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TICK PARALYSIS IN THE KAROO AREAS OF SOUTH AFRICA

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CONTENTS

	Page
A. Introduction	170
(1) Karoo Tick Paralysis	170
(2) Spring Lamb Paralysis	171
(3) Leg Weakness in Geese and Ducks	171
(4) Tick Paralysis in Man	171
B. Historical	171
C. Biology of *Ixodes rubicundus*	174
(1) Seasonal Occurrence	174
(2) Daily Activity	177
(3) Hosts and Intermediate Hosts	177
D. The Behaviour of the Tick on Sheep	178
(1) Attachment Sites	178
(2) Periods of Engorgement	180
(3) Variations during the Process of Engorging	181
(4) The Diminishing Chances of Engorgement	182
(5) Copulation	182
E. Survey Methods and Some Findings	184
(1) Tethering Experiments	184
(2) Dragging Experiments	184
(*a*) Apparatus	184
(*b*) Procedure	185
(*c*) Findings	187
F. The Free Living Tick and its Environment	189
(1) General Aspects	189
(2) Veld-Types	189
(*a*) Considerations in Mapping the Occurrence of the Tick	194
(*b*) Considerations in Mapping the Occurrence of Tick Paralysis	195
(3) Tick Densities in Different Types of Veld	197
(*a*) Introduction	197
(*b*) Findings in Other Countries	197
(*c*) Changes in the Composition of the Plant Associations in the Sneeuberg	198
(i) Initial Investigations	199
(ii) Second Series of Investigations	201
(iii) Third Series of Investigations	203

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G. The Ecology of the Tick 206
(1) Influence of Farm Management Upon the Presence of Tick Paralysis 206
(a) Alteration of the Plant Associations 207
(b) Dipping 208
(c) Resting of Veld 208
(d) Burning of Veld 209
H. The Control of *Ixodes rubicundus* on Woolled Sheep by Foot-Dipping, with Remarks on the Control of *Hyalomma* Spp. and *Rhipicephalus evertsi* 210
(1) Work of Other Investigators 210
(2) The Specific Efficacy of BHC and Dieldrin 212
(3) Diffusibility of the Insecticide in Wool 213
(4) Duration of Protection 214
(a) Against *Ixodes rubicundus* 214
(b) Against *Hyalomma* spp. and *Rhipicephalus evertsi* 217
I. Discussion and Recommendations 219
(1) Discussion 219
(2) Recommendations for the Control of *Ixodes rubicundus* 222
J. Summary 223
K. References 225
L. Acknowledgements 225

A. Introduction

Tick paralysis, which is found in several parts of the world, is one of the main problems of the sheep and goat farmer in certain parts of South Africa. In recent years in South Africa it has attracted special attention due to the fact that, not only has there been a tendency for the disease to make its appearance in areas where it was formerly unknown, but also, in that outbreaks of considerable severity have been encountered amongst stud stock.

In South Africa four different forms can be distinguished according to the causative tick, and to the clinical picture.

1. *Karoo Tick Paralysis*

The condition is caused by the bite of *Ixodes rubicundus,* Neumann (1904). The adult only has been incriminated. The period of activity of this tick is confined to the winter months. Sheep, goats and cattle, the latter to a lesser extent, are affected as also several species of antelope. Exceptionally, cases of paralysis in dogs and in red jackals have been reported. Other animals such as horses, cats and hares, have not been observed to become paralysed. Only female ticks have been incriminated thus far; the immature stages attach to the susceptible hosts in exceptional cases only. The symptoms appear during the last phase of engorgement of the tick and it is characteristic of the disease that all limbs of the host are affected simultaneously. The rate of recovery is high, provided the ticks are removed; in untreated sheep, however, losses may be considerable.

2. *Spring Lamb Paralysis*

The condition is caused by the bite of *Rhipicephalus evertsi* Neumann (1897). Young lambs mainly are affected, the condition making its appearance in the spring, as a rule; odd cases have been reported in adult sheep and in calves. Other hosts of this tick, which is present throughout the greater part of the Union throughout the year, have not been recorded as showing the disease. Outbreaks are experienced in the highveld of the eastern Orange Free State, reaching southwards to Sterkstroom in the Cape Province. In the Transvaal it is present only in the Belfast area. The tick has not been reported as being responsible for paralysis in other parts of the Union. The symptoms occur during the engorgement of the tick. The hind legs only are affected, to start with at least, regardless as to whether the tick is attached to the hind or forequarters (Clark, 1938). The recovery rate is high provided that the causative ticks are removed. Neitz and Jansen have been able to produce paralysis in sheep under experimental conditions (Neitz, 1956).

3. *Leg Weakness in Geese and Ducks*

The condition is caused by the bite of *Argas persicus* (Oken, 1867). Geese and ducks mainly are affected, but fowls also may suffer. According to Coles (pers. comm.) the disease has been observed in fowls on which larvae and adults were engorging simultaneously, but in geese and ducks adults can cause paralysis even when no larvae are attached to the hosts.

Outbreaks have been recorded from several parts of South Africa. As is the case with other ticks, not all *Argas persicus* adults are capable of producing the disease. The symptoms appear six-and-a-half to seven days after the engorgement of the tick and only the legs of the birds are affected. The recovery rate is low (Coles, 1937).

4. *Tick Paralysis in Man*

In South Africa, Zumpt and Glaichen (1950) have recorded one case of tick paralysis in an adult due to *Rhipicephalus simus* Koch (1844). The paralysis appeared as a general weakness with undisturbed sensitivity. Erasmus (1952) describes a case in an adult due to *Hyalomma truncatum* (Koch, 1844) and refers to a case in a child due to *Ixodes rubicundus*. Both cases of Erasmus showed a localised motor paralysis accompanied by a complete loss of sensation in the affected area. Erasmus also refers to a statement by an elderly man, that he had tick paralysis some 30 years ago due to a bontpoot tick, most probably *Hyalomma truncatum*. The chronic course in the above cases in man is strikingly different to the acute onset of symptoms and the quick recovery after the removal of the tick in both Karoo Tick Paralysis and Spring Lamb Paralysis in sheep.

