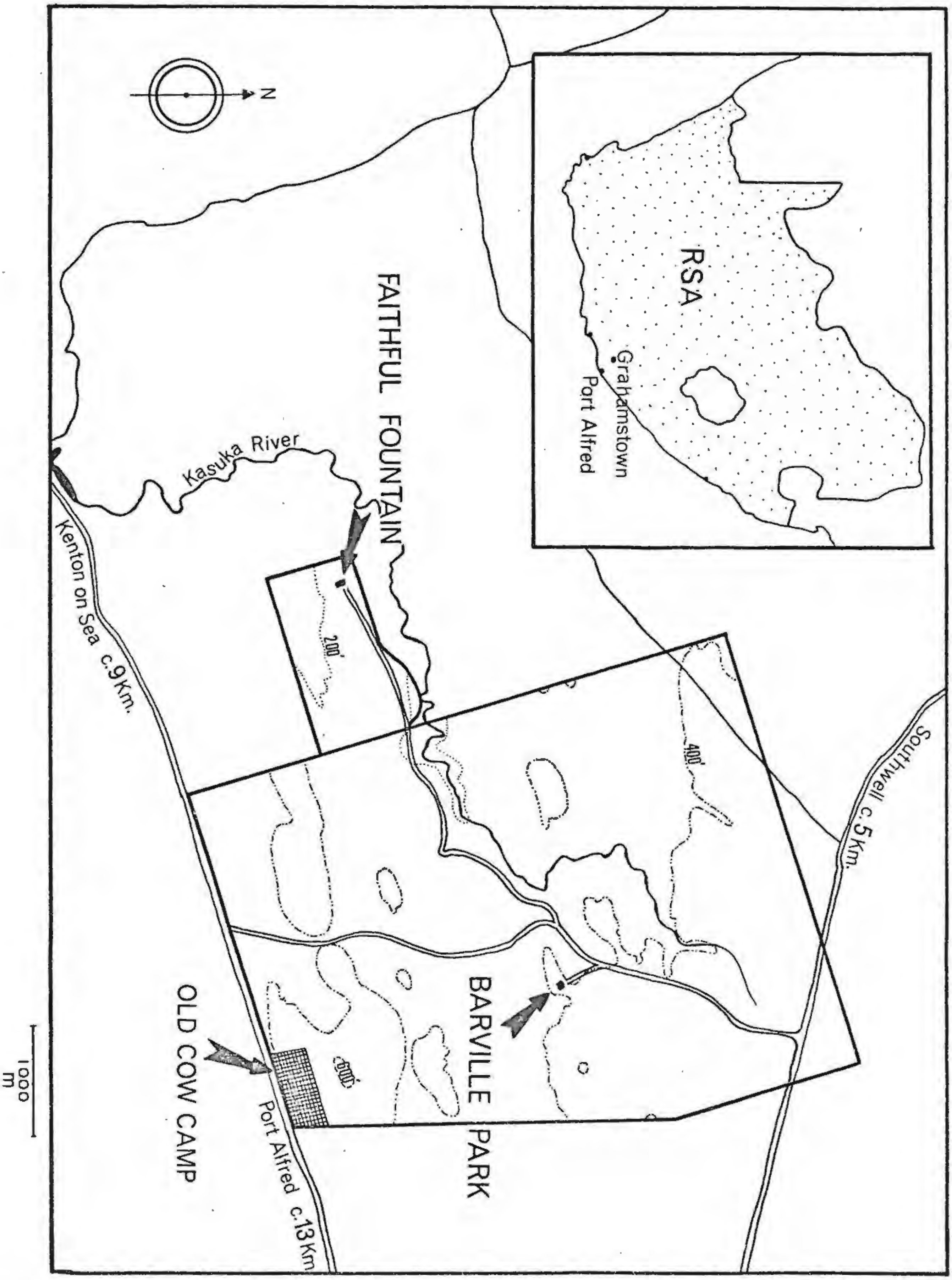
Choice of farms

It was decided that field surveys would be undertaken on coastal farms in the vicinity of Port Alfred as these farms were noted for high tick populations. It was thought that high tick populations might be most suitable for ecological investigations.

Two farms, within 80 Kilometres of the headquarters of the investigation (Rhodes University, Grahamstown), were selected. The two farms were Barville Park, owned by Miss E.R. Norton, and Faithful Fountain, owned by Mr G. Reed. Fig. 1 shows the geographical positions of these two farms. Barville Park was selected as it was considered to be one of the better managed farms in the Eastern Cape. An efficient spray race was operated at regular intervals, rotational grazing, using 55 camps each with its own water supply, was practiced and bush clearing and grass mowing were frequently undertaken. This farm was also selected as it presented a wide variety of vegetational situations.

Faithful Fountain, which bordered on Barville Park and therefore possessed similar climate and vegetation, was selected as it was considered to be a less efficiently managed farm. A certain amount of crop cultivation was practiced and this appeared to complicate the management of the relatively few head of cattle on the farm. Dipping was carried out at rather erratic intervals and was considered inefficient as many adult B. decoloratus were frequently seen on the cattle. Rotational grazing, although practiced, was undertaken using only a few camps, most of which lacked a water supply. It appeared that one or two camps, those with water, were very intensively grazed while the other camps appeared to be completely ungrazed and overgrown with tall grass. It was hoped that by selecting the above two farms that some differences in the tick populations would be detected and associated with the particular farming techniques.

Fig. 1. Map showing the position of Barville Park and Faithful Fountain in relation to the surrounding countryside.



Barville Park was used for the majority of the field work. A single camp, 'Old Cow Camp', was selected as it presented a very wide variety of vegetational situations. This camp, shown in Fig. 1, also appears in Plate 1. Plate 1 shows 'Old Cow Camp' to be largely covered with open grass except for a fairly dense 'forest' undergrowth at the north-west corner of the camp. This dense undergrowth has been called Alexandria Forest vegetation by Acocks (1953). Smaller, more isolated, clumps of trees and bushes were also in evidence. The Stevenson's screen, in which the Thermohygrograph was housed, was placed amongst the trees which can be seen in the centre foreground of Plate 1. This position was chosen as it prevented passing travellers from seeing and tampering with the equipment.

Categories of vegetational cover

The 'vegetation' in 'Old Cow Camp' was conveniently divided into a number of categories dependent on height and the degree to which it was protected by neighbouring trees and bushes. The term 'vegetation' refers to plants growing in the immediate vicinity of the ground, i.e. Bushes and trees excluded. Vegetation was described as 'short' (5-30 cms in height), 'medium' (30-50 cms in height), 'tall' (>50 cms in height), 'open' (not in the immediate vicinity of trees and bushes), 'protected' (laterally sheltered or incompletely covered by bushes and trees) and 'covered' (covered by a complete canopy of trees and bushes). Using these six main divisions eight different vegetation categories were defined.

i. Short open vegetation.
ii. Medium open vegetation.
iii. Tall open vegetation.
iv. Short protected vegetation.
v. Medium protected vegetation.
vi. Tall protected vegetation.

vii. Short covered vegetation.
viii. Medium covered vegetation.

Vegetation which would have been described as 'tall covered' was not found at Barville Park or Faithful Fountain. Plates 2-9 show examples of the above eight vegetation types.

Nature of vegetation in 'Old Cow Camp'

'Old Cow Camp' was surveyed with respect to the various types of vegetation found. The survey was limited to the grasses and other plants which might be assumed to harbour larval ixodids. The following list of plants collected in the camp were identified by Dr. A. Jacot-Guillarmod of the Botany Department of Rhodes University.

Gramineae :	*Hyparrhenia hirta* (L) Stapf.
	Panicum maximum Jacq.
	Panicum stapfianum Fourc.
	Digitaria eriantha Steud.
	Setaria pallide fusca (Schum) Stapf & Hubb.
	Aristida junciformis Trin & Rupr.
	Sporobolus capensis (Willd) Kunth.
	Sporobolus fimbriatus Nees.
	Cynodon dactylon (L) Pers.
	Chloris gayana Kunth.
	Eragrostis plana Nees.
Restionaceae :	*Leptocarpus paniculatus* Mast.
Cyperaceae :	*Mariscus dregeanus* Kunth.
	Scirpus thunbergianus (Nees) Levyns.
	Kyllinga alba Kunth.
	Kyllinga erecta K. Schum.
Iridaceae :	*Aristea anceps* Eckl. ex Klatt.
	Bobartia indica L.
Compositae :	*Metalasia muricata* Less.
	Disparago ericoides Gaertn.
	Helichrysum anomalum Less.

Although the above list is far from being complete it is a reasonable sample of the species present in the camp under discussion.

Sampling method.

The sampling apparatus used throughout the survey was a modified version of that described and used by both Stampa (1959) and Kraft (1961). Ten flannelette strips or 'tails' approximately 60 x 8 cms were attached at equal intervals down the length of a one metre long broom handle. This collecting apparatus or 'Tailbar', although only one metre long, was found to be quite convenient especially when sampling in dense undergrowth. The sampling procedure was as follows.

i. The 'tailbar' was swept over the vegetation for a set distance. Larvae situated at the tips of the vegetation would cling to the flannelette 'tails'. The distance traversed was usually 50 metres when conditions permitted. When the undergrowth was very dense, or when insufficient vegetation of the category involved was available, shorter distances were traversed. When shorter distances were used the numbers of larvae collected were adjusted so as to indicate the number that would have been expected in a 50 m^2 sample. This was done to facilitate comparisons. More than one sample was often taken in each category per sampling day and in these instances the average number per sample was calculated.

ii. Each flannelette 'tail' was examined at the end of each sample. When no larvae were found the next sample was taken. When only a few larvae were found, these were removed from the 'tails' by means of a pair of fine forceps and placed in small glass vials containing 70% ethyl alcohol (C_2H_5OH). On occasions when large numbers of larvae were collected the 'tails' were removed and placed in small plastic containers which were capped and taken back to the laboratory.

iii. Larvae were then examined, identified, counted and recorded in the laboratory.

Sampling period

Samples were taken in the mornings between approximately 10 am and noon and this was found to be the most convenient time. Dyk & Bouckova (1968)(vide Theiler 1969) have shown that the activity of ticks is dependant on the temperature and relative humidity. This suggests that there are certain peaks of activity in each 24 hour period. Stampa (1959) has shown that I. rubicundus has a peak of activity at approximately 10 pm. Very little is known about activity peaks in larval ixodids and as this aspect did not receive attention in the present investigation, sampling times were confined to the hours already mentioned so as to standardise the sampling procedure. The activity peaks of larvae are probably directly related to the periods during which the prospective hosts are active. As ticks which infest cattle were of prime interest, the sampling period used was probably the best on as cattle are particularly active during the morning hours. Activity peaks must certainly be given more attention in future work.

Larval identification

Larval Ixodidae are notoriously difficult to identify at specific level. With the vast majority of species it is necessary to clear and mount the specimens and examine them by means of a good compound microscope. In the present study larvae of five different species were collected and identified. It was found that these species could be relatively easily separated on characters of size, coloration and general shape of capitulum, scutum and idiosoma. The main difficulty was in ascertaining that a specimen, which appeared to be one of the five collected species, was in fact that species and not a closely related one. Since a great number of larvae were collected, it was not possible to study each specimen individually. The procedure for identification was therefore as follows.

i. Larvae, preserved in 70% ethyl alcohol, were given an 'initial identification' which was made with the aid of a stereo dissection microscope (Wild M5).

ii. The larvae were then placed in tubes of alcohol labelled with the specific name determined by the initial identification.

iii. At a convenient time a number of larvae were removed from each tube (usually 25) and mounted in polyvinyl lactophenol. These larvae were then studied using a compound microscope. Final identifications were then made by comparison with drawings made from standard specimens studied at Onderstepoort under the direction of Miss J.B. Walker, and with preserved specimens identified by Miss Walker herself.

iv. After a number of samples had been studied in the above way Table 1 was constructed.

Table 1.

The numbers of larvae studied and identified using the procedure outlined in the text.

Tick species	No examined with stereo microscope	No examined with compound microscope	No found not to agree with initial determination
I. pilosus	1984	200	0
H. silacea	985	200	1
A. hebraeum	772	200	0
B. decoloratus	208	150	0
R. evertsi	3	3	0

Table 1 shows that the initial identifications of larvae were in most cases adequate. The single specimen found not to be H. silacea was B. decoloratus and was probably accidentally misplaced during initial sorting.

Macroclimatic conditions over the survey period

Thermohygrograph records were kept over the survey period at Barville Park and Faithful Fountain. Fig. 2 shows the fluctuations in mean weekly saturation deficit calculated from these records. Fig. 2 shows only the records calculated from the data recorded at Barville Park. The Faithful Fountain records were very similar and for this reason have not been included.

Table 2 shows the mean monthly rainfall, recorded by Mr. G. Reed at Faithful Fountain, over the survey period.

Table 2.

The mean monthly rainfall recorded at Faithful Fountain over the period of the survey (mms).

1969										
F	M	A	M	J	J	A	S	O	N	D
33	118	41	35	62	46	29	66	38	24	5
1970										
J	F	M	A	M						
141	45	23	66	101						

The Easter Cape was declared a drought stricken area during the summer of 1969-70. This may have had an effect on tick populations.

Results

The results of the Barville Park survey are shown in Tables 3-6. These results are summarised in Tables 7-8. The results of the Faithful Fountain survey appear in Tables 9-13.

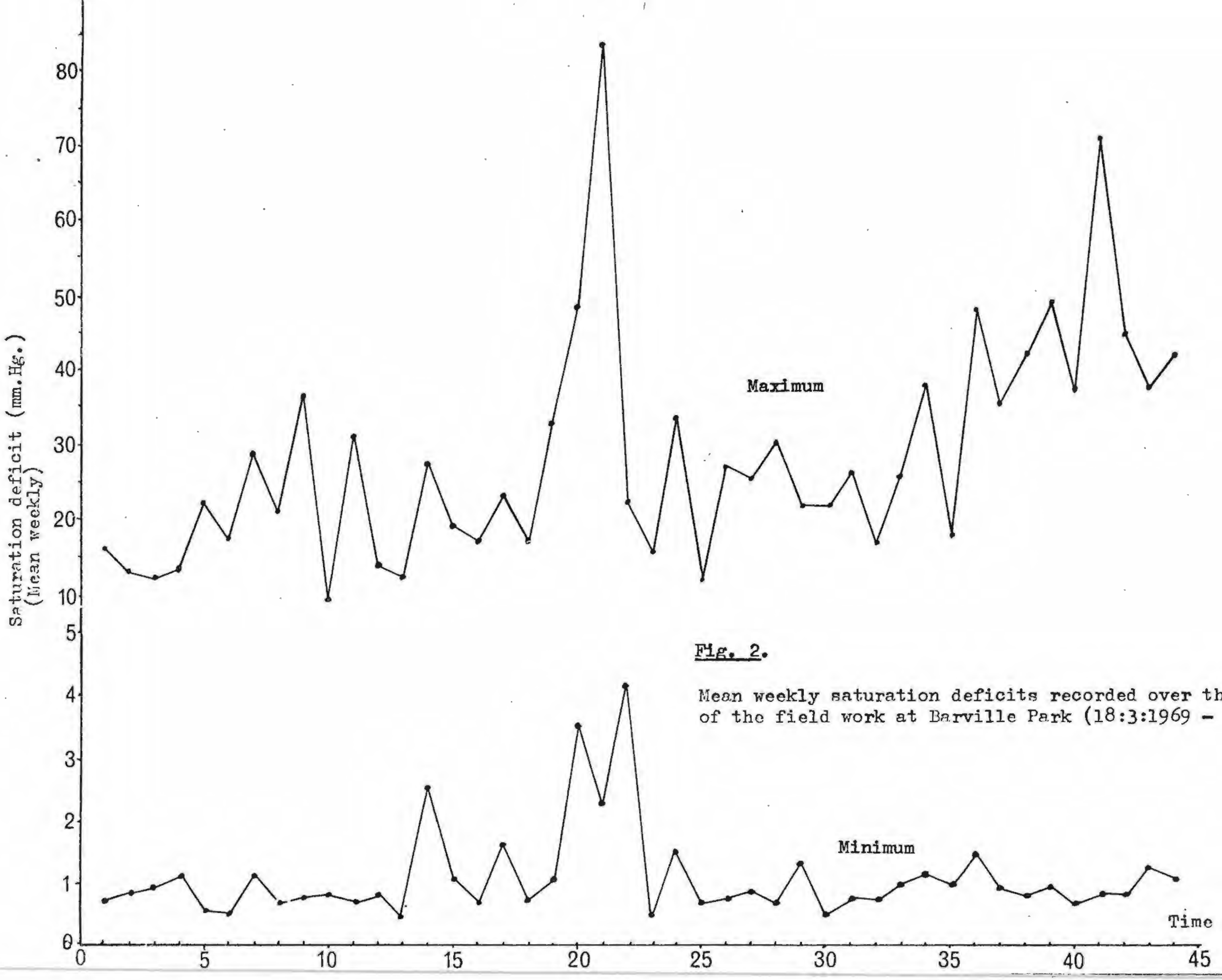


Fig. 2.

Mean weekly saturation deficits recorded over the duration of the field work at Barville Park (18:3:1969 – 2:2:1970).

Conclusions drawn from the Barville Park data

The results reported in Tables 3-8 show that the most commonly collected species was I. pilosus. This species was closely followed in numbers by H. silacea and A. hebraeum. B. decoloratus was only collected in small numbers. The distribution of the four species collected at Barville Park were in most cases fairly clearly defined by the nature of the vegetation. I. pilosus and H. silacea were collected predominantly from short covered vegetation while A. hebraeum appeared to be associated with medium to tall protected vegetation. Unfortunately B. decoloratus was collected in too small a number to allow any valid conclusions to be drawn from the data.

From the data presented in Tables 3 & 4 seasonal fluctuations can be detected for I. pilosus and H. silacea. Fig. 3 shows the average number of larvae, of both species, found in short covered vegetation (per 50^2metres) at various times throughout the survey period. Larval density was at its highest level during the cooler months of the year.

Conclusions drawn from the Faithful Fountain data

Although the results presented in Tables 9-13 are not conclusive it does appear that the population of B. decoloratus was of a higher density than at Barville Park. This suggestion is supported by the frequent observations of B. decoloratus adults on Faithful Fountain cattle. B. decoloratus larvae were predominantly collected from short protected vegetation. Initially it was decided that Barville Park would be surveyed over 1969 and Faithful Fountain over 1970. The severe drought of the summer of 1969-70, which was only finally broken in September 1970, altered the state of the vegetation so drastically that it was decided to cancel the

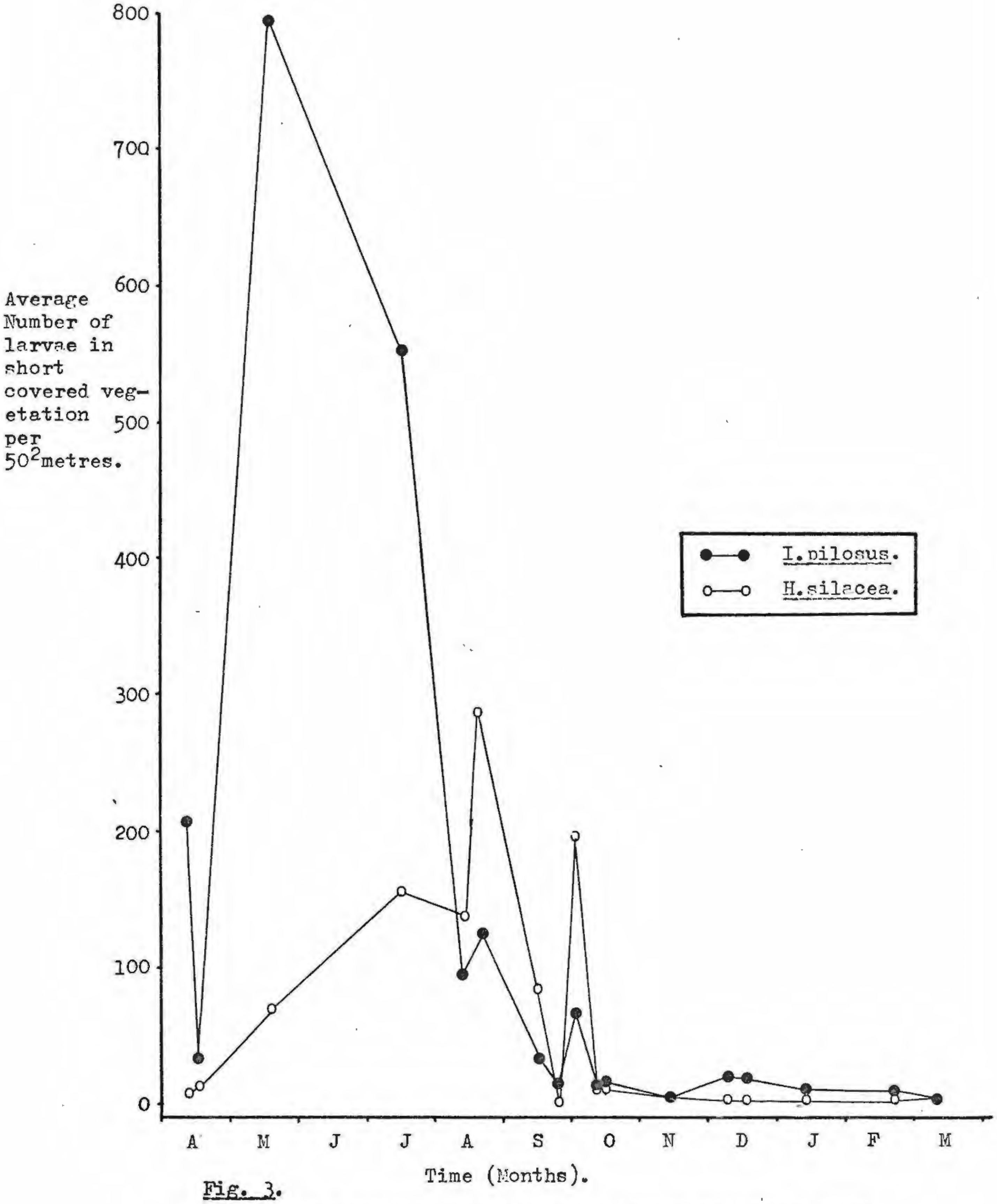


Fig. 3.

Numbers of I.pilosus and H.silacea larvae collected from short covered vegetation on Barville Park over 12 months.

(Constructed from figures in tables 3 and 4 respectively)

Faithful Fountain survey. Tick population densities also appeared to be very low over the drought which meant that comparisons with the 1969 data would have been impossible. These factors account for the presentation of only a few incomplete sampling records from Faithful Fountain.

Table 3. The average number of I. pilosus larvae collected per 50 m^2 from Barville Park over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	17/3	–	–	2	–	–	–	–	–	2
	23/3	–	0	–	–	–	–	–	–	0
	30/3	–	0	–	–	0	–	–	–	0
	5/4	–	0	0	–	–	0	–	–	0
	10/4	1	0	0	–	0	3	206	7	217
	16/4	0	0	2	36	11	2	33	–	84
	21/4	0	0	0	–	0	0	–	–	0
	8/5	0	0	0	–	0	–	–	–	0
	20/5	0	0	0	45	3	3	795	–	846
	17/7	0	0	0	20	2	–	552	–	574
	12/8	0	0	0	0	0	0	94	0	94
	18/8	0	0	0	0	0	0	122	0	122
	16/9	–	–	–	–	–	–	32	–	32
	26/9	0	10	4	5	6	–	15	15	55
	2/10	–	0	–	–	–	–	67	–	67
	8/10	0	0	0	2	0	0	11	26	39
	14/10	0	0	1	0	0	0	13	6	20
	11/11	0	0	0	0	0	0	3	0	3
	11/12	0	0	0	0	85	60	20	8	173
	17/12	0	0	0	0	60	20	18	10	108
1970	19/1	0	0	0	0	0	0	10	3	13
	26/2	0	0	0	0	0	0	9	2	11
	7/3	0	0	0	1	–	–	2	–	3
	Total	1	10	9	109	167	88	2002	77	2463

SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
TP = Tall Protected veg.
SC = Short Covered veg.
MC = Medium Covered veg.
– = No sample taken.
0 = No larvae collected in sample.

Table 4. The average number of H. silacea larvae collected per 50 m^2 from Barvilie Park over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	17/3	–	–	0	–	–	–	–	–	0
	23/3	–	0	–	–	–	–	–	–	0
	30/3	–	0	–	–	0	–	–	–	0
	5/4	–	0	0	–	–	0	–	–	0
	10/4	0	0	0	–	0	1	4	4	9
	16/4	1	2	2	3	1	8	10	–	27
	21/4	0	0	0	–	0	1	–	–	1
	8/5	0	0	0	–	0	–	–	–	0
	20/5	0	0	0	35	2	0	67	–	104
	17/7	0	0	0	95	5	–	152	–	252
	12/8	0	0	0	0	0	0	136	0	136
	18/8	0	0	0	0	0	0	288	0	288
	16/9	–	–	–	–	–	–	88	–	88
	26/9	0	0	0	3	0	–	3	30	36
	2/10	–	0	–	–	–	–	191	–	191
	8/10	0	0	0	0	0	0	13	34	47
	14/10	0	0	0	0	0	0	7	3	10
	11/11	0	0	0	0	0	0	2	2	4
	11/12	0	0	0	0	0	0	0	0	0
	17/12	0	0	0	0	0	0	0	0	0
1970	19/1	0	0	0	0	0	0	0	0	0
	26/2	0	0	0	0	0	0	0	0	0
	7/3	0	0	3	1	–	–	2	–	6
	Total	1	2	5	137	8	10	963	73	1199

SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
SC = Short Covered veg.
TP = Tall Protected veg.
MC = Medium Covered veg.
– = No sample taken.
0 = No larvae collected in sample.

Table 5. The average number of A. hebraeum larvae collected per 50 m^2 from Barville Park over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	17/3	–	–	0	–	–	–	–	–	0
	23/3	–	1	–	–	–	–	–	–	1
	30/3	–	2	–	–	202	–	–	–	204
	5/4	–	1	0	–	–	43	–	–	44
	10/4	0	0	0	–	4	52	14	1	71
	16/4	0	7	0	1	6	7	0	–	21
	21/4	1	1	2	–	0	24	–	–	28
	8/5	0	1	0	–	22	–	–	–	23
	20/5	0	0	0	2	13	14	2	–	31
	17/7	0	0	0	0	0	–	2	–	2
	12/8	0	0	0	0	0	0	0	0	0
	18/8	0	0	0	0	0	0	0	0	0
	16/9	–	–	–	–	–	–	4	–	4
	26/9	0	0	0	0	0	–	1	–	1
	2/10	–	0	–	–	–	–	3	–	3
	8/10	0	0	0	0	0	0	0	0	0
	14/10	0	0	0	0	0	0	0	0	0
	11/11	0	0	0	0	0	0	0	0	0
	11/12	0	0	0	0	0	0	0	0	0
	17/12	0	0	0	0	0	0	0	0	0
1970	19/1	0	0	0	0	0	0	0	0	0
	26/2	0	0	0	0	0	0	0	0	0
	7/3	2	1	0	1	–	–	0	–	4
	Total	3	14	2	4	247	140	26	1	437

SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
TP = Tall Protected veg.
SC = Short covered veg.
MC = Medium Covered veg.
– = No sample taken.
0 = No larvae collected in sample.

Table 6. The average number of B. decoloratus larvae collected per 50 m^2 from Barville Park over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	17/3	–	–	0	–	–	–	–	–	0
	23/3	–	0	–	–	–	–	–	–	0
	30/3	–	0	–	–	0	–	–	–	0
	5/4	–	0	0	–	–	0	–	–	0
	10/4	0	0	0	–	1	0	0	0	1
	16/4	0	0	0	0	0	0	0	–	0
	21/4	0	0	0	–	0	0	–	–	0
	8/5	0	0	0	–	0	–	–	–	0
	20/5	0	0	0	0	0	0	0	–	0
	17/7	0	0	0	0	0	–	0	–	0
	12/8	0	0	0	0	0	0	0	0	0
	18/8	0	0	0	0	0	0	0	0	0
	16/9	–	–	–	–	–	–	22	–	22
	26/9	0	0	0	0	0	–	0	0	0
	2/10	–	0	–	–	–	–	0	–	0
	8/10	1	1	0	0	0	0	0	0	2
	14/10	0	0	0	0	0	0	0	0	0
	11/11	0	0	0	0	0	0	0	0	0
	11/12	0	0	0	0	0	0	0	0	0
	17/12	0	0	0	0	0	0	0	0	0
1970	19/1	0	0	0	0	0	0	0	0	0
	26/2	0	0	0	0	0	0	0	0	0
	7/3	0	0	0	0	–	–	0	–	0
	Total	1	1	0	0	1	0	22	0	25

SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
TP = Tall Protected veg.
SC = Short Covered veg.
MC = Medium Covered veg.
– = No sample taken.
0 = No larvae collected in sample.

Table 7. The average number of larvae of the four species studied, collected per 50 m^2, from the eight vegetation categories.

Vegetation category	I. pilosus	H. silacea	A. hebraeum	B. decoloratus
SO	0	0	0	0
MO	0	0	1	0
TO	0	0	0	0
SP	8	10	0	0
MP	10	0	15	0
TP	6	1	10	0
SC	118	57	2	1
MC	7	7	0	0

(Figures expressed to the nearest whole number)

Table 8. A diagrammatic representation of the relative numbers of larvae collected from the eight vegetation categories as presented in Table 7.

Vegetation category	I. pilosus	H. silacea	A. hebraeum	B. decoloratus
SO	-	-	-	-
MO	-	-	X	-
TO	-	-	-	-
SP	X	XXX	-	-
MP	XXX	-	XXX	-
TP	X	X	XXX	-
SC	XXXXX	XXX	X	X
MC	X	X	-	-

- = less than 1.
X = greater than 0 and less than 10.
XXX = greater than 9 and less than 100.
XXXXX = greater than 99 and less than 1000.
SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
TP = Tall Protected veg.
SC = Short Covered veg.
MC = Medium Covered veg.

Table 9. The average number of I. pilosus larvae collected per 50 m^2 from Faithful Fountain over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	16/9	0	0	–	0	0	–	–	–	0
	22/9	0	–	–	–	0	–	16	–	16
	2/10	0	–	–	0	0	–	0	–	0
	8/10	0	0	–	–	–	–	0	–	0
1970	22/5	0	–	–	0	–	–	13	–	13
	Total	0	0	–	0	0	–	29	–	29

Table 10. The average number of H. silacea larvae collected per 50 m^2 from Faithful Fountain over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	16/9	0	0	–	0	0	–	–	–	0
	22/9	0	–	–	–	0	–	0	–	0
	2/10	0	–	–	0	0	–	0	–	0
	8/10	0	0	–	–	–	–	0	–	0
1970	22/5	0	–	–	2	–	–	44	–	46
	Total	0	0	–	2	0	–	44	–	46

Table 11. The average number of A. hebraeum larvae collected per 50 m^2 from Faithful Fountain over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	16/9	0	0	–	0	2	–	–	–	2
	22/9	0	–	–	–	2	–	2	–	4
	2/10	0	–	–	0	0	–	0	–	0
	8/10	0	0	–	–	–	–	0	–	0
1970	22/5	0	–	–	15	–	–	1	–	16
	Total	0	0	–	15	4	–	3	–	22

SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
TP = Tall Protected veg.
SC = Short Covered veg.
MC = Medium Covered veg.
– = No sample taken
0 = No larvae collected in sample.

Table 12. The average number of B. decoloratus larvae collected per 50 m^2 from Faithful Fountain over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	16/9	0	0	–	65	29	–	–	–	94
	22/9	0	–	–	–	3	–	0	–	3
	2/10	0	–	–	10	0	–	0	–	10
	8/10	2	3	–	–	–	–	0	–	5
1970	22/5	0	–	–	28	–	–	0	–	28
	Total	2	3	–	103	32	–	0	–	140

Table 13. The average number of R. evertsi larvae collected per 50 m^2 from Faithful Fountain over the period of the survey.

	Date	SO	MO	TO	SP	MP	TP	SC	MC	Total
1969	16/9	0	0	–	0	0	–	–	–	0
	22/9	0	–	–	–	0	–	0	–	0
	2/10	0	–	–	0	0	–	0	–	0
	8/10	0	0	–	–	–	–	0	–	0
1970	22/5	0	–	–	3	–	–	0	–	3
	Total	0	0	–	3	0	–	0	–	3

SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
TP = Tall Protected veg.
SC = Short Covered veg.
MC = Medium Covered veg.
– = No sample taken.
0 = No larvae collected in sample.

Discussion

Although Kraft (1961) used different vegetation categories and was concerned with larval clusters rather than individual larvae, it is possible to compare her 'Seaview' (a farm near the coast in the Alexandria district) findings with those of the present investigation. It is convenient to deal with each of the five species of ixodid tick larvae individually.

i. I. pilosus

This species has been found to live in high rainfall areas under sourveld (Theiler 1969). Kraft (1961) collected it from Seaview but did not find it on any of the farms which were located further inland. This is an indication that coastal farms are probably more suitable for the development of this species. Kraft (1961) collected I. pilosus from the following vegetation categories.

a. Level and South facing slopes, under complete and incomplete overhead cover.
b. Laterally-sheltered medium-height grass.
c. South facing slope, in laterally-sheltered short and medium-height grass.

The findings of the present investigation agree with those of Kraft (1961). The Barville Park and Faithful Fountain survey shows that this species, although collected from all protected and covered vegetation categories, was predominantly found in short covered and short protected vegetation. Kraft (1961) notes that larval clusters of this species were found in more open situations in Spring. The collection data of the 26th September 1969 (Table 3) supports this observation in that larvae were collected from both medium and tall open vegetation. The reason for this exception to what appears to be the rule can not be explained. It is possible that the movements of the host animals have some bearing on this observation. In both Kraft's (1961) and the present survey, numerous larvae were collected in autumn. Theiler (1969) states that

> "in general terms, most of the South African adult ticks are active in summer. I. rubicundus and Margaropus winthemi, however, are active in winter."

This is of interest as it suggests that the different stages may possess different activity peaks. i.e. Egg peak in autumn; larval peak in winter; nymphal peak in spring; adult peak in summer. The differences in population density of each stage relative to the seasons is important in the management of dipping programmes and should be thoroughly investigated in an endeavour to plan more efficient control.

ii. H. silacea

Theiler (1969) states that

> "Haemaphysalis silacea is confined to the hot dry Fish-river type of Karroid bush."

This statement is of interest as the coastal strip is not really of this type of vegetation. H. silacea is however well established at Barville Park as the survey data show. Kraft (1961) does not mention this species at all. This seems odd as it occurs very commonly with I. pilosus which she collected in large numbers. It is unlikely that Kraft (1961) mistook this species for another as it is a fairly distinctive one in that it lacks eyes and is in other respects easily recognised. The only explanation is that Kraft (1961) did collect this species but did not include it in her study. Although this species occurs commonly with I. pilosus it is unlikely that any interspecific competition exists, as the host lists, presented in the appendix, show. Fig. 3 shows that H. silacea also has a population density peak during the cooler months as does I. pilosus.

iii. A. hebraeum

Theiler (1969) states that A. hebraeum is found in tall grassveld, provided bush or tall scrub coverage is adequate. The Barville Park survey supports this statement as larvae of this species were collected predominantly from medium to tall protected vegetation. Kraft (1961) did not record A. hebraeum from her Seaview farm. As she did find it on her other farms it must be assumed that it was absent at Seaview. This fact is difficult to understand as this species is well established on coastal farms. Apart from collecting many specimens at Barville Park, numbers of adults were seen on the cattle at Faithful Fountain.

The number of A. hebraeum larvae collected at Barville Park declined rapidly around about the end of May 1969. This fall in density is thought to be associated with the fact that farm labourers entered Old Cow Camp on the 21st May, cleared a number of bushes from the area and cut down almost all the tall grass in the camp. It is quite possible that this incident effectively caused the removal of many suitable habitats which normally supported A. hebraeum larvae and thus caused a decrease in their numbers.

iv. B. decoloratus

Kraft (1961) collected B. decoloratus in the following vegetation categories at Seaview and an adjacent farm.

a. Laterally-sheltered Medium-height grass on level ground.

b. Medium-height grass on level ground.

c. Short grass on East facing slope.

d. Short grass on level ground.

e. Sparsely growing grass with no stones on a steep North facing slope.

Few larvae of this species were collected at Barville Park but numbers were collected from short protected vegetation at Faithful Fountain. Kraft (1961) appears to have collected this species predominantly from short grass (she does not define 'short') which received little protection from neighbouring plants. She did however collect larvae from laterally protected medium grass (again she does not define 'medium'). Kraft (1961) suggests that the distribution of B. decoloratus is closely related to the movements of the cattle. As this is a single host species this suggestion is probably true and is supported by the fact that larvae were only collected from the camps which were frequented by cattle and not from those camps which were infrequently grazed (i.e. those Faithful Fountain camps without water supplies).

v. R. evertsi

Kraft (1961) collected R. evertsi at Seaview in the following vegetation categories.

a. Laterally-sheltered Medium-height grass.
b. Laterally-sheltered short grass.
c. Medium-height grass.
d. Short Grass.

Only three specimens of this species were collected during the entire period of the survey reported in this investigation. This fact is difficult to explain as adults were frequently seen under the tails of cattle on both Barville Park and Faithful Fountain. The possible explanations for the species apparent absence in the non-parasitic larval form could be as follows. The species may not have its activity peak in the morning hours when samples were taken. The species may have inhabited the drier areas of Barville Park (i.e. the north camps) which were not studied. It is also possible that the 'tailbar' was unsuitable for the collecting of this species. This last suggestion does not seem very probable as Kraft (1961) collected R. evertsi using a similar type of 'tailbar'.

3. MICROCLIMATIC STUDIES

It is evident from the results of the survey carried out at Barville Park and Faithful Fountain that larval ticks are probably associated with broad vegetation categories. These categories, however, only represent the outward signs of particular factors involved in the ecology of larval ticks. It is felt that a thorough knowledge of the microclimatic conditions underwhich non-parasitic larval ticks live, and do not live, is essential. This type of information could partly explain the distribution of larvae as concluded from the study of the broad vegetational situations. Stampa (1959) and Kraft (1961) attempted to gain microclimatic information from thermohygrograph records, a procedure which has obvious limitations. The reason for the lack of knowledge of larval microclimates is partly due to the difficulty in measuring these with any accuracy. It was decided that some measurement of microclimatic temperatures and relative humidities should be attempted, using more refined instrumentation.

Instrumentation

Temperature measurement :

All microclimatic temperatures were measured with thermistors. The circuit used in the construction of the thermometer is shown in Fig. 4 and the thermometer itself is shown in Plate 10. The circuit was housed in a wooden container, as shown, and was easily carried in the field. Fig. 5 shows the galvanometer deflection in relation to temperature. The range of the instrument was 0-74°C which was thought to be adequate for the purposes of the investigation. Although two thermistor leads were incorporated into the circuit, only one of these was used throughout the investigation. Fig. 5 is applicable only to the particular lead used.

Fig. 4. The circuit diagram used in the construction of the thermometer.

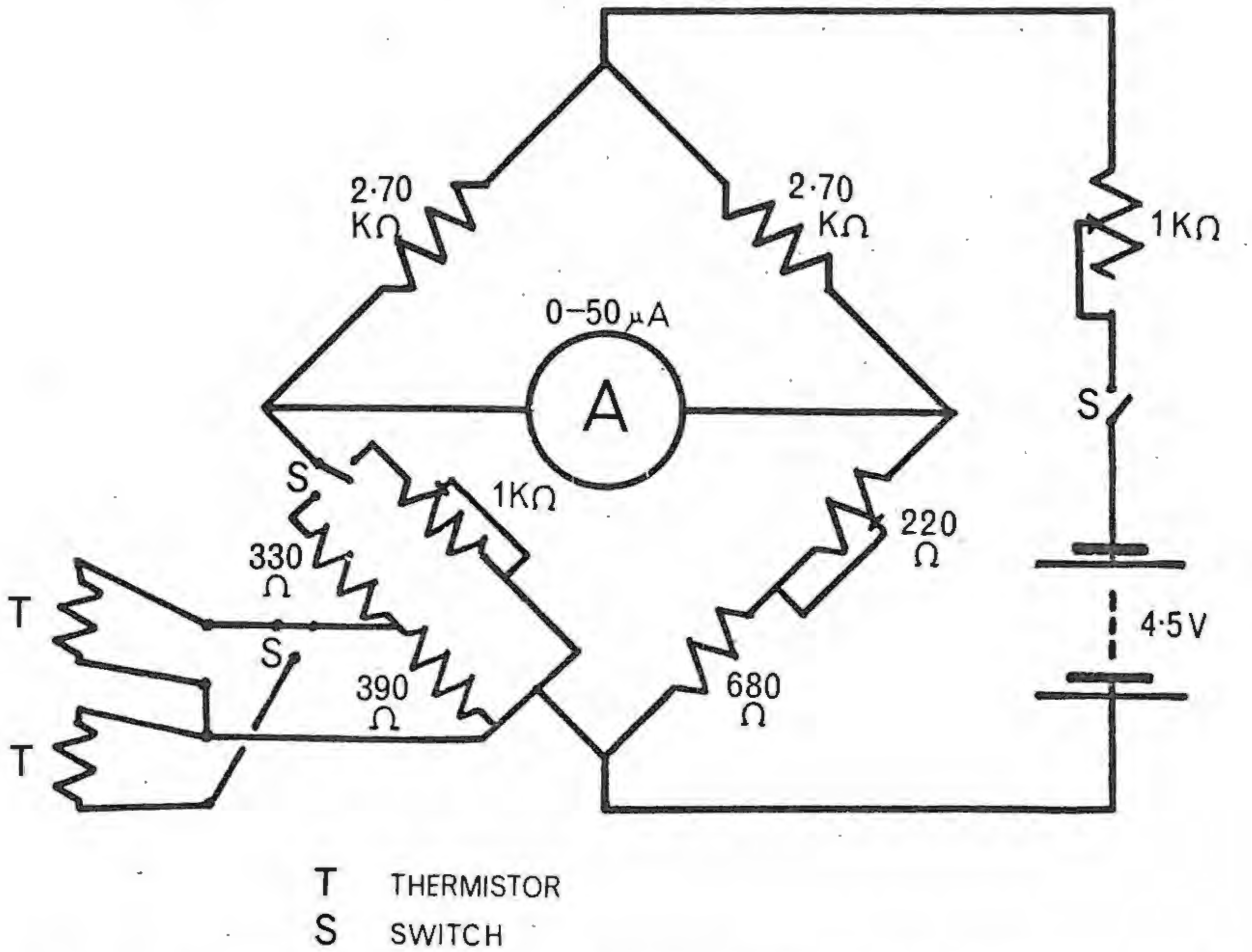
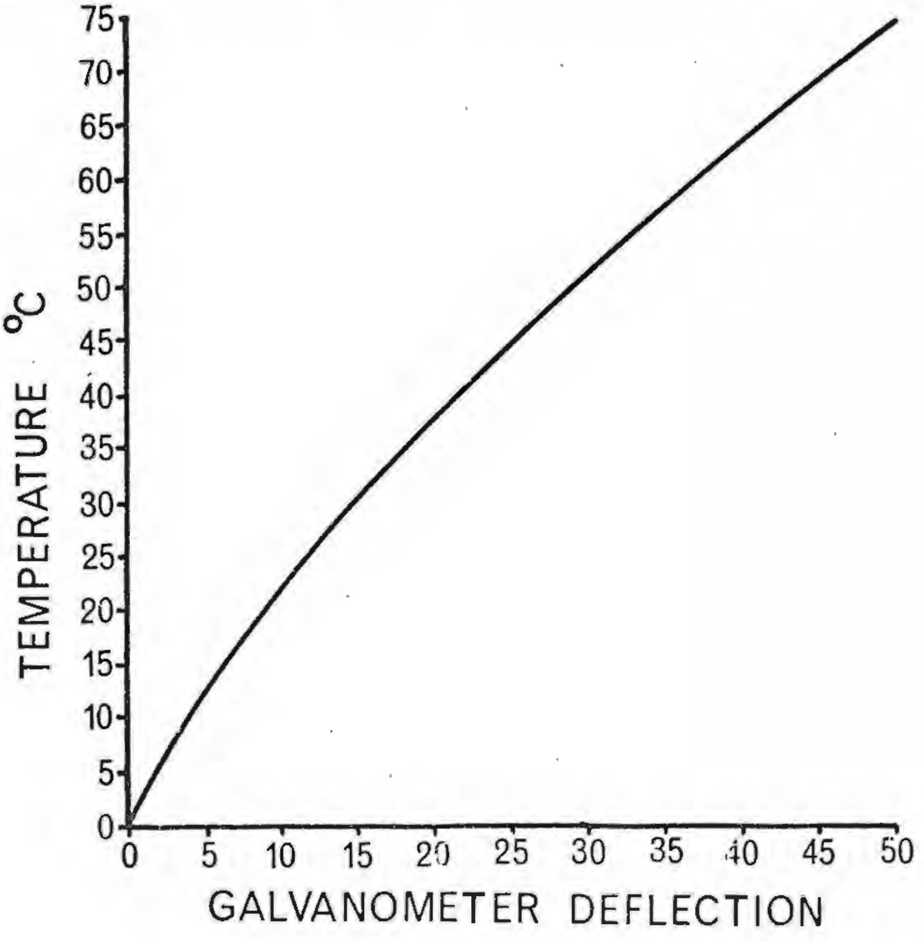


Fig. 5. The temperature curve characteristic of the thermistor used.