Of these four forms of paralysis, Karoo Tick Paralysis, caused by the bite of *Ixodes rubicundus*, is of the greatest economic importance and has, therefore, received more attention than the other three. All early references in South African literature refer to Karoo Tick Paralysis.

B. Historical

Hellier (1893) was the first to investigate the problem and report upon his findings. Mally (1904) recognised the tick as belonging to the Genus *Ixodes* but identified it incorrectly as *Ixodes pilosus* Koch (1844). We know today that he must have been dealing with *I. rubicundus* as has appeared from the zoological survey (Theiler, 1950). The latter species was described by Neumann (1904), subsequent to Mally's investigations.

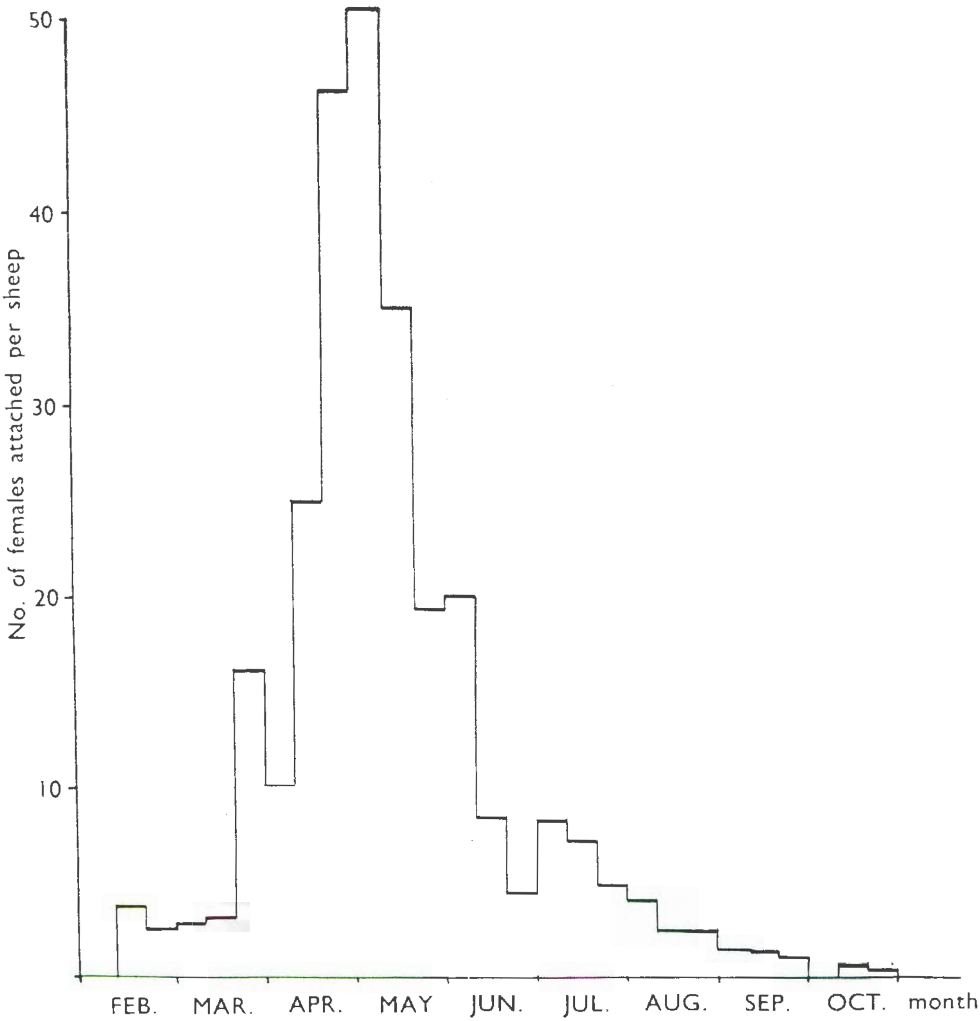
Borthwick (1905) gave a good description of the disease in sheep and had his specimen of the responsible tick identified by Lounsbury as *I. pilosus.* The latter author appears to have been unaware of the fact that he provided Neumann with the specimen from which *I. rubicundus* was described. Lounsbury (1905) stated that *I. pilosus* was the only species of the genus *Ixodes* present in South Africa.

Neumann (1904) names *I. rubicundus* as responsible for a disease in sheep which is not well known and this may well have referred to tick paralysis. Later authors confuse the two species in various ways. Thus Howard (1908) records both and names *I. pilosus* as the Paralysis Tick. Van Rensburg & Silcock (1927), van Rensburg (1928), Bedford & Graf (1939) and du Toit (1942) describe *I. pilosus* as the Paralysis Tick and *I. rubicundus* as the Karoo Paralysis Tick. Similar information appears in later references until Theiler (1949) showed that *I. rubicundus* alone is found in the areas from which tick paralysis has been recorded. Theiler (1950) also gives the distribution of the tick in South Africa by means of a map. Although this information is not yet complete, it indicates the areas involved. McHardy (1951) reports upon his investigations into the problem, but only a reference to his report is available and nothing of the work done by him during the years 1951–53 has appeared in print.

From correspondence and personal communication with McHardy and from information given by farmers in the Graaff-Reinet, Middelburg and Somerset East areas it is possible to deduce that not only has the range of *I. rubicundus* extended considerably in the Karoo but that the disease is spreading at an alarming rate in areas previously free from it.

Little authentic information can be supplied on the economic importance of the disease due to the absence of reliable records but, according to the State Veterinarian of the central Karoo areas, sheep losses attributable solely to it amounted to 10,000 during 1951 in the districts of Graaff-Reinet, Middelburg and Cradock alone. This was due to an unexpectedly early outbreak of the disease and resulted in mortality on certain farms of up to 15 per cent of the total stock. In other years losses were generally small on account of the timely preventive measures undertaken. It is even more difficult to estimate losses in terms of loss of condition, expense necessitated by regular mustering and inspection of sheep, dipping, etc., and it is possible that these amount to even more than the losses due to mortality.

Mally (1904) correlates the occurrence of the disease with the condition of the pasture and with the method of management which in his day included cattle as well as sheep farming and blames understocking as one of the main causes of the problem. The information that the tick is particularly prevalent in long grass pastures or in the presence of certain types of shrub is still frequently advanced by farmers.



GRAPH 1.—Seasonal Incidence of *Ixodes rubicundus* Females on Sheep.

Research into the biological aspects of the problem was commenced by de Vries and Belonje (1949) while the application of the modern synthetic insecticides for the control of the tick was investigated by McHardy (early 1950's). The spread of the tick, the losses attributable to it and the extra work and expense entailed in its control together with the fact that it is involved in the soil and veld conservation programme which is being recommended in the Karoo areas, have necessitated the investigation of the habits and ecology of the species and the conditions under which paralysis of stock occurs. More intensive investigations, as described in this article, were commenced in 1954 in the areas surrounding New Bethesda*, Cape Province, where there is a particularly high incidence of the tick and where severe losses of sheep have been experienced in recent years.

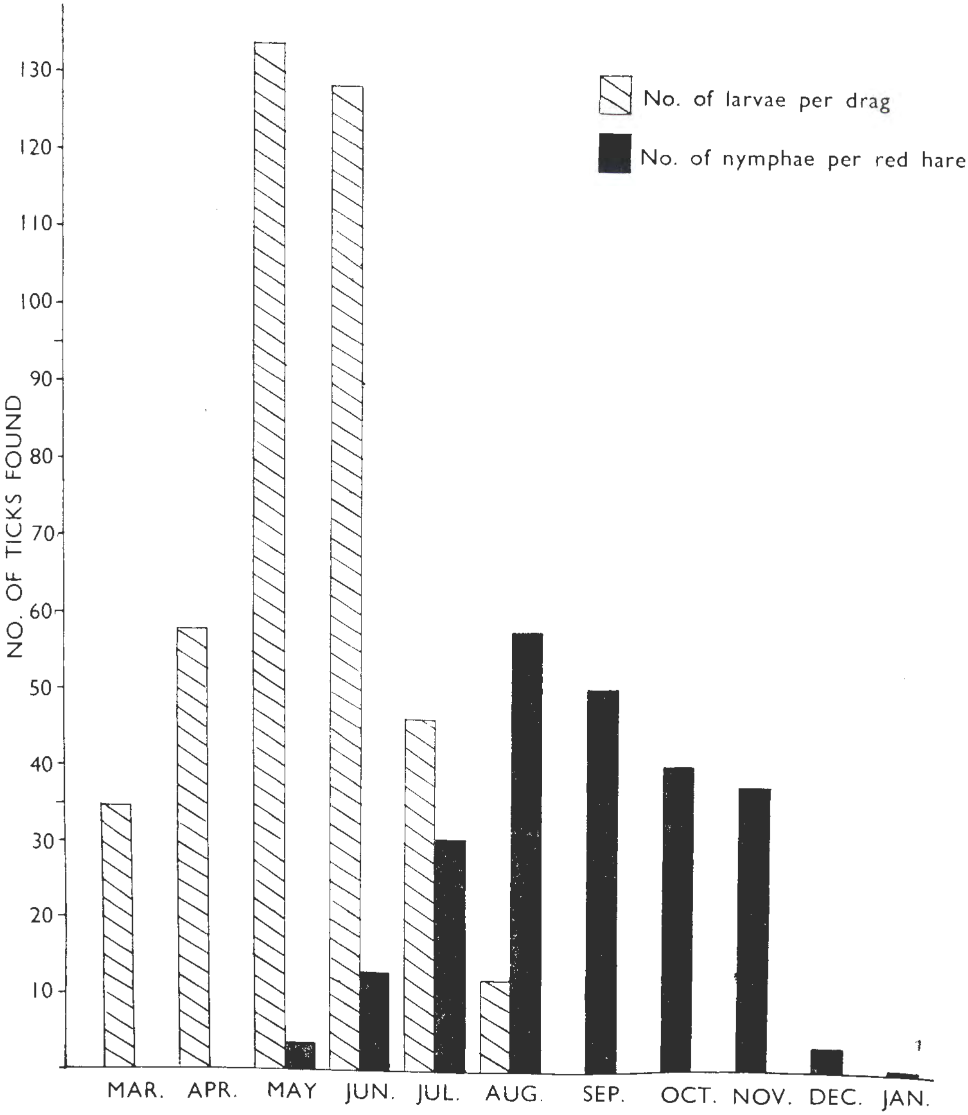
* Also spelt: Nieu Bethesda.