Relative humidity measurement :

Relative humidity (RH) is perhaps the most difficult condition to measure at a microclimatic level. Many excellent devices have been produced in order to fill the need for a sensitive humidity recorder. These devices are usually limited when used in small volumes of air. It was decided that, for the purposes of the present study, the use of Cobalt thiocyanate paper indicators was the most practical method. The method used was that of Solomon (1957). The apparatus used is shown in Plate 11. The standards available for use with the Lovibond comparator were 0, 10, 20, 30, 40, 50, 60, 65, 70, 75, 80, 85, 90, 95, 100 % RH. When an exposed paper indicated a value between two standards, a value half way between the two standards was recorded. e.g. If a paper indicated a RH value between 65-70 % RH, then 67.5 % RH was recorded. In this way an error of not greater than 5% RH was likely to be incurred while dealing with values between 0-60 % RH and 2.5 % RH when dealing with values between 60-100 % RH. All relative humidity values were corrected when measurements were made at a temperature other than 20°C, as indicated by Solomon (1957). All measurements were made by exposing the paper indicators for two hour periods.

Air speed measurement :

An indication of the way in which the wind might be expected to influence the microhabitats was also obtained by the use of an anemometer (Casella Air Meter) (Plate 12) calibrated between 0-100,000. metres. All readings were taken over one minute periods and are therefore expressed in terms of metres per minute.

Sites used in the analysis of microclimates

Eight sites were selected in 'Old Cow Camp' at Barville Park as representing the eight vegetation categories outlined in the previous chapter. Details concerning the nature of these sites, which are illustrated in Plates 2-9, are supplied in Table 14.

Table 14. Some details concerning the nature of the sites used in the microclimatic investigation.

Vegetation Category	Soil and surface	Protection	Position
SO	Dry sandy soil with little surface cover.	None.	Slight W slope.
MO	Dry sandy soil with little surface cover.	None.	Slight S slope.
TO	Dry sandy soil with little surface cover.	None.	Slight S slope.
SP	Firm sandy soil with little dead leaf matter on surface.	Dense bush on E side.	S slope.
MP	Sandy soil with a mat of dead leaves on surface.	Dense bush on NW side.	S slope.
TP	Sandy soil with little surface cover.	Dense bush on NW side.	Slight W slope in hollow.
SC	Sandy soil with a mat of dead leaves on surface.	Tree canopy overhead.	Slight S slope.
MC	Sandy soil with a mat of dead leaves on surface.	Tree canopy overhead.	Slight S slope.

SO = Short Open.
MO = Medium Open.
TO = Tall Open.
SP = Short Protected.
MP = Medium Protected.
TP = Tall Protected.
SC = Short Covered.
MC = Medium Covered.
N = North.
S = South.
E = East.
W = West.

The positions of the above sites are indicated diagrammatically in Fig. 6. The general positions of the sites should be noted for the following reasons.

i. Sites situated on south facing slopes can be regarded as being generally cooler and damper than other sites as the vegetation is usually denser on these slopes. South slopes are never

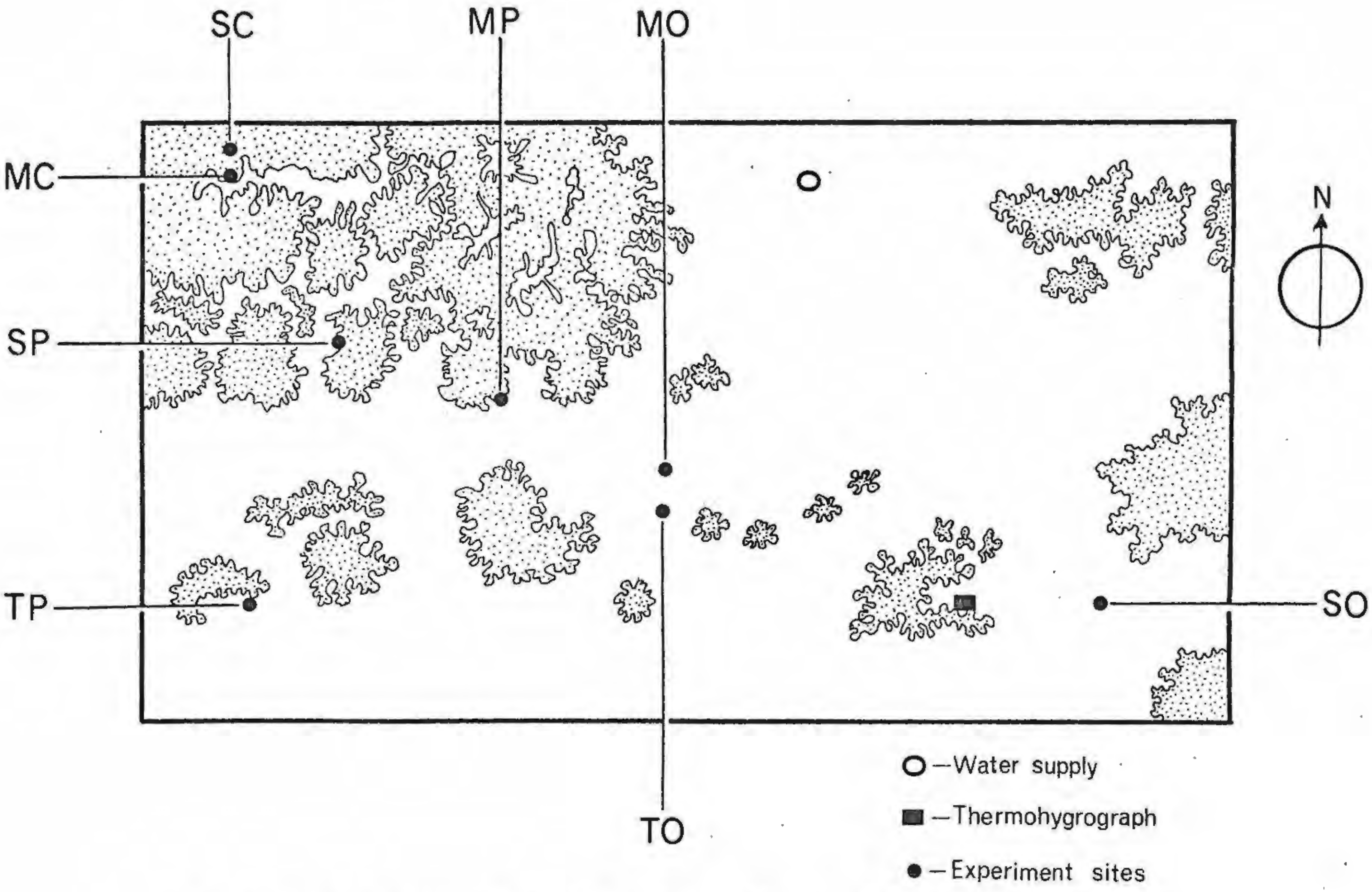


Fig. 6. The positions of the various sites used in the microclimatic investigation conducted in Old Cow Camp.

SO = Short open vegetation.
MO = Medium open vegetation.
TO = Tall open vegetation.
SP = Short protected vegetation.
MP = Medium protected vegetation.
TP = Tall protected vegetation.
SC = Short covered vegetation.
MC = Medium covered vegetation.

under the direct vertical rays of the sun, especially in winter.

ii. Sites on east slopes usually get direct sunlight in the mornings while those on west slopes in the afternoon. This means that east facing slopes are generally drier, as those facing west were often found to retain dew for longer periods.

iii. Sites protected by bushes on the west (i.e. shaded when the sun was in the west) can be regarded as being drier than those protected by bushes on the east as dew appeared to be retained longer in vegetation on the west side of bushes. The importance of shading in the survival and behaviour of <u>Boophilus microplus</u> (Canestrini) has been shown by Wilkinson and Wilson (1959). These workers found that larvae lived longer in shaded places than in unshaded ones. They also found that larvae tended to gather in shaded situations in preference to sunny situations. It will be shown later (page 38) that the microclimatic conditions are influenced by shading and this in turn must have an effect on the survival of larvae.

iv. North facing sites and slopes can be regarded as being generally much hotter and drier than other sites and slopes. This is naturally due to the fact that the sun is always in the northern sky in all southern hemisphere countries. Further evidence in support of this contention is given later (page 38).

The above considerations, although obvious, must be kept in mind when a study of microclimatic conditions is undertaken as one experimental site may differ greatly from another depending on the factors mentioned.

Procedure followed during microclimatic analysis

The procedure followed in all measurement of microclimatic temperatures and relative humidities was as follows.

i. Each experimental site was visited in strict order. The order was always Short Open, Medium Open, Tall Open, Medium Protected, Short Protected, Medium Covered, Short Covered and Tall Protected as this was found to be the shortest route and could be undertaken within an hour.

ii. At each site a dowel-stick (90 x 0.6 cms) was thrust into the ground among the plants in the particular habitat. Three small metal mesh cylinders were attached to each dowel by means of rubber-bands at levels corresponding to the top, middle and bottom of the vegetation concerned. Plate 13 shows one such arrangement of cylinders.

iii. Cobalt thiocyanate paper strips (3 x 1 cms) were then placed in the mesh cylinders.

iv. After an exposure of two hours each paper strip was removed and placed in a labelled vial containing liquid paraffin so as to prevent any further colour change. Temperatures were recorded at the same three levels used in relative humidity measurements at the time when the papers were removed from their cylinders.

v. Finally the thermohygrograph recordings were studied to facilitate correlations between microclimatic and macroclimatic conditions.

It should be noted that as Cobalt thiocyanate paper strips require two hours exposure (Solomon 1957), a detailed hour by hour examination of relative humidities was impossible. This was one of the drawbacks to the method. Another drawback was the fact that only two readings could be made in any 24 hour period as only two periods exist during which conditions remain fairly constant for at least two hours. These periods, established by studying thermohygrograph records, were at midday (between approximately 11 a.m. and 1 p.m.) and in the early morning (between approximately 3 a.m. and 5 a.m.). Measurements over these two periods were thought to be sufficient as the readings reflected the extremes experienced by any of the habitats involved.

Wind speeds (air currents) were measured as follows.

i. The anemometer was placed in an E/W direction (i.e. one side facing east the other west) at ground level. The prevailing wind being from the west on both occasions when measurements were taken. Three readings were then taken, each over one minute periods, from which a mean was calculated.

ii. Three further readings were then taken with the anemometer held in an E/W direction at the top of the vegetation. The height above the ground being dependant of the vegetation height.

iii. Each vegetation site was visited in order and the above procedure undertaken.

Results

The data collected from the eight vegetation sites in 'Old Cow Camp' at Barville Park appear in Tables 15-16. Microclimatic temperatures and relative humidity values have been expressed in terms of saturation deficits. This was done so as to allow easy and direct comparisons between the various levels in the vegetation and the various vegetation categories. As saturation deficit is a measure of the drying power of the air, this is of particular relevance to tick survival and is therefore a realistic means of expressing microclimatic

Table 15. Microclimatic conditions measured in eight sites representing eight vegetation categories. All figures expressed as saturation deficits (mm. Hg.).

Day conditions (measured between 11 a.m. and 1 p.m.)

Date	P	SO	MO	TO	SP	MP	TP	SC	MC	T/H
8/5/69	Top.	20.44	–	16.06	9.95	7.44	9.06	7.44	10.57	18.13
	Mid.	21.06	12.69	13.09	9.95	7.21	8.52	5.61	9.17	
	Bot.	11.67	1.00	0.00	3.26	1.36	2.42	2.88	3.36	
26/5/69	Top.	15.09	10.35	13.81	7.68	7.45	–	4.91	6.16	10.32
	Mid.	14.66	10.06	13.01	6.54	6.54	–	4.75	6.16	
	Bot.	12.02	6.39	7.36	3.26	2.12	–	2.00	1.99	
12/6/69	Top.	8.16	7.01	5.52	5.79	6.79	7.68	5.97	6.79	7.65
	Mid.	8.16	7.01	5.52	5.79	6.79	7.68	5.97	6.79	
	Bot.	8.41	0.77	4.05	1.61	2.56	3.26	2.56	1.99	
18/6/69	Top.	19.25	15.58	19.04	15.58	15.58	12.31	9.95	12.69	18.74
	Mid.	16.03	15.11	18.47	15.58	12.31	12.31	9.95	12.69	
	Bot.	8.40	11.04	0.91	8.16	3.16	0.94	7.92	9.95	
23/7/69	Top.	20.44	13.91	12.69	8.36	7.68	7.68	5.61	5.61	12.94
	Mid.	20.44	13.49	12.69	7.21	6.79	7.21	4.21	5.44	
	Bot.	13.81	7.68	7.92	2.40	3.16	4.21	2.97	4.08	
18/8/69	Top.	13.41	8.67	9.75	9.95	6.15	6.15	7.92	7.92	9.95
	Mid.	11.32	8.67	9.75	9.92	6.15	6.15	7.68	7.68	
	Bot.	11.67	10.57	9.75	6.15	6.15	4.34	7.68	7.92	
16/9/69	Top.	13.09	9.35	10.88	8.52	6.08	7.62	8.52	8.25	11.57
	Mid.	29.45	10.42	10.88	8.52	6.08	7.62	8.52	8.25	
	Bot.	30.26	13.09	10.42	6.78	5.37	5.27	10.55	8.25	
14/10/69	Top.	22.34	20.24	12.25	17.55	12.25	17.36	12.31	16.06	18.50
	Mid.	22.23	20.24	20.24	21.69	12.25	11.57	12.31	16.06	
	Bot.	71.44	20.24	20.24	26.50	18.13	17.36	18.47	13.09	
1/12/69	Top.	18.60	13.13	19.14	14.66	8.40	10.66	10.66	8.92	40.79
	Mid.	17.10	15.66	21.41	12.02	9.27	8.40	10.66	8.92	
	Bot.	+	26.43	16.71	12.02	10.66	13.01	10.66	10.08	
6/1/70	Top.	46.42	24.97	14.32	39.84	15.63	22.24	15.22	24.26	35.15
	Mid.	54.45	24.97	22.24	39.84	12.54	22.24	15.22	24.26	
	Bot.	+	24.97	15.33	+	7.68	22.24	22.24	24.26	

(Table 15 continued on following page)

Table 15 continued :

Night conditions (measured between 3 a.m. and 5 a.m.)

Date										
31/5/69	Top.	0.13	0.13	0.13	0.13	0.13	0.13	0.55	0.55	0.34
	Mid.	0.13	0.13	0.13	0.13	0.13	0.13	0.55	0.55	
	Bot.	0.00	0.00	0.00	0.00	0.00	0.00	0.55	0.55	
18/6/69	Top.	0.13	0.13	0.13	0.13	0.13	0.13	0.55	0.55	0.34
	Mid.	0.13	0.13	0.13	0.13	0.13	0.13	0.55	0.55	
	Bot.	0.00	0.00	0.00	0.00	0.00	0.00	0.55	0.55	
24/1/70	Top.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.83
	Mid.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
	Bot.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	

P = Position in vegetation (Top, Middle and Bottom)
SO = Short Open veg.
MO = Medium Open veg.
TO = Tall Open veg.
SP = Short Protected veg.
MP = Medium Protected veg.
TP = Tall Protected veg.
SC = Short Covered veg.
MC = Medium Covered veg.
T/H = Thermohygrograph reading.
– = Spoilt readings.
\+ = Value higher than the limits of the method.

Table 16. Wind speeds recorded on two fairly windy days at Barville Park.

Date 30/6/1969.

Vegetation category	Position	E/W wind (m/min)
SO	Top of veg.	239.5 W
	Ground.	66.5 W
MO	Top of veg.	238 W
	Ground.	4 W
TO	Top of veg.	283.5 W
	Ground.	0 -
SP	Top of veg.	8.5 W
	Ground.	0 -
MP	Top of veg.	60 W
	Ground.	0 -
TP	Top of veg.	17.4 W
	Ground.	0 -
SC	Top of veg.	0.5 E
	Ground.	0 -
MC	Top of veg.	13 W
	Ground.	0 -

Additional reading : 6' above ground in open 529 m/min W.

Date 29/9/1969

Vegetation category	Position	E/W wind (m/min)
SO	Top of veg.	217 W
	Ground.	28 W
MO	Top of veg.	138 W
	Ground.	22 W
TO	Top of veg.	153 W
	Ground.	0 -
SP	Top of veg.	25 W
	Ground.	0 -
MP	Top of veg.	40 W
	Ground.	0 -
TP	Top of veg.	180 W
	Ground.	0 -
SC	Top of veg.	0 -
	Ground.	0 -
MC	Top of veg.	32 W
	Ground.	0 -

E = East. W = West. SO = Short Open veg. MO = Medium Open veg. TO = Tall Open veg. SP = Short Protected veg. MP = Medium Protected veg. TP = Tall Protected veg. SC = Short Covered veg. MC = Medium Covered veg.

conditions. All saturation deficit values were calculated using the following basic formulae.

$$\boxed{\begin{array}{l} SVP = \frac{100 \times VP}{\%RH} \\ SD = SVP - VP \end{array}}$$

SVP = Saturated Vapour Pressure.
VP = Vapour pressure (dependant on temperature).
RH = Relative Humidity.
SD = Saturation Deficit (mm. Hg).

Peterson (1953) published useful vapour pressure/temperature tables which were used throughout the investigation. Table 15 also includes thermohygrograph recordings as indications of the macroclimatic conditions which prevailed during the microclimatic measurements, these are also expressed as saturation deficits.

Discussion of results

From the results shown in Tables 15-16 the following conclusions can be drawn.

i. Open habitats are generally hotter, drier and 'windier' than protected and covered ones.

ii. During the cooler months ground conditions were generally cooler and damper than higher up in the vegetation. However, during summer, before rain had fallen, the reverse pertained. Air currents were usually very slight at ground level, especially in protected and covered habitats which meant that these categories were likely to be damper than open vegetation categories (Schütte and King 1965).

iii. Conditions of saturation deficit in nearly all the habitats examined, approximated 0 mm.Hg. during the early morning hours. This appeared to be true for both summer and winter. Open categories were found to be damper than protected and covered ones as dew was not found to be present to any great extent under trees and bushes. Open vegetation was found to be very wet, especially during the winter. The importance of free water to the survival of larval Ixodidae has been demonstrated by Wilkinson and Wilson (1959) and will be discussed in Chapter 4.

iv. Microclimatic conditions measured in open vegetation categories were found to be drier and hotter than those recorded by the thermohygrograph. This was probably due to the fact that the thermohygrograph was sheltered from the direct rays of the sun by the Stevenson's screen in which it was housed. Protected and covered vegetation categories were usually found to be cooler and damper than conditions within the Stevenson's screen. It appeared that the conditions found in Tall Open vegetation most closely resembled those recorded by the thermohygrograph. It is obvious that the prediction of microclimatic conditions from macroclimatic conditions could be very misleading. As some past workers have attempted to do this, their predictions should be viewed with discretion.

v. Generally equable conditions appeared to prevail when the day was windy or overcast. This fact is not readily concluded from the results presented in Tables 15-16 but was recorded during the investigation.

As many of the conclusions expressed above may only apply to the particular sites used in the investigation it was thought necessary to get some idea of the possible range of conditions which might be expected within each vegetation category. It was suspected that conditions within the open and covered habitats would vary only slightly between different sites. Protected habitats might, however, be expected to vary quite considerably between different sites dependant on the position of the site with respect to the protecting trees and bushes. It was decided that a study of various sites which could be classified under the same broad category (eg. Short Protected etc) should be undertaken. For this investigation short vegetation of open, protected and covered types were dealt with.

Comparison of various short open vegetation sites

Six examples of short open vegetation were compared with the site used in the microclimatic studies already reported. Table 17 shows the values of saturation deficit calculated for all seven sites at three different levels in the vegetation. Microclimatic temperatures and relative humidities were measured at the same time in all sites.

Table 17. Saturation deficits calculated for seven short open sites.

Date : 2/5/1969

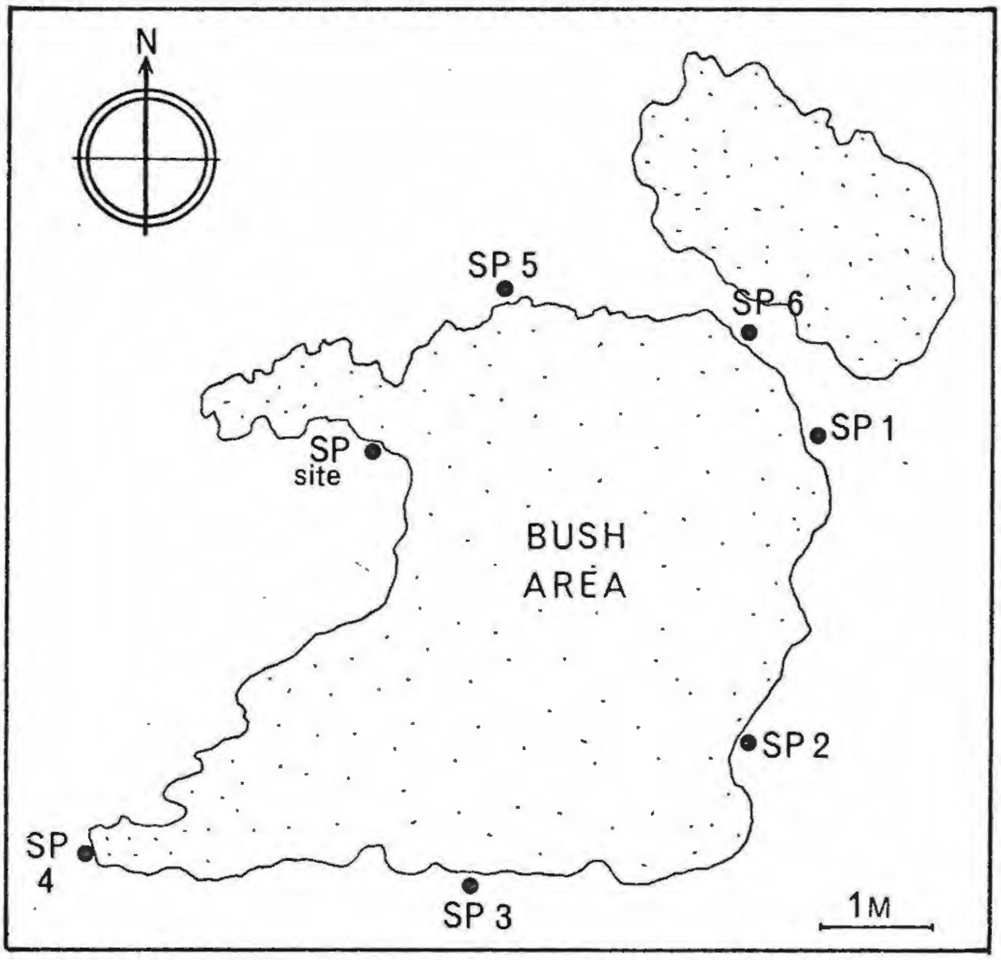
Position in vegetation.	Saturation deficit (mm.Hg.)							
	SO 1	SO 2	SO 3	SO 4	SO 5	SO 6	SO site	T/H
Top.	19.04	19.04	19.04	19.04	19.04	19.04	19.04	18.47
Middle.	19.63	19.63	19.63	19.63	19.63	19.63	19.63	
Bottom.	16.06	16.06	16.06	19.63	16.06	16.06	16.06	

SO (1-6) = Short Open sites.
SO site = Short Open site used in microclimatic study.
T/H = Thermohygrograph (Macroclimatic conditions).

The results above show that all short open sites are likely to differ only very slightly from each other microclimatically. The site used throughout the already reported investigation could be regarded as typical.

Comparison of various short protected vegetation sites.

Six examples of short protected vegetation were selected in the vicinity of the site used during the microclimatic work already reported. Fig. 7 shows a diagramatic representation of the positions of all seven sites under discussion. Table 18 shows the saturation deficits calculated at the three levels in each site.



SP = Short Protected vegetation category.

site = Actual site used in microclimatic work.

<u>Fig. 7</u>.

The positions of various short protected sites used for comparative purposes in microclimatic studies.

Table 18. Saturation deficits calculated for seven short protected sites.

Date : 2/10/1969.

Position in vegetation.	Saturation deficit (mm.Hg.) SP 1	SP 2	SP 3	SP 4	SP 5	SP 6	SP site	T/H
Top.	7.68	6.16	6.19	9.64	19.25	7.68	9.06	
Middle.	8.67	6.16	5.44	9.35	20.40	6.75	9.06	16.37
Bottom.	9.75	4.62	4.08	4.34	40.72	5.06	5.61	

SP (1-6) = Short Protected sites.
SP site = Short Protected site used in microclimatic study.
T/H = Thermohygrograph (Macroclimatic conditions).

Table 18 shows that north facing sites (i.e. SP 5) are far hotter and drier than other sites. The results show that east facing sites were cooler and damper than west facing ones. This is easily explained by the fact that the vegetation was thicker on the eastern side of the bushy area. The time of study was over the midday period and therefore humidity papers were collected from the eastern side of the bush after that side had fallen into shadow. The temperatures were therefore lower than those recorded on the western side of the bushy area as this side was then in direct sunlight.

The above short discussion shows just how readings can be effected by position as regards protecting vegetation. The site which was used for the microclimatic study reported earlier appeared to be slightly drier and warmer than some of the other short protected sites. However, it was probably ultimately the best site, as the conditions were between the extremes found in the results reported in Table 18. It is evident that if a north facing site had been used in the microclimatic work earlier reported some erroneous results could certainly have been reported.

Comparison of various short covered vegetation categories

The results of a study of six short covered vegetation sites and the site used in the microclimatic study are reported in Table 19.

Table 19. Saturation deficits calculated for seven short covered sites.

Date : 22/9/1969.

Position in	Saturation deficit (mm. Hg.)							
vegetation.	SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC site	T/H
Top.	10.47	9.64	9.64	8.62	9.64	8.62	9.64	18.12
Middle.	10.47	9.64	9.64	8.62	9.64	8.62	9.64	
Bottom.	10.74	9.46	7.68	8.62	7.68	7.68	9.64	

SC (1-6) = Short Covered sites.
SC site = Short Covered site used in microclimatic study.
T/H = Thermohygrograph (Macroclimatic conditions).

Table 19 shows that there were some slight differences between the sites studied. These differences can probably be explained by the uneven nature of the overhead tree canopy. Some of the sites were probably effected by direct sunlight more than others.

Although all the vegetation categories have not been studied in the above way, these three examples do point to some of the possible errors which may be expected in a microclimatic study of the sort reported in this chapter. If the information in Table 14 is taken into consideration however, some of the effects of site position, especially with regard to the protected vegetation categories, might be predicted. It is felt that the microclimatic data presented in Table 15 can be taken as reasonable indications of the conditions found in the eight types of vegetational situations.

A further discussion of the importance of the results obtained in this chapter will be made in the next chapter which deals with the water relations of larval ticks.

4. WATER RELATIONS OF TICK LARVAE

The survival of terrestrial arthropods is, in general, dependent on factors such as the availability of sufficient food, adequate living space, the absence of severe predation and the maintenance of water balance. When dealing with the non-parasitic larval stage of ticks, the availability of food is of no immediate importance. Larvae naturally depend on the location of a host for ultimate survival but as they can live for considerable periods without food it is of no vital concern that food is immediately available.

When considering 'adequate living space' in an ecological investigation, a factor usually of importance is the competition for food. Ixodid tick larvae do not compete for food in the usual sense but they may compete for a position of rest at the tip of a grass stem. As many larvae are able to collect at the tip of any one grass stem and as many of these are able to scramble onto a passing host (as was noticed when sampling at Barville Park) it appears to be unlikely that this type of competition for space is of great importance in determining the survival of larvae.

The absence of severe predation is largely dependent on the number and efficiency of the parasites and predators concerned. Only a few parasites, predators and pathogenic organisms have been reported as affecting tick populations. A discussion of the various parasites, predators and pathogens affecting ticks has been presented in Chapter 6. It appears likely that larval ticks are not affected to any great extent by parasites and predators. It is therefore suggested that this aspect probably does not play an important role in the survival of larvae.

It appears that the maintenance of water balance is the most important factor concerning larval survival in the field. It is obvious that survival as regards the water relations of larvae implies that a balance is maintained between water lost from the tick and water taken up by it. This chapter covers water balance in tick larvae under the following two categories.

A. Water loss in ixodid tick larvae.
B. Water uptake in ixodid tick larvae.

A. Water loss in ixodid tick larvae

Water can be lost in four main ways by terrestrial anthropods.

i. Evaporation from the tracheal linings or other respiratory surfaces.
ii. Evaporation from the main body openings.
iii. Excretion in faeces and urine.
iv. Evaporation through the general body surface.

These four headings are convenient guides to further discussion and presentation of experimental work.

i. Evaporation from the tracheal linings or other respiratory surfaces.

Water loss by this means is common to a large number of insects (Wigglesworth 1965). Lees (1946) has shown that the adults and nymphs of Ixodes ricinus L., which possess trachea and spiracles, lose little water during respiration as a spiracular opening and closing mechanism exists at each respiratory opening. Ixodid tick larvae do not possess trachea and spiracles but respire directly through the body surface. Water loss by evaporation directly through the body surface is dealt with presently.

ii. Evaporation from the main body openings

Tick larvae have two main body openings, the mouth and the anus. The anus is usually held tightly closed and therefore evaporation from this opening is minimal. The hypostome is usually held tightly between the pedipalps so that it is hardly visible. This may reduce the amount of water lost by evaporation from the mouth. Although it would seem likely that water is lost through evaporation from the mouth this amount is unlikely to seriously effect the larva concerned unless the various means of water uptake are unable to operate for long periods. Of interest is the work of Tatchell (1967a, 1967b, 1969) on salivary secretion in B. microplus. He has shown that water is passed back into the host via salivary secretions after feeding has taken place. This means of water loss does not however concern the non-parasitic larval stage.

iii. Excretion in faeces and urine

Faeces are voided only once during the non-parasitic larval stage, i.e. soon after hatching. Waste products of larval development are excreted in the form of a dry white pellet. It is unlikely that very much water is contained in this faecal matter. Urination has not been reported in Ixodidae.

iv. Evaporation through the general body surface

Although it has been shown that ixodid ticks possess a layer of cuticular wax (Lees 1946, Cherry 1969 and others) it still appears that the main source of water loss is through the cuticle. The work on cuticular waxes has been confined almost entirely to adult ticks, it is probable, however, that larvae possess this feature. Lees (1946) studied water loss and survival in a number of tick species including I. ricinus. He demonstrated that each species studied lost water in a specific way and survived for different periods in dry air. The three species of Ixodes studied by Lees (1946) lost water more rapidly and lived far shorter periods than the other species studied. The argasid Ornithodorus moubata Murray on the other hand lost water only slowly and survived for a relatively longer period. As the conditions underwhich tick larvae live will determine the way in which they will lose water, it was decided to study water loss in a few southern African species of Ixodidae.

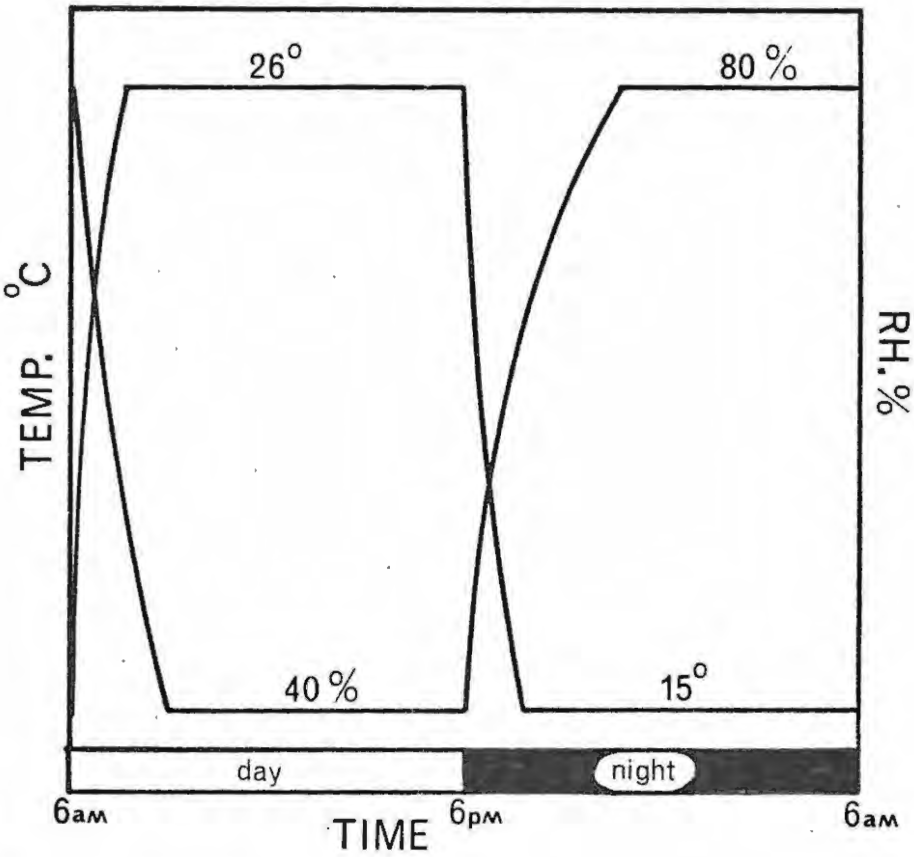
Most of the work reported in this investigation was done under either one of two environment room regimes. Fig. 8 shows these two regimes, called conditions A and B. These conditions will be referred to in the majority of the work which follows.

Six species of ixodid tick larvae were used in the following work on water loss and survival. These were A. hebraeum, I. pilosus, B. decoloratus, R. evertsi, R. appendiculatus and R. simus. All the above species were maintained in laboratory cultures. They were kept in an incubator held at 26°C and 95 % RH. I. pilosus was, for some unknown reason, the only exception because it was difficult to maintain in the incubator and therefore supplies of this species had to be brought in from the field for experimental purposes.

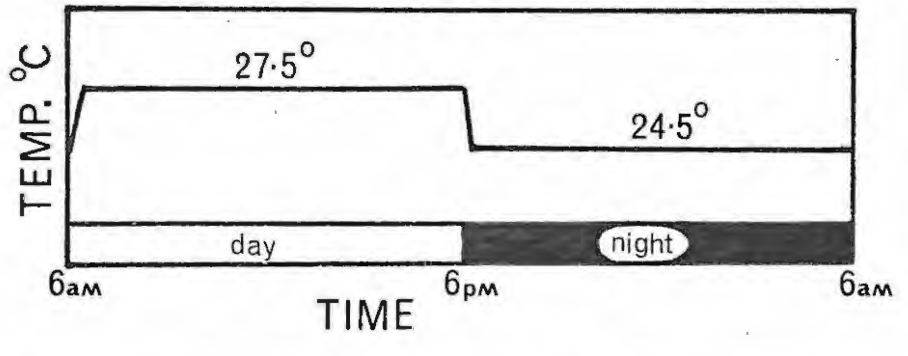
Eight desiccators were placed in the constant environment room with a regime as shown by Fig. 8 (Condition B). Different conditions of relative humidity were maintained in each desiccator with varying solutions of potassium hydroxide (KOH) details of which appear in Table 20. The required KOH concentrations were obtained from Peterson (1953).

Table 20. The treatments received by eight desiccators in producing eight different conditions of relative humidity.

Dessicator No	Wt.KOH/100 ml. H_2O (gms)	Expected RH. %	Measured RH. %
1	0.0	100	100
2	10.0	90	90
3	25.0	80	80
4	37.5	69	70
5	50.0	61	60
6	62.5	50	50
7	75.0	39	40
8	87.5	31	30



Environmental room condition A.



Environmental room condition B. Humidity conditions are ignored as relative humidity was controlled by some other means (see text).

Fig. 8. The two environmental room regimes used during the various experiments conducted in this investigation.

Live larvae of the six species were placed in small glass vials which were loosely stoppered with cotton wool. The rate of diffusion into such tubes was studied by placing a series of vials containing cobalt thiocyanate papers into each of the eight desiccators already described. A single vial was then removed from each desiccator every two hours. In this way the rate of diffusion of air in each desiccator was investigated. The results appear in Fig. 9. The results show that any vial placed in any of the desiccators could be expected to achieve the required internal relative humidity within approximately 12-14 hours. Some vials achieved the required values much more rapidly than others as all the vials were held at 50 % relative humidity for 48 hours prior to the examination.

Seven or eight vials of larvae, of each species, were placed in each desiccator. A single vial, of each species, was then removed daily and the number of living and dead larvae counted. In this way the mortality due to desiccation could be followed for each species. The only exception to the above method was that adopted for I. pilosus larvae which were not plentiful enough to allow more than a single vial of larvae per desiccator. For this reason only a single vial was used in each desiccator. Vials were therefore replaced after counting instead of being discarded as in the case of the other five species. Examination of the vials usually entailed emptying the respective vials into a soap solution (in order that they should sink) so that counting would be made easier. In the case of I. pilosus counting was merely by holding the vials under a stereo microscope.

Difficulty was encountered in determining the point of death and therefore the following criteria of death were adopted.

i. Larvae which did not move when stimulated with the pressure from a needle were taken as dead.

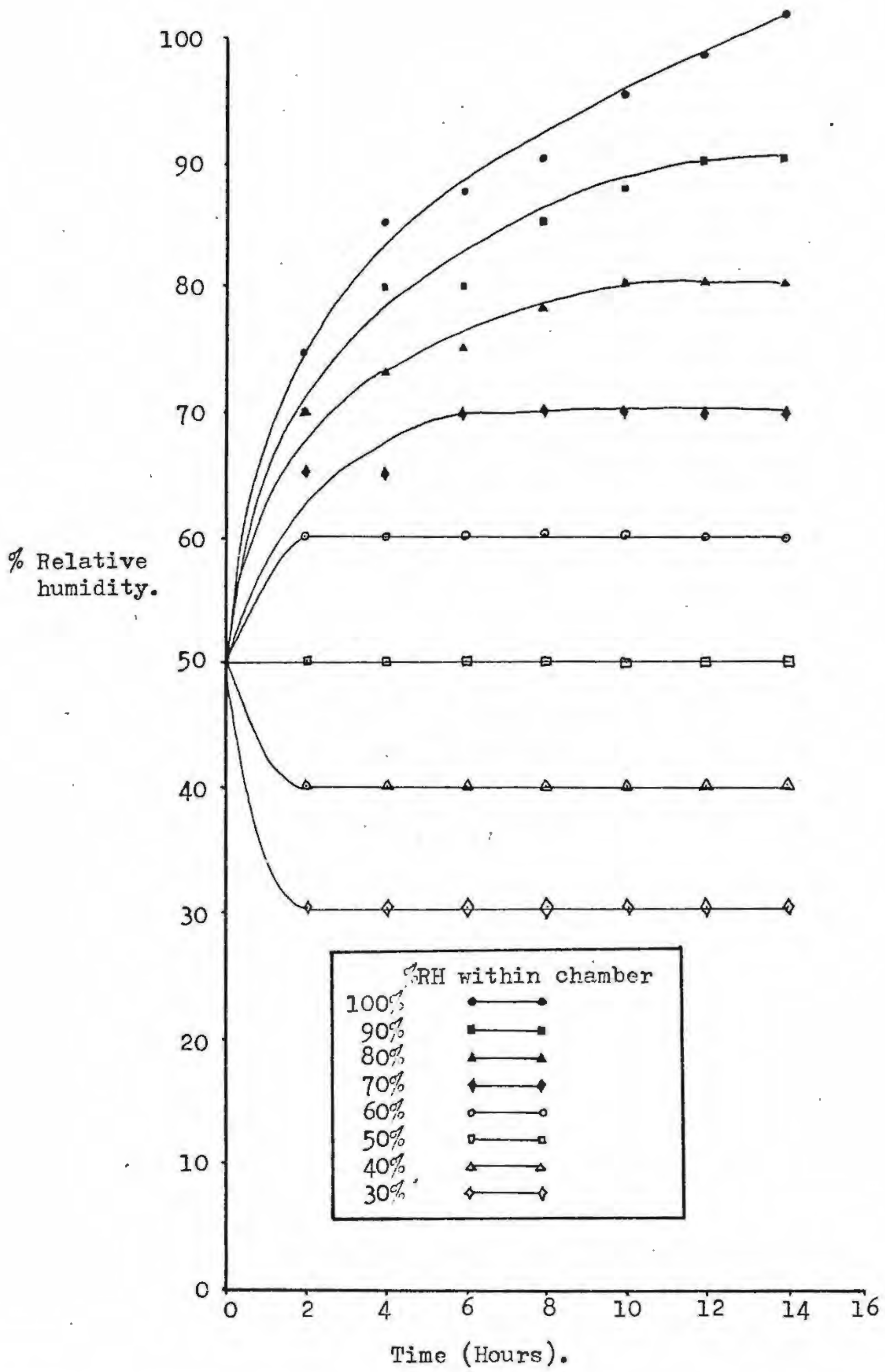


Fig. 9. The development of relative humidity within the experimental tubes at a temperature of 26°C. (All tubes were at 50 % RH at the begining of the experiment.)

ii. Larvae which floated in the dilute soap solution and appeared to be a little darker in colour (probably due to air bubbles trapped in the limbs and body) were taken as dead.

iii. In the case of I. pilosus, if larvae could be induced to move by rubbing the vial up and down on the hand (which had the effect of warming the vial) they were taken as living. If they remained motionless they were taken as dead.