C. BIOLOGY OF IXODES RUBICUNDUS

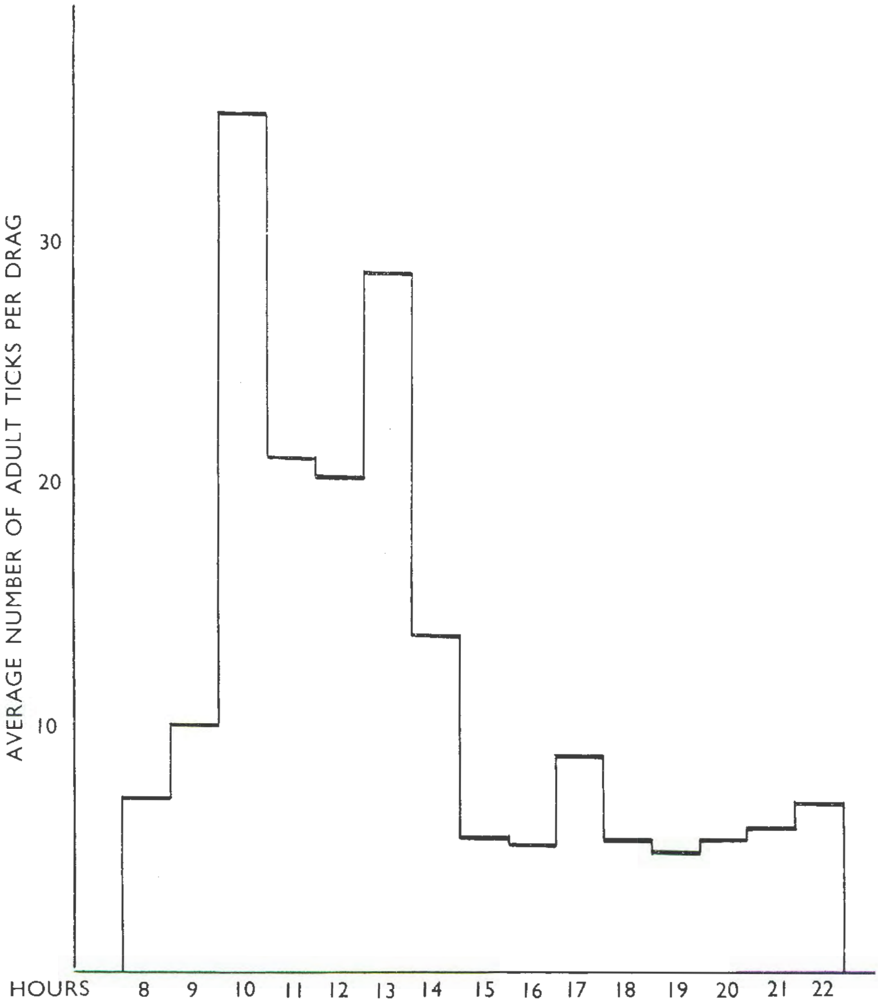
1. *Seasonal Occurrence*

The seasonal incidence of *I. rubicundus* adults in a camp grazed continuously is demonstrated in Graph 1. Tick counts were made at weekly intervals on six sheep during the first year of the investigations and on 10 sheep during the succeeding years. The graph gives the average number of ticks per sheep at intervals of 10 days over three seasons.

The onset of activity of the adults occurs rather suddenly in the second half of February. The peak period is observed during April and May. There-



GRAPH 2.—Seasonal Incidence of Larvae and Nymphae of *Ixodes rubicundus.*



GRAPH 3.—Daily Activity of *Ixodes rubicundus*.

after the activity curve declines very steeply to end with only the odd tick found in October and occasionally even in November. When stock is removed from infested veld during the first part of the active season of the tick a comparatively higher incidence of adults occurs when sheep are reintroduced in the later part of the season; accurate data, however, are not available.

The active period of larvae was determined by dragging, using a modification of the standard flagging method. The average larval count per drag is given for each month in Graph 2. Counts were made on well-infested pasture with a uniform coverage.

It was not possible to employ this method for the nymphae. The active period of the nymphae was established by tick counts on the main intermediate host, the Cape Red Hare, *Pronolagus rupestris saundersiae*. Graph 2 gives the average nymphal counts per red hare for each month.

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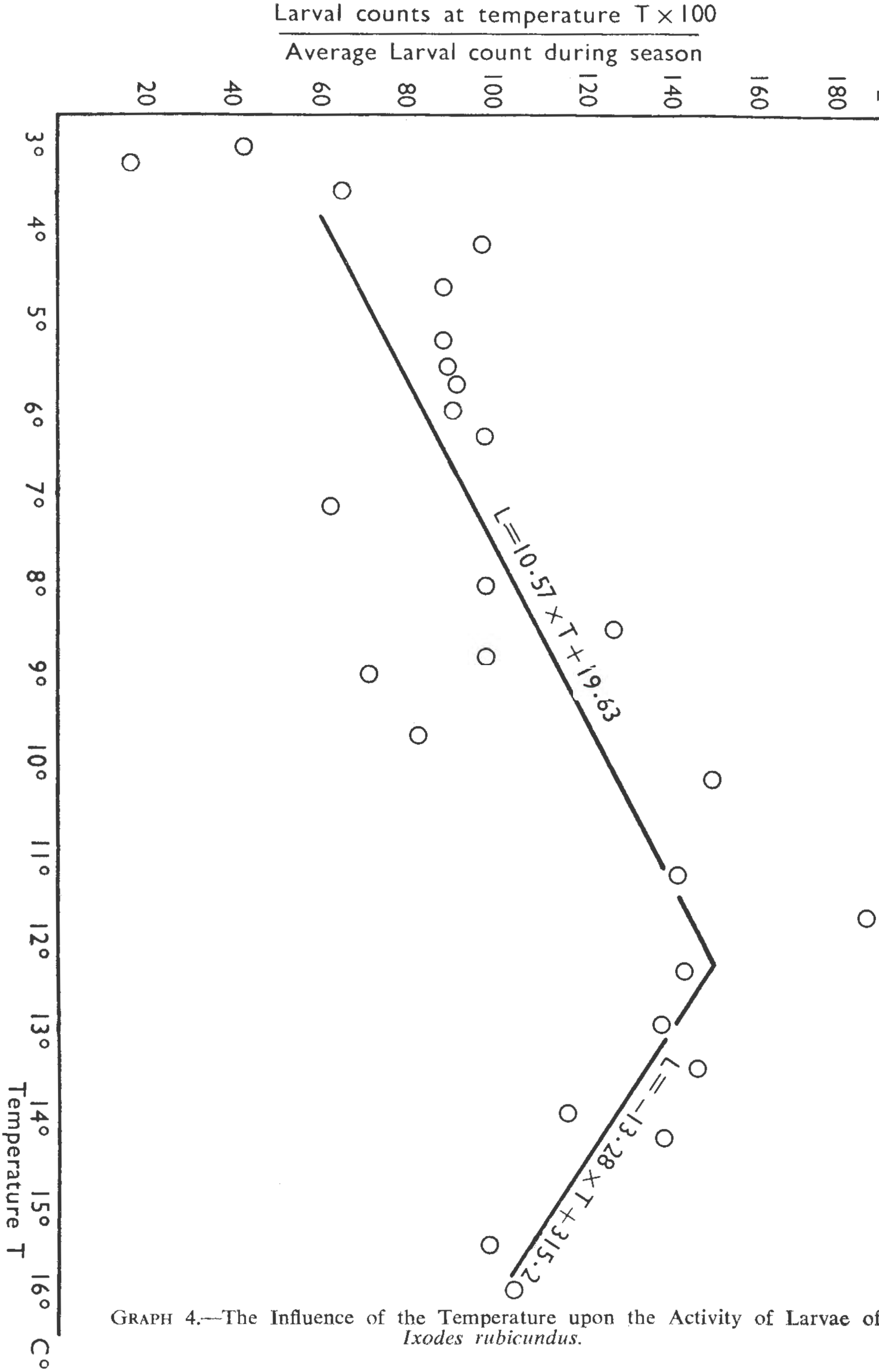


GRAPH 4.—The Influence of the Temperature upon the Activity of Larvae of *Ixodes rubicundus*.