Results

The results of the various experiments are presented in Figs 10-15, each specie being dealt with in a separate figure. All the species studied appeared to react in a similar way to the various relative humidity values. A large number of larvae survived the duration of the experiments (7-8 days) when placed in relative humidities between 80-100 %. Below 80 % RH mortality increased with decrease of relative humidity. These results suggest that the 'equilibrium humidity' (that humidity value at which water loss is equal to water uptake) of all the tick species studied probably lies between 70-80 % RH. Lees (1946) demonstrated an 'equilibrium humidity' in the region of 92 % RH for I. ricinus. As this species was also shown to be the least resistant to desiccation when compared with seven other species a fairly high 'equilibrium humidity' was to be expected.

Although the species studied in the present investigation reacted in a similar way to various atmostpheric relative humidities some appeared to be more resistant to desiccation than others. In order to compare the six species studied quantitatively, in respect of the degree of resistance to desiccation, probits of the percentage survival of each species at 70 % RH were plotted against time (Fig. 16). Table 21 shows the times of survival at the 75 %, 50 % and 25 % quartiles.

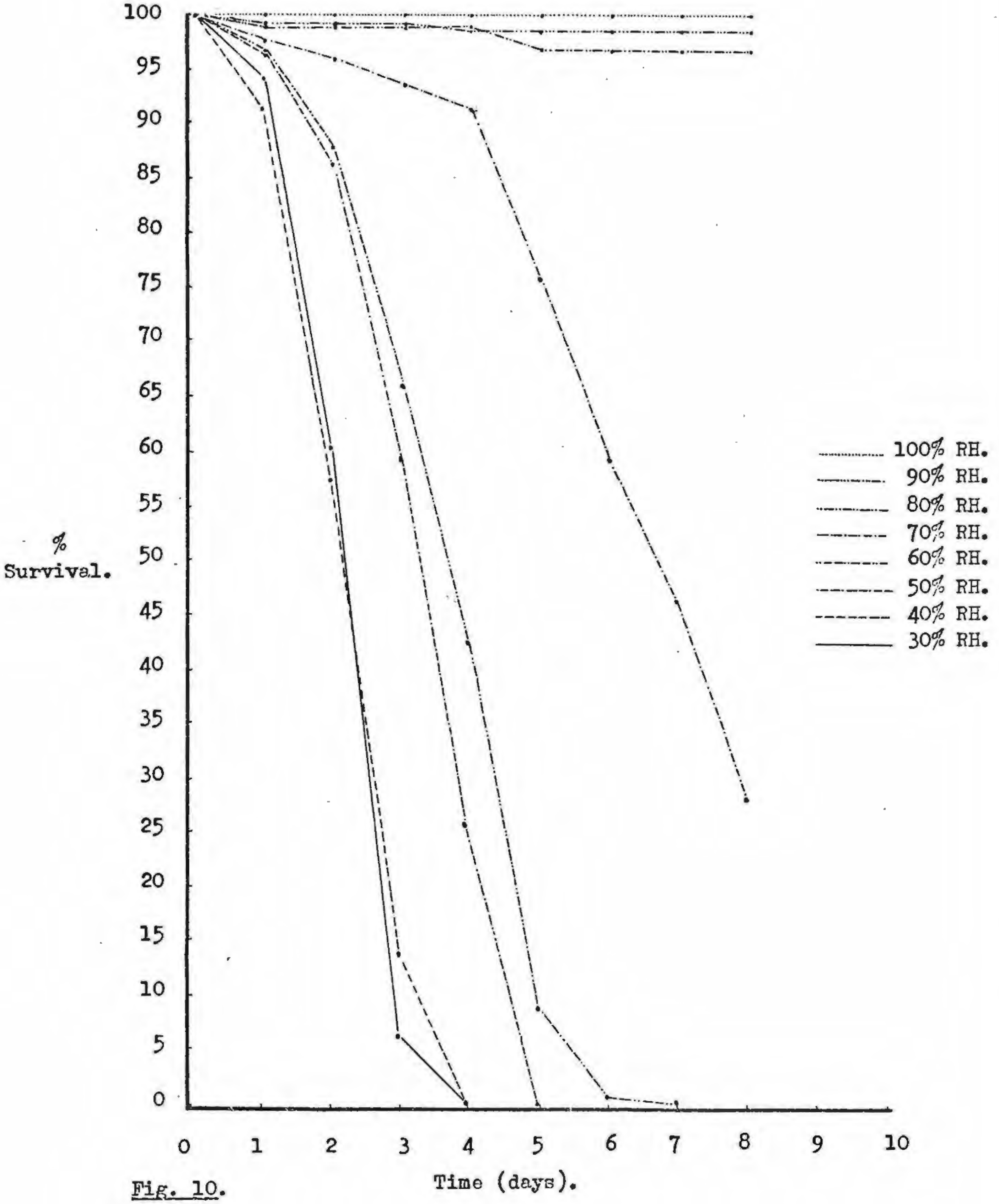


Fig. 10.

The survival of Amblyomma hebraeum larvae under various conditions of relative humidity and constant temperature (26°C).

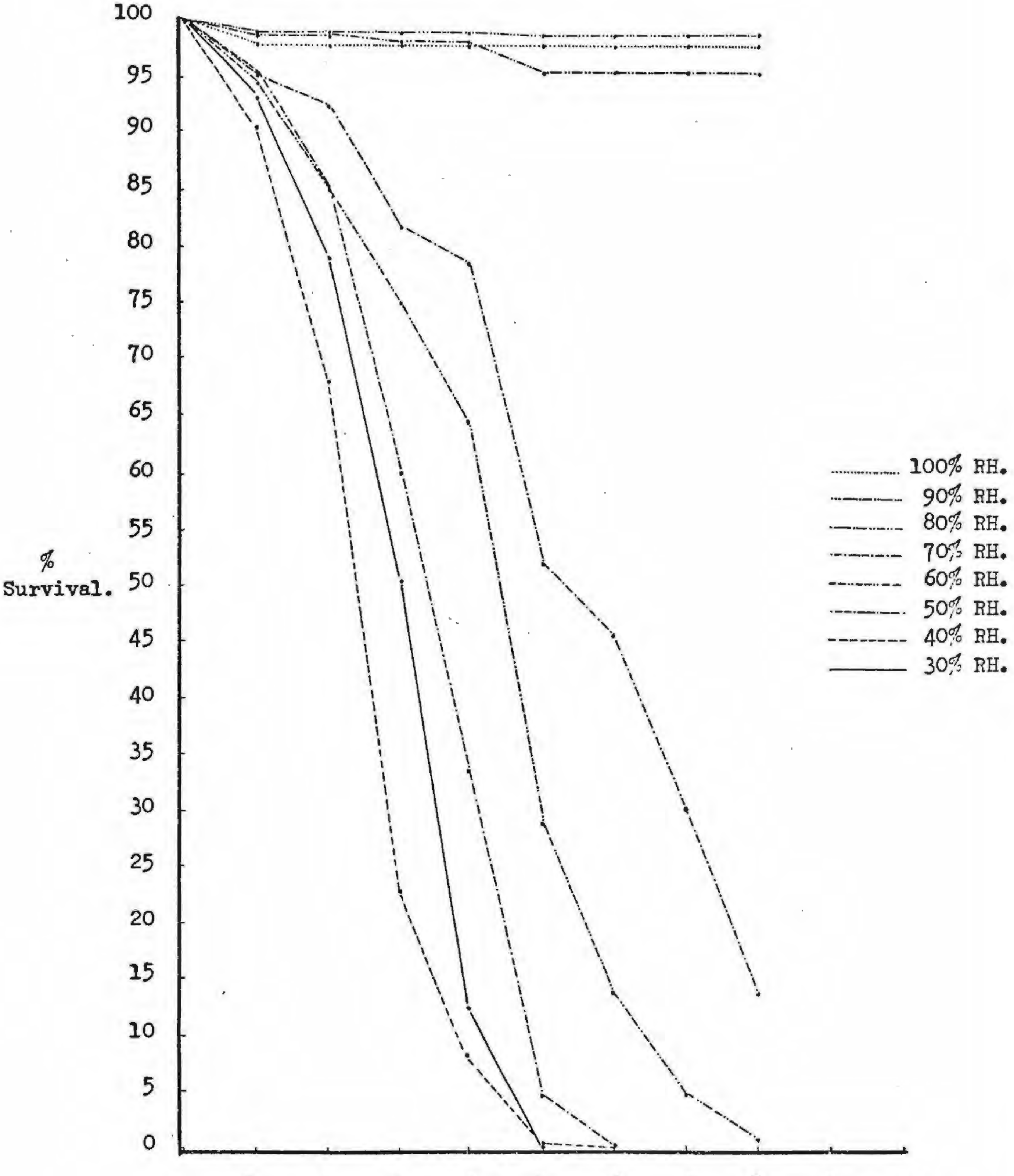


Fig. 11.

The survival of *Boophilus decoloratus* larvae under various conditions of relative humidity and constant temperature (26°C).

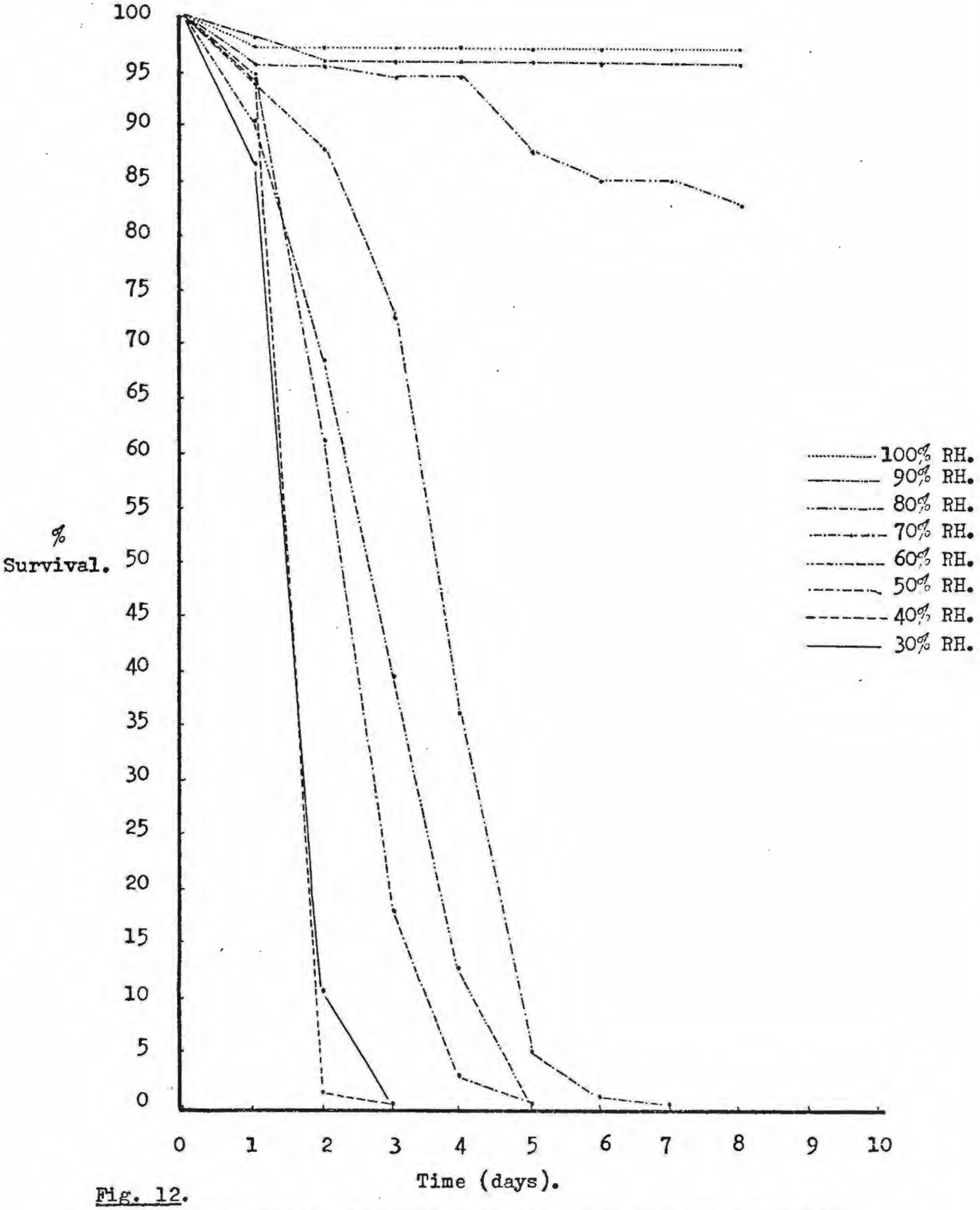


Fig. 12.

The survival of Ixodes pilosus larvae under various conditions of relative humidity and constant temperature (26°C).

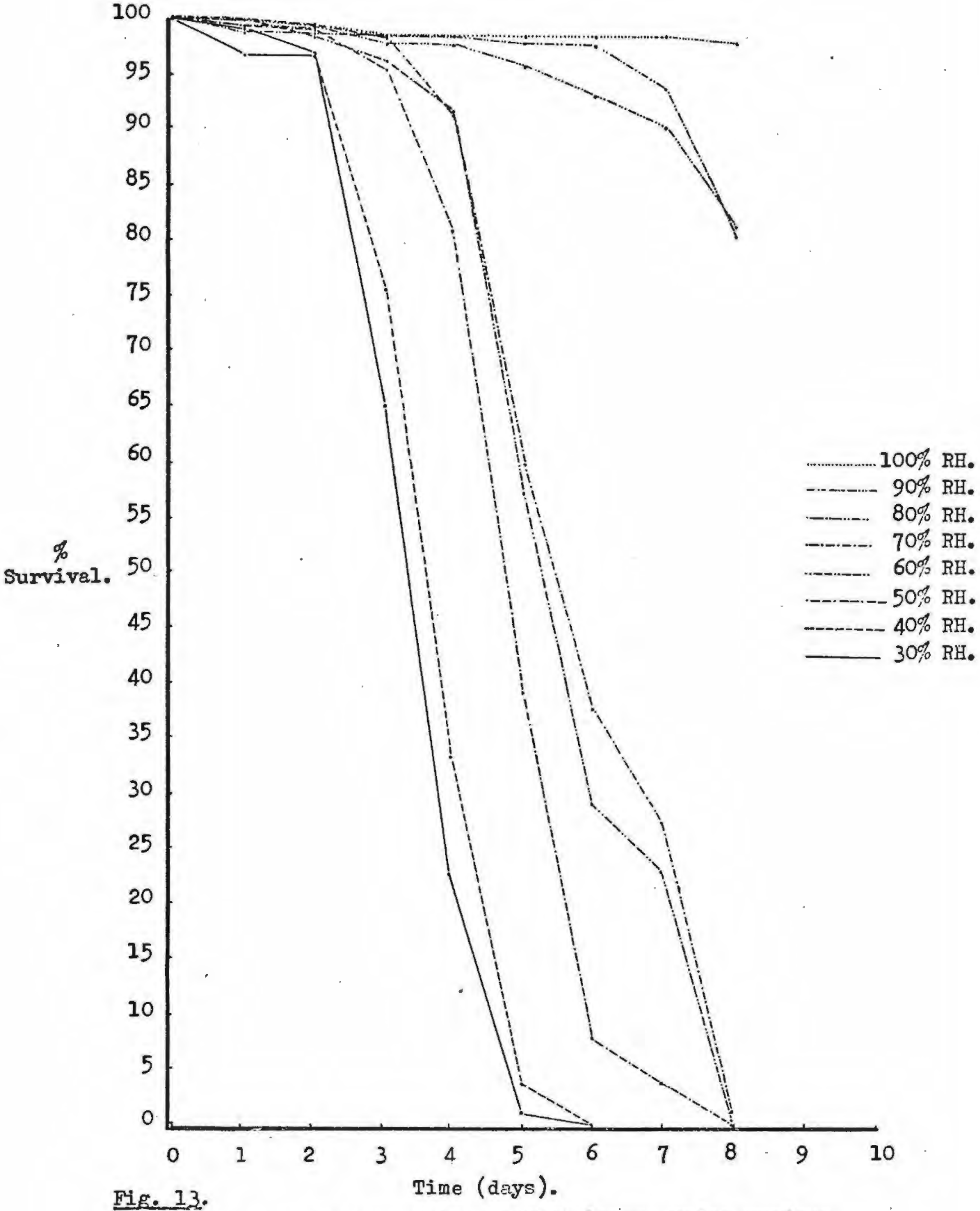


Fig. 13.

The survival of *Rhipicephalus evertsi* larvae under various conditions of relative humidity and constant temperature (26°C).

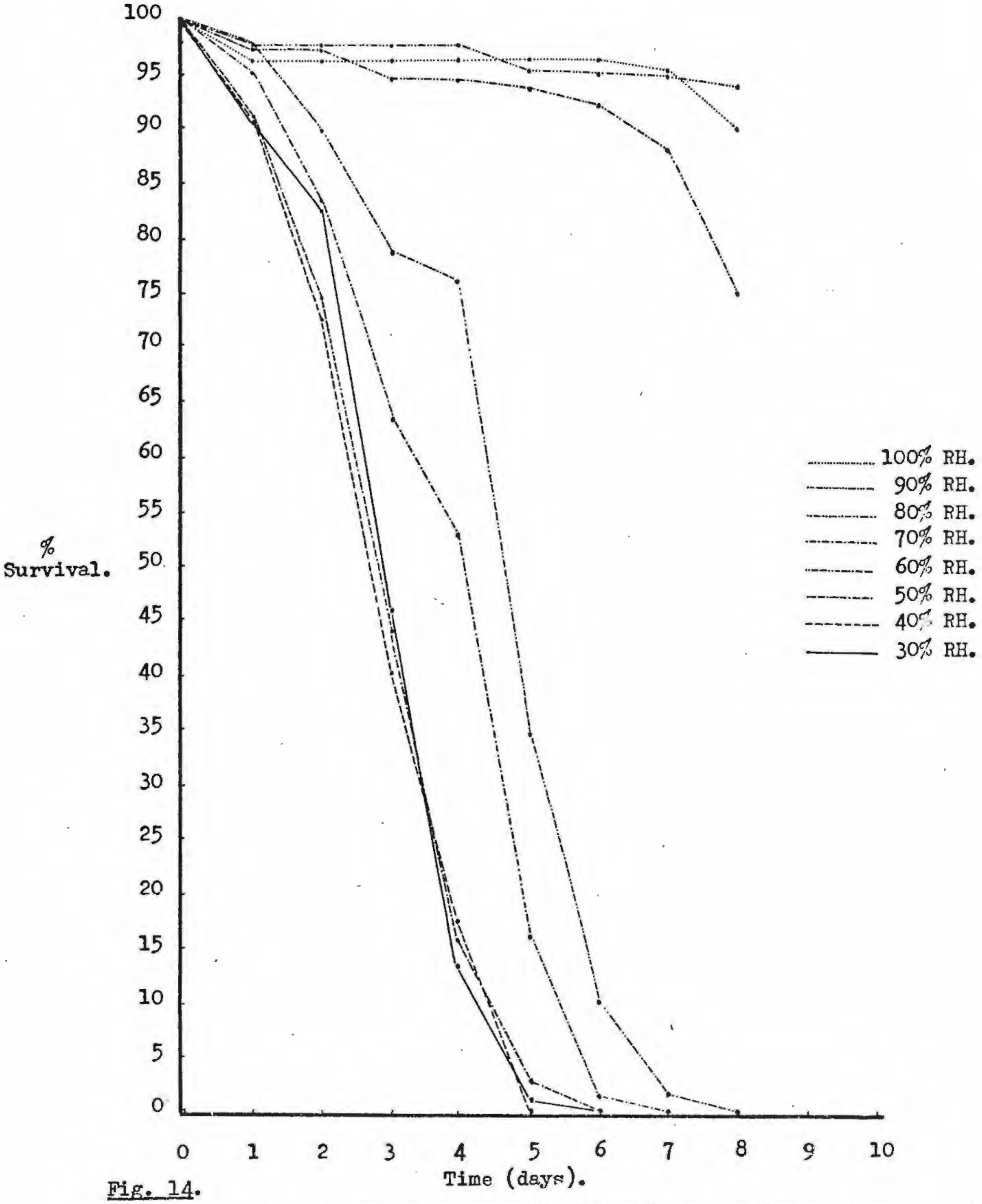


Fig. 14.

The survival of Rhipicephalus appendiculatus larvae under various conditions of relative humidity and constant temperature (26°C).

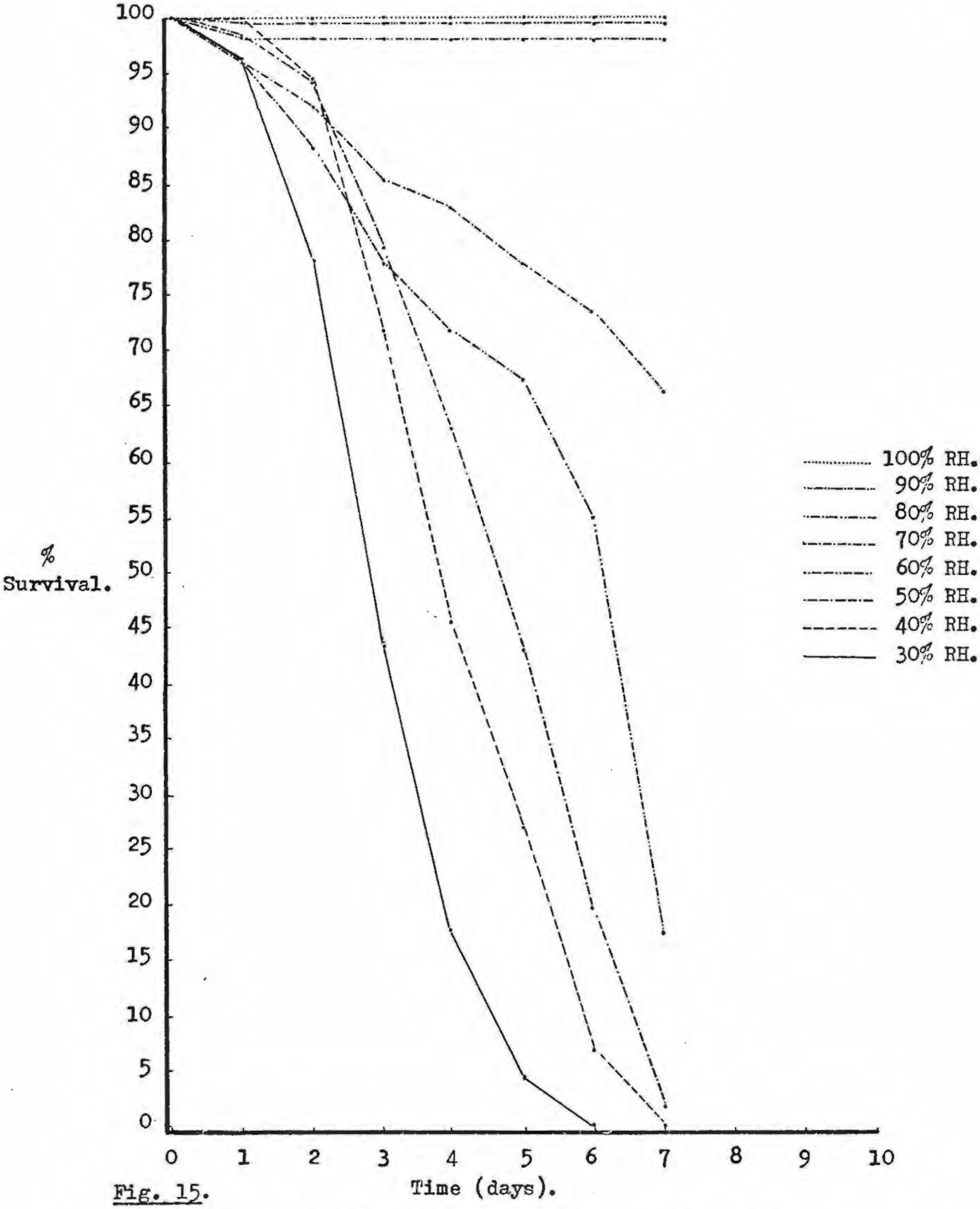


Fig. 15.

The survival of *Rhipicephalus simus* larvae under various conditions of relative humidity and constant temperature (26°C).

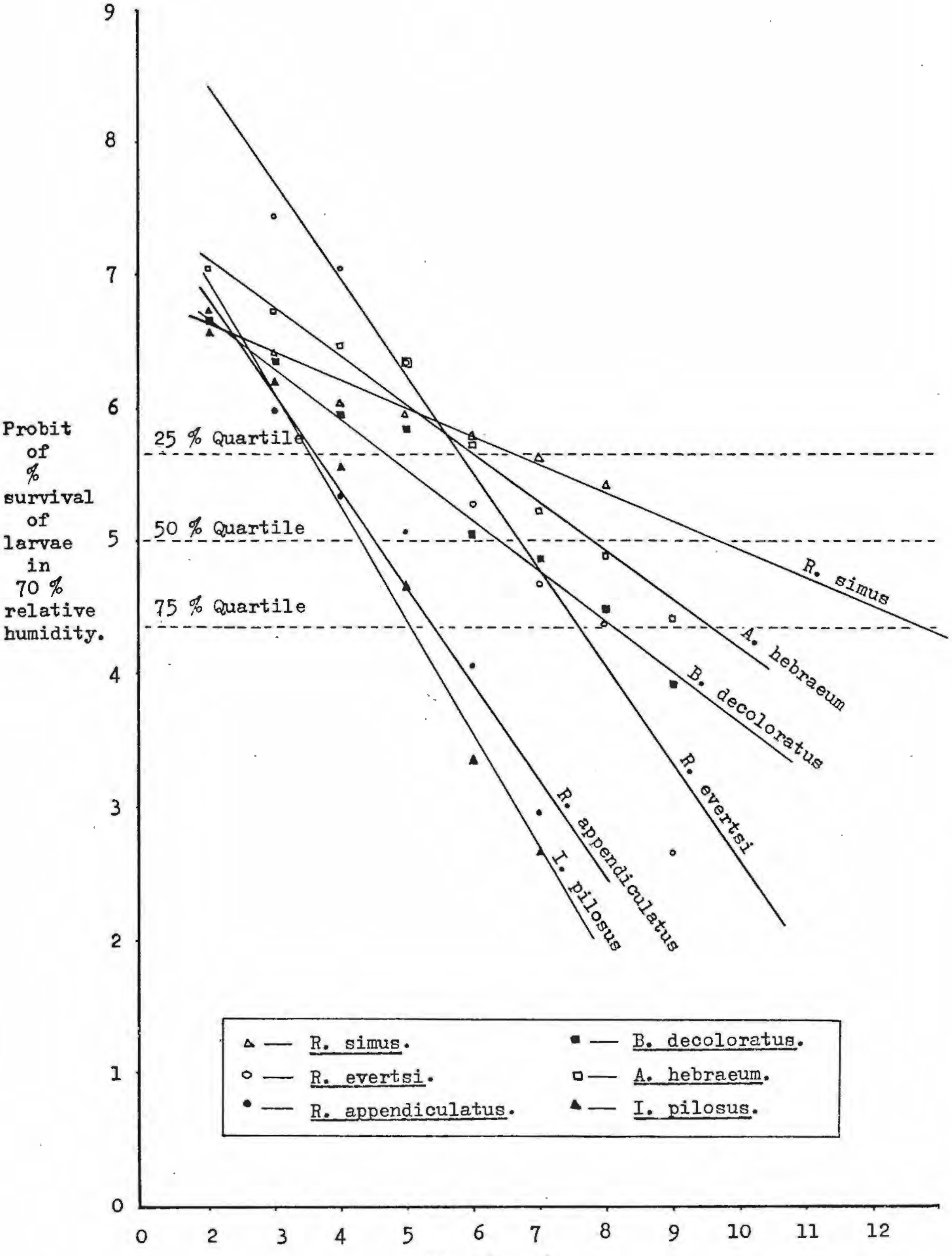


Fig. 16.

Probits of the percentage survival of tick larvae in an atmosphere of 70 % relative humidity plotted against time in days. Survival at the 25 %, 50 % and 75 % quartiles are indicated.

Table 21 Survival times of six tick species in an atmostphere of 70 % RH at 26°C.

Species	Survival time (days)		
	75% quartile	50% quartile	25% quartile
R. simus	5.7	8.8^{+}	11.8^{+}
A. hebraeum	5.0	6.8	8.6^{+}
B. decoloratus	3.7	5.4	7.1
R. evertsi	4.8	5.7	6.6
R. appendiculatus	2.6	3.5	4.4
I. pilosus	2.5	3.3	4.1

+ = by extrapolation.

From Fig. 16 and Table 21 it can be seen that there are basically four different reactions to desiccation. These may be listed as follows.

i. An initial resistance to desiccation followed by a slow increase in mortality. e.g. A. hebraeum.

ii. An initial resistance to desiccation followed by a rapid increase in mortality. e.g. R. evertsi.

iii. A slow increase in mortality with no initial resistance to desiccation. e.g. R. simus and B. decoloratus.

iv. A rapid increase in mortality with no initial resistance to desiccation. e.g. I. pilosus and R. appendiculatus.

Because of the above four different reactions to desiccation it is difficult to state which species is most 'resistant to desiccation'. If the survival times at the 50 % quartile are taken as the 'standard' at which an assessment should be made then the six species could be arranged in the following order with respect to the ability to resist desiccation. R. simus being the most resistant.

i *R. simus*
ii *A. hebraeum*
iii *R. evertsi*
iv *B. decoloratus*
v *R. appendiculatus*
vi *I. pilosus*

Although the above list is useful it should be stressed that if the six species are examined at any other quartile a slightly different order would emerge.

The results presented above are interesting in that they suggest that some species are more able to resist desiccation than others. Lees (1946) also reported this sort of phenomenon. This phenomenon could help in the understanding of larval distribution in the field. From the work reported above it would be expected that *I. pilosus* should be confined to microhabitats which possess high relative humidities. This has been found to be true. Similarly the other species would be expected to occur in drier habitats than *I. pilosus*. This has also been shown to be true in the case of those species collected during the Barville Park survey (i.e. *B. decoloratus*, *A. hebraeum*).

In order to provide quantitative evidence that death in dry atmostpheres is due to desiccation the following short experiment was conducted.

Large numbers of *R. appendiculatus* larvae were placed in small glass tubes (Fig. 17). Six such tubes were then placed in a desiccator at 40 % RH. An equal number of tubes were also placed in a second desiccator at 95 % RH. Both desiccators were kept in the constant environment room at a regime as shown in Fig. 8, condition B. The tubes were weighed using a Sartorius single pan balance at the commencement of the experiment and at various intervals during their submission to the experimental conditions. Results are presented in Fig. 19. The larvae held at 40 % RH lost water at a greater rate than those held at 95 % RH.

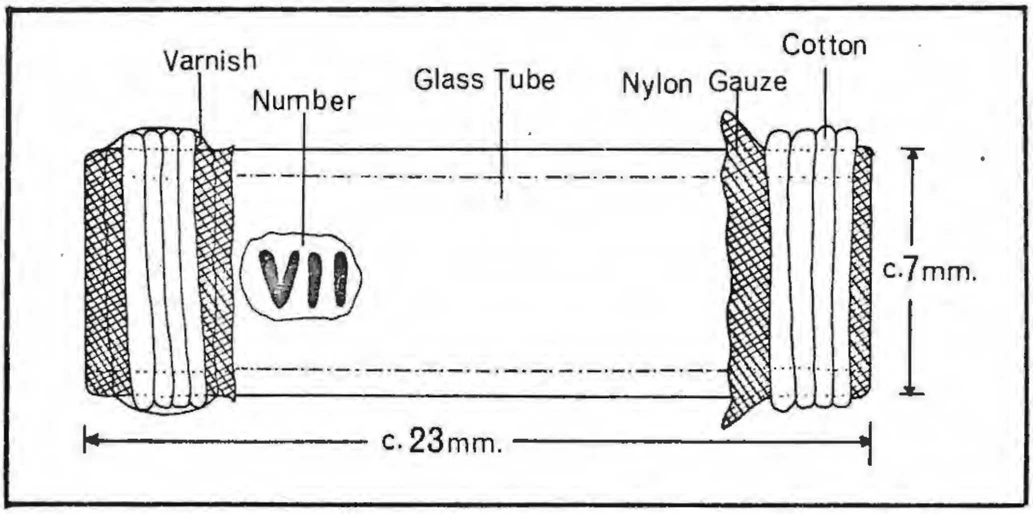


Fig. 17. The type of glass tube used in all the experiments involving weighing.

Fig. 18. The water-bath and other apparatus used in the temperature studies.

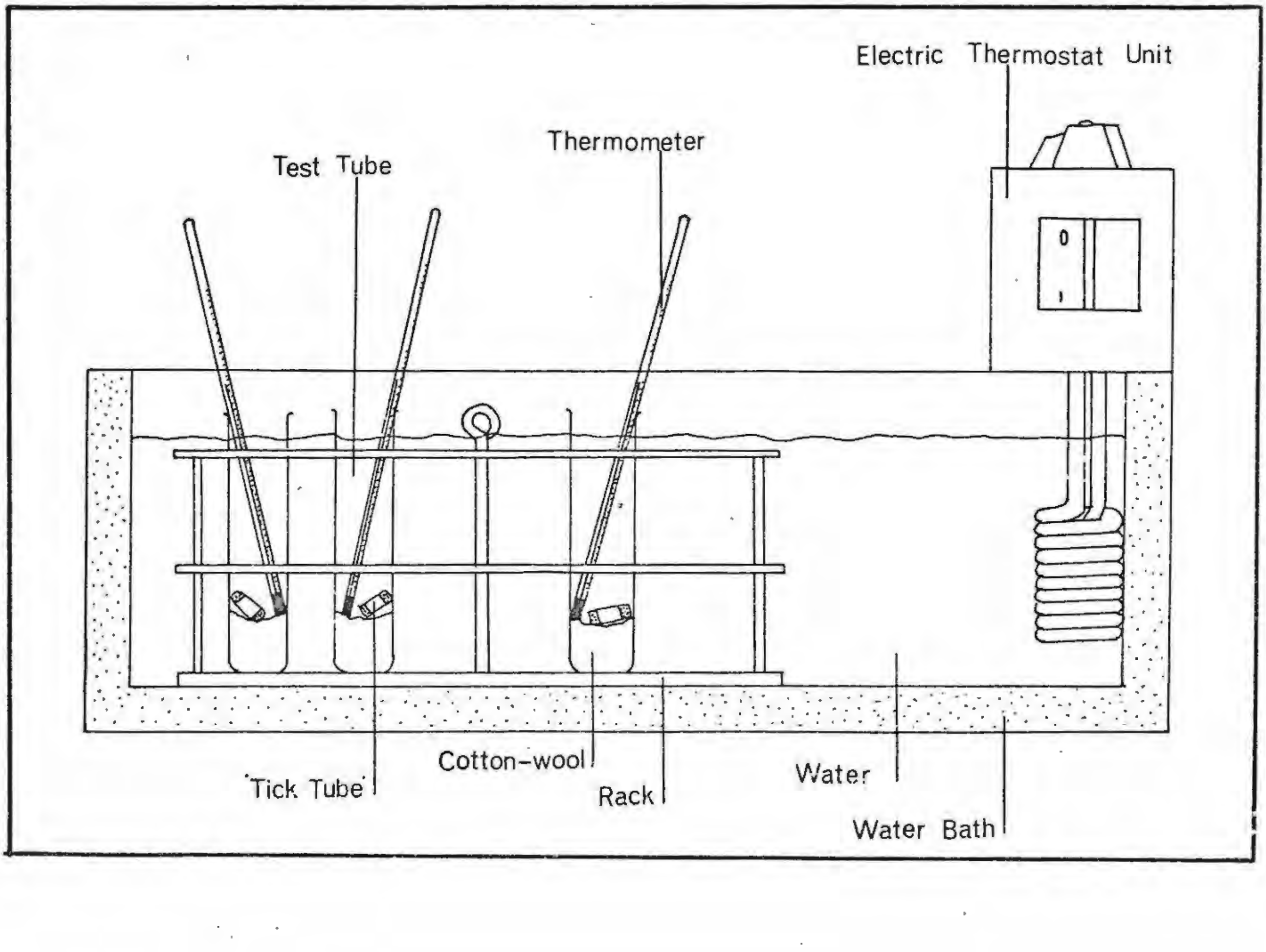
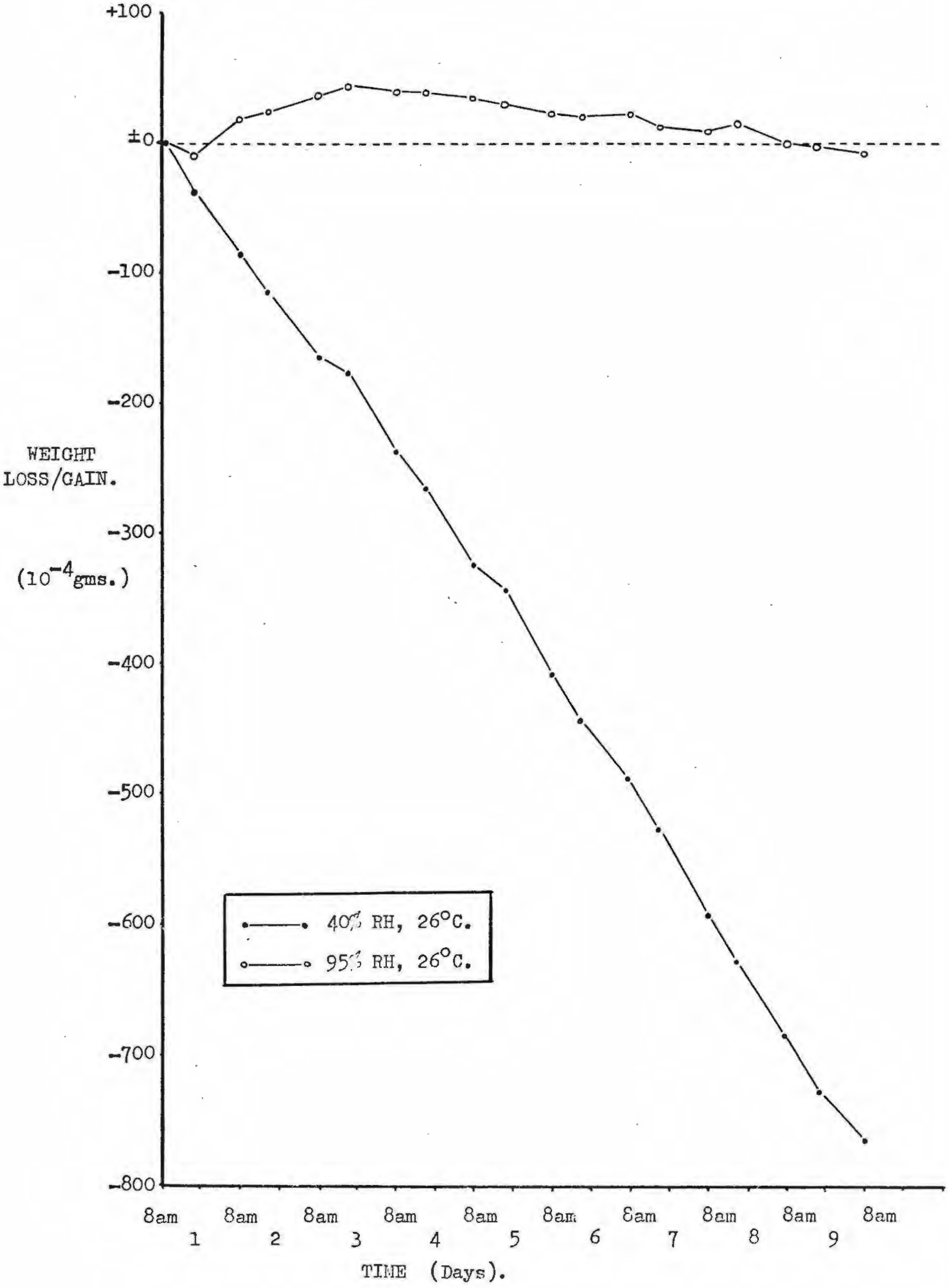


Fig. 19. The effects of low relative humidity on *R. appendiculatus* larvae.



The slight rise in the weight of the control batch kept at 95 % RH was probably due to water uptake. Apart from the above evidence it was obvious that larvae were losing water when placed in 40 % RH as they became very flattened, especially the distal end of the idiosoma, due to a loss in body volume which was probably a result of water loss. A similar phenomenon was reported by both Lees (1946) and Wilkinson (1953).

Because relative humidity is related to temperature it is important to know the effect temperature has on water loss through evaporation by larval Ixodidae. The following species were dealt with in this brief examination. R. evertsi, A. hebraeum and B. decoloratus.

Tubes of larvae, similar to those used in the last experiment (Fig. 17), were placed inside test tubes stoppered with cotton-wool which were placed in a water-bath (Fig 18). Each tube (three of each species) was weighed at the start of the experiment. The temperature of the water in the bath was then raised by 5°C every half-an-hour, the tubes being weighed at the end of each half hour period. The results are reported in Figs 20-22. In order to determine the effect of death on water loss, R. evertsi larvae, both living and dead, were compared in the same way as described above. The results of this comparison appear in Fig. 23.

The results show that larvae lose weight, considered to be due to water loss, in a rather characteristic manner over the range of temperature to which they were subjected (usually 20-75°C). At first this loss was slight, then, at about 40°C the rate increased rapidly. At approximately 55-60°C the maximum weight loss was recorded. At this temperature range death usually occurred. The rate of weight loss decreased progressively with the increase of temperature from 65°-70°C above which point no further weight loss was recorded.

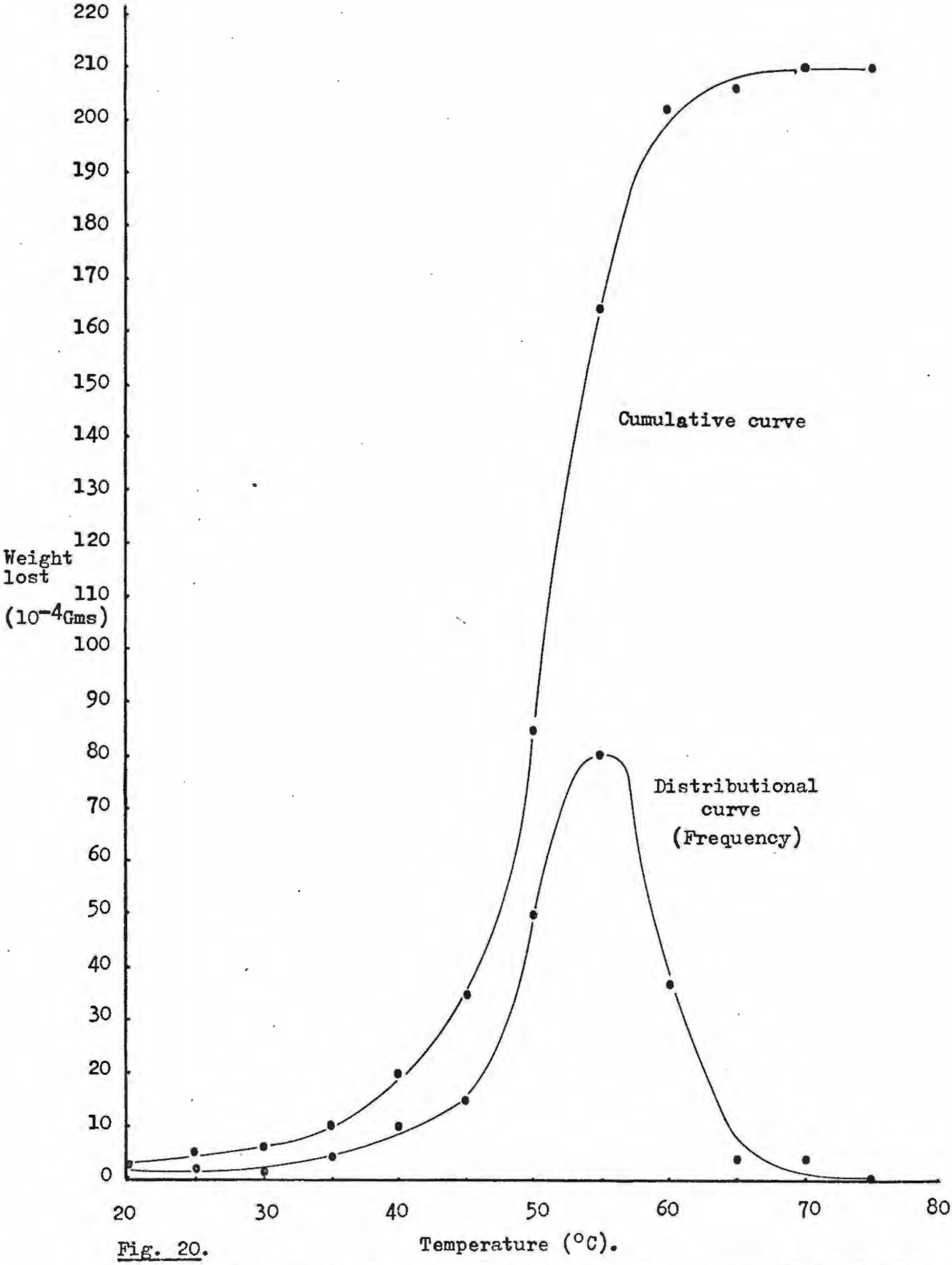


Fig. 20.

Weight lost by Rhipicephalus evertsi larvae when exposed for half hour intervals to increasing temperature values.

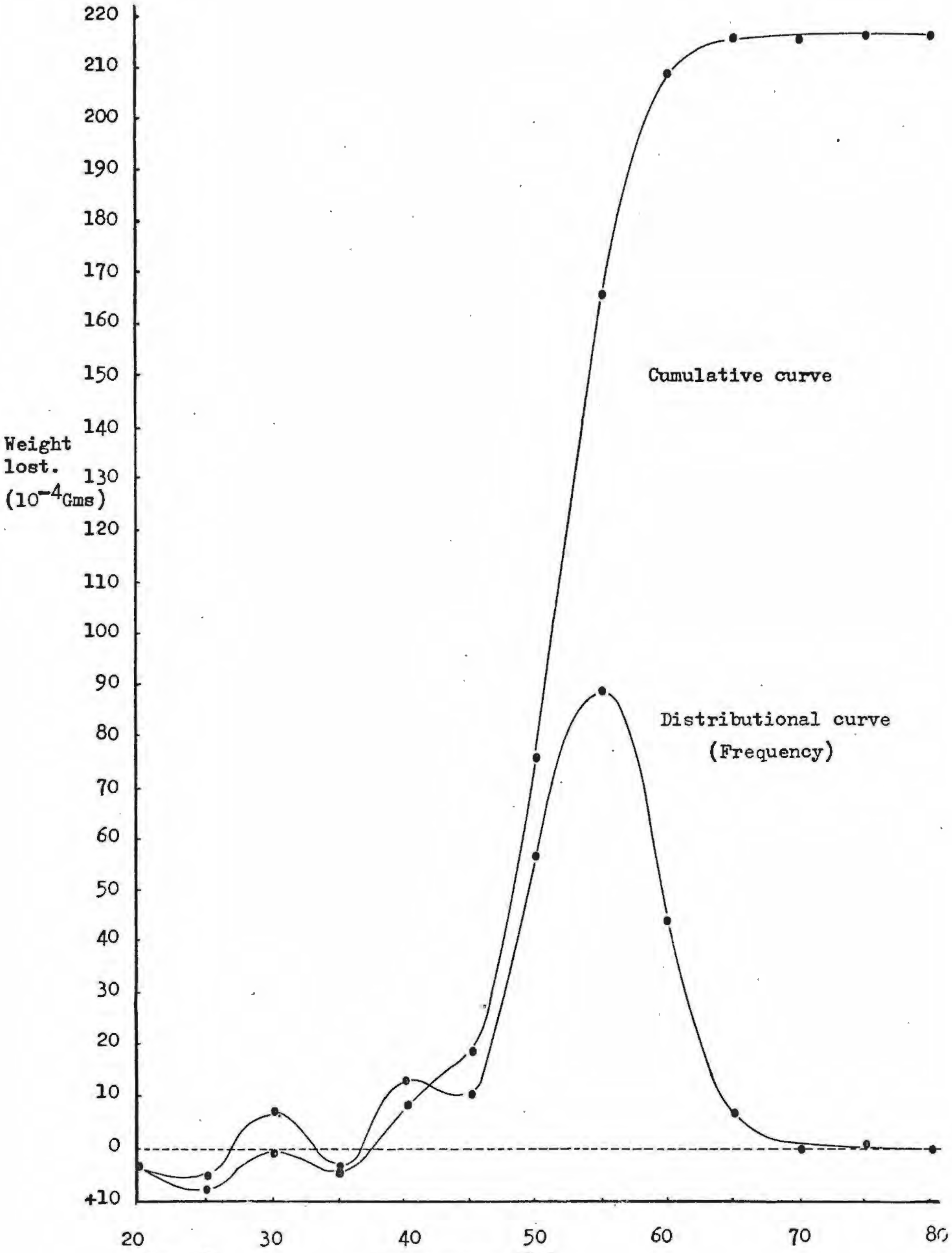


Fig. 21.

Weight lost by Boophilus decoloratus larvae when exposed for half hour intervals to increasing temperature values.

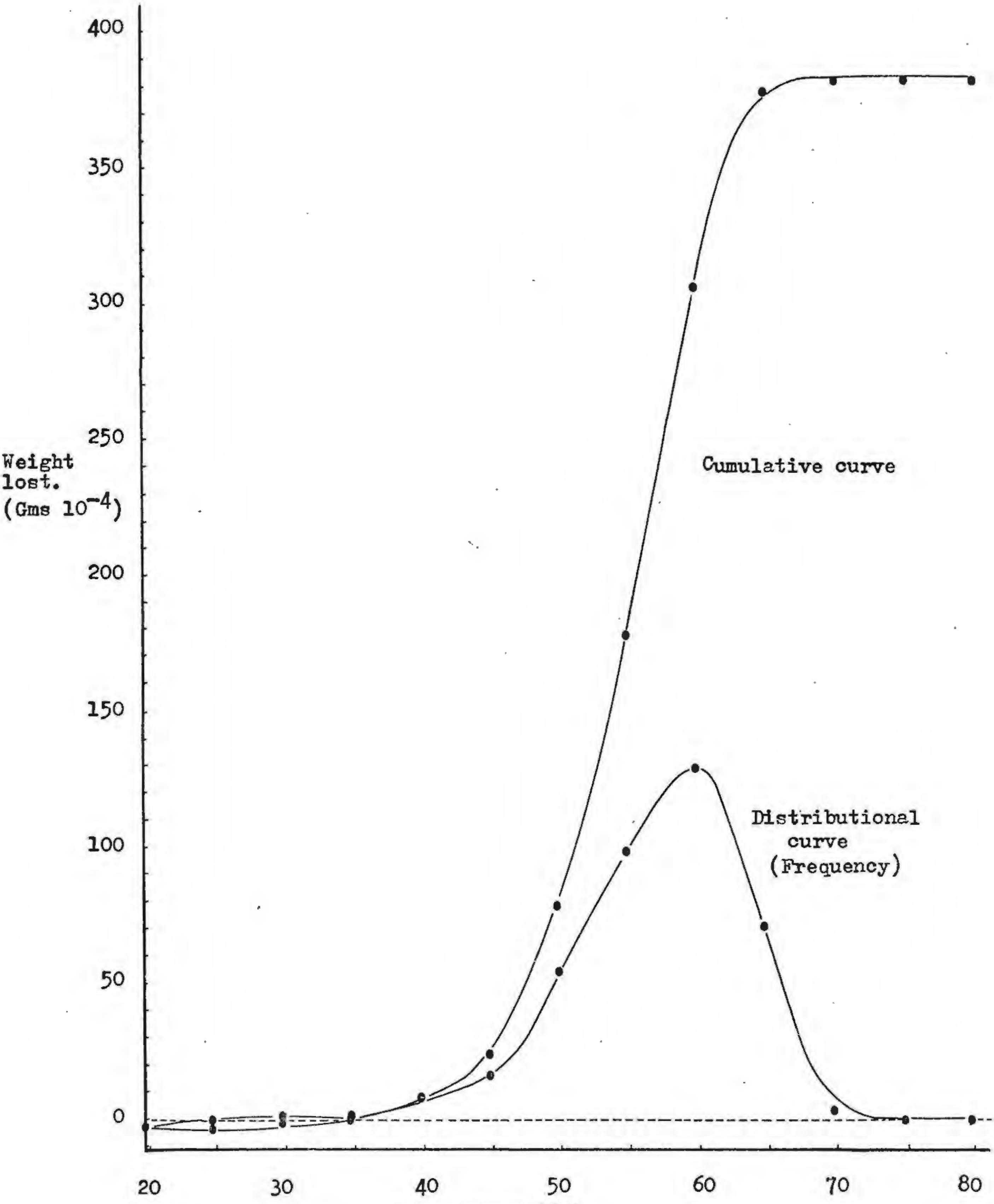


Fig. 22.
Weight lost by Amblyomma hebraeum larvae when exposed for half hour intervals to increasing temperature values.

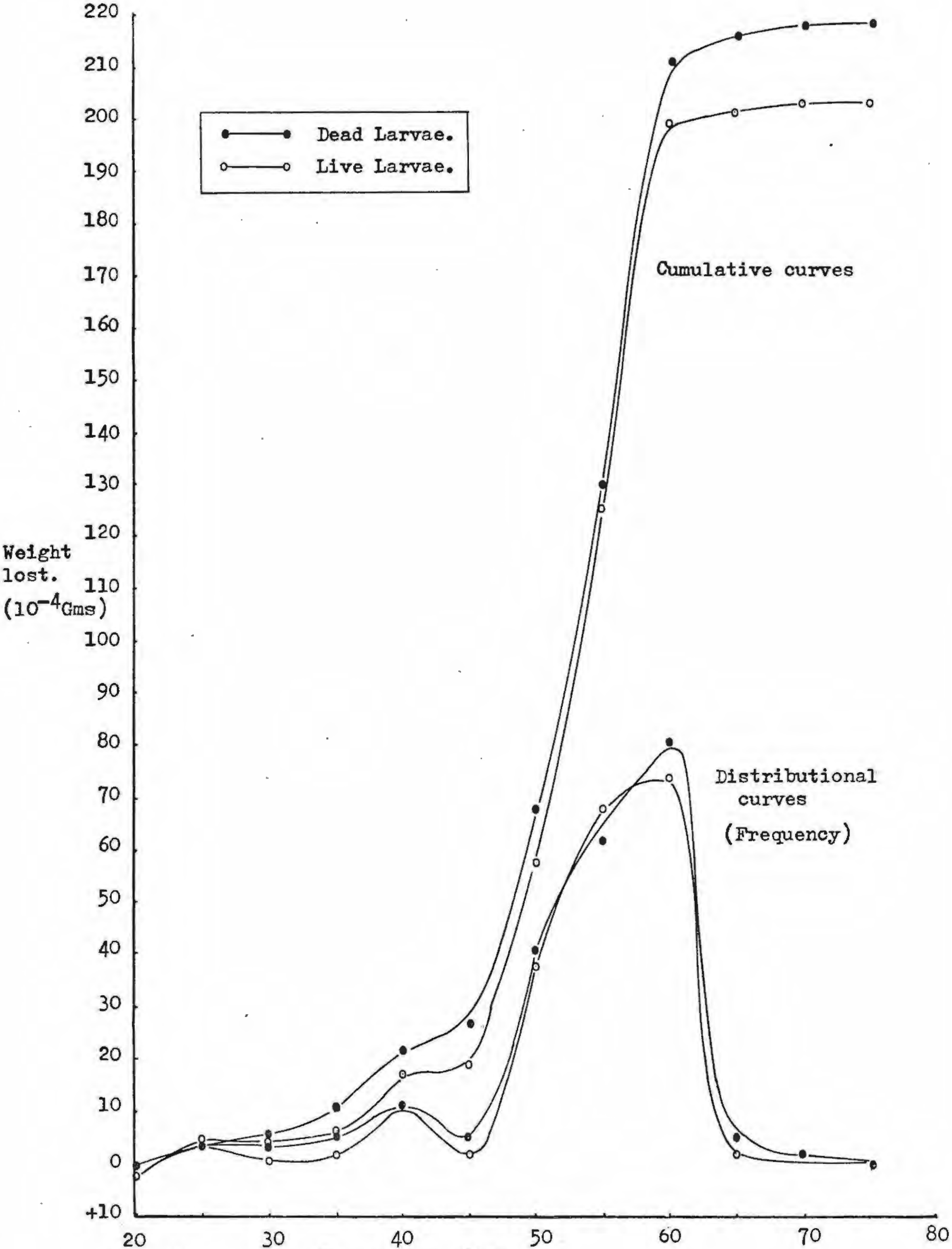


Fig. 23.

A comparison of the weight lost by dead and live *Rhipicephalus evertsi* larvae when exposed for half hour intervals to increasing temperature values.

The sudden rise in the rate of weight loss, between 55-60° C, could be attributed to one or a combination of the following factors.

i A breakdown in the structure of the epicuticular wax layer, which normally prevents excessive evaporation of water molecules. Little is known about this phenomenon in ticks.

ii The breakdown of some active process which may be responsible for replacing water which is evaporated from the larva. i.e. The active process of water uptake, discussed later, may be impeded by high temperature.

iii The death of the larvae may result in the sudden increase in water loss. This seems unlikely from the results reported in Fig. 23 where dead and living larvae appear to lose weight in an identical manner.

Probably the most important fact which arises from the above study of the effects of temperature on water loss is that no great increase occurs within the temperatures normally encountered by tick larvae in the field, i.e. the highest temperature recorded in the field was approximately 42°C. This was at ground level in short open vegetation where larvae were never found. It is probably unlikely that temperatures as encountered in the field in the eastern Cape Province will, in itself, effect the survival of tick larvae.

The important factor in the survival of tick larvae in the field appears to be relative humidity. Temperature, although effecting the rate of water loss when high, would only be likely to influence survival if maintained at a high level for fairly lengthy periods. This does not normally occur in the field.

General discussion of water loss by larval Ixodidae

The most important way in which larval ticks lose water appears to be through evaporation from the general body surface. Water has been shown to be lost by larvae when exposed to relative humidities below 80 % RH at a temperature of 26°C. If this equilibrium humidity is taken as being approximately 70 % RH at 26°C then the saturation deficit would be in the region of 10 mm.Hg. It is of interest to note that larvae were not commonly collected in microhabitats which experienced midday saturation deficits in excess of 10 mm. Hg. It could be suggested that any saturation deficit in excess of 10 mm. Hg. constitutes a condition of 'stress' in that larvae will lose water to the atmostphere. Temperature does not appear to have a very marked effect on the rate of water evaporation at values normally experienced by larvae in the field.

A further discussion of water loss will be made at the end of the next section on water uptake, as these two events are usually combined and contribute towards the general water balance of larval ticks.

B. Water uptake in ixodid tick larvae

Water can be gained by terrestrial arthropods in a number of different ways.

i Water absorbed from food.
ii The production of metabolic water.
iii The direct absorption of liquid water through the cuticle.
iv Drinking.
v Active uptake of water vapour from the air.

The above points serve as convenient headings in the presentation of experimental work undertaken in the present study as well as for the introduction of brief discussions on water uptake by ixodid tick larvae.

i Water absorbed from food

Ixodid tick larvae naturally take up large quantities of water while feeding on their host's blood. As non-parasitic larvae (before the host is located) obviously do not feed, this means of water uptake does not play any role in their survival.

ii The production of metabolic water

Lees (1946) states that

> "Metabolic water is unlikely to be of any significance, for the fasting tick survives for only a very limited period at low humidities, while in humid air other, and more efficient, mechanisms for gaining water come into operation."

Little can be added to this statement at present. More work on this aspect of water 'uptake' should be undertaken.

iii The direct absorption of liquid water through the cuticle

This means of water uptake has received some attention by Lees (1946) and he has shown that the nymphs and adults of *I. ricinus* are able to absorb water directly through the cuticle. Lees (1946) states that his results

> "suggest that the normal unfed tick is to some extent able to prevent the entry of water in contact with the cuticle; after desiccation, however, water is taken up so rapidly from this source that uptake is exaggerated and the ability to control its entry is finally lost."

As far as the non-parasitic larval stage is concerned it is very probable that when the opportunity arises, water could be taken up directly through the cuticle in order to supplement supplies already in the animal. The uptake discussed by Lees (1946), quoted above, appears to be of no survival value, unless the ticks can move away from the water, as the ticks eventually lose control of the uptake and literally 'burst' with the large quantities of water taken up.

The reason why it is suggested that larvae can take up water directly through the cuticle as a survival mechanism will be outlined in the section on drinking. Briefly, however, it was found that larvae possess a behavioural pattern which involves 'squatting' on wet surfaces so that their ventral surfaces are in contact with the surface. This type of behaviour suggests an association with water absorption. This aspect is at present only surmise and requires further examination.

iv Drinking

Lees (1946) states

"*Ixodes* does not drink."

On the otherhand Wilkinson (1953) and later Wilkinson and Wilson (1959) show that *B. microplus* does imbibe water. These conflicting opinions suggested that this aspect of water uptake, in some of the species available, might be investigated. The species selected for this brief investigation were *R. evertsi*, *R. appendiculatus*, *B. decoloratus* and *A. hebraeum*.

Larvae of these four species were placed in the centre of a petri dish in which a piece of filter paper, cut in the shape of a hollow-square, had been placed (Fig. 24). The filter paper was moistened with distilled water. All the larvae, irrespective of species, displayed a similar behavioural reaction to the moist paper. The behaviour pattern observed was as follows.

i At first larvae would walk in a direct path towards the moist filter paper.

ii On arrival within about 5 mm. of the wet paper, larvae would exhibit 'avoiding' behaviour in that they would hesitate and turn away from the path which would lead directly to the wet filter paper. As the paper formed a barrier all around the larvae, they were obliged, once again, to approach the wet paper. Larvae

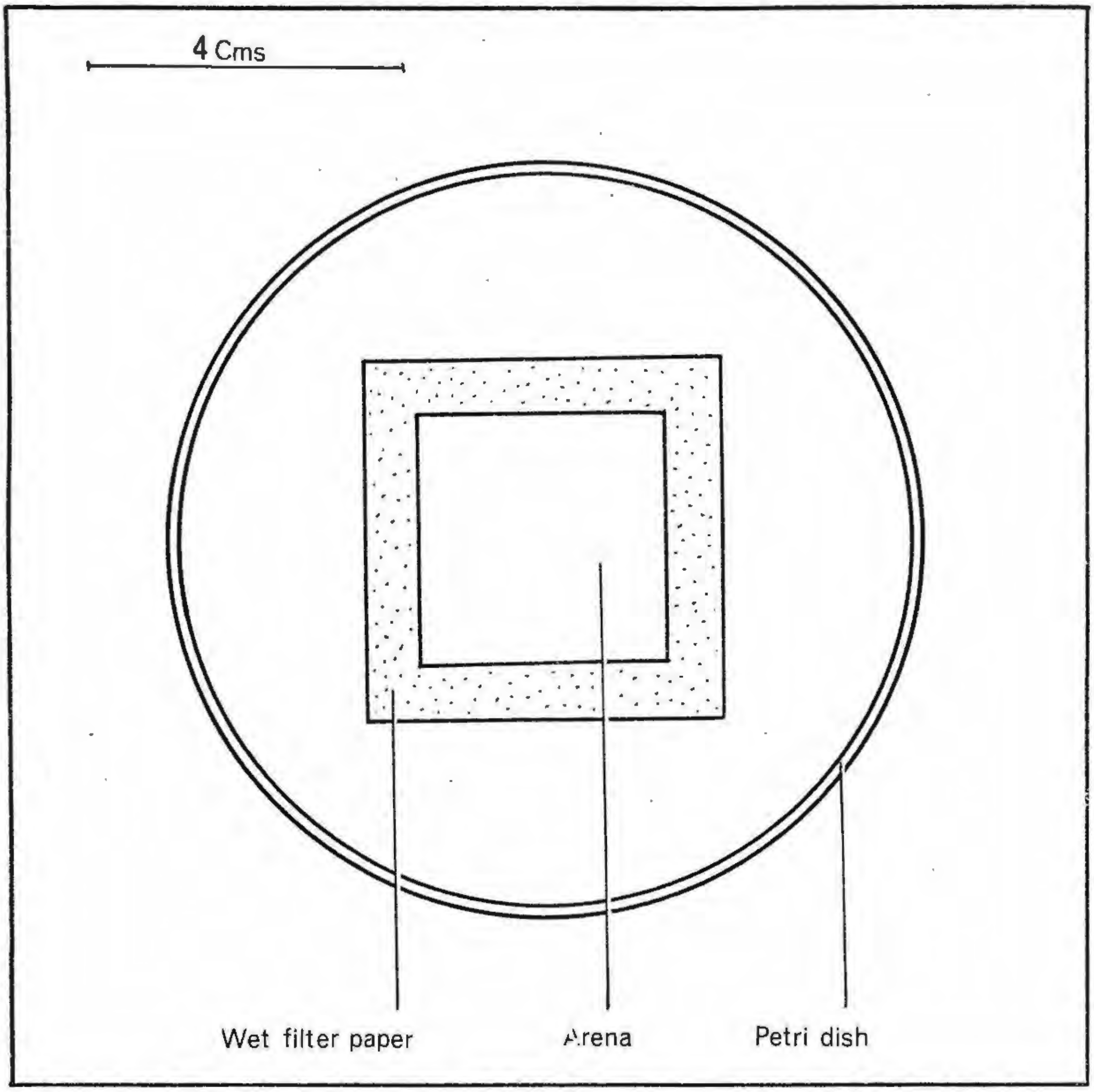


Fig. 24.

The apparatus used during observations on 'drinking' behavior of larval ticks.

would repeat this 'avoiding' behaviour a number of times before the next stage was observed. The value of this 'avoiding' behaviour is not known. As high relative humidities are usually considered to be most suitable for larval survival it is odd that larvae should react in this way to the damper region in the immediate vicinity of the wet filter paper. A possible explanation could be that larvae which possess sufficient water are negatively hygrotrophic. This explanation would, however, not explain the behaviour which follows.

iii After a number of consecutive 'avoiding' reactions it was noticed that larvae would at each attempt, approach increasingly closer to the wet filter paper until eventually they would come into contact with it.

iv Larvae would then either, hesitate, turn around and continue the 'avoiding' behaviour a little longer, or approach the paper slowly and thrust the hypostome into the water at the edge of the paper. Plate 14 shows an A. hebraeum larva in the process of drinking water at the edge of the filter paper. Larvae which thrust their hypostomes into the water always splayed the pedipalps outwards as shown in the photograph. The pedipalps were usually not actually submerged in the water and appeared to be hydrophobic. Arthur (1962) shows that this is the position of the pedipalps adopted during feeding from a host. In some cases the hypostome was thrust between the fibres of the filter paper during this drinking behaviour.

v Larvae would then become motionless. During this period active movements of the anterior region of the gut were observed through the partially transparent scutum.

vi After varying periods of time larvae would suddenly become active again and would withdraw their hypostomes and either turn away from the water or slowly walk onto the wet surface of the filter paper. Larvae which moved onto the wet surface often then demonstrated a further behavioural characteristic. They would 'squat' on the surface of the wet filter paper and lie motionless for a while. As has already been mentioned in an earlier comment on this behaviour, there is the possibility that water may be taken up directly through the cuticle of the larva during this 'squatting' behaviour. Some larvae would demonstrate this behaviour without actually having imbibed water as described earlier. This would suggest that these two patterns of behaviour are distinct.

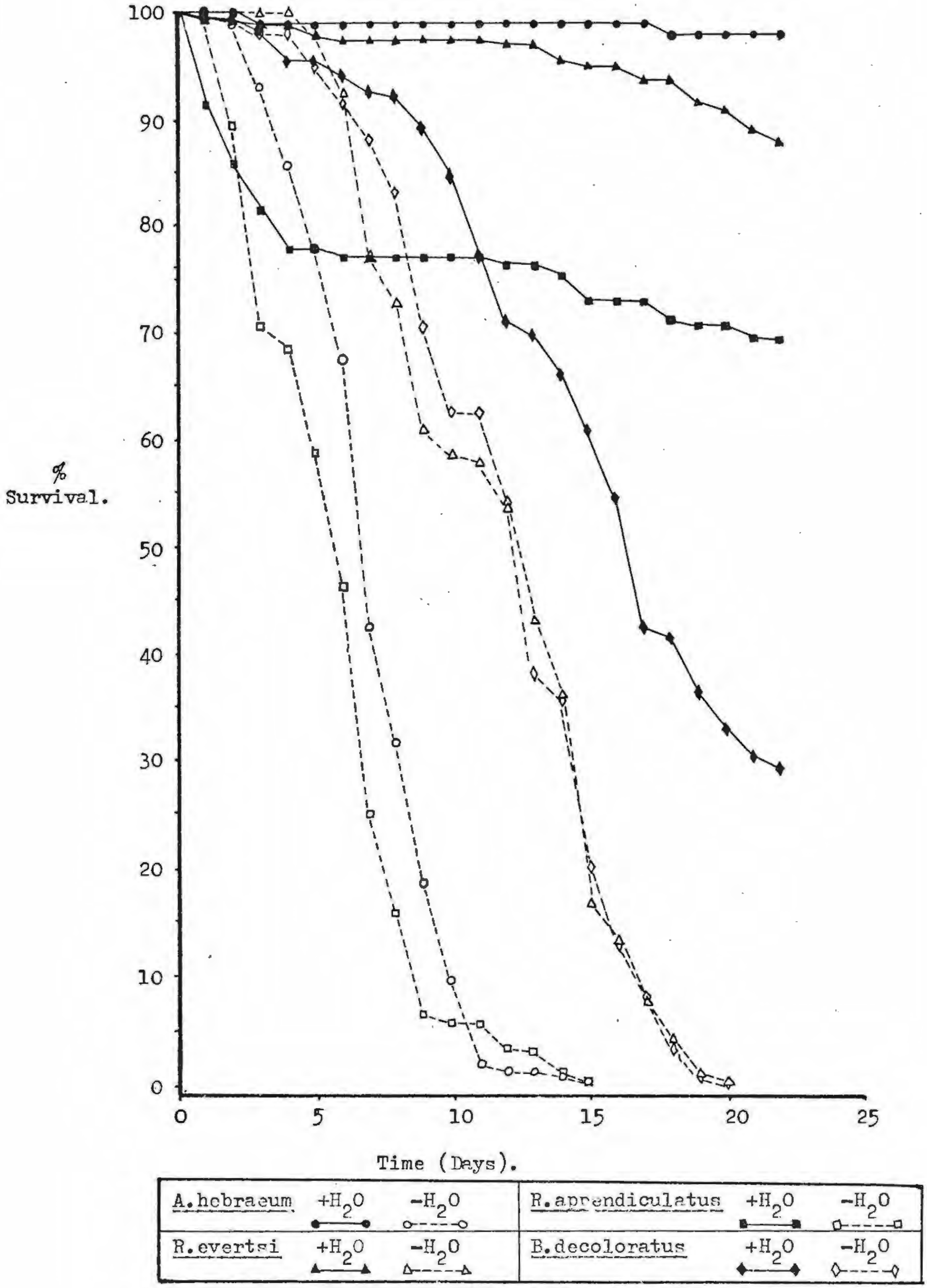
The behaviour described above is of great interest as it suggests that larvae are able to imbibe water in liquid form as would be presented by dew or raindrops. They would be able to replenish, rather rapidly, any water lost during a period of desiccation. In order to establish whether the larvae were taking up water during this 'drinking' behaviour, various dyes were added to the water. Methylene blue was found to be most satisfactory. Plate 15 shows a photograph of three larvae in various stages of dye uptake. The larva at the left hand side of the photograph had not taken up any dye at all, the one in the centre had been interrupted during its dye uptake, the larva on the right hand side of the photograph had been allowed to take up as much of the dye as it had wanted. It is obvious that the last mentioned larva appears darker in colour than the other two. Wilkinson (1953) has presented similar evidence of water uptake in B. microplus while Wilkinson and Wilson (1959) reported larval B. microplus drinking from dew. These findings appear to be in contradiction with those of Lees (1946) in respect of I. ricinus.

As it is the survival value of drinking which is of most interest, some further consideration was given to this aspect. Wilkinson and Wilson (1959) have shown that B. microplus larvae supplied with 'dew' live longer than those deprived of liquid water.

The importance of free water in the survival of ixodid tick larvae was studied using the following species, R. evertsi, R. appendiculatus, B. decoloratus and A. hebraeum. Four replicate batches of larvae were placed in a series of plastic petri dishes. The larvae were confined to the dishes with a ring of vaseline applied around the edge of each dish. A piece of filter paper (4 x 4 cms) was then placed in each dish. All the petri dishes were placed in the constant environment room under the regime shown as Condition A in Fig. 8. Two dishes of each species were supplied with distilled water every 12 hours, this being added to the filter paper squares. The number of living and dead larvae in each petri dish were then counted daily. The results appear in Fig. 25. These results show that larvae which were supplied with water lived longer than those without. The species can be arranged in the following order with respect to the ability to survive when liquid water is available. A. hebraeum, R. evertsi, R. appendiculatus and B. decoloratus. As these species can be listed in the same order in respect of hypostome length it is suggested that larvae with long hypostomes are more able to efficiently imbibe water than those with short hypostomes. This is however only surmise.

A further experiment, using A. hebraeum larvae only, in which the effects of high and low night relative humidities were coupled with the availability of free water, was undertaken. The constant environment room was again set to condition A as shown in Fig. 8. The petri dishes, similar to those already described, were placed in atmostpheres of different relative humidity values during the night. These values were 100 %, 90 %, 80 % and 50 % RH respectively. Two petri dishes were placed in each of the four different night conditions, one of which was supplied with a few drops of free water as described in the last experiment. During the day the petri dishes were placed in the general environment room conditions (40 % RH and 26°C). The results are shown in Fig. 26. The results show that larvae in high night relative humidity values (80-100 % RH) are only slightly effected by the presence of free water. This suggests that they are able to survive quite well without it. This contention is supported in later work on active uptake of water vapour. Larvae kept at a relative humidity of 50 % at night reacted differently from those kept at 80-100 %. Those larvae kept at 50% RH at night and not supplied with free water survived only eight days while those supplied with free water lived much longer (i.e. less than 50 % mortality in 30 days).

Fig. 25.
The importance of free water to the survival of some ixodid larvae.



Environment room condition A was used throughout experiment.

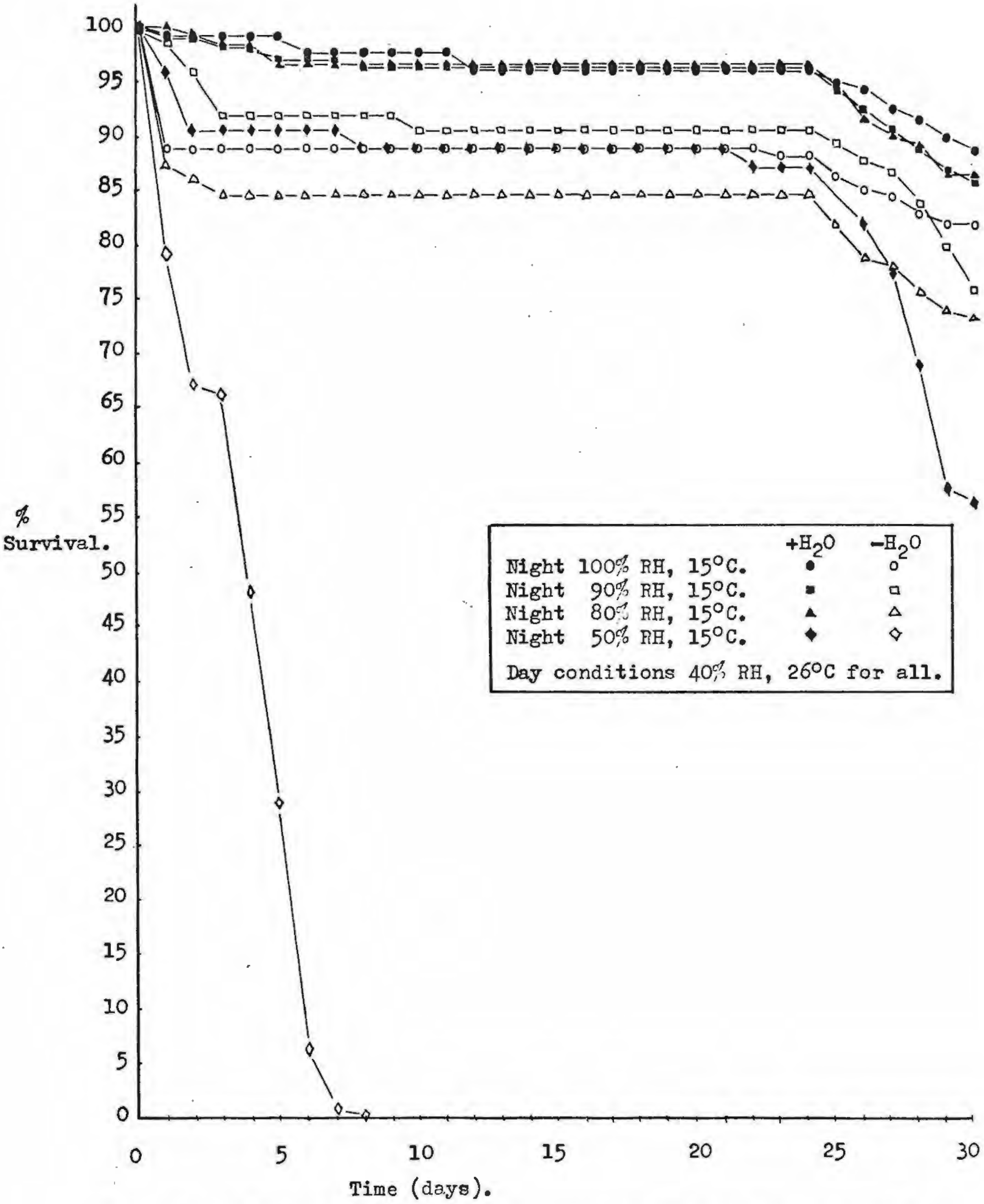


Fig. 26. The effects of different atmospheric relative humidities and the presence or absence of free water on the survival of *Amblyomma hebraeum* larvae.

From these results it can be concluded that free water can be of great survival value when atmostpheric relative humidities are not sufficiently high enough to allow active uptake of water vapour. However, it is unlikely that dew or raindrops would be present when atmostpheric relative humidities are low. It is suggested that the value of drinking behaviour is mainly as a means of rapidly regaining water. The taking up of atmostpheric water, which is duscussed anon, appears to take more time.

Although free water appears to be of some survival value to larval ticks, it could be that they might drown in copious supplies of water such as heavy dew or rain. In order to examine this possibility, larvae of R. evertsi, R. appendiculatus, B. decoloratus and A. hebraeum were placed in glass petri dishes and submerged in drops of water released from a dropper held immediately above them. In all cases the larvae were able to pull themselves free of the water droplets, even when the footing was as inadequate as that offered by the smooth surface of the glass petri dishes.

Larvae were also placed in sealed vials of water and the number of living and dead counted daily. In this experiment larvae of only R. appendiculatus and A. hebraeum were used. The results, which are presented graphically in Fig. 27, show that total immersion for 24 hours caused no mortality. As total immersion for 24 hours in the field would be most unlikely, death by drowning is very unlikely.

v. Active uptake of water vapour from the air

It appears that this means of water uptake is of the greatest survival value to ixodid tick larvae. A summary of the findings of Lees (1946) in this regard are listed below.

a. I. ricinus (unfed nymphs and adults) lose water to the air by evaporation at atmostpheric humidity values of less than 92 % RH. Water is gained by active uptake of vapour from air at a relative humidity of higher than 92 % RH. Thus 92 % RH can be considered as the 'equilibrium humidity' of this species.

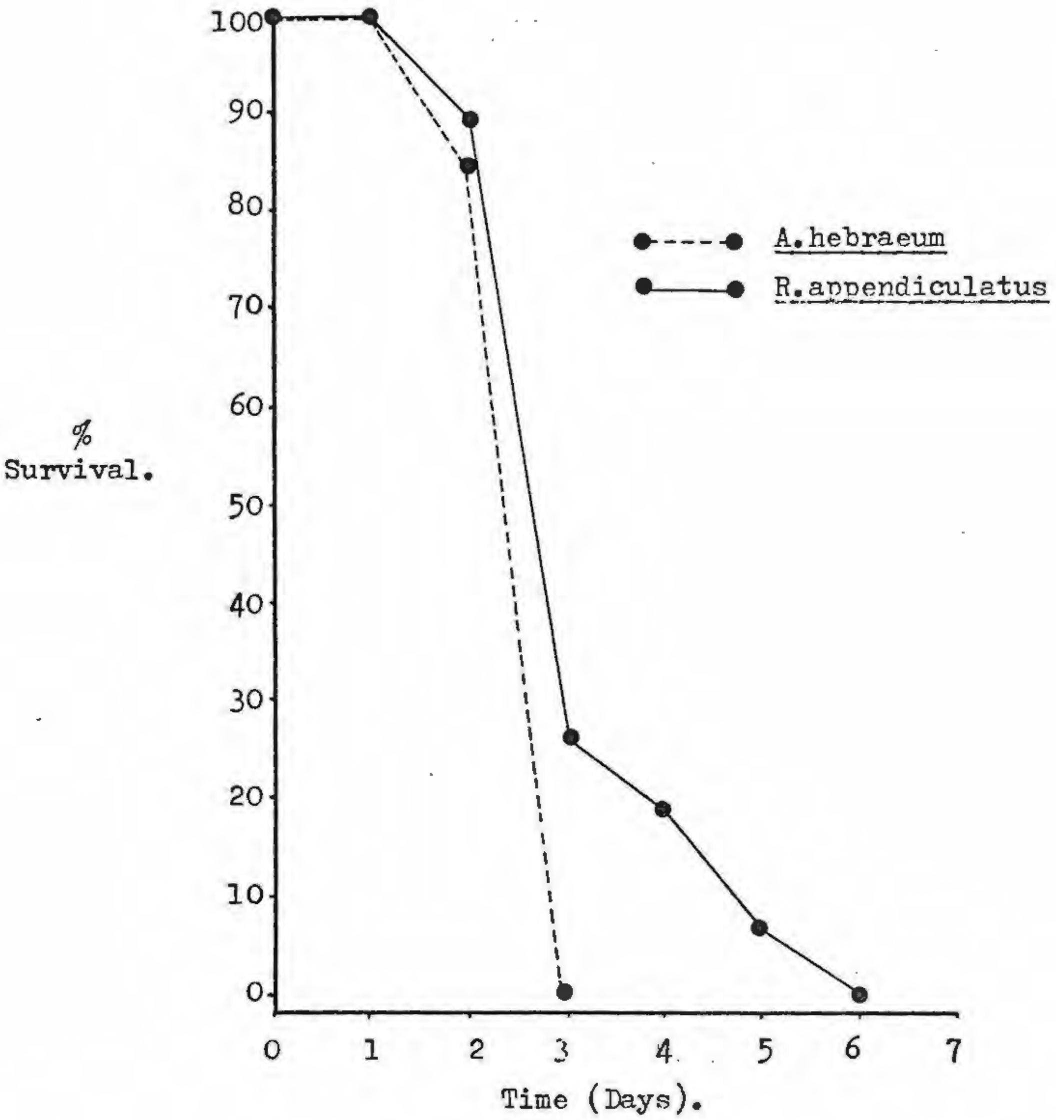


Fig. 27.
The survival of larval ticks completely submerged in water.

b. The evidence supplied to demonstrate that the process of water vapour uptake is active included the fact that temporarily asphyxiated ticks lost the ability to take up water. Ticks, the cuticle of which had been abraded, even over a very small surface area, lost the ability to take up water. The process was also dependant on temperature, from which Lees (1946) deduced that it was an active one. In addition to the above facts Lees (1946) points out that water vapour is taken up against a gradient. He suggests that if the haemolymph of ticks was assumed to have an osmotic pressure approximately equivalent to a 1% sodium chloride solution, this solution would have a relative humidity in the region of 94 % RH. As he demonstrated that ticks take up water vapour from the air at relative humidities of less than 94 % RH, he concluded that this was against the gradient.

c. The epidermal cell layer was considered to be the site of the active uptake process. Lees (1946) demonstrated that pore canals traverse the endocuticle and he suggests that these might play an important role in water uptake.

d. The loss or gain of water in the region of the 'equilibrium humidity' was determined by the relative humidity and not the saturation deficit of the air, over a wide range of temperature.