Larval activity begins a little later than does that of the adults, namely, in the middle of March, and its peak is also somewhat later, namely, in May-June. The first nymphae only appear in May on red hares. The peak of nymphal activity is found to be during August and September.

2. *Daily Activity*

Graph 3 shows the averages of adult counts on the dragging apparatus on four different days plotted against the time of the day. The work was discontinued during the greater part of the night. A peak is evident from 10 a.m. to 2 p.m.

The immature stages were found to be inactive during the day-time. They become active approximately half-an-hour after sunset and their active period was shown to last for several hours, but it may be terminated by a drop in temperature or by dew formation.

The influence of temperature upon the activity of the larvae is demonstrated in Graph 4. Temperatures are given as the average of two readings at hourly intervals. The number of larvae found by dragging per hour is given as a percentage of the total number of larvae found in the portion of field involved during the whole season, divided by the total number of repetitions.

The tendency of temperature to influence larval activity is shown by two straight lines determined by the method of least squares. It is noteworthy that larvae were found to be active at temperatures as low as 3·1° C. It may be remarked that the larvae of *Rhipicephalus evertsi* were found to be active even at temperatures close to freezing point.

3. *Hosts and Intermediate Hosts*

Table 1 gives the wild mammals trapped or shot in infested areas and examined for all stages of the tick. On 40 birds representing 19 different species no stage of *I. rubicundus* was found.

TABLE 1

List of Wild Hosts of Ixodes rubicundus

Name of Animal	No. of Animals Examined	No. of Ticks Found			
		Larvae	Nymphae	Females	Males
1. *Elephantulus capensis karroensis*.	7	88	77	0	0
2. *Elephantulus vandami*...........	2	X	X	0	0
3. *Proteles cristatus cristatus*.......	1	0	1	2	0
4. *Caracal caracal caracal*.........	3	0	0	X	X
5. *Felis lybica cafra*...............	3	0	0	X	X
6. *Thos mesomelas mesomelas*......	2	0	5	1	0
7. *Redunca fulforufula*.............	1	0	0	1	3
8. *Pelea capreolus*................	3	0	0	17	12
9. *Raphicerus campestris campestris*.	3	0	0	4	9
10. *Aethomys namaquensis centralis*..	12	0	1	0	0
11. *Lepus capensis centralis*.........	9	0	1	0	0
12. *Lepus saxatilis albaniensis*.......	10	20	8	14	6
13. *Pronolagus rupestris saundersiae*..	76	660	2,029	9	3

X = Some ticks found.

The imagines are found mainly on domestic stock Nymphae have been collected off sheep occasionally. A single larva has also been collected off a sheep. Other domestic animals are free of immature stages.

The following animals taken on infested pastures were found to be free of all stages of *I. rubicundus,* figures in brackets indicating the number of animals examined:—

Crocidura argentata (1), *Myonax pulverulentus ruddi* (1), *Surricata surricata sur.* (1), *Procavia capensis vanderhorstii* (21), *Damaliscus albifrons* (4), *Antidorcas marsupialis marsupialis* (4) — this species has been found by Belonje (pers. comm.) to carry imagines — *Oreotragus oreotragus oreotragus* (2), *Hysterix africae-australis* (3), *Pedetes cafer albaniensis* (9), *Graphiurus ocularis* (3), *Gerbillus paeba paeba* (1), *Malacothrix typicus typicus* (1), *Petromyscus collinus* subsp. nova * (3), *Leggada minutoides minutoides* (1), *Myomys colonus colonus* (1), *Rhabdomys pumilio cradockensis* (5).

The host list shows that the *Menotyphla* (*Elephantulus*) and the *Lagomorpha* (*Lepus and Pronolagus*) are the main intermediate hosts, followed in importance by the *Canidae* (*Proteles and Thos*). The *Rodentia* appear not to act as intermediate hosts as a rule, the one nymph found on one out of 34 animals of this order examined is obviously an exception. The adult tick is found on *Artiodactyla* (*Redunca, Pelea, Rhaphicerus* and *Antidorcas*). The absence from *Damaliscus* can be attributed to the custom of this species of avoiding the mountains. The Carnivora (*Proteles, Caracal, Felis* and *Thos*) serve as incidental hosts of the adult tick. The absence of the tick from the two Carnivora (*Myonax* and *Surricata*) could be accidental. Some adults were found on *Lepus saxatilis* and *Pronolagus,* but the number was small.

Lepus capensis obviously is only an exceptional host. What was said about *Damaliscus* can be applied to this hare, which also avoids the mountains. The one specimen on which the one nymph was found, was shot in a flat camp covered by *Danthonia disticha* (see Influence of Veldtype).

The view expressed by Milne (1948) for *I. ricinus* that there is a tendency for the smaller host species to carry the smaller stages of the tick and vice versa also appears to hold for *I. rubicundus.*

D. The Behaviour of the Tick on the Sheep

During the course of the investigations in the Sneeuberg area of New Bethesda, information was gathered as to the site of attachment, the period of engorgement of the female and of copulation on the sheep, all factors of considerable significance in control by dipping. Also, the findings on the time required for engorgement may assist in an understanding of the conditions under which the tick is capable of causing paralysis.