In view of Lees's (1946) findings on I. ricinus it was decided to investigate the possible existence of a similar water uptake mechanism in R. appendiculatus larvae. This species was selected as large numbers of larvae were readily available.

R. appendiculatus larvae were placed in small glass tubes such as that illustrated earlier (Fig. 16). Tubes were placed for an initial period of 12 hours in a desiccator held at 95 % relative humidity and then weighed. The tubes were then transferred to a desiccator containing dry air, created by the use of silica-gel, for a period of 24 hours. At the end of this period the tubes were once again weighed before being distributed among eight desiccators containing relative humidity values of 30, 40, 50, 60, 70, 80, 90 and 100 % RH respectively. The tubes in each desiccator were weighed on a Sartorius single pan balance at intervals over a period of 96 hours. The entire experiment took place in the constant environment room set as condition B of Fig. 8. The results are presented graphically in Fig. 28.

The results show that water is lost by larvae when placed in dry air. When the tubes were placed in an atmostphere of various relative humidity values after the initial period of desiccation larvae reacted in different ways depending on the environment in which they were placed.

a. Those placed in relative humidities of 100 % and 90 % RH regained water very rapidly and even achieved weights greater than the initial values recorded before the experiment commenced.

b. Larvae placed in a relative humidity of 80 % also took up water, but to a smaller extent than those in 100 % and 90 % RH.

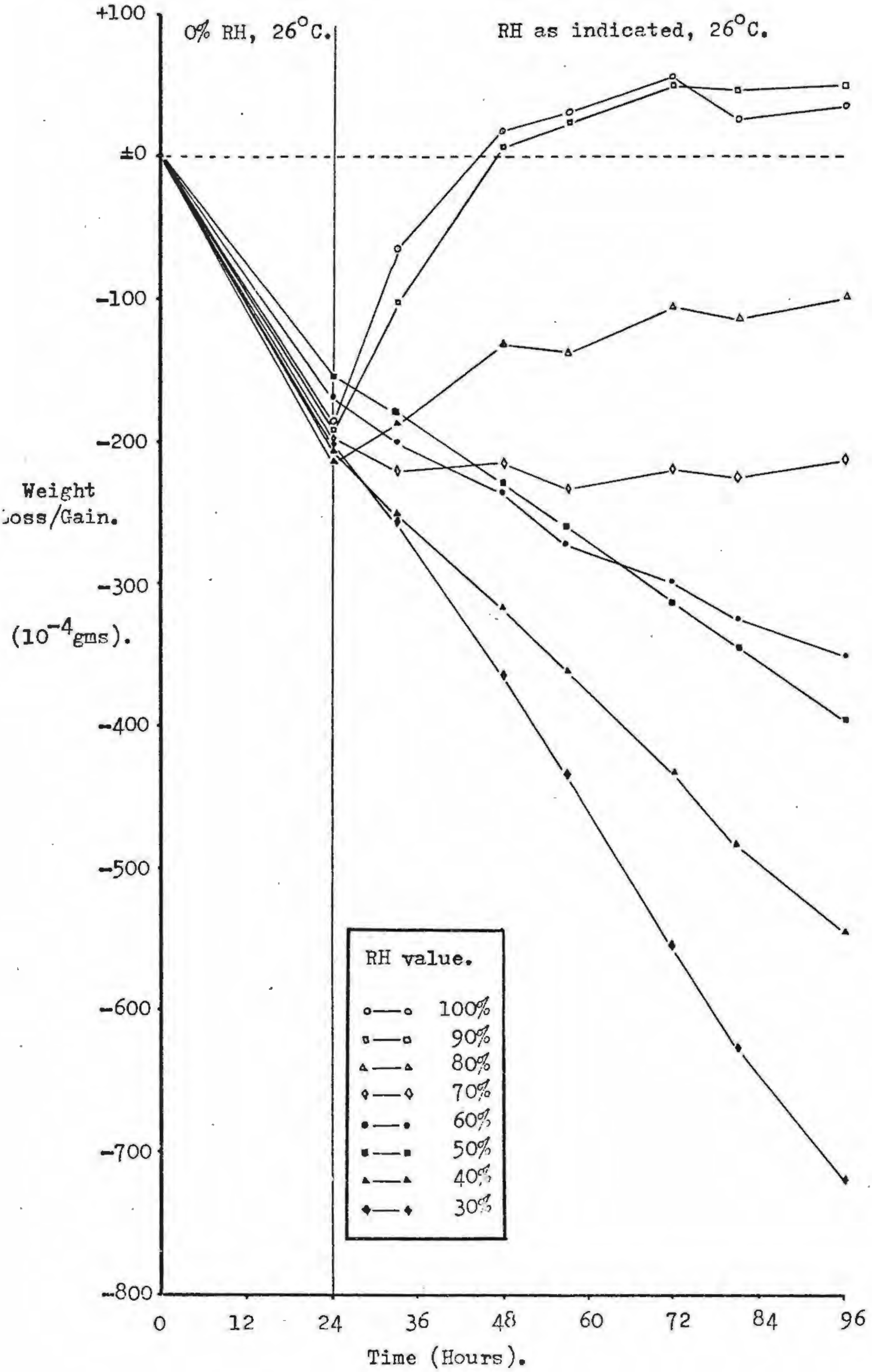
c. Larvae placed in a relative humidity of 70 % appeared to maintain their body weight. This is what was expected as larvae examined earlier in survival experiments (Figs 10-15) showed only a gradual loss of water (indicated by the gradual increase in the rate of mortality) in an atmostphere of 70 % relative humidity.

d. All larvae placed in an atmostphere of less than 70 % relative humidity showed a progressive drop in weight which was directly related to the relative humidity value. i.e. those placed in an atmostphere of 30 % relative humidity lost water proportionately faster than those in an atmostphere of slightly higher relative humidity.

From the way in which larvae of R. appendiculatus reacted at various relative humidities it would appear that this species has an 'equilibrium humidity' in the region of 70% relative humidity. From the results presented earlier (Figs 10-15) it may be possible to suggest that all the species dealt with in this investigation have

Fig. 28.

The ability or inability of water uptake from various atmospheric relative humidities by R.appendiculatus larvae. (Temperature constant at 26°C.)



'equilibrium humidities' of this order. Apart from this suggestion, it is possible to predict the way in which larvae of R. appendiculatus, and possibly all ixodid species, will react to changes in relative humidity throughout any 24 hour period. Fig. 29 represents the changes in relative humidity over a period of 24 hours (generalised) and the probable way in which larvae might take up from, or lose water to, the air over the same period. This suggested pattern shows that the rate of uptake increases with increase in relative humidity. The rate of uptake is greatest when the relative humidity is highest (i.e. in the early hours of the morning). Similarly at midday when the relative humidty is at its lowest value, larvae lose water at the greatest rate. The 'equilibrium humidity' is achieved twice during the theoretical day shown in Fig. 29. i.e. at approximately 7.30 a.m. and 8.30 p.m.

In the last experiment it was shown that water uptake is dependent on the relative humidity of the atmostphere. It was thought that the degree of desiccation might also influence the rate at which water is taken up. In order to investigate this possibility the following brief investigation was undertaken.

Twelve small glass tubes, similar to those already described (Fig. 16), were filled with R. appendiculatus larvae. All the tubes were placed for an initial period of 12 hours in an atmostphere of 95 % relative humidity. The tubes were then weighed and then handled in groups of three in the following way.

a. A group was placed in a desiccator at 90 % relative humidity and weighed every 12 hours over a period of ten days as a control.

b. A second group of three tubes of larvae were placed in a desiccator containing dry air for a period of 12 hours, weighed, and then transferred to an atmostphere of 90 % relative humidity.

c. A third group was desiccated in the dry air for a 24 hour period and then transferred to an atmostphere of 90 % relative humidity.

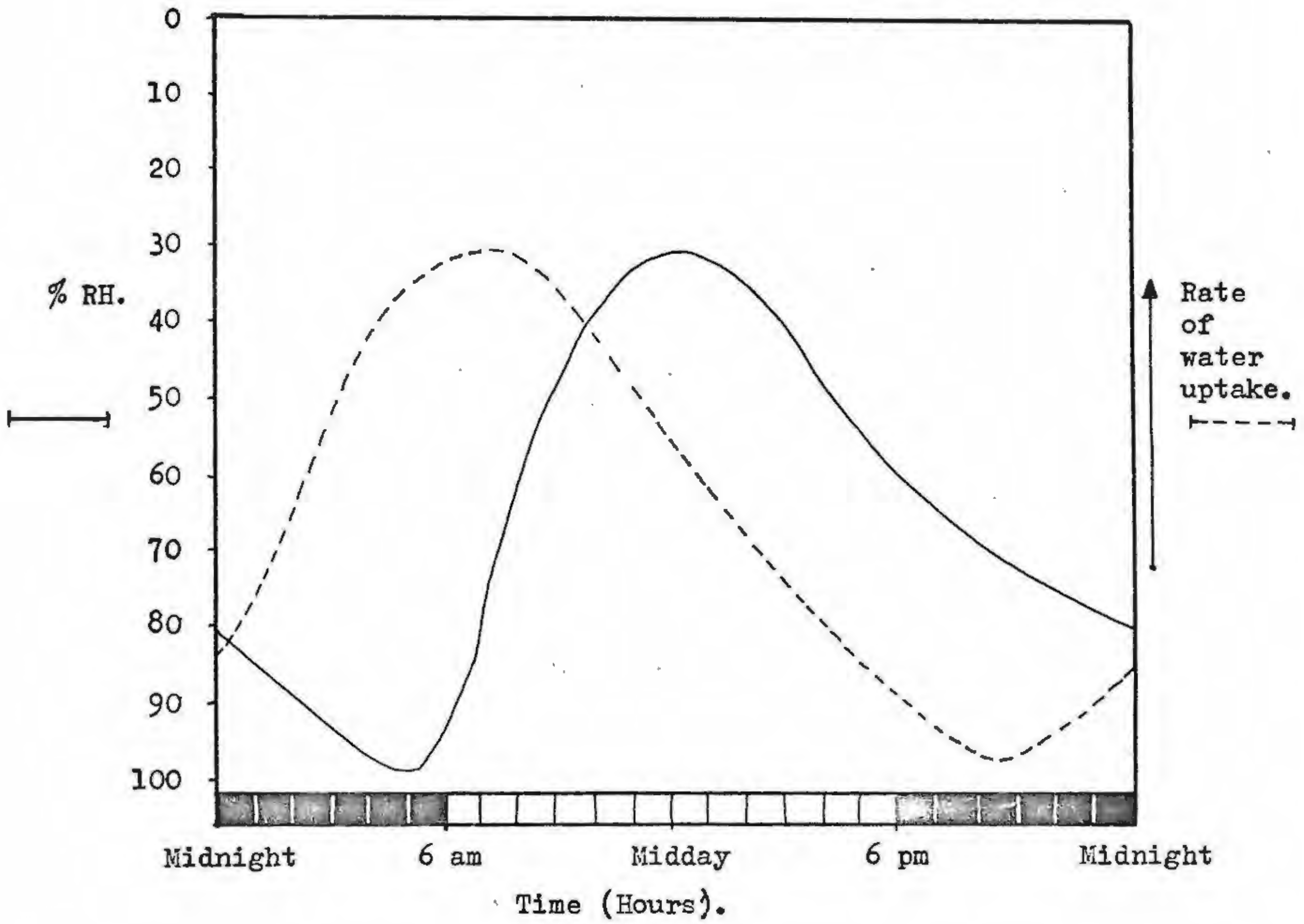


Fig. 29. A possible way in which a larval tick might gain from and lose water to the atmosphere throughout a 24 hour period. Based on the information shown in Fig. 28.

d. The last group of three tubes of larvae were desiccated in dry air for 36 hours, weighed and transferred to an atmostphere of 90 % relative humidity.

The entire experiment was conducted in the constant environment room under condition B as shown in Fig. 8. The results are presented in Fig. 30. These results show that the rate of water uptake is unlikely to be dependent on the degree to which larvae have been desiccated. The curves representing the recovery of larvae when placed in an atmostphere of 90 % relative humidity show similar slopes. Of interest is the fact that these curves rose above the control line. This means that the process of water uptake continues to operate after the equilibrium weight has been achieved. The slope of the control curve does not lie parallel to the X axis as would be expected if the larvae were maintaining their water content at a fairly constant level. The reason for the decline in weight is not known. A similar but less marked decline can be seen in the control curve reported in Fig. 18. It is also apparent that the rate of weight loss fluctuates from one 12 hour period to the next. This is thoughtto be due to the temperature regulating mechanism of the constant environment room. A small difference in night and day temperatures occurs even when these are set to be identical. This small change in temperature may have effected the rate of water loss and thus weight loss.

General discussion of water uptake by larval Ixodidae

Water uptake by larval Ixodidae is achieved mainly by the active uptake of water vapour from moist air. Drinking and the uptake of liquid water directly through the cuticle may also supplement water uptake. Larvae of R. appendiculatus are able to take up water vapour from atmostpheres which have relative humidities higher than 70 %. The 'equilibrium humidity' appears to be between 70-80 % relative humidity for this species. It is suggested that all the other species mentioned in this investigation have similar 'equilibrium

Fig. 30. The effects of different degrees of desiccation on the uptake of water vapour on subsequent exposure to high humidity by *R. appendiculatus* larvae.

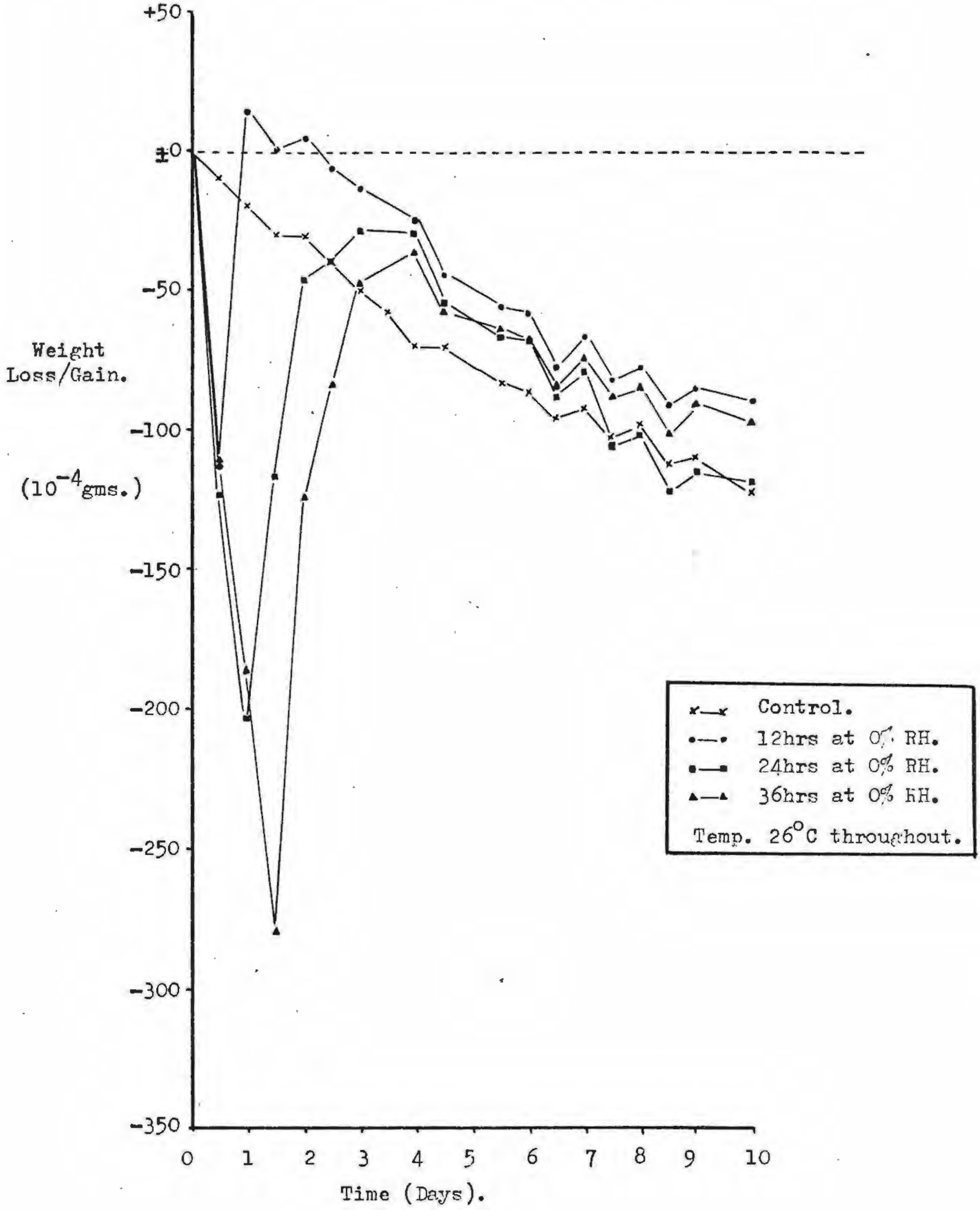
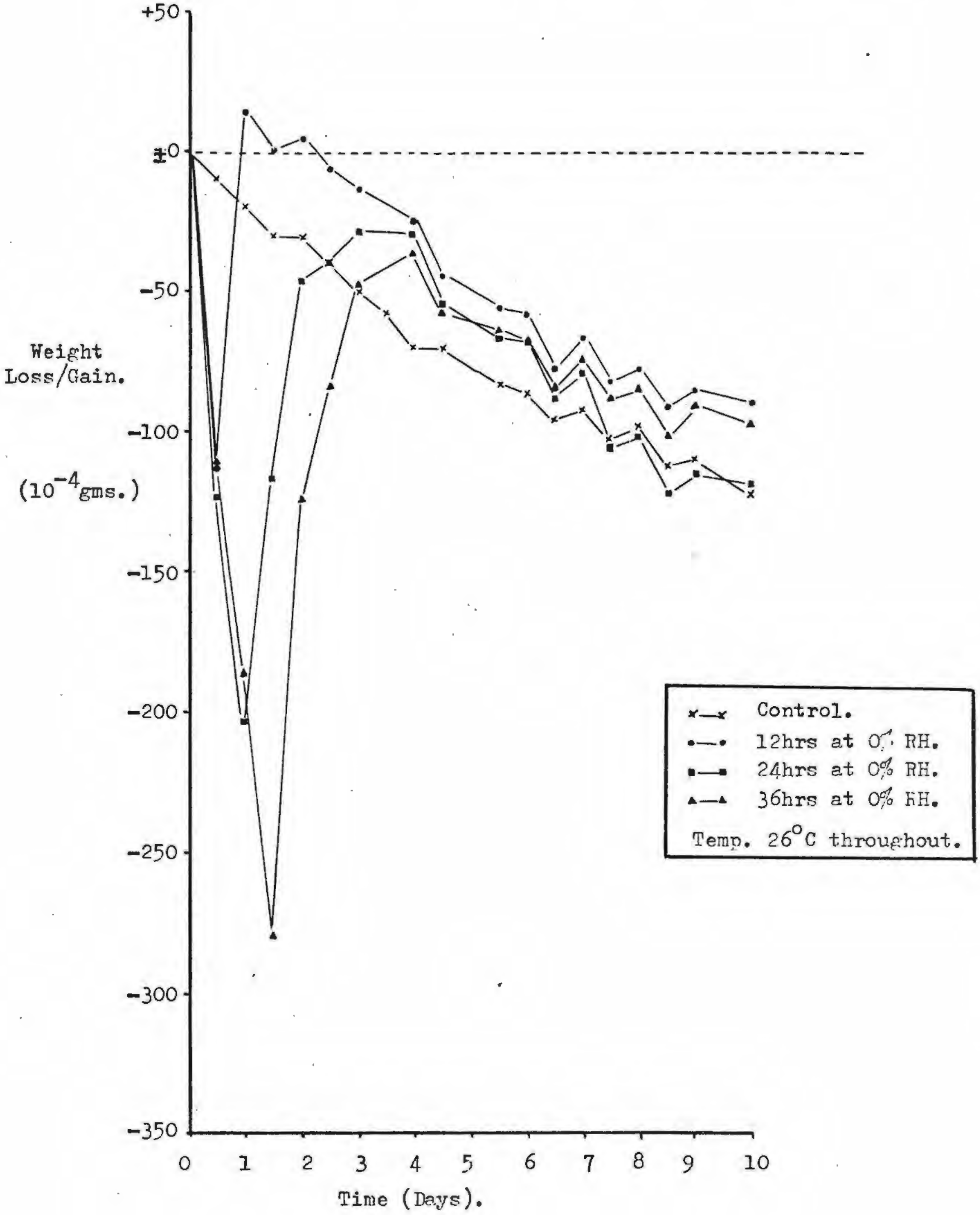


Fig. 30. The effects of different degrees of desiccation on the uptake of water vapour on subsequent exposure to high humidity by *R. appendiculatus* larvae.



humidities'. The results obtained in the present investigation are very similar to those obtained by Lees (1946) using I. ricinus except that the 'equilibrium humidity' for this species was found to be higher than that suggested for R. appendiculatus and the other species mentioned in this study. Water vapour uptake appears unrelated to the degree to which larvae are desiccated.

General conclusions and discussions resulting from the work reported in this chapter

It is evident both from the results of the present investigation and the findings of Lees (1946), Wilkinson and Wilson (1959) and others, that a balance between water uptake and loss is maintained by ixodid ticks. Tick larvae lose water mainly by evaporation through the cuticle. Water uptake is likewise through the general body surface. Lees (1946) has suggested that the process is an active one. The imbibing of liquid water probably supplements uptake through the cuticle.

Lees (1946) demonstrated that I. ricinus possesses a characteristic 'equilibrium humidity' in the region of 92 % relative humidity. The results of work done on R. appendiculatus in the present investigation, show that this species probably has an 'equilibrium humidity' in the region of 70-80 % relative humidity. As the survival of R. appendiculatus larvae in various relative humidity values is comparable with a number of other species (R. evertsi, R. simus, B. decoloratus, A. hebraeum and I. pilosus) it may be suggested that these species have very similar 'equilibrium humidities'.

The distributional data reported earlier (Tables 7-8) show that larvae collected at Barville Park and Faithful Fountain are found in definite vegetational situations. If 70-80 % relative humidity is considered as being the approximate 'equilibrium humidity' of the species studied during the distributional work,these species would not be expected to occur in habitats experiencing relative humidities much in excess of this approximate value. Using Fig. 31, which shows the relationship of relative humidity to saturation deficit at 26°C, an 'equilibrium saturation deficit' of approximately 10.00 mm. Hg. may be suggested as being characteristic of the species studied. Habitats which yielded larval ticks during the distributional survey hardly ever experienced conditions of saturation deficit much greater that 10.00 mm. Hg. (Table 15). When higher values were recorded these were over the midday period and usually did not occur at all levels in the vegetation. Larvae which experienced these short periods of desiccation over midday appear to have had adequate time to recoup the water lost during the relatively long periods during which the saturation deficit was well below 10.00 mm. Hg. (i.e. The relative humidity would have been higher than 70-80 %).

Although other factors, such as host behaviour, egg development and larval behaviour probably influence larval distribution, there appears to be a definite correlation between larval distribution and microclimate.

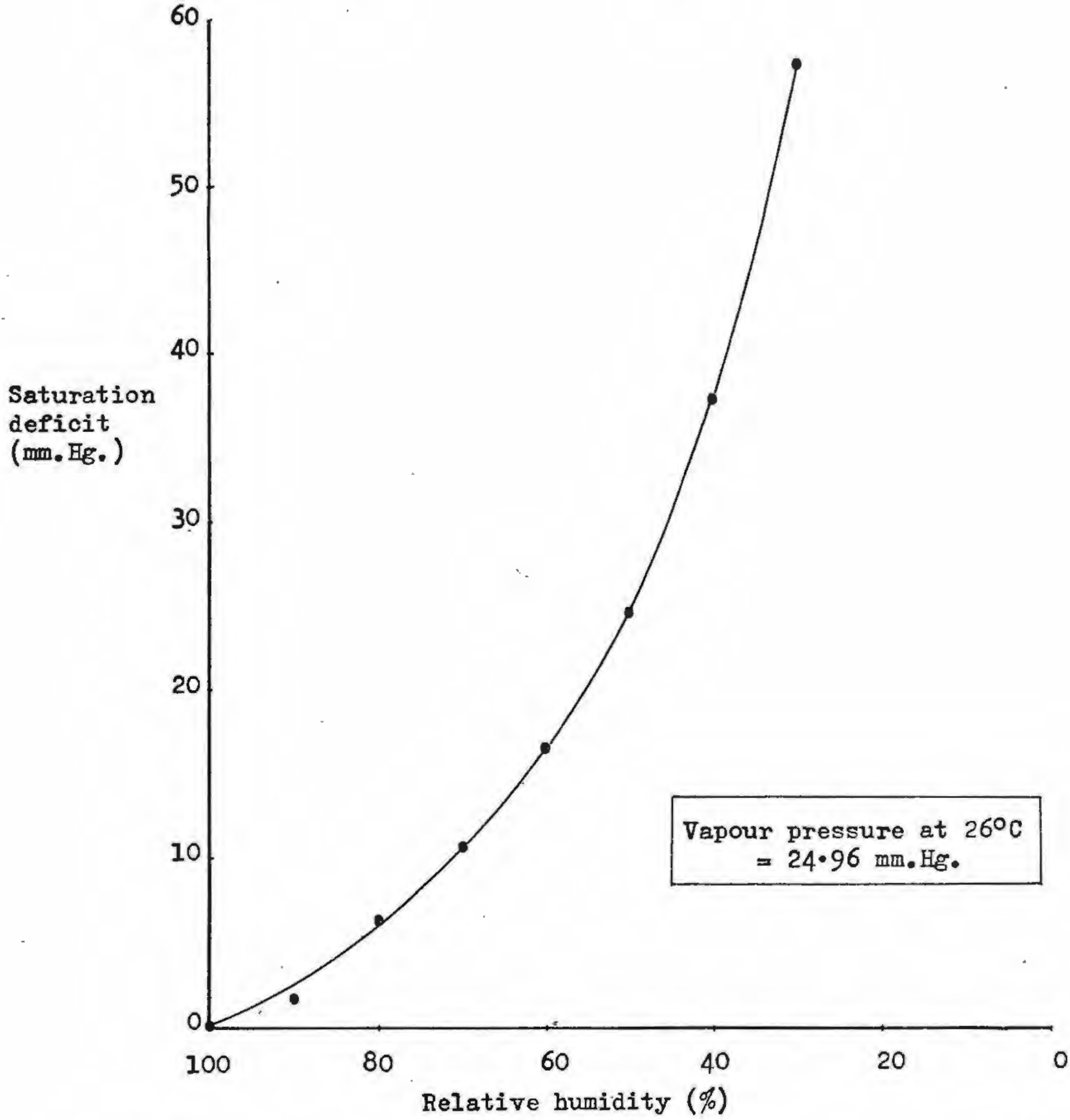


Fig. 31.

The relationship between Saturation deficit and Relative humidity at 26°C.

5. SOME ASPECTS OF THE BEHAVIOUR OF LARVAL TICKS

It has become evident, from the evidence presented in the preceeding chapters, that the distribution of ixodid tick larvae is probably related to microclimate. It is also probable that other factors are involved in delineating larval distribution. The results of the distributional survey undertaken at Barville Park and Faithful Fountain show that there is a close relationship between vegetation height and larval distribution. The height of the vegetation has been shown to affect the microclimatic conditions found in the habitats concerned. The height of the vegetation may, however, also have some direct influence on larval behaviour.

A number of workers have reported on the sensory physiology and behaviour of various ixodid ticks, among these are Lees (1948) and Lees and Milne (1951) working on I. ricinus, Wilkinson (1953) working on B. microplus, Camin (1963) and George (1963) working on Haemaphysalis leporispalustris and Goldsmid (1967) working on B. decoloratus. The aspect with which most of the above workers have been concerned is the behaviour which eventually results in ticks attaining vantage points at the tips of grass stems, from which they are in a position to eventually encounter a passing host. Such stimuli as gravity, light, encounters with the tip of the stem, humidity gradients and temperature gradients have been given attention. As a number of conflicting opinions exist as to which of the above stimuli is most important in this 'orientation behaviour', some of the work reported by the above workers has been repeated using southern African tick species.

An aspect which has not received much attention is the possible importance of vegetation height in 'orientation behaviour'. This aspect has therefore been given special attention in the present investigation as it was thought that vegetation height may relate directly to larval distribution. The behavioural work undertaken is reported in two sections.

A. The possible importance of vegetation height in the distribution of non-parasitic larval ticks.

B. The stimuli which might govern 'orientation behaviour' in larval ticks.

Discussions of the relevant work previously done in this field of tick behaviour will be presented in the above sections.

A. The possible importance of vegetation height in the distribution of non-parasitic larval ticks.

As larval distribution appears to be related to vegetation height (i.e. I. pilosus, H. silacea and B. decoloratus were collected predominantly from short vegetation and A. hebraeum from medium to tall vegetation) this aspect was investigated further. It was thought that if larvae are in fact limited to certain specific vegetation heights they would possess the necessary 'behavioural pattern' to limit them to this height. The experiments presented in this section were designed to determine, firstly, whether vegetation height is of any relevance and secondly the nature of the 'behavioural pattern' involved.

Material and Methods

The living material consisted mainly of A. hebraeum larvae for the following reasons. This species was collected and correlated with a particular vegetation height in the distributional survey undertaken at Barville Park. A. hebraeum larvae are also large when compared with other species and this facilitated easy handling and counting.

At the end of this section a brief examination of other available species is reported, the species involved are B. decoloratus,

R. appendiculatus, R. evertsi and I. pilosus. With the exception of I. pilosus all the above species were easily maintained in the laboratory. I. pilosus larvae were brought in from field collections for experimental purposes.

Other material used consisted mainly of glass rods which served as satisfactory models of grass stems. Each rod was approximately 0.4 cms in diameter. The lengths of the rods varied with the experimental requirements. Each rod had one end drawn out into a point of a diameter of approximately 0.5 mm. This pointed end will be referred to as the tip of the rod in all further discussion. Glass rods were used in preference to real grass stems for a number of reasons. Glass rods could be cut to any length. Lengths far longer than any available grass stems could be obtained. Glass rods, being transparent, were ideal for observing climbing larvae. Glass rods also had the advantage of being easily washed and re-used with minimum possibility of 'contamination'. Goldsmid (1967) has suggested that a clustering 'pheromone' may exist, which could be deposited on the rods, thus affecting further experimental findings. This 'pheromone' will be discussed later in this chapter. Glass rods had a further advantage over grass stems in that they could be permanently marked off at 1 cm intervals or bent into any desired shape.

Other material used will be described in the relevant experiments.

Observations on the behaviour of individual A. hebraeum larvae climbing different lengths of glass rod

In the following experiments individual A. hebraeum larvae were permitted to climb on six different lengths of glass rod. The lengths used were 10, 15, 30, 40, 50 and 90 cms respectively. All observations were conducted in the laboratory where temperatures were maintained between 20° and 22°C by the use of an electric heater with built-in fan. The relative humidities recorded during observations were between 60% and 65%. Dyk and Boučkova (1968) (vide Theiler 1969) have shown that the activity of I. ricinus larvae is dependent on the relative humidity of the atmostphere. As A. hebraeum larvae, and larvae of the other species studied, were found to be quite active at the relative humidity values measured in the laboratory, it was assumed that the conditions were satisfactory for activity.

All experiments were conducted using the following procedure.

i An individual larvae was introduced onto the glass rod by means of a fine paintbrush (No 1). The point of release was dependent on the length of rod to be climbed i.e. if a length of 40 cms was used the larva was released just below the 40 cm mark on a glass rod. The glass rods used were always a little longer than the required length so as to facilitate release at the required distance from the tip.

ii The larva was then observed as it climbed the rod. If the larva climbed downwards it was removed and replaced by another larva. This did not however, happen often. When the larva climbed upwards it was carefully observed and its movements recorded using the method described by Lees (1948).

iii Once a larva had commenced its first trip up the rod, it was left undisturbed until it either returned past the point of release or came to rest on the rod for a period of at least 30 minutes. The larva was then considered as having completed the requirements of the test. Ticks which returned past the point of release were removed as it was clear that in the field a larva in this position would have reached the ground and would therefore have the opportunity of choosing another grass stem of a different height. Those larvae which came to rest on the rod were removed as they were considered to have achieved the position required by a larva in order to encounter a passing host.

iv On completion of the experimental requirements the larva concerned was usually destroyed so as to ensure that no larva was used more than once.

The diagrammatic representations of the movements of ten individual larvae were recorded for each rod length. The exception being the 40 cm rod on which the movements of 20 larvae were recorded. The 'tracks' are shown in Figs 32-37. Although considerable variation was displayed by the tracks they were able to be analysed. Table 22 shows the type of information which can be calculated from the individual tracks of the larvae shown in Figs 32-37. Table 22 shows that the height of the rod may well be of some importance. The main effects of rod length are listed below.

i Generally speaking larvae appear to walk to the tip of the vertical rod on the first upward trip, except in the case of the 90 cm rod where larvae only walked approximately half way up the rod before turning back and descending. It can be seen that turning back before the tip is reached also occurs on the shorter rod lengths but to a lesser extent. Goldsmid (1967) stated that, in the case of <u>B. decoloratus</u> larvae, turning <u>never</u> took place on the upward trip. He was, however, concerned with rod lengths of between 8-10 cms (Goldsmid 1969) which may explain this statement.

ii Larvae usually reached the tip of the rod during the time spent on it, even if not on the first upward trip. The exception was again the 90 cm rod, where the average maximum height attained was only 64.7 % of the total height possible.

iii The average duration of movement in minutes was greatest for larvae placed on the 50 cm rod. The short times spent on the 10, 15 and 30 cm rods was attributed to the fact that larvae frequently returned past the point of release after the first passage up these rods. The numbers actually coming to rest at the tips of these rods were small. In the case of the 90 cm rod the time spent by a larva on the rod was less than that spent on the 50 cm rod. This can

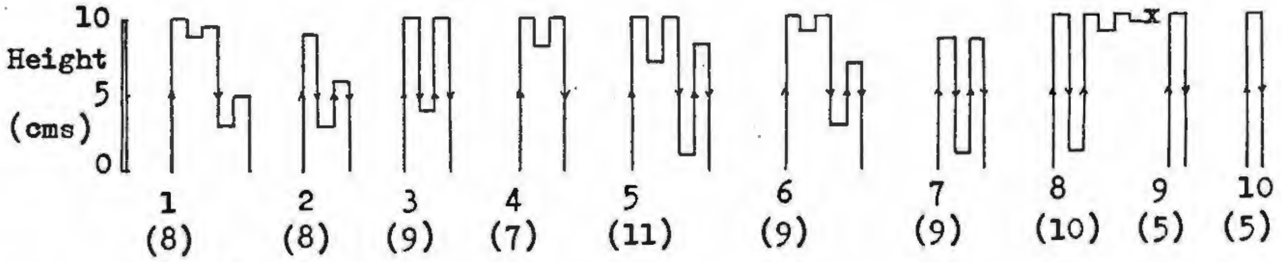


Fig. 32.

The individual tracks of ten Amblyomma hebraeum larvae on a 10 cm. rod.

x = Position at which larva came to rest.

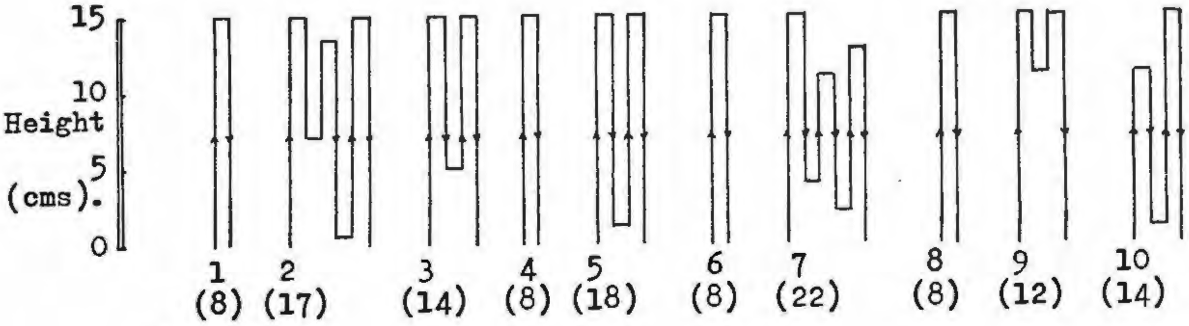


Fig. 33.

The individual tracks of ten Amblyomma hebraeum larvae on a 15 cm. rod.

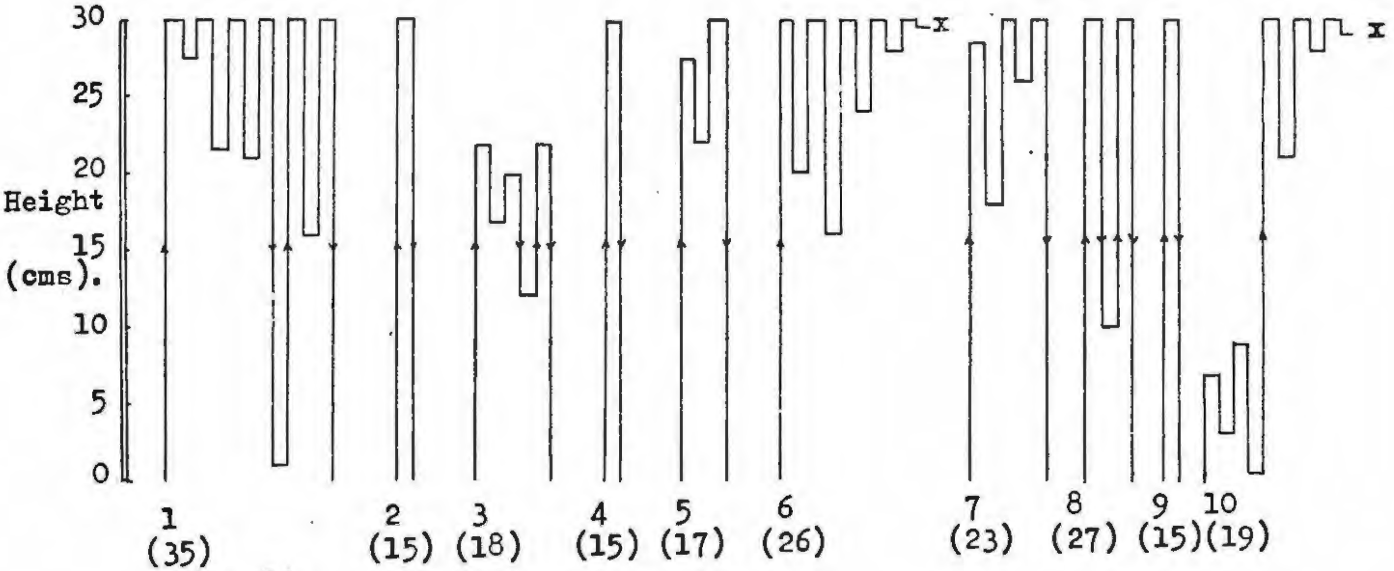


Fig. 34.

The individual tracks of ten Amblyomma hebraeum larvae on a 30 cm. rod.

(Figures in brackets indicate time (in Mins.) taken to complete eack track)

x = Position at which larva came to rest.

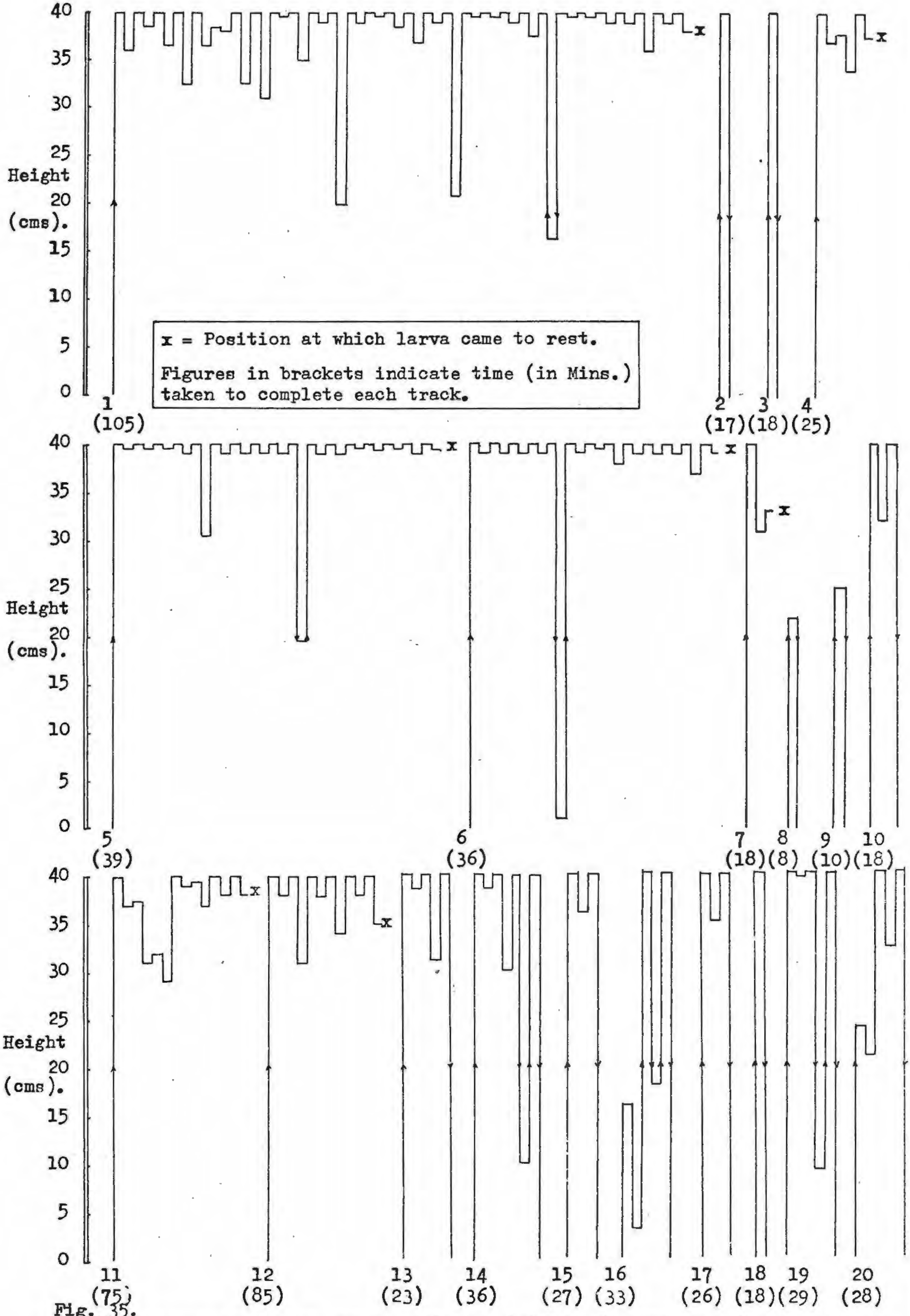
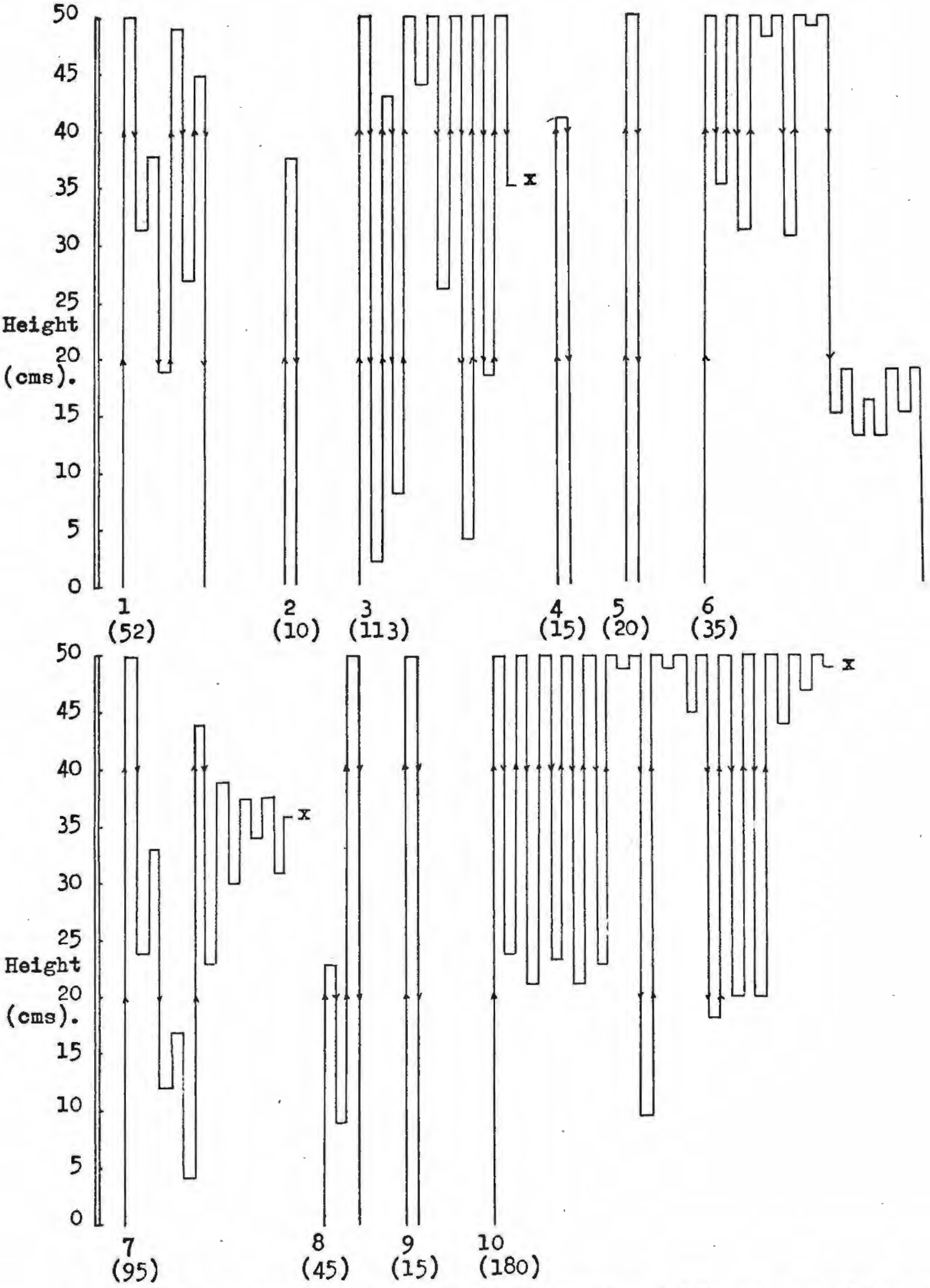


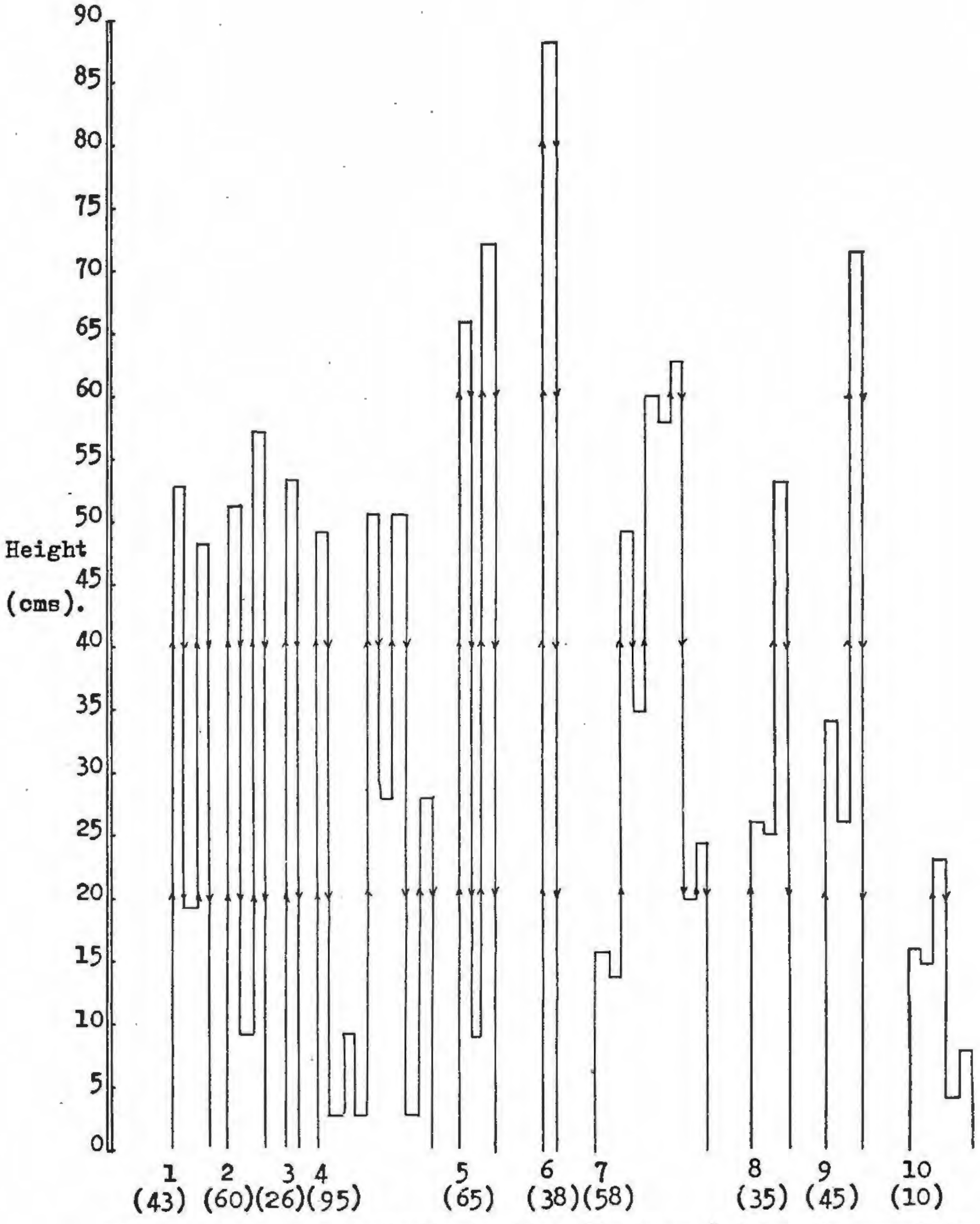
Fig. 35.
The individual tracks of twenty Amblyomma hebraeum larvae on a 40 cm. rod



Figures in brackets indicate time (in Mins.) taken to complete each track.

Fig. 36.
The individual tracks of ten *Amblyomma hebraeum* larvae on a 50 cm. rod.

x = Position at which larva came to rest.



Figures in brackets indicate time (in Mins.) taken to complete each track.

Fig. 37.

The individual tracks of ten Ambylomma hebraeum larvae on a 90 cm. rod.

x = Position at which larva came to rest.

Table 22 An analysis of the individual tracks recorded for *A. hebraeum* larvae walking on six different lengths of glass rod (Figs 32-37).

Length of rod (cms)	10	15	30	40	50	90
Average length of 1st trip (cms)	9.8	14.6	26.5	36.4	45.2	45.0
% of maximum height possible	98.0	97.3	88.3	91.0	90.4	50.0
% larvae reaching tip on 1st trip	80.0	90.0	60.0	80.0	70.0	0.0
Average maximum height achieved in any trip (cms)	9.8	15.0	29.2	38.4	47.9	58.3
% of maximum height possible	98.0	100.0	97.3	96.0	95.8	64.8
% larvae reaching tip on any trip	80.0	100.0	90.0	90.0	80.0	0.0
Average duration of movement on rod (to nearest min.)	8	13	21	34	58	48
% actually coming to rest at tip	10.0	0.0	20.0	35.0	30.0	0.0
No larvae tested	10	10	10	20	10	10

be attributed to the fact that larvae on the longer rod climbed fairly high on the rod before returning almost immediately past the point of release. The relatively long periods spent on the 40 and 50 cm rods was for another reason. In these cases time was occupied by frequent short trips to and from the tip before the larva finally came to rest in the region of the tip. The movements involved will be discussed later.

A further analysis of the individual tracks (Figs 32-37) was made. In this analysis an attempt was made to compare the activity of larvae at various levels on the rods. The graphic representations of activity against rod region (Fig. 38) for the six defferent rods was produced in the following way.

i Each rod was demarkated into a number of 5 cm long regions. (i.e. the 40 cm rod was therefore made up of 8 regions). The bottommost region was considered as the first (i.e. No 1).

ii The total number of centimetres through which larvae moved, in both upwards and downwards directions, in each region was then calculated for each rod length from the individual tracks recorded during the observations (Figs 32-37). A mean was then calculated for each region by dividing by the number of larvae used (i.e. 10 except in the case of the 40 cm rod where 20 were used). In other words a value was obtained which represented the mean number of centimetres moved through per larva in each region of each rod length.

iii Curves were then plotted; activity (i.e. the average number of centimetres traversed per larva) against region of rod. This concept of 'activity' at first appears to lack the factor of time. This is, however, not the case as larvae were found to walk at a remarkably constant speed (approximately 15 seconds were required to move through 1 cm) and thus the concept as applied here is useful.

iv Finally a line was drawn parallel to the X axis and passing through the 10 cm mark of the Y axis. The significance of this line is briefly as follows. Should a larva walk up the rod through a region, without any turning movements, and then return downwards through the same region, again without any turning movements, it would have moved through a total of 10 cms in that region. This means that should any part of any of the six curves (Fig. 38) lie below the line described, it is an indication that larvae were, on the average, not merely passing up and down the particular region in the simple manner outlined above. Larvae would however either be passing through the region once only, on the average, or passing through only part of the region before turning and returning back through that part. Similarly should any part of a curve lie above the line described, it is an

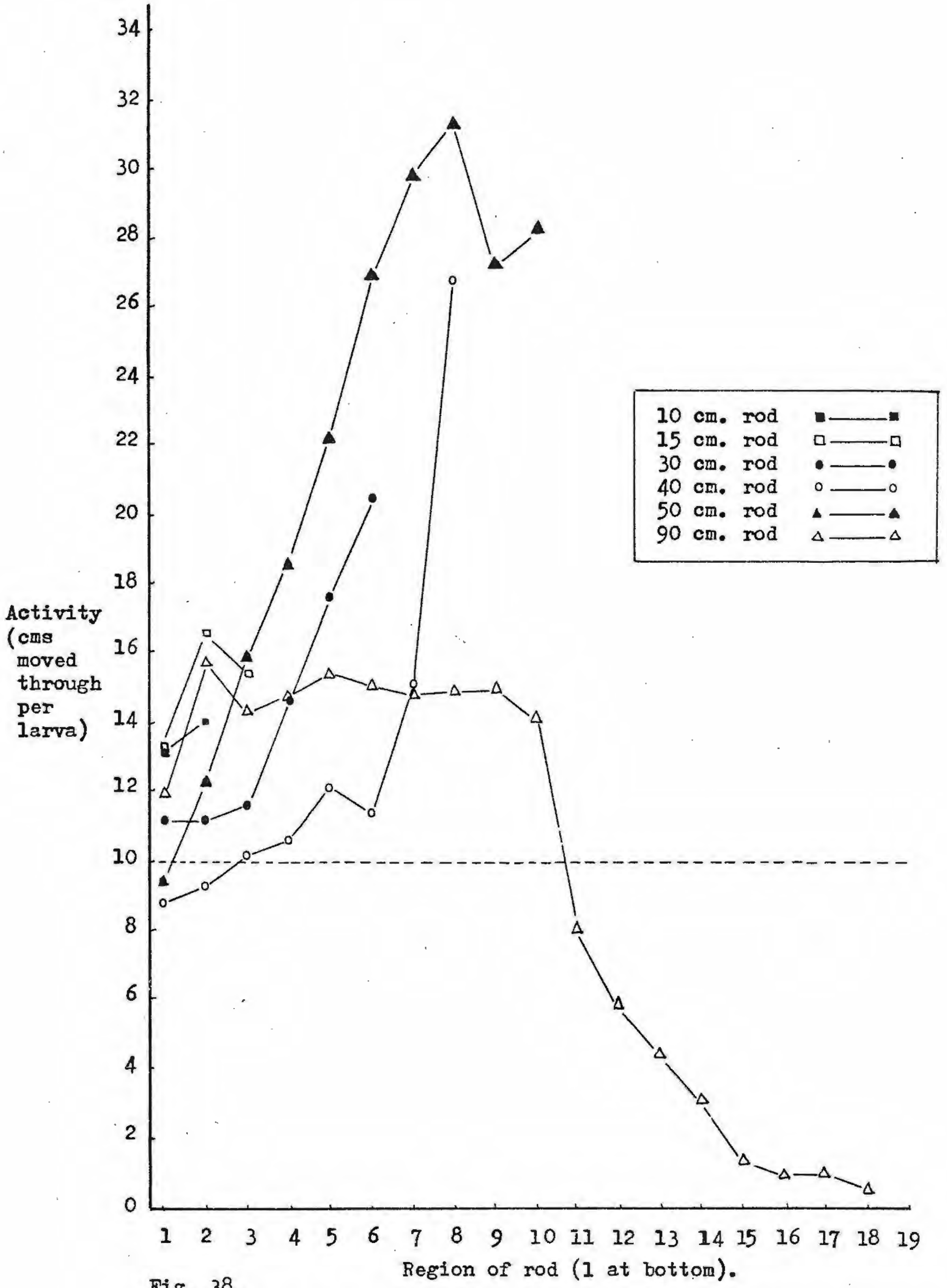


Fig. 38.

The activity of Amblyomma hebraeum larvae on six different lengths of glass rod.

indication that larvae were either walking up and down a region more than once or moving about within a region with many turning movements.

It is possible to make the following comments after a study of the curves presented in Fig. 38.

i In most cases activity increased with region height (i.e. Activity was greatest in the regions at the top of the rod). Activity however tended to drop off after the eighth region, as seen in the 50 and 90 cm rods.

ii Activity in the first 10 regions of the 90 cm rod was fairly constant. There was then a rapid decrease in activity over the last eight regions.

iii On the average, larvae on the 90 cm rod did not reach levels higher than the 10th region. Larvae were also not passing more than once or twice through the first 10 regions of this rod.

iv Larvae climbing on the 40 and 50 cm rods tended to pass through the lower regions in one direction only. Their greatest activity took place in the region of the tip of the rods.

The above analyses suggest that there is an optimal height of rod needed by A. hebraeum larvae in order that they should achieve resting positions in the region of the tip of the rod. This height appears to correspond with the eighth region from the bottom of a rod i.e. between 35-40 cms. This height corresponds with the height of the vegetation from which A. hebraeum larvae were collected in the distributional survey at Barville Park (i.e. Medium - tall vegetation).

Choice experiments involving numerous larvae and a number of rods of different lengths

In the following experiments A. hebraeum larvae were exposed to glass rods of 10 different lengths viz. 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 cms long respectively. This 'multi rod' arrangement is illustrated diagrammatically in Fig. 39. The control consisted of

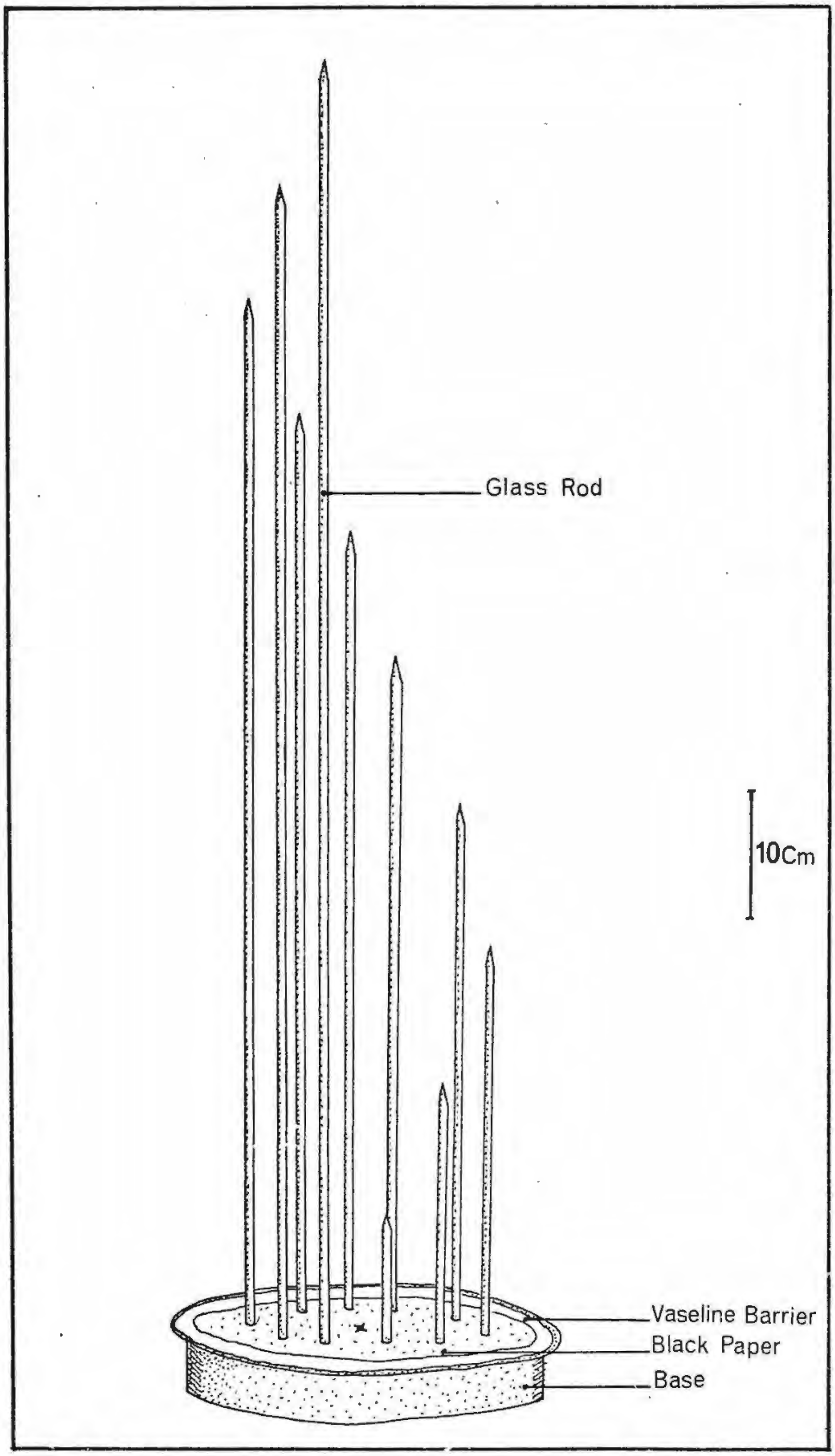


Fig. 39. The apparatus, consisting of 10 different rod lengths, used during choice experiments involving numerous larvae.

an identical arrangement of rods all of exactly the same length (30 cms). A large number of larvae were placed on the black paper in the centre of the circle formed by the bases of the 10 rods. Each tick had therefore the same chance, initially, of walking towards any one of the 10 rods. Thereafter larvae would naturally be closer to the rods immediately next to the original rod towards which they had moved. The apparatus was placed in the constant environment room under condition A (Fig. 8).

It is important to note that the black paper was replaced and the glass rods carefully washed after each experimental replicate. Goldsmid (1967) pointed out that larvae of some tick species have been shown to produce a 'substance' which brings about larval clustering. This 'substance', as yet not identified, remains on the substrate after larvae have been removed. Other larvae, of the same species, placed on the same substrate formerly occupied by clusters of larvae respond by clustering in exactly the same positions as the larvae had previously clustered. It was therefore important to see that this 'substance', if produced by A. hebraeum, was effectively removed from the rods and paper base, as it may have produced misleading results.

Experimental runs were 24 hours in duration. This period was found to be sufficient for the majority of larvae to achieve a resting position somewhere on the rods or base board. After this 24 hour period, larvae were observed and those which had come to rest within 5 cms of the rod tips, counted. All other larvae were ignored. The results are shown in Tables 23-24 and Figs 40-41. The test involving 10 different rod lengths was replicated five times while the control was replicated three times.

The results show that there is probably a tendancy for A. hebraeum larvae to come to rest at the tips of rods shorter than 40 cms, in preference to those taller than 40 cms. The 20 cm. rod had the largest number of larvae congregating at its tip. The high numbers of larvae

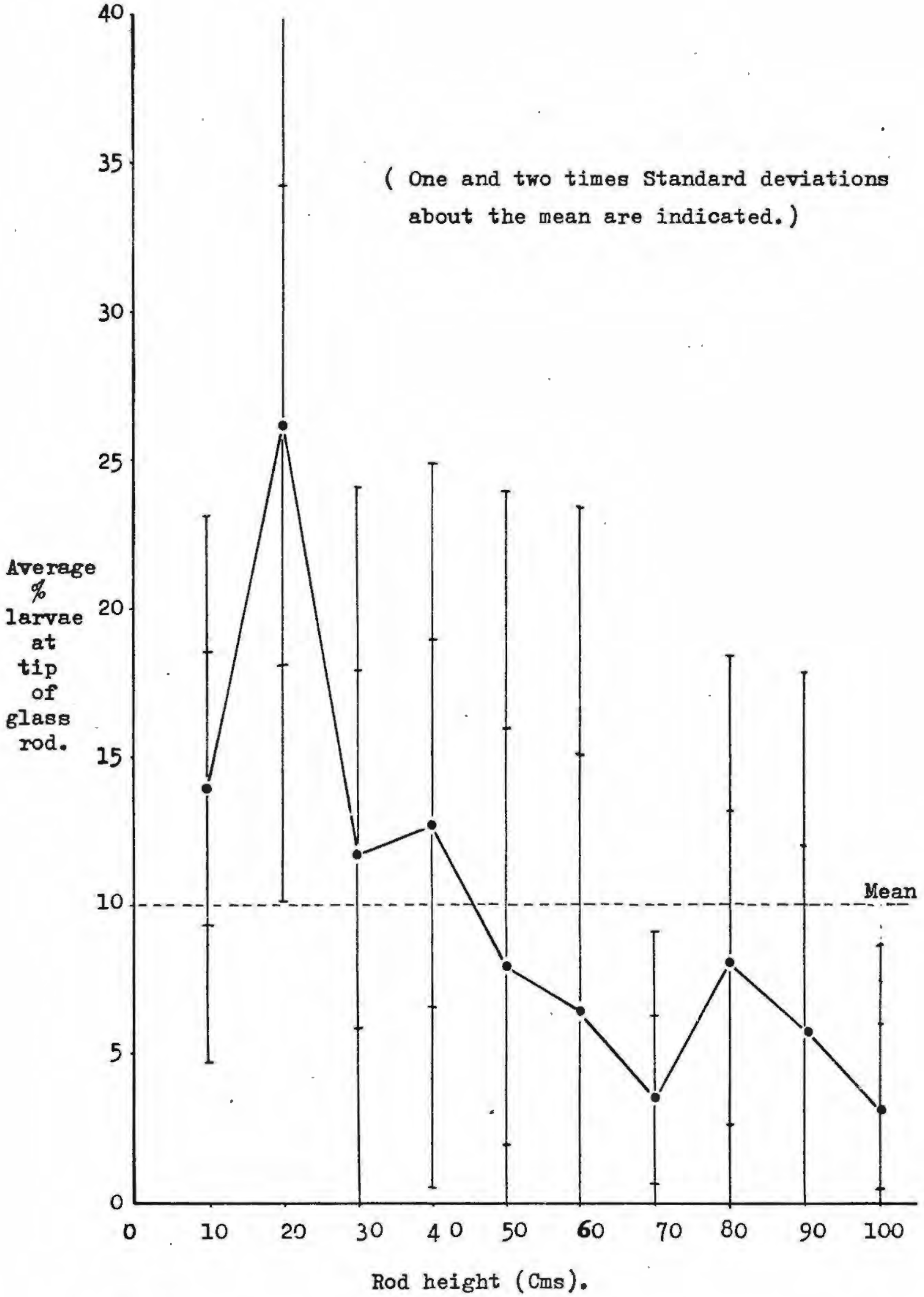


Fig. 40.
Average percent of larvae coming to rest at the tips of ten glass rods of different height.

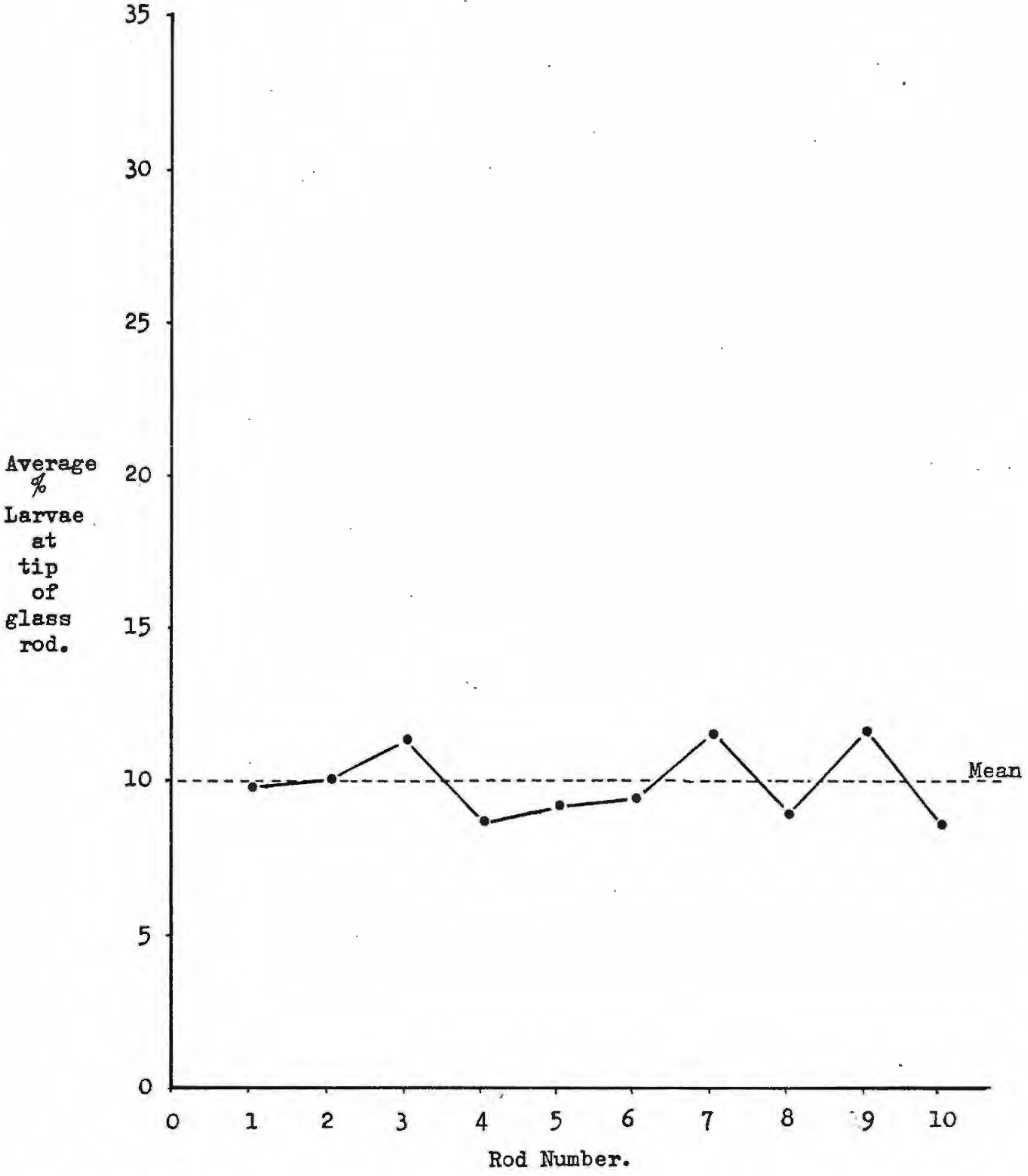


Fig. 41.

Average percent of larvae coming to rest at the tips of ten 30 cm. glass rods.

Table 23 The numbers, and percentages, of A. hebraeum larvae coming to rest near the tips of 10 glass rods of different heights.

Rod length (cms)	Replicate Number 1		2		3		4		5		Total		Mean Total
	No	%	No	%	No	%	No	%	No	%	No	%	%
10	25	8.6	23	18.5	67	10.6	81	13.5	44	18.9	240	70.1	14.0
20	47	16.1	39	31 4	149	23.5	141	23.6	86	36.9	462	131.5	26.3
30	43	14.8	11	8.9	77	12.2	19	3.2	46	19.8	196	58.9	11.8
40	49	16.8	17	13.7	96	15.2	96	16.1	5	2.1	263	63.9	12.8
50	9	3.1	24	19.4	16	2.5	82	13.7	3	1.3	134	40.0	8.0
60	61	21.0	1	0.8	52	8.2	7	1.2	3	1.3	124	32.5	6.5
70	18	6.2	1	0.8	35	5.5	32	5.3	1	0.4	87	18.2	3.6
80	9	3.1	7	5.7	34	5.4	99	16.5	22	9.4	171	39.1	8.1
90	21	7.2	1	0.8	100	15.8	6	1.0	9	3.9	137	28.7	5.7
100	9	3.1	0	0.0	7	1.1	35	5.9	14	6.0	65	16.1	3.2
Total	291	100	124	100	633	100	598	100	233	100	1879	--	100

Table 24 The numbers, and percentages, of A. hebraeum larvae coming to rest at the tips of 10 glass rods all 30 cms in height (Control).

Rod length (cms)	Replicate Number 1		2		3		Total		Mean Total
	No	%	No	%	No	%	No	%	%
30	35	11.3	26	5.3	69	13.0	130	29.6	9.9
30	32	10.4	39	7.9	62	11.7	133	30.0	10.0
30	44	14.2	21	4.3	84	15.8	149	34.3	11.4
30	21	6.8	86	17.4	25	4.7	132	28.9	9.6
30	22	7.1	52	10.6	52	9.8	126	27.5	9.2
30	25	8.1	69	14.0	31	5.8	125	27.9	9.3
30	40	12.9	51	10.3	60	11.3	151	34.5	11.5
30	17	5.5	70	14.2	38	7.1	125	26.8	8.9
30	46	14.9	46	9.3	57	10.7	149	34.9	11.6
30	27	8.8	33	6.7	54	10.1	114	25.6	8.6
Total	309	100	493	100	532	100	1334	-	100

congregating at the tip of the 20 cm rod are difficult to explain. The following short experiment supplies rather scanty evidence that the actual cluster of larvae at the tip of a rod effects the movements of other larvae in the process of orientation to the tip of the rod. It is possible that, for some unknown reason, the influence of the cluster is strongest in the case of the 20 cm rod.

Two glass rods of equal length (i.e. 30 cms) were placed in the constant environment room (Condition A of Fig. 8). One rod possessed a cluster of 25 larvae at the tip while the other did not. The larvae used were A. hebraeum. Five individual larvae of the same species were then introduced at the base of each rod, individually, and their final positions recorded. Results of these observations are presented in Table 25.

Table 25 The influence of a larval cluster on the behaviour of larvae orientating to the tip of a glass rod.

Rod	Larva No	Final position of larva	Time taken (mins
Tick free rod (30 cms long)	1	Returned to base.	27
	2	Returned to base.	21
	3	Came to rest 2 cms from tip.	85
	4	Returned to base.	36
	5	Came to rest 5 cms from tip.	63
Rod with 25 larvae clustering at its tip. (30 cms long)	1	Came to rest at cluster.	10
	2	Came to rest at cluster.	15
	3	Returned to base.	25
	4	Came to rest at cluster.	21
	5	Came to rest at cluster.	22

The above results suggest that there may be a tendency for larvae to stop and settle at a cluster of larvae of the same species. There is a strong possibility that the influence which might be involved is of the same nature mentioned by Goldsmid (1967) when discussing the probable release of some chemical stimulant to bring about clustering behaviour. Little is known of the effects of the chemical which has been suggested as being laid down by tick larvae and this aspect requires further investigation.

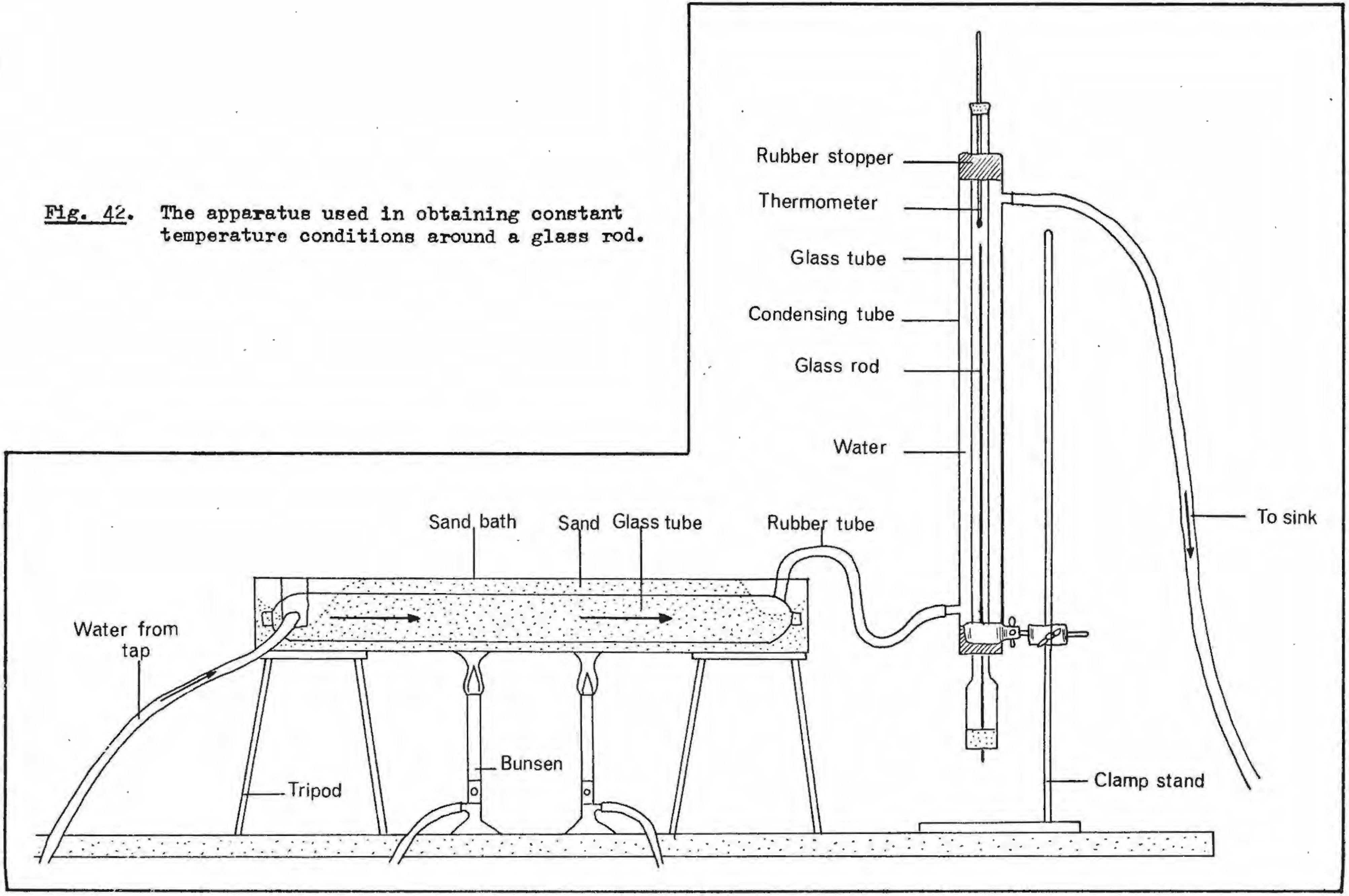
The effects of rod length on other species of ixodid tick larvae

It was decided that a brief examination of some other species of tick larvae on glass rods might be of interest. It was considered possible that an estimation of the 'optimal vegetation heights' of these species might be obtained. A. hebraeum was shown to have an optimal height of approximately 35-40 cms by studying the movements of individual larvae on different lengths of glass rod. It was decided that a comparison of the behaviour of other ixodid larvae on a 40 cm. rod may lead to an estimation of the heights which may be associated with these species. 10 larvae of each of the following species were tested. I. pilosus, B. decoloratus, R. evertsi and R. appendiculatus.

The following experiment was carried out in the laboratory as described earlier in the work on A. hebraeum. The 40 cm. rod was however, placed in the centre of a condensing tube as shown in Fig. 42. This apparatus allowed for an accurate control of the temperature at 21°C throughout the experiments. Larvae were introduced singly at the base of the rod. Their movements were recorded in the same manner as shown earlier in the work on A. hebraeum. The individual tracks recorded are shown in Figs 43-46 respectively. An analysis of the individual tracks is shown in Table 26. To facilitate comparison the data presented earlier in respect of A. hebraeum larvae (Table 22) climbing on a 40 cm. rod are repeated in Table 26.

It has already been suggested that A. hebraeum can be associated with a height of approximately 35-40 cms. At this rod length larvae eventually come to rest at the tip of the rod. Longer or shorter rods appeared to be 'inadequate' for successful 'orientation behaviour'. This height, 35-40 cms, appears to be almost equivalent to the value calculated (Table 22) for the average maximum height achieved in any 'trip' up the rod. On this basis the following heights may be suggested as being the approximate 'optimal vegetation heights' of the other four species.

Fig. 42. The apparatus used in obtaining constant temperature conditions around a glass rod.



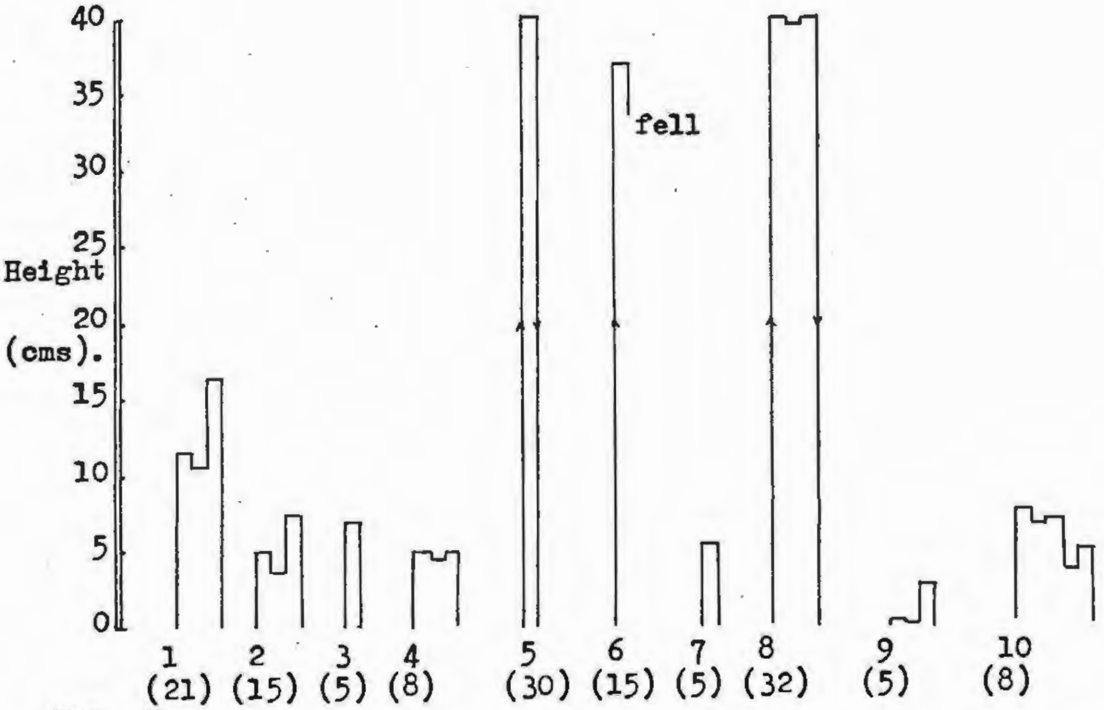


Fig. 43.
The individual tracks of ten Ixodes pilosus larvae on a 40 cm. rod.
(Figures in brackets indicate time (in Mins.) taken to complete each track)

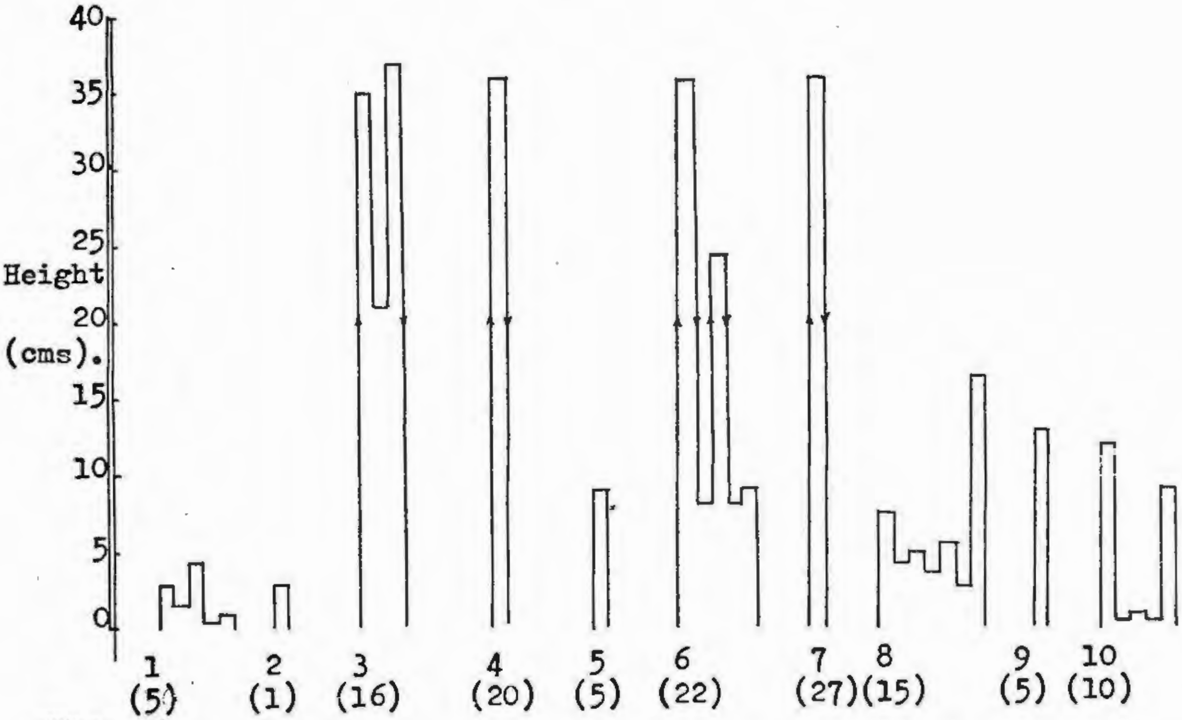


Fig. 44.
The individual tracks of ten Boophilus decoloratus larvae on a 40 cm. rod.