1. *Attachment Sites*

The female of *I. rubicundus* attaches to the ventral aspect of the body, and to the legs from the knee or hock to the fetlocks and heels (Stampa & Du Toit, 1957). For purpose of record the areas of attachment have been subdivided into 10 regions. Table 2 gives the number out of 955 attached to each region

* The assumption that the *Petromyscus* sp. represents a new subspecies has been confirmed by Mr. Davis, S.A.I.M.R.

as observed on ewes. Table 3 gives similar information regarding 539 females attached to lambs, two to six weeks old. The tables also give the number of ticks attached to each region which reached full engorgement, the number that died and the number removed by the sheep.

TABLE 2

*Place of Attachment and History of Female Ticks on Ewes**

Region	Total No.		Incompletely Observed	Engorged		Died		Removed by Sheep	
	No.	%	No.	No.	%	No.	%	No.	%
Bare parts of head..........	34	3·6	4	22	73·4	8	26·6	0	—
Woolled parts head and neck	48	5·0	9	35	89·7	4	10·3	0	—
Shoulders and sternum......	82	8·6	8	68	91·8	6	8·2	0	—
Woolled parts of forelegs....	144	15·1	34	99	90·0	9	8·2	2	1·8
Bare parts of forelegs.......	100	10·5	13	71	81·6	13	14·9	3	3·5
Woolled parts of thorax.....	95	9·9	16	75	95·0	4	5·0	0	—
Bare parts of thorax........	127	13·3	17	97	88·2	12	10·9	1	0·9
Woolled parts of belly......	44	4·6	17	25	92·5	2	7·5	0	—
Woolled parts of hindquarters	189	19·8	46	125	87·5	18	12·5	0	—
Bare parts of hindquarters...	92	9·6	18	58	78·4	16	21·6	0	—
TOTAL................	955	—	182	675	—	92	—	6	—
Total head and neck........	82	8·6	13	57	82·6	12	17·4	0	—
Total forequarters..........	466	48·8	80	342	88·6	38	9·8	6	1·6
Total hindquarters.........	281	29·4	64	183	84·4	34	15·7	0	—
Total for bare parts........	353	37·0	52	248	82·4	49	16·3	4	1·3
Total for woolled parts.....	602	63·0	130	427	90·5	43	9·1	2	0·4

* For footnote see table 3 on following page.

The woolled parts of the body are preferred to the bare parts. This applies more to ewes carrying wool of one inch or more in length, than to lambs. In ewes twice as many ticks attached to the woolled parts of the body than to the bare parts, while the proportion was 1·25:1 in the lambs. In this respect the behaviour of *I. rubicundus* is different from that of *I. ricinus*, where Milne (1947) found only 16 per cent of the *I. ricinus* females attached to the woolled parts of sheep.

These tables show that the chances of reaching full engorgement are greater for the ticks attached to woolled parts than for those attached to bare parts. Removal of ticks by the sheep plays only a minor part in accounting for this, more ticks being removed by lambs than by ewes.

Only very few ticks are found attached to the head; of these a considerable percentage fails to reach full engorgement. In this *I. rubicundus* also differs from *I. ricinus*, where Milne (1947) and Evans (1951–52) record a high percentage of *I. ricinus* engorging on the head.

On the bare parts of the hindquarters the percentage of ticks that fail to reach full engorgement is also high.

TABLE 3

*Place of Attachment and History of Female Ticks on Lambs**

Region	Total No.		Incompletely Observed	Engorged		Died		Removed by Sheep	
	No.	%	No.	No.	%	No.	%	No.	%
Bare parts of head.........	9	1·7	3	2	33·3	3	50·0	1	16·7
Woolled parts of head and neck	10	1·9	6	3	75·0	1	25·0	0	—
Shoulder and sternum......	72	13·4	26	42	91·4	4	8·6	0	—
Woolled parts of forelegs....	36	6·7	14	20	91·0	2	9·0	0	—
Bare parts of forelegs.......	98	18·2	34	54	84·5	10	15·5	0	—
Woolled parts of thorax....	34	6·3	11	23	100·0	0	—	0	—
Bare parts of thorax........	84	15·6	16	63	88·3	5	11·7	0	—
Woolled parts of belly......	29	5·4	19	10	100·0	0	—	0	—
Woolled parts of hindquarters	125	23·2	35	76	84·5	11	12·2	3	3·3
Bare parts of hindquarters...	42	7·8	9	26	78·8	3	9·1	4	12·1
TOTAL................	539	—	173	319	—	39	—	8	—
Total head and neck........	19	3·5	9	5	50·0	4	40·0	1	10·0
Total for the forequarters...	252	46·7	75	160	90·4	17	9·6	0	—
Total for the hindquarters...	167	31·0	44	102	83·0	14	11·4	7	5·7
Total for bare parts........	233	43·2	62	145	84·8	21	12·3	5	2·9
Total for woolled parts.....	306	56·8	111	174	89·2	18	9·2	3	1·5

* The ticks attached to each region are given as a percentage of the total number. The numbers of ticks that were not observed during their whole period of attachment are deducted from the totals for each region. Of those with complete records, the numbers and percentages are given which reached full engorgement, died *in situ* and were removed by the sheep.

In lambs, Evans (1951-52) found more *I. ricinus* females attached to the hindquarters and fewer to the head than in the long-woolled ewe. A similar tendency is apparent, although not proved, by the figures presented in Tables 2 and 3. The explanation offered by Evans, namely, that the tick is handicapped by the long wool in its migration from head to hindquarters might also be applicable to *I. rubicundus*.

2. *Period of Engorgement*

Most of the females reached full engorgement within four to seven days, in some cases even within three days. Exceptionally long periods of attachment were observed in cases where sheep had grazed for several weeks in tick-infested veld, as also when the temperature rose to over 25° C maximum. Ticks which failed to engorge within 10 days reached full engorgement only in very exceptional cases; as a rule they died *in situ* or dropped off semi-engorged and failed to lay eggs.

The quickest engorgement recorded was when the temperature remained for a long period between 8° C and 15° C. Sometimes, however, when the temperature had approached 20° C for several days, rapid engorgement took place within a single night after the temperature had dropped to hard frost level. Engorgement is also much more rapid when the sheep is paralysed.