(Figures in brackets indicate time (in Mins.) taken to complete each track)

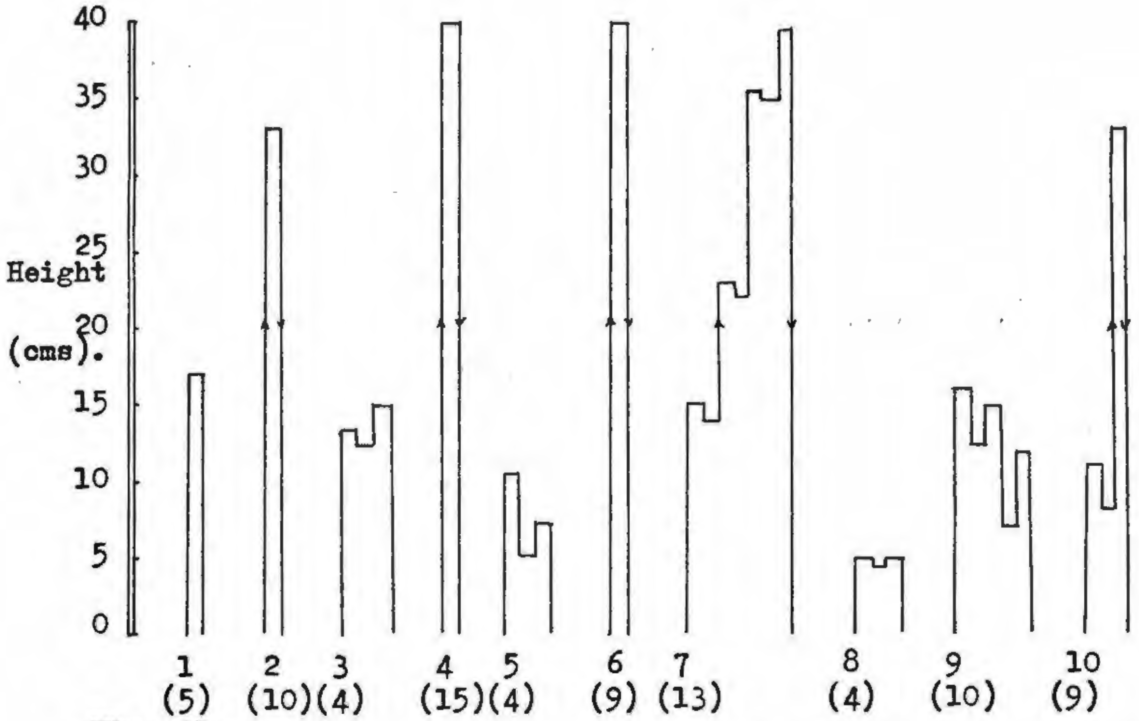


Fig. 45.
The individual tracks of ten Rhipicephalus evertsi larvae on a 40 cm. rod.

(Figures in brackets indicate time (in Mins.) taken to complete each track)

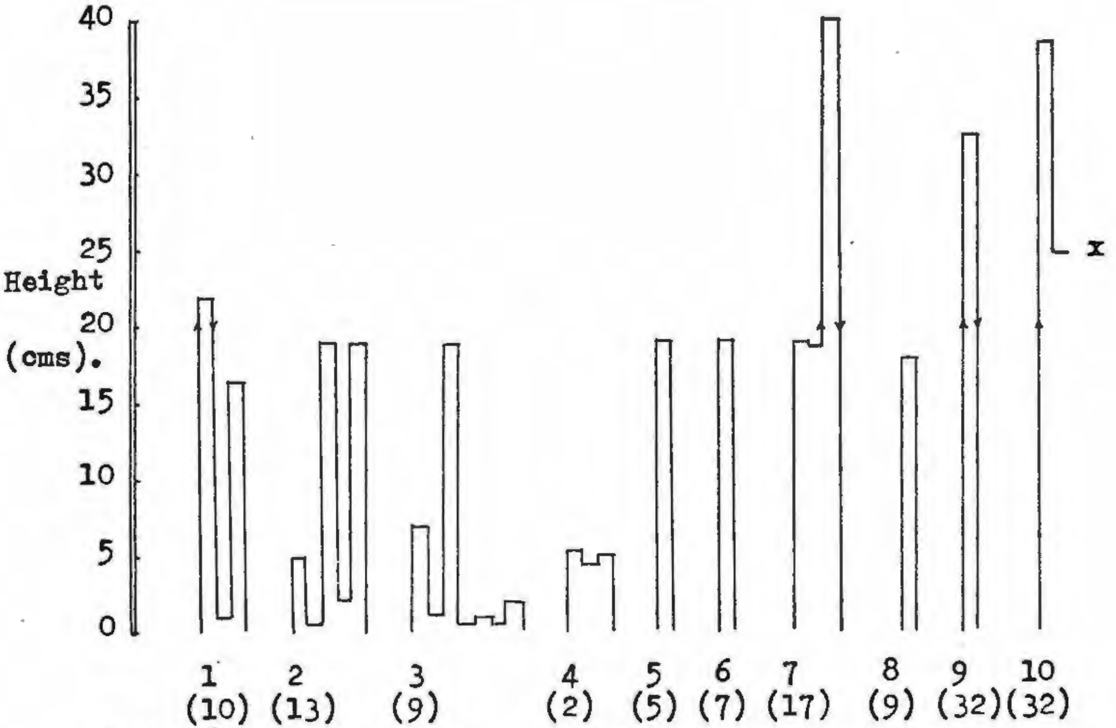


Fig. 46.
The individual tracks of ten Rhipicephalus appendiculatus larvae on a 40 cm. rod.

(Figures in brackets indicate time (in Mins.) taken to complete each track)

x = Position at which larva came to rest.

Table 26 An analysis of the individual tracks recorded for five species of ixodid tick larvae walking on a 40 cm high rod. (*A. hebraeum* data as supplied earlier in Table 22).

	Species				
	I.pilosus	*B.decoloratus*	*R. appendiculatus*	*R.evertsi*	*A.hebraeum*
Average length of 1st trip (cms)	12.7	19.1	18.6	20.2	36.4
% of maximum height possible	31.7	47.7	46.5	50.5	91.0
% larvae reaching tip on 1st trip	20.0	0.0	10.0	20.0	80.0
Average maximum height achieved in any trip (cms)	17.1	20.3	23.3	24.8	38.3
% of maximum height possible	42.7	50.7	58.2	62.0	96.0
% larvae reaching tip on any trip	20.0	0.0	10.0	20.0	90.0
Average duration of movement on rod (to nearest min.)	14	13	14	9	34
% actually coming to rest at tip	0.0	0.0	0.0	0.0	35
No larvae tested	10	10	10	10	20

i *I. pilosus*............15-20 cms.
ii *B. decoloratus*........20 cms.
iii *R. appendiculatus* .....20-25 cms.
iv *R. evertsi*............25 cms.

The above analysis showed that none of the four species actually came to rest at the tip of a 40 cm rod. The species appeared to react in much the same way as *A. hebraeum* larvae reacted to a 90 cm rod. This means that 40 cm was too high for *I. pilosus*, *B. decoloratus*, *R. appendiculatus* and *R. evertsi*. The approximate values of the 'optimal vegetation heights' for these species appear to be, at least in the case of *I. pilosus* and *B. decoloratus*, similar to the vegetation heights in which the species were collected in the distributional survey at Barville Park. R. evertsi and R. appendiculatus may be suggested as living in vegetation in the height range of approximately 20-30 cms. This suggestion needs support in the form of distributional information from the field.

The five species studied may be arranged in the following order in respect of the calculated 'optimal vegetation height' obtained from the behavioural experiements reported. A. hebraeum being associated with the highest vegetation.

i A. hebraeum.
ii R. evertsi.
iii R. appendiculatus.
iv B. decoloratus.
v I. pilosus.

This order is also the apparent order of larval size, A. hebraeum being the largest and I. pilosus the smallest species. It may be argued that it is merely a case of the largest larva climbs the highest. This may be used as a criticism of the present work but it is suggested that this fact does not negate the suggestion that each species is associated with a very definite vegetation height. The actual way in which this association between species and vegetation height is controlled is not known. It is possible that there is a behavioural pattern which regulates it, but it may merely be a function of larval size.

It is of some interest to consider the biological implications of larvae possessing 'optimal vegetation heights'. This 'optimal vegetation height' may best be defined as the height at which larvae will eventually attain a resting position at the tips of the vegetation. Larvae have been shown to live on vegetation of a particular height (Barville Park survey) and it may be suggested that this height relates to the height at which the larvae normally locate their hosts. This height must, in turn, be related to the actual heights of the hosts themselves.

From the lists of hosts prepared by Theiler (1962) it is possible to gain some idea of the relative sizes of the hosts normally parasitized by larvae of the species collected at Barville Park. The appendix to this thesis contains the lists of hosts which have been recorded for the four species of ticks viz. H. silacea, I. pilosus, B. decoloratus and A. hebraeum. These lists have been compiled from those given by Theiler (1962) but as many of the scientific names were found to be either incorrect or placed in synonymy, these names were checked using the works of Roberts (1951, 1957). The names given by Roberts (1951, 1957) have been given in the lists presented in the appendix together with the common names of the animals. Hosts on which both adults and immature stages have been found have been listed. Special note must however be taken of the hosts on which immature stages (larvae and nymphae) were collected as this investigation has been concerned with larval ticks.

The lists of hosts (appendix) show that in most cases the heights of the hosts fall within the range of vegetation heights in which the larvae were found to occur. Tall hosts may be accessible to the larvae by first climbing onto the legs before proceeding to the prefered feeding site which may be at a position corresponding to a far greater vegetation height. The only probable exception to the above statement appears to be A. hebraeum which has been associated with medium to tall vegetation. The larvae of this species apparently feed on a wide variety of hosts of which the birds form the largest group. It is difficult to imagine how larvae manage to locate their bird hosts from the tips of tallish grass. Some of the birds may be classified as 'ground living' birds, in which case larvae may be able to encounter them with relative ease. Many of the birds are, however, small and might be called 'tree living birds' in which case it is difficult to imagine how larvae encounter these hosts.

From the above discussion it seems feasible to suggest that in most instances height to which larvae climb has some direct bearing

[illegible]

on the size of the hosts they normally parasitize. Presumably larvae which are not actually at the tips of grass or other vegetation of the correct height have less chance of encountering a host (this is supported with evidence later in this thesis). This fact may have provided the selection pressure which led to the selection of 'optimal vegetation heights'.

B. The stimuli which may govern 'orientation behaviour' in larval ticks

As it has been suggested that the height of vegetation is of some importance in the distribution of tick larvae, it was decided that some of the more important stimuli governing the behaviour of larvae climbing on grass stems should be studied. There is little in the literature on this subject which pertains to southern African tick species other that the work of Goldsmid (1967) on *B. decoloratus* larvae. A number of overseas workers have however contributed to our knowledge in this field. These include Lees (1948), Lees and Milne (1951) and George (1963). The above authors, and others, are not in agreement as to the nature of the stimuli which govern 'orientation behaviour'. Although most of these workers agree that gravity, light, relative humidity gradients and other stimuli constitute stimuli which could influence climbing behaviour on grass stems, they appear to have different views as to which of these stimuli is of the greatest importance. Before examining some of the stimuli studied by past workers it is felt that a brief introduction to the various aspects of larval behaviour is important. The place occupied by what is here called 'orientation behaviour' will then become obvious. The movements carried out by larvae during this 'orientation behaviour' will then be examined and discussed before further studies and discussions of the stimuli involved in directing the movements of larval ticks during this 'orientation behaviour' are dealt with.

It seems reasonable to assume that some type of 'reaction chain' (Tinbergen 1951) exists in the behaviour of tick larvae from the time they embark on their first trip up a grass stem to the moment when they actually attach and feed on the host. The following stages are suggested as possible 'links' in such a 'reaction chain'.

i. Orientation to the top of the vegetation. i.e. Movements directed towards the eventual attainment of a resting position at the tip of a grass stem.

ii. Questing reactions to stimuli presented by an approaching host and active clinging to the host when contact is made with it.

iii. Reactions to stimuli on the host which ultimately lead the larva concerned to the predeliction site.

iv. Attachment of the hypostome and the onset of feeding.

Camin (1963), discussing the work of Lees (1948), lists three "phases" of behaviour.

i. Passive phase. i.e. Movement to a vantage point.

ii. Questing phase.

> "in which the tick is alerted to the approach or the presence of a host, orients to the hosts and climbs onto it."

iii. Host discrimination phase. i.e. The larva either attaches and feeds or rejects the host and falls off to seek another.

Essentially Camin's (1963) first and second phases are equivalent to the first and second links suggested in the 'reaction chain' above. The third phase is a rather debatable one and it is suggested that this phase can not be considered as a link in a 'reaction chain'. If the host is rejected then the chain is broken. A feature of 'reaction chain' is that one stage leads on to another. This means that if the questing phase is successfully undertaken a suitable host has been located. This is not always the case however, and therefore discrimination does have to take place as Camin (1963) suggested. The important thing to realise however, is that this does not form a link in a 'reaction chain'. The third link in the chain as suggested in the present work is probably the sort of link which Camin (1963) had in mind. If successful reactions to stimuli presented by the host are undertaken then the larva would find itself on a suitable host. This is one suggested way in which discrimination could be brought about. Discrimination may however take place during the fourth phase. The actual 'testing' of the host may occur during attachment and the onset of feeding. This may be the most likely time. The following study will be concerned with the first link in the suggested 'reaction chain' and some evidence will be provided in support of the suggestion that the second link of the chain can not be embarked upon until the first has been completed. It should be noted that although the suggested 'reaction chain' is a useful model it would be a mistake to become mesmerized by it.

Orientation behaviour in *A. hebraeum* larvae

The following observations were conducted in the laboratory where conditions of temperature were between 19-21°C and humidity between 50-60 % relative humidity. All observations were made on *A. hebraeum* larvae walking on a 40 cm vertical glass rod, unless otherwise stated. The following general pattern of behaviour was recorded for *A. hebraeum* larvae but casual observations on larvae of other species available suggested that they may react in a very similar way. Fig. 47 should be consulted in conjunction with the following chain of events.

i. The larva climbs up the rod towards the tip (Fig. 47a).

ii. The larva reaches the tip (Fig. 47b) and either hesitates, when the forelegs do not contact further substrate, turns around and proceeds down the rod, or continues slowly onto the actual tip of the rod (Fig. 47c).

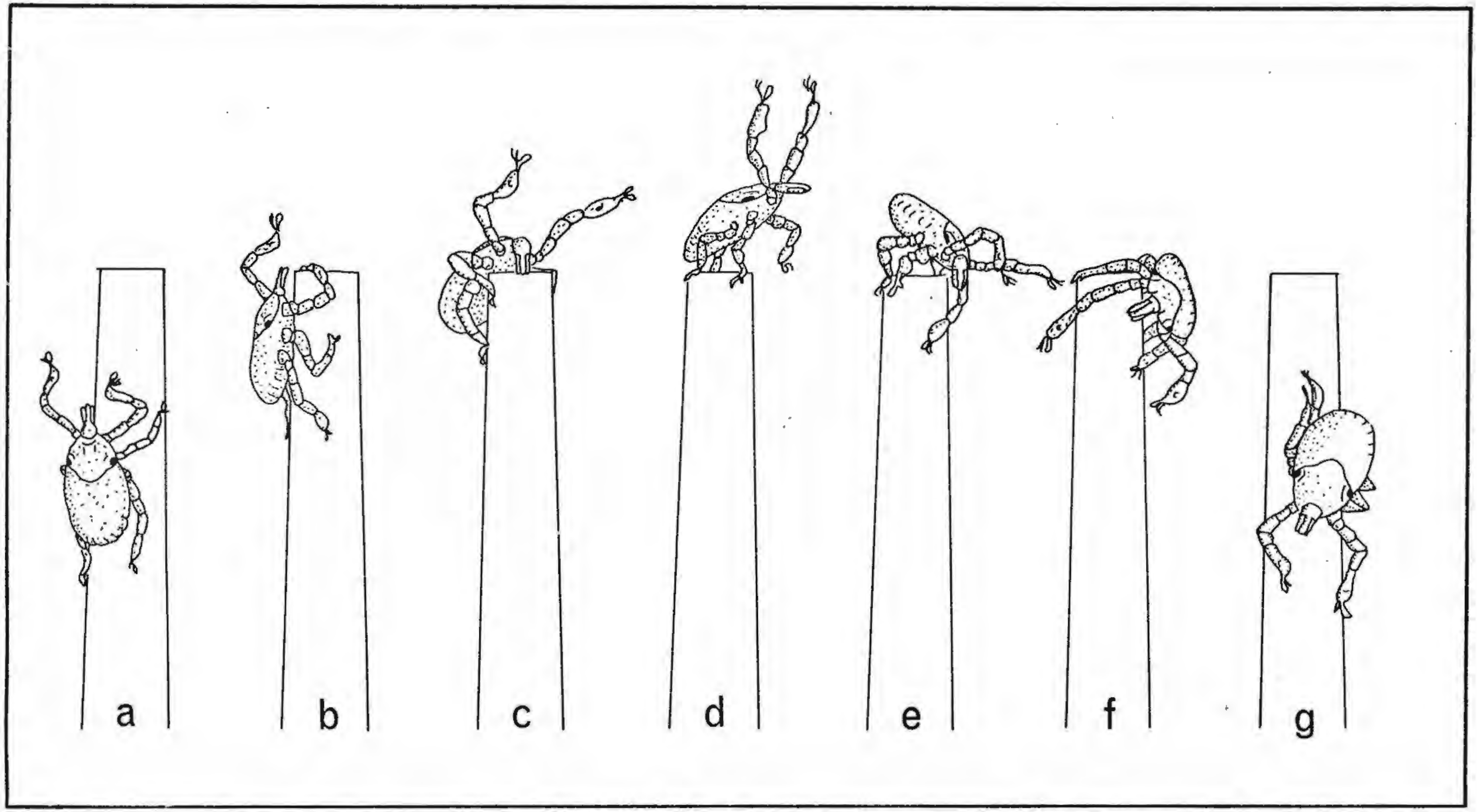


Fig. 47. The movements of a larval tick at the tip of a glass rod.
(Drawn from photographs)

iii. The larva then reaches upwards with the forelegs, waving them up and down as if trying to reach further substrate above. The second pair of legs are then often also raised, very briefly, off the substrate, leading togreater instability (Fig. 47d).

iv. The larva then either falls forward, due to the instability of its stance, and brings its forelegs into contact with the rod again (Fig. 47e), or slowly climbs over the tip of the rod after lowering the legs onto the tip.

v. The larva then proceeds to walk down the other side of the rod (Fig. 47f & g).

vi. After proceeding a short distance down the rod (variable distance but usually shorter than the upward trip) the larva turns around and again ascends the rod.

vii. After a number of encounters with the tip, the larva eventually comes to rest at or within a short distance of the tip. The resting position is nearly always such that the longitudinal axis of the body is vertical and the capitulum uppermost. The same position has been described by Lees (1948) for the nymphs of I. ricinus.

The above sequence of events are in essence identical to those described by Lees (1948) for the nymphs of I. ricinus. It is suggested that the questing which takes place at the tips of rods is not always 'host questing' behaviour as implied by Lees (1948) and subsequently by Lees and Milne (1948) and Dethier (1957). It is believed that there are two distinct types of questing behaviour which can be conveniently termed 'host questing' and 'substrate questing' respectively. The important differences between these are briefly as follows.

Substrate questing behaviour

This involves movements of the forelimbs up and down, in turn, through a fairly wide arc. These movements are carried out at various intervals during 'orientation behaviour' on a glass rod as well as at the actual tip of the rod. The movements are carried out in a rather methodical and unexcited manner. Although Camin (1963) does not actually make a distinction between this type of questing and 'host questing' he does state : -

> "If the tip of the vegetation is reached before the tick has travelled approximately 40 cms, it responds tactually to the nothingness beyond the tip by questing with the anterior legs, turning, climbing downward for a short distance, climbing to the tip again, and questing."

As Camin (1963) then separates the behaviour of host location into the various phases already discussed and places this type of behaviour in his 'Passive Phase' (i.e. in which the tick is orientating to the tip of the grass stem), he has in fact separated it from the questing which takes place in response to the approach of a host. His comments on 'host questing' as defined in the present investigation will be discussed under host questing behaviour.

Host questing behaviour

This takes place, it appears, only when the larva has achieved a resting place at the tip of a rod. If the resting larva (which adopts a typical posture with the legs tucked up closely under the body) is stimulated by casting a shadow over it or gently blowing on it, it very excitedly raises the forelegs (simultaneously) and holds them aloft. In this position the limbs appear to quiver, especially at the distal ends, so that the arc through which they move is small. At the same time the larva usually stands erect on the remaining four legs so that the body is lifted high off the substrate. When the larva is not situated at the tip of the rod, it may make a very hurried trip to the tip and carry out the behaviour as already described.

Camin (1963) while discussing the behaviour of ticks to the approach of a prospective host states : -

> "Any sudden movement of the vegetation or sudden decrease in light intensity, such as a host and its shadow might cause, immediately elicits a questing response".

It appears that the suggestion that this type of response is different from that described as 'substrate questing' is in fact supported by the work of Camin (1963). The terms 'substrate questing' and 'host questing' will be used in all future discussions.

Stimuli governing orientation behaviour

Five main stimuli are possibly involved in larval orientation to the tip of a rod or grass stem. These may be listed as follows.

i Gravity.
ii Light.
iii The tip of the rod.
iv The humidity gradient up the rod.
v The temperature gradient up the rod.

Previous workers are not in agreement as to which of these stimuli is of most importance in governing 'orientation behaviour', or whether in fact a combination of some or all of these stimuli direct the movements of larvae so that they attain a position of rest at the tip of a rod or stem.

Lees (1948) and Lees and Milne (1951) suggest that gravity is the most important stimulus, The nymphae of I. ricinus are negatively geotactic. They also state that a kinesis ("upward turning near the tip") is present. It is thought, however, that they do not adequately explain the nature of this kinesis. Finally these two workers provide evidence that the behaviour on grass stems is modified to some extent by the humidity gradient along the grass stem. Minerov (1939) (vide Dethier 1957) demonstrated that Ixodes persulcatus Schulze reacts to both gravity and humidity gradients in order to determine the height to which they will climb on vegetation. Wilkinson (1953) working on B. microplus and Jenkins (1948) (vide Dethier 1957) working on various mites, both present evidence to support the contention that the ascent of these acarina to the tips of vegetation is a response to light rather than to gravity. Goldsmid (1967) demonstrated that larvae of B. decoloratus respond to gravity as well as to encounters with the tip of the rod. The tip response is a strong one which can override the gravity response (i.e. larvae would collect at the tip even if it was directed downwards). Goldsmid (1967) also points out that larvae respond to linear temperature gradients, eventually coming to rest at the coolest end of the gradient irrespective of the temperatures involved. This was because walking speed was dependent on temperature and thus those in higher temperatures would walk faster and eventually all the larvae would be found at the lowest temperatures, provided the temperature was not too low to allow movement.

Camin (1963), working with the rabbit tick H. leporispalustris states that :-

> "Unfed larvae and nymphs respond positively to light and negatively to moisture, moving towards the lowest humidity available. This combination of reactions draws them up to the tips of the vegetation. After a few hours in a dry atmostphere, desiccation causes a reversal of the response to moisture and the ticks also become insensitive to light. Therefore, they follow the humidity gradient back down to the ground, where the lost body water is replenished."

Lees and Milne (1951) have very similar thoughts on this matter.

It appears from the above brief survey of some of the ideas which prevail on this subject, that a number of factors may be involved in the orientation behaviour of ixodid larvae. It also appears that some of these stimuli may be able to override others depending on the prevailing conditions and the 'physiological state' of the larva.

The following experiments were conducted using A. hebraeum larvae in order to establish the validity of gravity, light and 'the tip of the rod' as stimuli to orientation behaviour. It is suggested that the conditions of temperature and relative humidity will determine the 'physiological state' of the larvae and will thus influence their reactions to both temperature and relative humidity gradients. For example, larvae in a partially desiccated state would probably avoid the higher regions of the vegetation where conditions are likely to lead to further desiccation, and direct their movements towards places of higher relative humidity and lower temperatures. It is suggested that temperature and humidity gradients can only modify the basic behavioural reactions to such stimuli as gravity, light and 'the tip of the rod', which are uneffected by af microclimatic conditions. For this reason the present study excludes observations on reactions to these gradients. The importance of the gradients is not being disputed and it is clear that more work in this field is desirable.

Gravity, light and 'the tip of the rod' as orientation stimuli

During the preceding experiments it was noticed that larvae usually commenced walking in an upward direction when placed on a glass rod. This suggested that larvae react to gravity and are negatively geotactic. The following short experiment provides some evidence for this suggestion.

A 40 cm. long glass rod was placed in such a position, in the laboratory, that it was uniformly illuminated. The conditions underwhich observations were made were similar to those described earlier in this chapter. 20 *A. hebraeum* larvae were individually placed at the 20 cm. mark of the vertical rod. When a larva had progressed 10 cms along the rod (either in an upward or downward direction) the rod was rotated through 180° so that the larvae would be proceeding in the opposite direction with respect to gravity. The movements of each larva were recorded and Table 27 shows the results of an analysis of these individual records.

Table 27 The results of experiments involving gravity as an orientation stimulus

% larvae moving upwards on the first trip	90
% larvae moving downwards on the first trip	10
% of those moving upwards on the first trip responding to rod reversal by turning around	83.4
% of those moving downwards on the first trip responding to rod reversal by turning around	50
Average distance moved after rod reversal before responding (nearest cm.)	2
No of larvae tested	20

These results show that there is a definite response to gravity and that larvae are usually negatively geotactic. When the rods are reversed, larvae are suddenly made to change the direction in which they are moving with respect to gravity. The larvae react by turning around within a fairly short distance and proceeding once again in the direction in which they had formally been going. Goldsmid (1967) also demonstrated that B. decoloratus larvae are negatively geotactic. He draws attention to the fact that the reactions of larvae changed with respect to their age. Larvae younger than nine days old were positively geotactic after which they became negatively geotactic. These observations may well hold for A. hebraeum, in principle, and for this reason larvae of more than one month old were used in all the observations.

It became obvious that the above type of study was in many respects inadequate. It is not an easy matter to deal with the effects of any one of the stimuli thought to govern orientation behaviour without having to include one or more of the others. In order to evaluate the effects of each stimulus and to get some idea of the relative importance of each, the following experiment was done.

In this experiment all three stimuli (gravity, light and 'the tip of the rod') were taken into account simultaneously and it is suggested that the results can be relied upon to give a good indication of the effects of the three stimuli.

Eight tubes of approximately 37 cms in length and 23 mms internal diameter were used. Glass rods similar to those already described were placed in each tube as indicated in Fig. 48. All eight tubes were clamped in a vertical position. A number of the tubes were covered in various ways with black paper so as to eliminate light from the whole of, or part of, the tubes (Fig. 48). Eight different conditions were created by modifying the construction of the apparatus as shown in Fig. 48. These were :-

i Tip uppermost; both halves of rod in light.
ii Tip downwards; both halves of rod in light.
iii Tip uppermost; both halves of rod in darkness.
iv Tip downwards; both halves of rod in darkness.
v Tip uppermost; bottom half of rod in darkness, top in light.
vi Tip downwards; bottom half of rod in darkness, top in light.
vii Tip uppermost; top half of rod in darkness, bottom in light.
viii Tip downwards; top half of rod in darkness, bottom in light.

A number of A. hebraeum larvae were placed on the rods at a point approximately midway along the length. The apparatus was then left undisturbed for two hours after which time counts were made of the number of larvae on each quarter (lengthwise) of each rod. The results obtained from three replicates are shown in Table 28.

Fig. 48. The eight conditions formed by the various positions of rods and covering black paper.

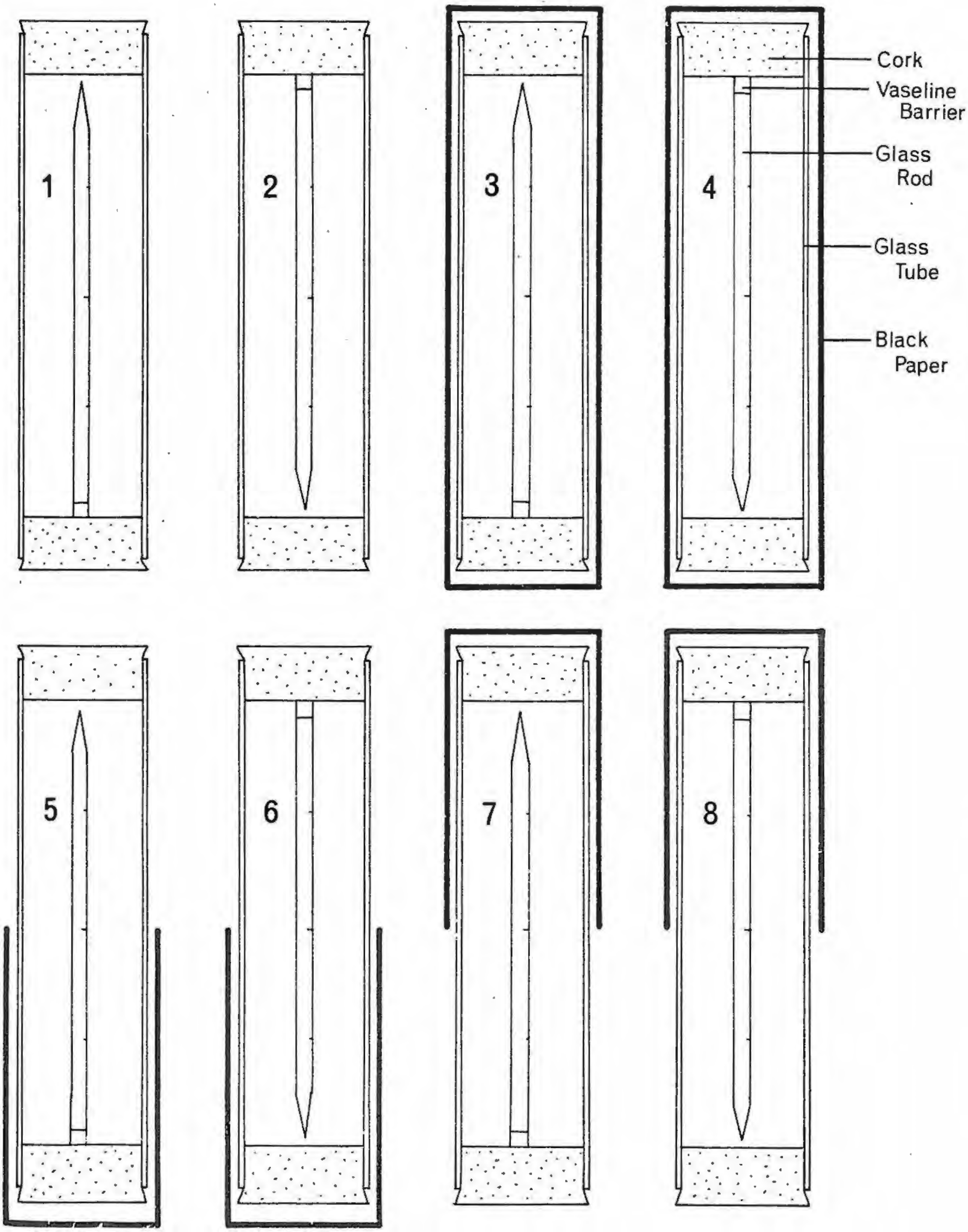


Table 28 The numbers of larvae coming to rest on eight glass rods, each of which demonstrated different characteristics as regards the position of the tip and illumination.

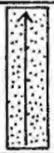
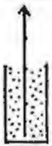
Condition	Replicate No			Total	Condition	Replicate No			Total
	1	2	3			1	2	3	
i 	24	28	23	75	ii 	2	13	6	21
	1	0	0	1		2	0	1	3
	0	0	0	0		2	2	3	7
	0	0	0	0		20	12	16	48
Totals	25	28	23	76	Totals	26	27	26	79
iii 	20	23	31	74	iv 	10	12	17	39
	0	0	0	0		6	7	6	19
	0	0	0	0		0	1	0	1
	0	0	0	0		3	4	3	10
Totals	20	23	31	74	Totals	19	24	26	69
v 	23	26	28	77	vi 	0	11	20	31
	0	0	0	0		14	6	1	21
	0	0	0	0		11	6	7	24
	0	0	0	0		0	3	3	6
Totals	23	26	28	77	Totals	25	26	31	82
vii 	22	26	18	66	viii 	3	12	13	28
	2	0	3	5		0	0	3	3
	0	1	0	1		21	7	10	38
	1	0	0	1		3	1	0	4
Totals	25	27	21	73	Totals	27	20	26	73

Table 28 is not very easy to interpret but the following conclusions can be arrived at.

i Larvae under all eight conditions exhibit a response to gravity.

ii The gravity response appears to be strongest when the tip is uppermost (conditions i, iii, v and vii). This suggests that there is a response to the tip of the rod which reinforces the response to gravity. The conditions of light appear to be completely unimportant when such a combination is present.

iii When the tip is directed downwards and the effects of light are the same along the entire length of the rod (conditions ii and iv) it appears that the gravity and tip responses are to some extent separated in that numbers of larvae collect at both ends. This suggests that the two stimuli are working against each other.

iv When the tip is directed downwards and the effects of light are not the same at both ends of the rods (conditions vi and viii) it appears that some response to the unevenness of the illumination is detectable. Larvae tend to gather at the interface between light and dark. The tip response appears to be almost overridden while the gravity response is still evident.

From the points mentioned above it appears that larvae under natural conditions (which would most probably approximate condition v most closely) the response to gravity is the strongest. This response is probably coupled with a response to the tip of the rod or grass stem. The combination produces a strong stimulus and practically all larvae achieve a resting position at the tip of the rod. A response to light does appear to exist but this does not seem to be a simple case of positive or negative phototaxy. It appears that larvae tend to congregate in the region where light and dark converge. When the tip is uppermost this light effect is not detectable and therefore can not play an important role in orientation to the tips of grass stems as these are under natural conditions directed upwards. It is possible that the artificial conditions under which this light response was detected causes larvae to exhibit this anomalous response. Under natural conditions it probably seldom occurs. It is known from work by Lees (1948), that ticks are positively phototactic. The experiments were however invariably conducted on a horizontal plane and it is just possible that the unnatural conditions offered to the larvae in the above experiment (condition viii) caused behaviour which normally only occurs on a horizontal plane. It is suggested that the response to light is far weaker than the responses to the other two stimuli studied.

The nature of the responses to gravity, light and the tip of the rod

Gravity

The response to gravity is often mediated in many arthropods by some type of statocyst organ, but it appears that the position of the body in relation to the limbs is the most common means of mediation (Wigglesworth 1965). Lees (1948) suggested that in I. ricinus the size and weight of the idiosoma is of great importance. It is obvious that the weight of the idiosoma, especially in the case of Ixodes species where the legs are usually situated far forward, would tend to orientate ticks so that their capitulae would face in an upwards direction on a grass stem. Lees (1948) states that engorged nymphs and adults can still ascend stems but can not walk downwards as the distribution of body weight does not allow it. In unengorged nymphae this is not the case and it is probable that in these nymphs and in larvae, the position of the idiosoma is important in mediating the gravity response.

Light

In most ixodid ticks it is probable that the eyes mediate the response to light. In some genera (i.e. Ixodes and Haemaphyasalis) however, eyes do not appear to be present and dermal light receptors have been postulated by both Lees (1948) and George (1963). George (1963) working on H. leporispalustris demonstrated that the "dorsum of the podosoma" (i.e. the scutum) was the most sensitive region to light. Painting over the region however, did not eliminate the response to light and therefore George (1963) postulated that the cuticle, being thin, allowed light penetrating it to stimulate the ganglia directly. He further postulated that paired intensity receptors must be present as the path taken by walking ticks was straight. The work of George (1963) points to the lack of knowledge in this field and it is suggested that although Ixodes and Haemaphysalis species appear to lack eyes, these may still be present but are not easily seen in superficial studies. The matter might be clarified by electron microscopic studies of the appropriate tissues.

The tip of the rod

The response to the tip of the rod (or grass stem) is difficult to explain. It is possible that larvae have a built in mechanism which causes them to undertake turning movements on a vertical rod. These turning movements might then be affected by encounters with the tip such that the rate of turning increases. This may be the type of kinesis envisaged by Lees (1948) and Lees and Milne (1951). This matter will however need further study. It was demonstrated by Lees (1948), using curved rods, and Lees and Milne, using bent grass stems, that larvae did not always react to the tip of the rod or stem but often to the highest point along the support. Larvae were observed to congregate in the regions of the curves of curved rods rather than at their tips which were some distance below the highest points. This work suggests that it is not so much the tip that is important but an encounter with the highest point. As the work of Goldsmid (1967) shows that larvae will gather around the end of a rod even when it is directed downwards appears to contradict this view, a closer look at his experiments is required. Goldsmid's (1967) rods were arranged so that the highest point accessable to the larvae was the section of rod just below a vaseline barrier. In other words the larvae were not actually able to encounter the end of the rod but merely a vaseline barrier. This may well explain why the larvae tended to gather around the tip which was directed downwards rather than at the highest point. The curved grass stems and rods of Lees (1948) and Lees and Milne (1951) allowed the larvae to actually walk over and therefore fully encounter the highest point along the particular support. This full encounter is probably essential as larvae collected at this point.

It was wondered whether the distance between the highest point of a curved rod or stem and the actual tip was important. If the curve in the rod was near the tip (i.e. the tip only a short distance from the top or highest point) it may be likely that larvae would continue over the highest point and encounter the tip, react to it and finally find a resting place in its vicinity. Lees (1948) demonstrated that when the tip of a curved rod was some distance below the highest point, which will be called the top in further discussions, nymphs would hardly ever encounter it as they would have to walk downwards, against the stimulus of gravity, for some distance before they would reach it. In order to establish whether the position of the tip of a curved rod was of some relevance in larval 'orientation behaviour' the following brief study was undertaken.

Firstly, two rods, one curved and the other straight, were arranged so that both possessed a maximum height of 20 cms. The curved rod however had its tip 15 cms from the top or highest point. Both rods were placed side by side in the constant environment room (condition B or Fig. 8). A number of larvae were introduced to the bases of each rod and after a period of two hours their positions recorded. The experiment was replicated three times and the results appear in Table 29.

Table 29 The final positions of rest of larvae of A. hebraeum climbing on two glass rods, one curved and one straight.

Curved rod	Final resting positions			
Replicate No	No at tip	No at top	No elsewhere	Total
1	2	15	1	18
2	1	18	2	21
3	2	16	0	18
Totals	5	49	3	57
Straight rod				
Replicate No	No at tip	No at top	No elsewhere	Total
1	21		1	22
2	20		0	20
3	18		1	19
Totals	59		2	61

Note : In the straight rod the tip and the top are the same point.

The results shown in Table 29 support the suggestions made by past workers. A greater number of larvae were found to settle at the highest point of the curved rod than at its tip. The straight rod, which can be considered as a control, showed that practically all the larvae came to rest at the tip. This was to be expected as it was shown earlier that larvae collect at the tips of straight glass rods.

Secondly, in order to establish the effects of different distances between the tip and the top of a bent rod the following experiment was done.

Five rods, one straight, and four with the tips at different distances from the top, were treated in the same way as the rods in the last experiment. The tips of the four curved rods were 2, 5, 10 and 15 cms from the highest points respectively. Table 30 shows the results of three replications of this experiment. The species used was once again A. hebraeum.

Table 30 shows that, after a two hour exposure to the rods, larvae were observed to come to rest at the highest points of the rods regardless of the distance of this point from the actual tip of the rod. These results support the suggestion that the response is one directed towards the highest point rather than the tip of the rod. Naturally when the tip is the highest point, as in the case of a straight rod the response can be called a 'tip response' but perhaps the term 'top response' should be used to avoid any confusion.

From the work reported in this section so far it can be suggested that there are two main stimuli which direct the movements of larvae during orientation behaviour on glass rods or stems. The first is gravity, the second is a response to encounters with the highest point of the rod or stem. The actual nature of this 'top response' is not understood. There also appears to be a weak response to the stimulus

Table 30 The final positions of rest of *A. hebraeum* larvae climbing on five glass rods, one straight and four with the tips at various distances from the top.

Replicate No	No at tip	No at top	No elsewhere	Total
Straight rod				
1	23		1	24
2	21		0	21
3	17		2	19
Totals	61		3	63
Tip 2 cms from top				
1	1	21	1	23
2	2	16	0	18
3	0	18	0	18
Totals	3	55	1	59
Tip 5 cms from top				
1	2	21	2	25
2	0	18	1	19
3	3	16	0	18
Totals	5	55	3	63
Tip 10 cms from top				
1	0	18	1	19
2	1	16	2	19
3	0	21	2	23
Totals	1	55	5	61
Tip 15 cms from top				
1	0	26	2	28
2	2	21	1	24
3	1	22	9	32
Totals	3	69	12	84

of light which only manifests itself under very unnatural experimental conditions. The light response is considered as being of very minor importance in orientation behaviour. The three stimuli considered can be listed as follows to show their relative importance.

Gravity response $>$ Top response $\gg$ Light response.

Culimination of orientation behaviour

As suggested earlier, it may be possible that a reaction chain exists in the behaviour of larval ticks. It was suggested that orientation behaviour must be completed before encountering the host can take place. i.e. A position of rest must be attained in the region of the tips of the vegetation before active movements can be made in response to stimuli presented by an approaching host. The following few observations on the behaviour of A. hebraeum larvae are presented in support of this contention.

Larvae were closely observed while either resting at the tips of glass rods or actually undergoing orientation behaviour, and their responses to being 'shadowed' recorded. The shadow response is well known among the Ixodidae in general (Lees 1948, Lees and Milne 1951, Wilkinson 1953, Dethier 1957, Goldsmid 1969).

Larvae were placed in a fairly strong beam of artificial light, and allowed to get accustomed to it. The larvae were then divided into two groups for observation. The first group were larvae which were static, having achieved a resting site at the tip of a glass rod, while the second group were larvae which were still performing orientation movements. The larvae were suddenly placed in shadow by either turning off the light source or passing an opaque object over the source of light. In all the larvae studied (50), those which had achieved resting positions reacted immediately to being 'shadowed' by exhibiting 'host questing' behaviour. Those in the process of orientation movements however, did not react to being 'shadowed'.

The above observations suggested that the actual attainment of a resting site marks the end of orientation behaviour and also the first link in the reaction chain earlier suggested.

6. DISCUSSION

In Capter 1 it was suggested that the control of ticks by purely chemical means has limitations. It was further suggested that ecological investigations could lead to the eventual formulation of alternative control programmes. Doutt and De Bach (1964) state:-

> "It is almost axiomatic that to reduce a pest population one must increase the unfavourability of its environment. Aside from the use of chemical pesticides, various possibilities exist for modifying the environment; therefore, it is imperative that any agricultural entomologist engaged in field research be familiar with ecological principles and use them whenever possible."

The reasons why ecological work should be done on ticks is obvious. Ticks have for many years, been pests and it has become obvious that although control by acaricidal application is progressively improving and is sufficient at present to keep ticks at an economic level, the costs of these products is continually increasing. In time it may prove completely uneconomical to control ticks entirely by chemical means. It is believed that if an intergrated control programme could be developed this would be as effective as pure 'chemical control' and probably cheaper. A reduction in the intensity of chemical application would probably also delay the development of resistant populations. In order to develop such an intergrated control programme it is necessary to know considerably more about the tick species involved and its interactions with the environment in which it lives. Adequate control by manipulation of the environment presupposes a thorough knowledge of the environment and the 'weak links' in the life cycle of the pest at which environmental effects could be directed. Unfortunately little is known about the constituent factors of the environment or the factors required to ensure the successful completion of a life cycle. This chapter is devoted to a discussion of the present state of our knowledge of tick ecology and the contribution made by the present investigation. An attempt is also made to briefly analyse the value of the information presented in this thesis in the field of applied acarology.

Fig. 49 represents a suggested model of a tick ecosystem. This proposed model included all the main groups of environmental factors with which the tick species probably interacts. A three host species was selected when the model was constructed as this type has the most complex ecosystem. In the case of a single and two host species the model would need to be modified. Although the host has been indicated as a single unit in the model, it should be emphasised that many tick species have a wide variety of hosts on which they can develop successfully, as well as 'prefered' hosts for each parasitic stage in the life cycle.

Mac Leod (1962) presented a mechanical analogue representing some of the community relations in which I. ricinus was envolved (Fig. 50). In Fig. 50 the wheels represent community factors. Any wheel, if turned in a clockwise direction represents an increase, anticlockwise a decrease. The central pulleys are the drive wheels and the peripheral ones the pick up. The uninterrupted line belts indicate ecological action, the interrupted lines coaction and the dotted lines reaction. It can be seen, for example, that as 'Good Grass' cover increases, all the other factors are affected in some way. For a fuller account of the operation of this model see both Mac Leod (1962) and Arthur (1965). Mac Leod's (1962) model shows the various community relationships very adequately. It does not however show the factors involved at the level of each population or the individuals within each population. Mac Leod (1962) indicates a pulley system labelled 'Ticks'. The population density of the ticks is however dependant on a number of factors which are not shown in Fig. 50. Fig. 49, it is thought, fills this need in part. A brief consideration of the interactions illustrated in Fig. 49 is relevant at this point in the duscussion.

In the environment off the host, abiotic factors such as relative humidity, temperature, rain and dew define the microclimatic conditions in which the non-parasitic ticks live. Lees and Beament (1948) working with I. ricinus and Sonenshine and Tigner (1969) working with Dermacentor

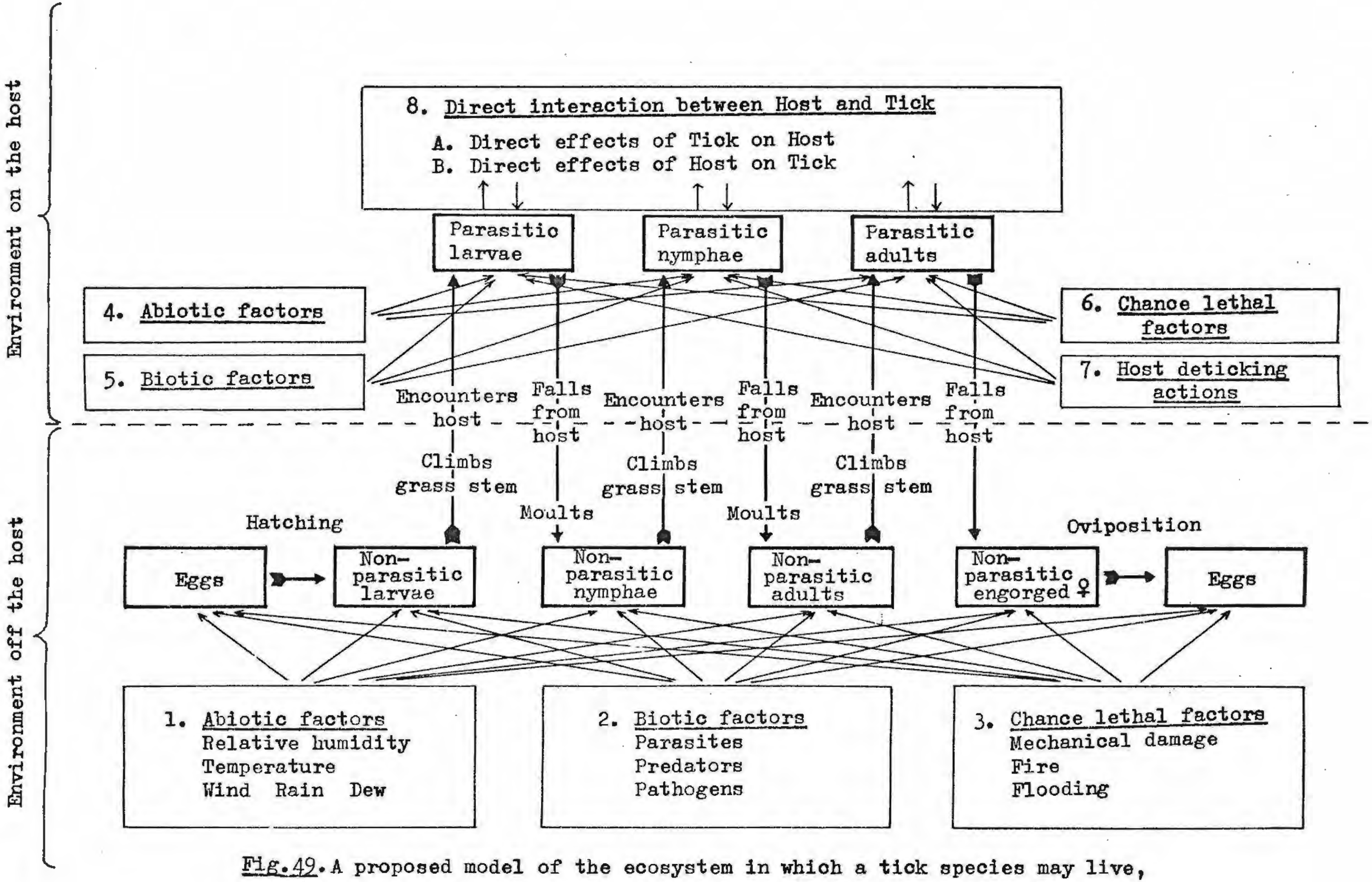


Fig.49. A proposed model of the ecosystem in which a tick species may live, showing the main environmental factors interacting with the stages in the life cycle of the tick species.

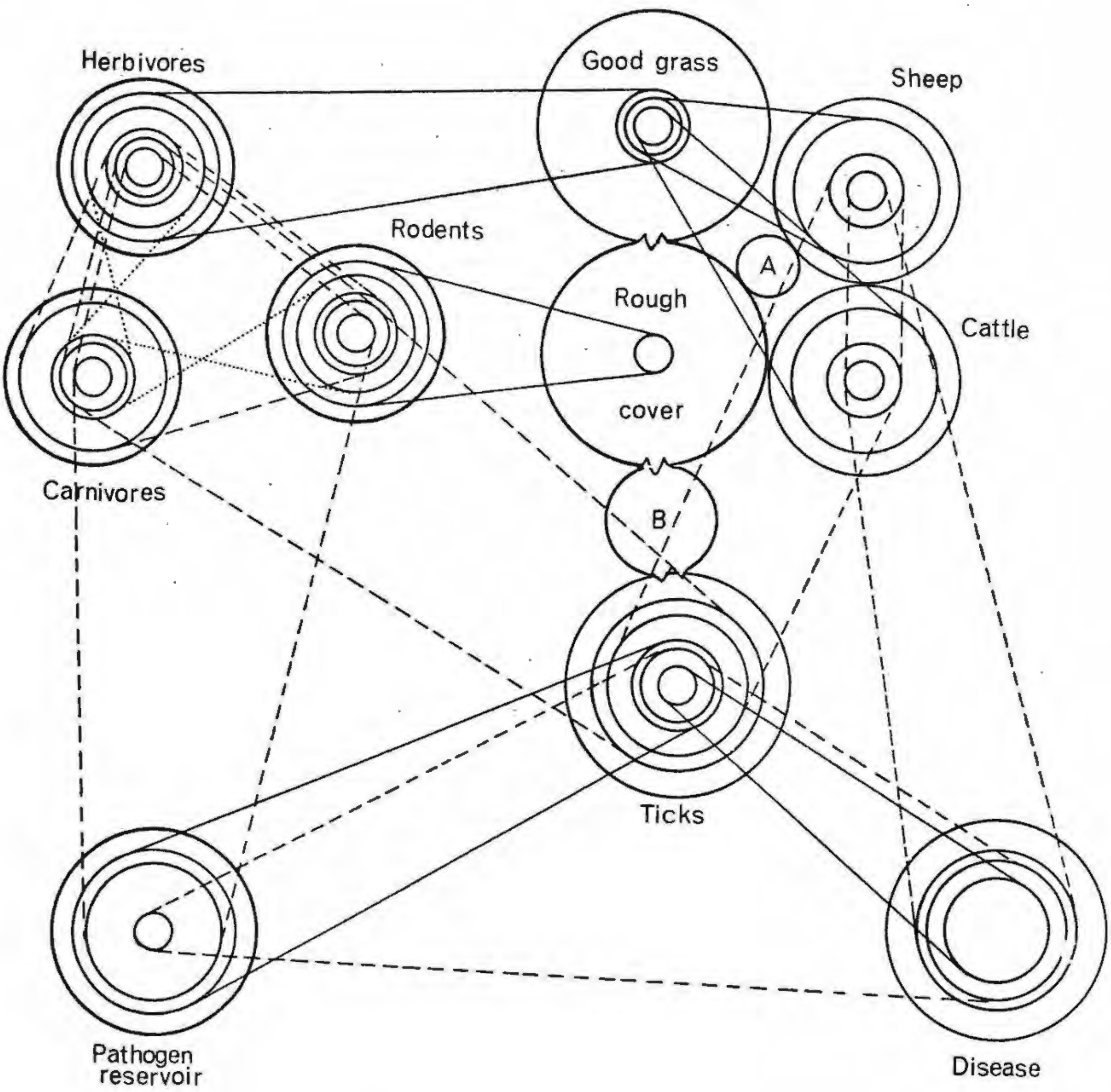


Fig. 50 A model of the dynamic community relations in which Ixodes ricinus L. participates.

Clockwise rotation indicates increase.

A = Selective grazing of sheep,

B = Microclimatic humidity,

—— = Ecological action,

--- = Coaction,

········ = Reaction.

(From: Mac Leod 1962 and Arthur 1965).

variabilis (Say) and *Amblyomma americanum* L. have shown that eggs become desiccated if the atmostpheric relative humidity is below a certain value. Hall and Wilkinson (1960) demonstrated that if eggs are flooded for a period of 24 hours or more, they fail to hatch. Lees (1946) and Milne (1952) working on *I. ricinus* and Hitchcock (1955) and Wilkinson (1953) on *B. microplus* have shown that the survival of non-parasitic ticks was greatly influenced by their water relationships. Lees (1946) demonstrated that unfed *I. ricinus* nymphs and adults lost water at relative humidities lower than 92 % and took up water vapour from the atmostphere at values lower than 92 % RH. 92 % RH was therefore called the 'equilibrium humidity' for *I. ricinus*. Milne (1952, and earlier papers) demonstrated that the distribution of *I. ricinus* could be correlated with the physical character of the sward. The ticks were found in vegetation which provided cover. The role of the cover was to maintain the high humidities required for survival. Stampa (1959) was able to show a similar relationship in the case of *I. rubicundus* in the Karoo. This type of information is very valuable as it immediately allows the distribution of the tick species to be defined. In this thesis I have attempted to define the limits of the distribution of a few tick species in relation to microclimatic conditions. It was shown, in the case of *I. pilosus*, *A. hebraeum*, *B. decoloratus* and *H. silacea*, that distribution could be correlated with vegetation type. *I. pilosus* and *H. silacea* were both predominantly collected from short covered vegetation, *B. decoloratus* from short protected vegetation and *A. hebraeum* from medium to tall protected vegetation. A microclimatic study of the various vegetation categories demonstrated that ticks were infrequently collected from habitats which normally experienced a midday saturation deficit value in excess of approximately 10 mm. Hg. This finding was supported by experimental evidence in that, at 26°C, 70-80 % relative humidity (i.e. approximately 10 mm. Hg. saturation deficit) was found to be the approximate equilibrium humidity of all the species studied.

Wilkinson (1953) was first to show that non-parasitic ticks (in this case B. microplus larvae) were able to imbibe liquid water through the mouthparts. Wilkinson and Wilson (1959) demonstrated that this means of water uptake was of survival value. I have shown in this investigation that the non-parasitic larvae of all the species studied (i.e. A. hebraeum, R. evertsi, R. appendiculatus and B. decoloratus) were able to drink water and that this uptake was of survival value. Drinking of dew in the field was observed by Wilkinson and Wilson (1959) and I suggest that as this means of water uptake appears to be rapid, larvae are able to replenish all the water lost through evaporation, over many hours, in a comparatively short period.

The biotic factors of the environment off the host have received comparatively little attention by tick ecologists as this aspect is naturally more difficult to study than the effects of abiotic factors. Very few tick parasites, predators and pathogens have been recorded. Cooley (1934), Fiedler (1953) and Kaiser and Hoogstraal (1958) reported the occurance of a few chalcidoid (Encyrtidae) parasites of tick nymphs. Among these were Hunterellus hookeri Howard and Hunterellus theilerae Fiedler, both of which were recorded from African tick species including R. evertsi and R. appendiculatus. Little is known about these hymenopterous parasites. Fiedler (1969) reported the occurance of an acaricidal micro-organism in Southern Africa. This pathogen, identified as a very virulent strain of Bacillus thuringiensis Berliner, was shown to be highly lethal to ticks. The principle problem in utilising this pathogenic organism as a control measure is that it must be introduced into the digestive tracts of the ticks. In the laboratory work (Fiedler 1969) introduction was done artificially.

Birds probably constitute the main tick predators. The cattle egret, Bubulcus ibis (L) although thought to be a well established tick predator needs further study. The value of the red-billed and yellow-billed oxpeckers, Buphagus erythrorhynchus (Stanley) and Buphagus africanus (L), as tick predators does not seem to have been evaluated.

Roberts (1957) states that an examination of the gut contents of these birds have shown very large numbers of tick fragments. Wilkinson and Wilson (1959) reported that engorged B. microplus adults were sometimes taken by spiders and ants. Kraft (1961) suggested that small mammals, such as rats and mice, may eat engorged adult ticks. Very little is known about these predators and their effects on tick populations.

Fig. 49 shows a third group of environmental factors affecting ticks off the host. These have been called 'chance lethal factors' and are probably very closely related to abiotic factors. As they are, however, not usually present they have been placed separately. These factors include mechanical damage, which could be produced in countless ways, fire and flooding.

Five main groups of environmental factors have been indicated in Fig. 49 as probably existing in the environment of parasitic ticks. Very little is known of the abiotic and biotic factors with which ticks must interact while on the host. It is probable that the microclimate on the host is affected only slightly by macroclimatic conditions as the host is, in many cases, a homoiothermic animal. This is pure conjecture however, as no work appears to have been done on this aspect of tick ecology. H. hookeri and H. theilerae probably attack ticks while on the host as well as off the host. Kaiser and Hoogstraal (1959) reported the latter species from a Hyalomma rufipes Koch nymph from a migrant bird in Egypt.

Probably the most important interaction which takes place on the host are those concerned with the host itself. Snowball (1956) and Bennett (1969) have shown that 'self licking' in cattle has a great effect on the parasitic tick stages. Other deticking activities such as scratching, probably also effect the survival of ticks on the host. Although Ducasse (1969) has shown that ticks have 'predeliction sites' on the host I suggest that these are probably determined largely by the deticking abilities of the host.

The most important 'chance lethal factor' in the environment of the parasitic tick is probably the presence of toxic substances. These toxic substances, acaricides, constitute man's main weapon against tick infestations at present. A few tick species, e.g. B. decoloratus and B. microplus, have however, evolved strains which are resistant to certain groups of toxic substances.

The direct effects of the tick on the host are well known. Ticks are the vectors of many disease organisms (Arthur 1962). Little is known about the actual process involved in the release of these organisms into the hosts blood. Arthur (1965, 1970)has studied, very fully, the feeding and digestive mechanisms in ticks and other ectoparasites and it is probable that this information will lead eventually to a more complete understanding of disease transmission. The direct physiological effects of the host on the tick is an aspect not well studied. Reik (1956, 1962) and Roberts (1968 a,b & c) have shown that some cattle possess a natural 'immunity' to tick infestation. The actual reason why this should be the case is not known.

An interesting interaction between a host and tick species was reported by Tatchell (1967 a & b, 1969). It was shown that B. microplus adults were able to eliminate water, taken up in the blood meal, by excreating this through salivary secretions back into the host, thus causing a concentrated blood meal to accumulate in the gut.

A rather important aspect of tick ecology, which is not adequately shown in Fig. 49, is the behaviour of ticks. It is obvious that the successful completion of a life cycle is dependant on the ticks successfully undertaking certain behavioural patterns. Probably the most important behavioural patterns are those concerned with the encounter with the host. Lees (1948, 1952) has shown that grass climbing and host questing behaviour is of considerable importance to tick survival. The work reported in this thesis contributes to the knowledge of non-parasitic larval behaviour in that it has been shown that vegetation height is probably of importance in the successful orientation of larvae to the tips of grass stems. A. hebraeum larvae appeared to successfully locate a resting place at the tip of the rod only when the rod was approximately 40 cms high. This height was correlated with the height of vegetation in which this species was collected in the field. Host questing behaviour has been studied by Lees (1948, 1952), Goldsmid (1967) and others. Arthur (1965, 1970) has studied feeding behaviour. Mating behaviour has received a little attention since the early work of Lounsbury (1899). Gladney and Drummond (1970) have reported interesting observations on the mating behaviour of *A. americanum*. 'Drop-off' behaviour has been studied by Hadani and Rechav (1969) who show the existence of a cicadian rhythm in this behaviour.

I have attempted to cover a number of aspects which have received attention by tick ecologists. These findings must, however, be evaluated in terms of their possible 'control' value. It is almost pointless to study, for instance, the grass climbing behaviour of larvae, if this behaviour is not analysed in terms of its potential in the field of applied acarology.

Numbers of suggestions have arisen from the findings of ecological investigations on tick species. Pasture improvement as a means of control was studied by Milne (1948, 1952). Although pasture improvement has an adverse effect on the population of *I. ricinus* this was considered to be an uneconomical means of control. Alteration of the environment was also suggested by Stampa (1969) as a means of controlling *I. rubicundus*. At present it is not known if this idea is economically feasible. Similar suggestions can arise from the results reported in this thesis. For example, *A. hebraeum*, larvae were shown to occur predominantly in medium to tall vegetation. It may be possible to limit the population density of this species by reducing the amount of tall grass in the grazing camps. This suggestion received unexpected support when labourers cut down a lot of the tall grass in Old Cow Camp. It was found that after this event the population of *A. hebraeum* larvae appeared to be greatly reduced. How practical this practise of grass mowing is as a means of tick control has not been determined. The results of the behavioural work concerned with vegetation height supports the above suggestion in that it has been demonstrated that vegetation of the 'wrong' height is probably unfavourable for the successful achievement of a vantage point at the tip of a grass stem. By altering the vegetation height, either by cutting or intensively grazing it, a serious effect on the survival of larvae and hence the continuation of the life cycle of the species, could be introduced.

Another suggestion can be made which is based on the information reported in this thesis. B. decoloratus was found predominantly in short protected vegetation at Faithful Fountain. It may prove economically feasible to either limit the movements of the cattle to other vegetation types or to treat the areas of short protected vegetation in some way. The application of an acaricide or the burning of the particular areas should be investigated.

Ecological findings have led to more efficient dipping programmes in Australia and additional control measures such as 'pasture spelling' (Wilkinson 1957) have been applied with some success (Wharton et al 1969). It was shown in this thesis that larval populations were higher in winter than in any other season. In the past, dipping appears to have been undertaken more conscientiously during the warmer summer months as farmers are able to actually see adult ticks on their cattle. In winter, when the animals have thicker coats the numerous larvae are probably not noticed and hence dipping is irregularly undertaken as farmers think that their cattle are 'clean'. The results of the ecological work therefore suggest that better results might be achieved if special attention to dipping and spraying is given during the winter months. This may prove to have a considerable effect not only on the parasitic larval stage but also on the adult population normally so evident in summer.

From this short discussion of some of the possible ways in which ecological findings can be applied in the field of tick control, the importance of a thorough knowledge of tick ecology becomes apparent.

So many aspects have been poorly studied that it is impossible at present to suggest which should receive the most attention. I feel that the non-parasitic larval stage is a very important one and should receive more attention. This is, in all species, a 'contact stage' (i.e. a stage which encounters a host), and in the case of single host tick species it is the only contact stage; as such it warrants special attention. The non-parasitic larval stage may eventually prove to be one of the weakest links in the tick life cycle at which effective control measures could be directed.

7. SUMMARY

The work conducted and discussed in this present investigation can be summarised in the following way.

i Surveys were carried out on two farms near the coast in the Port Alfred district. The results of these surveys demonstrated that there were four main species present on both farms (I. pilosus, H. silacea, B. decoloratus and A. hebraeum). It was found that these species were collected from very definite vegetation categories.

ii A study of the microclimatic conditions in each vegetation category was undertaken. The results of this study demonstrated that, although the various habitats were visibly different, they were very different microclimatically. The actual measurements of temperature and relative humidities for each of the three levels studied in each vegetation category were presented in terms of saturation deficit. It appeared that larvae were not found in habitats which experienced midday saturation deficits of greater than 10 mm. Hg.

iii Studies on the water relations of larval ticks revealed that water was mainly lost by the ticks through evaporation from the general body surface. Water uptake was mainly facilitated by the active uptake of water vapour from damp atmostpheres. It appeared that the species studied could take up water vapour from atmos~~t~~pheres of above approximately 70% relative humidity. Drinking was also shown to be of survival value. From the various experiments it became obvious that the distribution of larval ticks in the field was to some extent determined by the microclimatic conditions in which they live.

iv As it appeared that larval ticks may be influenced in their distribution by the actual height of the vegetation, investigations into the behaviour of larval ticks climbing glass rods were undertaken in the laboratory. It was found that vegetation height was likely to play an important role in the attainment of a resting position at the tips of grass stems. The heights to which the tick species appeared to be associated in the laboratory appeared to correlate with the vegetation heights in which these species were found in the field.

v Brief considerations of the stimuli responsible for directing 'orientation behaviour' on glass rods, similating grass stems, were also made. It was found that gravity was the main stimulus and that encounters with the tip of the rod were probably also of importance. Light appeared to be unimportant as a stimulus to 'orientation behaviour'. A little evidence was presented which supported the suggestion that the attainment of a resting position at the tip of a glass rod marked the end of a behavioural 'link' in a reaction chain.

vi A brief discussion was made of the present state of our knowledge concerning the ecology of non-parasitic larvae. The contribution made by the present investigation was discussed briefly.

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LIST OF PLATES

Plate 2

Short open vegetation at Barville Park.

Main species comprising vegetation

Panicum maximum
Panicum stapfianum
Digitaria eriantha
Seteria pallide-fusca
Aristida junciformis
Cynodon dactylon
Leptocarpus paniculatus
Mariscus dregianus
Kallinga erecta
Kallinga alba
Aristea anceps
Helichrysum anomalum
Metalasia muricata
Disparago ericoides

Plate 3

Medium open vegetation at Barville Park.

Main species comprising vegetation

Hyparrhenia hirta
Panicum maximum
Panicum stapfianum
Digitaria eriantha
Sporobolus capensis
Sporobolus fimbriatus
Chloris gayana
Eragrostis plana
Leptocarpus paniculatus
Scirpus thunbergianus
Metalasia muricata

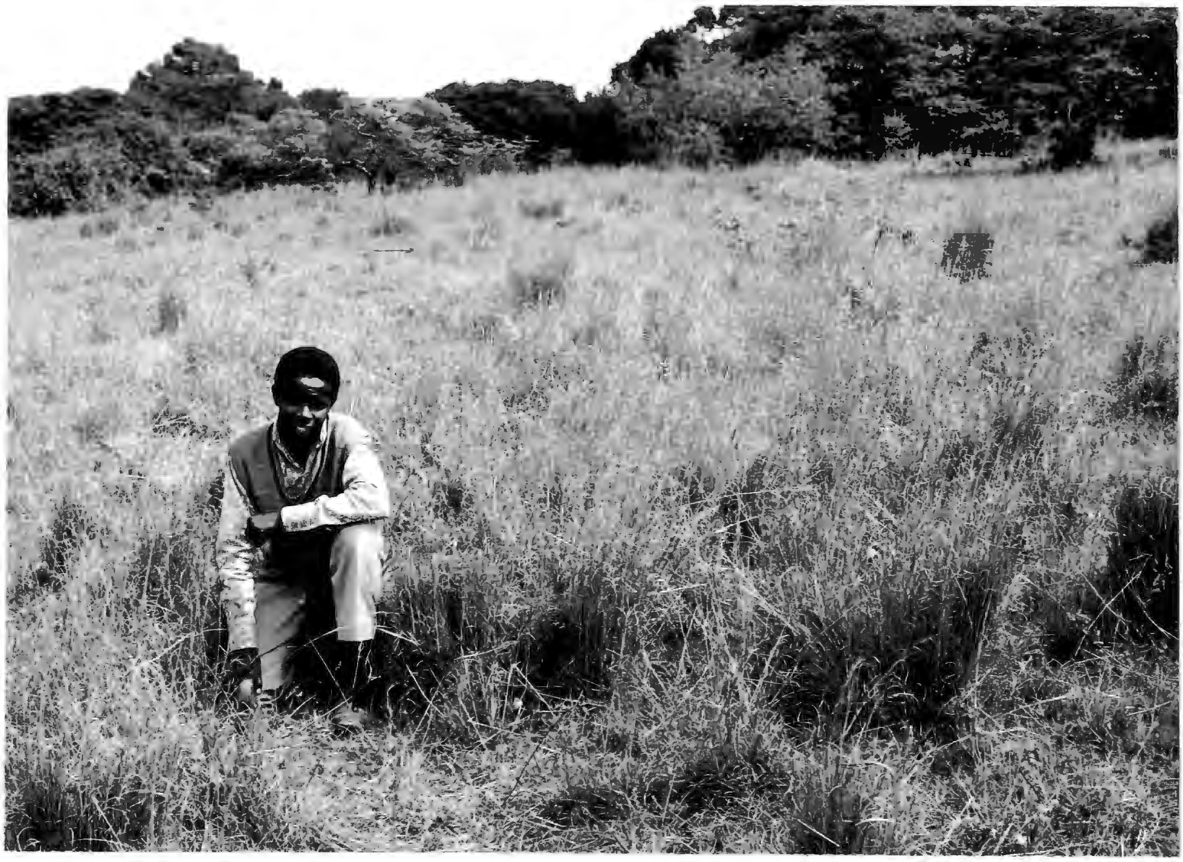

Plate 4

Tall open vegetation at Barville Park.

Main species comprising vegetation

Hyparrhenia hirta
Panicum maximum
Sporobolus capensis
Sporobolus fimbriatus
Chloris gayana
Eragrostis plana

Plate 5

Short protected vegetation at Barville Park.

Main species comprising vegetation

Setaria pallide-fusca
Cynodon dactylon
Leptocarpus paniculatus
Mariscus dregianus
Kallinga erecta
Kallinga alba
Disparago ericoides
Helichrysum anomalum

Plate 6

Medium protected vegetation at Barville Park.

Main species comprising vegetation

Panicum stapfianum
Digitaria eriantha
Cynodon dactylon
Kallinga erecta
Helichrysum anomalum

Plate 7

Tall protected vegetation at Barville Park.

Main species comprising vegetation

Hyparrhenia hirta
Eragrostis plana
Scirpus thunbergianus

Plate 8

Short covered vegetation at Barville Park.

Main species comprising vegetation

Cynodon dactylon and other unidentified dicotyledenous plants.

Plate 9

Medium covered vegetation at Barville Park.

Main species comprising vegetation

Setaria pallide-fusca
Cynodon dactylon

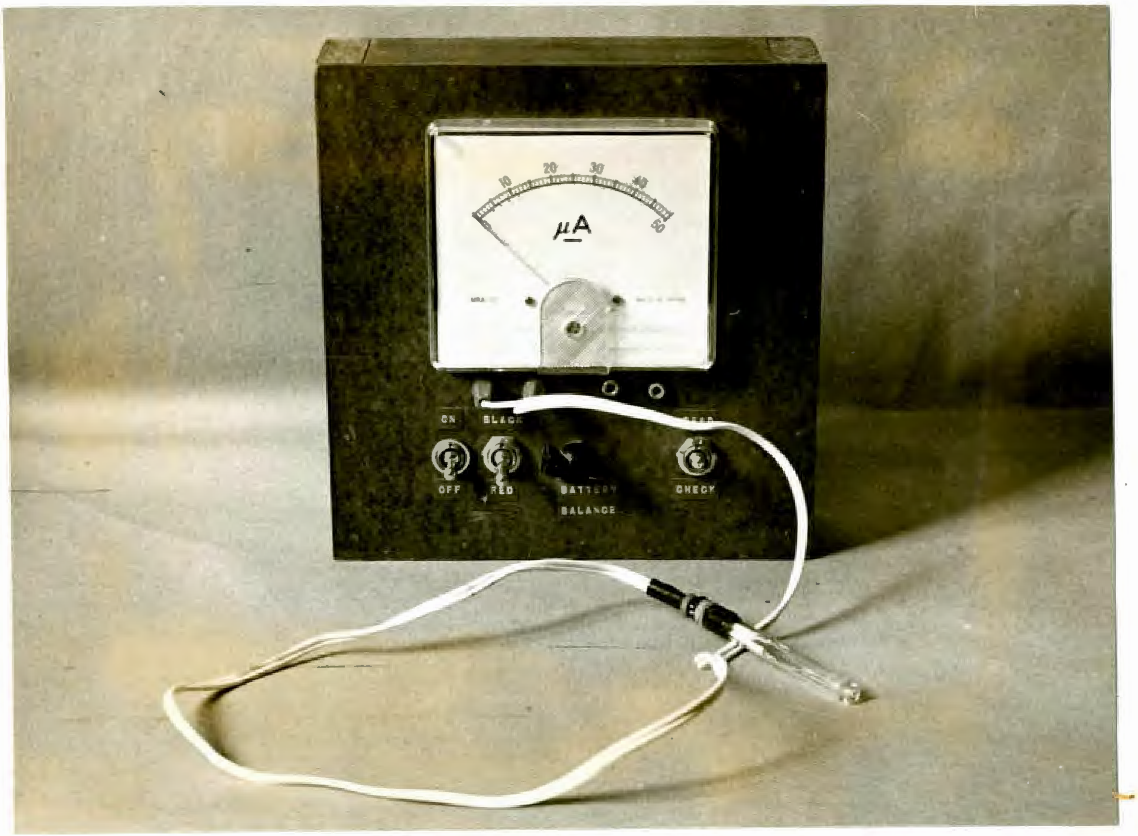

Plate 10

The thermometer used in the microclimatic work undertaken at Barville Park.

Plate 11

The apparatus used in the estimation of relative humidity values in the micro-climatic studies undertaken at Barville Park.

Plate 12

The Casella air meter used to measure wind speeds during the microclimatic studies undertaken at Barville Park.

Plate 13

The arrangement of mesh cylinders as used during relative humidity determinations at three different levels in the vegetation.

Plate 14

Amblyomma hebraeum larva drinking water.

Plate 15

Amblyomma hebraeum larvae after drinking Methylene Blue water for various lengths of time. (See text)

APPENDIX

Recorded host animals of Haemaphysalis silacea Robinson

Host as recorded by Theiler (1962)	Name as given by Roberts (1951,1957)	Common Name	Stage found
Bostrychia hagedash	Hagedashia hagedash	Hadeda	AI
Numida meleagris	Numida meleagris	Crowned Guinea-fowl	AI
Ichneumia albicauda	Ichneumia albicauda	White-tailed Mungoose	AI
-	-	'Hare'	AI
Sylvicapra grimmia	Sylvicapra grimmia	Grey or Common Duiker	A
Tragelaphus angosi	Tragelaphus angosii	Nyala	A
Tragelaphus scriptus	Tragelaphus scriptus	Chobe Bushbuck	AI
Tragelaphus strepsiceros	Strepsiceros strepsiceros	Kudu	A
Cephalophus monticola	Guevei caerula	Blue Duiker	AI
-	-	'Mongoose'	AI

Recorded host animals of Ixodes pilosus Koch

Host as recorded by Theiler (1962)	Name as given by Roberts (1951,1957)	Common Name	Stage found
Elephantulus rupestris	Elephantulus rupestris	Rock Elephant Shrew	AI
Cercopithecus aethiops	Cercopithecus aethiops	Vervet Monkey	AI
Canis mesomelas	Thos mesomelas	Black-backed Jackal	A
Genetta rubiginosa	Genetta rubiginosa	Rusty-spotted Genet	A
Herpestes pulverulentus	Myonax pulverulentus	Cape Grey Mungoose	AI
Mungos mungo	Mungos mungo	Banded Mungoose	AI
Suricata suricatta	Suricata suricatta	Suricate	A

A = Adult Stage
I = Immature stages (larvae and nymphs)

Ichneumia albicauda	Ichneumia albicauda	White-tailed Mungoose	AI
Felis caracal	Caracal caracal	Caracal	AI
Felis libyca	Felis lybica	Cape Wild Cat	A
Potamochoerus porcus	Potamochoerus porcus	Bush Pig	A
Phacochoerus aethiopicus	Phacochoerus aethiopicus	Warthog	A
Cephalophus monticola	Guevei caerula	Blue Duiker	A
Cephalopus natalensis	Cephalophus natalensis	Red or Natal Duiker	A
Pelea capreolus	Pelea capreolus	Grey Rhebok	A
Sylvicapra grimmia	Sylvicapra grimmia	Grey or Common Duiker	A
Redunca arundinum	Redunca arundinum	Reedbuck	A
Tragelaphus scriptus	Tragelaphus scriptus	Chobe Bushbuck	A
Syncerus caffer	Syncerus caffer	Cape Buffalo	A
Lepus saxatillis	Lepus saxatillis	Southern Bush Hare	A
Pronolagus crassicaudatus	Pronolagus crassicaudatus	Natal Red Hare	AI
-	-	'Wild Hare'	AI
Rattus chrysophilus	Aethomys chrysophilus	African Rat	AI
Saccostomys campestris	Saccostomys campestris	Pouched Mouse	AI
-	-	'Reed Rat'(?)	AI

Recorded host animals of Boophilus decoloratus Koch

Host as recorded by Theiler (1962)	Name as given by Roberts (1951,1957)	Common Name	Stage found
Phalacrocorax africanus	Phalacrocorax africanus	Reed Cormorant	A
Numida meleagris	Numida meleagris	Crowned Guinea-fowl	A
Panthera leo	Felis leo	Lion	A
Equus sp.	Equus	Horse/Zebra etc.	A

A = Adult Stage
I = Immature stages (larvae and nymphs)

Equus burchelli	Equus burchellii	Burchell's Zebra	AI
Giraffe camelopardalis	Giraffe camelopardalis	Giraffe	AI
Kobus ellipsiprymnus	Kobus ellipsiprymnus	Waterbuck	I
Aepyceros melampus	Aepyceros melampus	Impala	AI
Oryx gazella	Oryx gazella	Cape Oryx	A
Hippotragus equinus	Ozanna equina	Roan Antelope	A
Damaliscus lunatus	Damaliscus lunatus	Tsesseby	A
Connochaetes gnou	Connochaetes gnou	Black Wildebeeste	A
Connochaetes taurinus	Connochaetes taurinus	Blue Wildebeeste	AI
Tragelaphus scriptus	Tragelaphus scriptus	Chobe Bushbuck	AI
Tragelaphus spekei	Limnotragus spekii	Situtunga	A
Tragelaphus streptoceros	Streptoceros streptoceros	Kudu	AI
Taurotragus oryx	Taurotragus oryx	Cape Eland	AI
Syncerus caffer	Syncerus caffer	Cape Buffalo	A
Lepus sp.	Lepus	Hare	I

Recorded host animals of <u>Amblyomma hebraeum</u> Koch

Host as recorded by Theiler (1962)	Name as given by Roberts(1951,1957)	Common Name	Stage found
Gerrhosaurus validus	Gerrosaurus vallidus	Plated Rock Lizard	A
Varanus albigularis	Varanus albigularis	White Throated Monitor	AI
Bitus arietans	Bitus arietans	Puff Adder	(?)
Struthio camelus	Struthio camelus	Ostrich	A
Scopus umbretta	Scopus umbretta	Hamekop	I
Aquila rapax	Aquila rapax	Tawny Eagle	I

A = Adult Stage
I = Immature Stage (larvae and nymphs)

Tchagra senegala	Tchagra senegala	Black-crowned Tchagra	I
Chlorophoneus sulfureopectus	Chlorophoneus sulfureopectus	Orange-brested Bush Shrike	I
Lamprotornis chalybeus	Lamprotornis chalybeus	Blue-eared Glossy Starling	I
Plocepasser mahali	Plocepasser mahali	White-browed Sparrow-weaver	I
Erinaceus frontalis	Aethechinus frontalis	South African Hedgehog	AI
Galago crassicaudatus	Otolemur crassicaudatus	Bush-Baby	I
Cercopithecus aethiops	Cercopithecus aethiops	Vervet Monkey	I
Papio ursinus	Papio ursinus	Cape Chacma Baboon	I
Manis temmincki	Smutsia temminckii	Scaly Anteater	A
Canis adustus	Thos adustus	Side-striped Jackal	I
Canis mesomelas	Thos mesomelas	Black-backed Jackal	I
Vulpes chama	Vulpes chama	Silver Jackal	A
Ichneumon albicauda	Ichneumon albicauda	White-tailed Mungoose	I
Gennetta genetta	Gennetta felina	Small-spotted Genet	I
Gennetta rubiginosa	Gennetta rubiginosa	Rusty-spotted Genet	I
Mungus mungo	Mungus mungo	Banded Mungoose	I
Helogale parvula	Helogale parvula	Dwarf Mungoose	I
Suricata suricatta	Suricata suricatta	Suricate	A
Proteles cristatus	Proteles cristatus	Aardwolf	A
Crocuta crocuta	Crocuta crocuta	Spotted Hyena	I
Felis caracal	Caracal caracal	Caracal	I
Panthera leo	Felis leo	Lion	AI
Panthera pardus	Panthera pardus	Leopard	I

A = Adult Stage
I = Immature stage (larvae and nymphs)

Procavia capensis	Procavia capensis	Rock Dassie	I
Diceros bicornis	Diceros bicornis	Black Rhinoceros	AI
Diceros simus	Ceratotherium simum	White Rhinoceros	I
Potamochoerus porcus	Potamochoerus porcus	Bush Pig	AI
Phacochoerus aethiopicus	Phacochoerus aethiopicus	Warthog	AI
Giraffe camelopardalis	Giraffe camelopardalis	Giraffe	AI
Sylvicapra grimmia	Sylvicapra grimmia	Grey or Common Duiker	AI
Raphicerus campestris	Rhaphicerus campestris	Steenbok	AI
Pelea capreolus	Pelea capreolus	Grey Rhebuck	A
Redunca arundinum	Redunca arundinum	Reedbuck	AI
Aepyceros melampus	Aepyceros melampus	Impala	AI
Connochaetes taurinus	Connochaetes taurinus	Blue Wildebeeste	A
Tragelaphus angasi	Tragelaphus angosii	Nyala antelope	AI
Tragelaphus scriptus	Tragelaphus scriptus	Chobe	AI
Tragelaphus strepsiceros	Strepsiceros strepsiceros	Kudu	AI
Taurotragus oryx	Taurotragus oryx	Cape Eland	A
Syncerus caffer	Syncerus caffer	Cape Buffalo	AI
Lepus capensis	Lepus capensis	Cape Hare	I
Lepus saxatilis	Lepus saxatilis	Southern Bush Hare	I
Pronolagus sp.	Pronolagus sp.	Natal Red Hare ?	I
Pedetes capensis	Pesetes cafer	Spring Hare	I
Otomys unisulcatus	Otomys unisulcatus	Bush Otomys	I
Rhabdomys pumilio	Rhabdomys pumilio	Cape Striped Field Mouse	I
Tatera sp.	Tatera sp.	Gerbille	A

A = Adult Stage
I = Immature stage (larvae and nymphs)