The average time for reaching full engorgement for the different regions of the body is given in Table 4.

TABLE 4

Average Engorgement Times on the Different Parts of the Body of Ewes and Lambs

Region of the Body	Ewes		Lambs	
	No. of Ticks Observed	Engorgement Time in Days	No. of Ticks Observed	Engorgement Time in Days
Bare parts of head	22	5·4	2	5·0
Woolled parts of head and neck	35	7·0	3	6·3
Shoulder and sternum	68	6·0	42	4·9
Woolled parts of forelegs	99	5·3	20	4·9
Bare parts of forelegs	71	5·3	54	5·4
Woolled parts of thorax	75	7·6	23	5·1
Bare parts of thorax	97	5·2	63	5·2
Woolled parts of belly	25	6·3	10	5·2
Woolled parts of hindquarters	125	5·5	76	5·7
Bare parts of hindquarters	58	5·7	26	5·6

On ewes ticks require more time to engorge on the woolled parts of the head, neck, thorax and belly than on other parts. In lambs no difference in the engorgement times between the ticks attached to the different regions is found. It is noteworthy that the tick does not engorge more rapidly when attached to sites where the prospects of reaching full engorgement, e.g. woolled parts of thorax, appear to be better than elsewhere, e.g. bare parts of the head (cf. Tables 2 and 4). The average engorgement time for all ticks observed on ewes is 5·8 days, on lambs 5·46 days.

The effect of movement by the sheep upon the rate of engorgement was examined in two groups of three lambs each. The lambs were kept under observation for four weeks during which the one group was chased every day for 1½ miles and the other not. For the remainder of the day both groups remained tethered in tick-infested veld. Fifty-one females were picked up by each group. The average engorgement time was 5·22 days for the exercised group and 5·25 days for the other, i.e. approximately the same.

3. *Variations During the Process of Engorging*

Two distinct stages can be recognised during the course of engorgement of the tick; the first, from attachment to about half the final size, the second, from half to full engorgement. In this respect *I. rubicundus* behaves like *I. ricinus*, Lees (1946), and Balashov (1955).

The first stage is completed usually within three to five days, exceptionally within two days. When half engorged, the tick sometimes remains unchanged at this size for a couple of days, after which full engorgement is reached within 24 hours, generally during the night, and detachment occurs in the morning. The tick retains a reddish-brown colour during the first stage of engorgement and assumes a slate blue colour when fully engorged.

However, when ticks attach themselves to sheep that have been grazing in tick-infested veld for several weeks they may fail to complete the second stage, although they may slowly increase in size without changing colour, finally dying without reaching full engorgement, or detaching, dropping off and failing to lay eggs. Others re-attach at a different site where they sometimes reach full engorgement. Almost replete specimens under these conditions lay eggs but fewer than do those which engorge normally.

A small abscess is frequently seen at the site of detachment. This condition suggests the "local immunity" described by Enigk (1953).

4. *The Diminishing Chances of Engorgement*

During the period of normal viability of the tick the longer sheep are kept on tick-infested veld the greater becomes the percentage of female ticks that die after attachment. Table 5 records the number of females that died *in situ* expressed as a percentage of all females observed and plotted against the time the sheep spent in tick-infested veld.

TABLE 5

Females that Failed to Engorge in Relation to the Time the Sheep Spent in Tick-infested Veld. Averages of 6 Sheep

Week	1	2	3	4	5	6	7
Ticks dead	4·4	10·8	10·3	6·9	18·5	26·9	24·3

The percentage of ticks that die *in situ* increases from 4·4 to 24·3 per cent. Although the number of repetitions in this test is small it can, however, be accepted that the chance of the tick reaching full engorgement diminishes with the length of time the sheep spends in tick-infested veld.

5 *Copulation*

Records of copulating couples were kept for 797 females. These were checked once daily throughout the entire duration of attachment during which all reached full engorgement. Of these ticks 283 were never found copulating, 483 copulated for one continuous period of one to nine days, 31 copulated twice with an interval between the two copulations.

The number of ticks (283) that were never found in copulation is strikingly high, many of these engorged in as short a period as three to four days. It is possible that they may have copulated on the ground before attaching. That this can happen has been established by direct observation. It is also possible that copulation over a very short period could have taken place between observations.

TABLE 6

Number of Ticks Found in copulo *During the Number of Days Specified in Relation to the Period of Engorgement*

Period to Reach Engorgement	Number of Ticks *in copulo*									
	Number of Days *in copulo*									
	0	1	2	3	4	5	6	7	8	9
3 days...............	10	10	2	3	—	—	—	—	—	—
4 days...............	67	23	21	27	7	—	—	—	—	—
5 days...............	77	56	28	43	28	11	—	—	—	—
6 days...............	77	55	33	35	21	9	5	—	—	—
7 days...............	33	14	19	8	4	4	3	1	—	—
8 days...............	13	10	6	5	2	3	2	1	0	—
9 days...............	2	2	2	1	0	1	0	0	0	1
10 days...............	0	3	0	1	0	0	0	0	0	0
11 days...............	2	1	0	0	0	0	0	1	1	0
12 days...............	2	0	0	0	0	0	0	0	0	0
13 days...............	0	0	0	0	0	0	0	0	1	0
TOTAL..........	283	174	111	123	62	28	10	3	2	1

Copulation as from the first day of attachment does not necessarily result in the female engorging more quickly. There is, however, a strong tendency for this to be the case as is shown in Table 7.

TABLE 7

Commencement of Attachment and of Copulation

Period to Reach Engorgement	Number of Females *in copulo*							
	Days of Attachment on which Copulation Started							
	1st	2nd	3rd	4th	5th	6th	7th	8th
3 days............................	4	5	6	—	—	—	—	—
4 days............................	17	34	19	8	—	—	—	—
5 days............................	24	42	43	34	23	—	—	—
6 days............................	11	32	39	37	26	14	—	—
7 days............................	3	3	8	17	12	8	3	—
8 days............................	3	4	4	5	6	1	4	2
TOTALS.................	62	120	119	101	67	23	7	2

The table shows that the bulk of the ticks reaching full engorgement within a short period are *in copulo* early. The greater number of the females reaching full engorgement within as long a period as seven or eight days are *in copulo* as from the fourth or fifth day of their attachment.

E. Survey Methods and some Findings

Tick population counts in the field can be made on sheep pastured on tick-infested areas, or can be obtained by the blanket dragging or flagging method (Milne, 1943). Milne found that reliable results could be obtained from groups of 20 sheep grazing freely in specified localities and examined at weekly intervals. For comparative surveys by dragging he recommends comparison on the basis of uptake per drag, each made over 50 yards, these to be carried out simultaneously.

It is difficult to make counts on sheep grazing freely in paddocks under Karoo conditions in that the camps are usually very large and the mustering of sheep for inspection very laborious. Also it is impossible to compare tick densities in the different types of veld (pasture) by allowing free grazing, in that in most instances, several veld types are included within a single camp.

1. *Tethering Experiments*

To overcome these difficulties and drawbacks sheep were tethered by means of chains, 5·68 meters long to stakes driven into the ground. The uptake of ticks was recorded daily and the sheep were moved to a new site each day. The method has the advantage that tick densities in the different veld types encountered in each camp can be compared and the necessity for mustering sheep was obviated. Although the movement of tethered sheep is limited in comparison with that of sheep running free in camps, it was found as a rule, that more ticks were picked up by them, than by the free-running controls. Practically all the data referred to in Section E. of this article were obtained by this method. However, for gathering data on tick densities in different localities less time-consuming ways had to be found.

2. *Dragging Experiments*

A. Apparatus

The standard dragging method, entailing the drawing of cloth fabrics over the grass so much favoured overseas, was found to be unsuitable for Karoo conditions, in that the cloth sheet "rides" over the coarse shrubs and fails to make contact with the ticks.

The first successful assay was done with an apparatus consisting of a wooden bar, 6 feet in length, to which 12 "tails" of tanned sheep skin with wool attached were fastened so as to trail behind the bar when this was dragged horizontally over the veld. Weights were attached to the end of each "tail" in order to keep it down within the vegetation. This apparatus picked up the adults of *I. rubicundus* very satisfactorily but had the disadvantage that the "tails" did not last long.

Dragging showed that the immature stages of the tick occur at higher levels in the vegetation than do the adults. Although the ordinary sheet fails to pick up worthwhile numbers of larvae and nymphae the modified flag picked up large numbers when no weights were attached to the ends of the "tails". The weights required for dragging in the case of adult ticks were reponsible for extensive damage by tearing the "tails".

Different fabrics were tested in order to find the one most attractive to the ticks. These tests were simple to carry out in that six " tails " of each of two materials to be compared were attached simultaneously to the bar. Strips of a strong flannelette material four inches in width were folded along the length and the edges stitched together to form tubes 18 × 2 inches with the fluffy side out, as illustrated in Fig. 1 and 2. These were found the most satisfactory in picking up the immature stages. Adults were strongly attracted to corduroy material, whereas not a single immature stage was picked up by this fabric. Tests were also conducted with the skins of antelopes. The skins of *Redunca fulvorufula, Pelea capreolus* and *Raphicerus campestris* pick up adults but not immature stages. This observation may explain why the immature stages were not found on these antelopes.

FIG. 1.—Modified Dragging Apparatus.

The " tails " of tanned sheepskin did pick up the immature stages but not in any numbers.

The highest larval count for any one drag was 206, the highest nymphal count eight. Up to 64 adults were picked up per drag with the weighted sheepskin tails but only odd ones with the ordinary apparatus using flannelette " tails ".

B. Procedure

The following procedure has been found to yield the most reliable results in the collection of tick populations for comparison in the different types of veld.

FIG. 2. Modified Dragging Apparatus.

In each area to be surveyed 12 traverses, 50 meters in length and 8 meters apart, were marked out by means of painted numbered stakes, different colours being used to denote even and odd numbers. A stake avery three to four yards was adequate.

Surveys began half-an-hour after sunset, paraffin pressure lanterns being used for illumination. Dragging was done at a slow pace so that each 50 meter traverse was covered in approximately $1\frac{1}{2}$ minutes. The larvae were usually found on the flattened sides of the flannelette tubes comprising the " tails " but sometimes also on the edges. All the larvae from each " tail " were placed on cellotape (Scotch Tape) and the strip of cellotape for each " tail " representing a single drag was stuck to a recording card with the date and locality noted. With the dorsal side up identification of the larvae is possible by examination through the transparent tape using the low or medium power of a field microscope. If the ventral side is up the tape must be removed from the card and the larvae identified from the other side.

Besides *I. rubicundus*, larvae of the following species have been found: *Rhipicephalus arnoldi*, *R. capensis*, *R. evertsi*, *R. oculatus*, *Amblyomma marmoreum* and *Hyalomma* spp.. *R. evertsi*, *A. marmoreum* and *Hyalomma* spp. can be differentiated from *I. rubicundus* by the naked eye.

Temperatures were taken at hourly intervals four inches above ground level, in the middle of each area surveyed. The influence of temperature upon larval activity is seen to be striking (Graph 4). The differences of temperatures recorded in plots only a couple of hundred yards apart were found to be marked, particularly where readings were taken on slopes facing in different directions.

Larval counts were low when the temperature dropped below 3·8° C or when dew formation commenced, as also when a strong wind was blowing. All alterations in the weather experienced at the time were recorded on the cards to which the ticks captured were attached.

For comparison of tick populations in different veld types only those figures were used which were obtained under similar conditions. Results obtained under windy conditions and those obtained when dew began to form or when the temperature dropped below 3·8° C were discarded. The larval counts were corrected for temperature, using the correction coefficients found in Graph No. 4. The "Chi-Square-test" and the "Analysis of Variance" were used to indicate the significance of the differences.

C. *Findings*

Distribution of Larvae in the Field. The uniformity of larval distribution is remarkable as is evident in Table 8.

TABLE 8

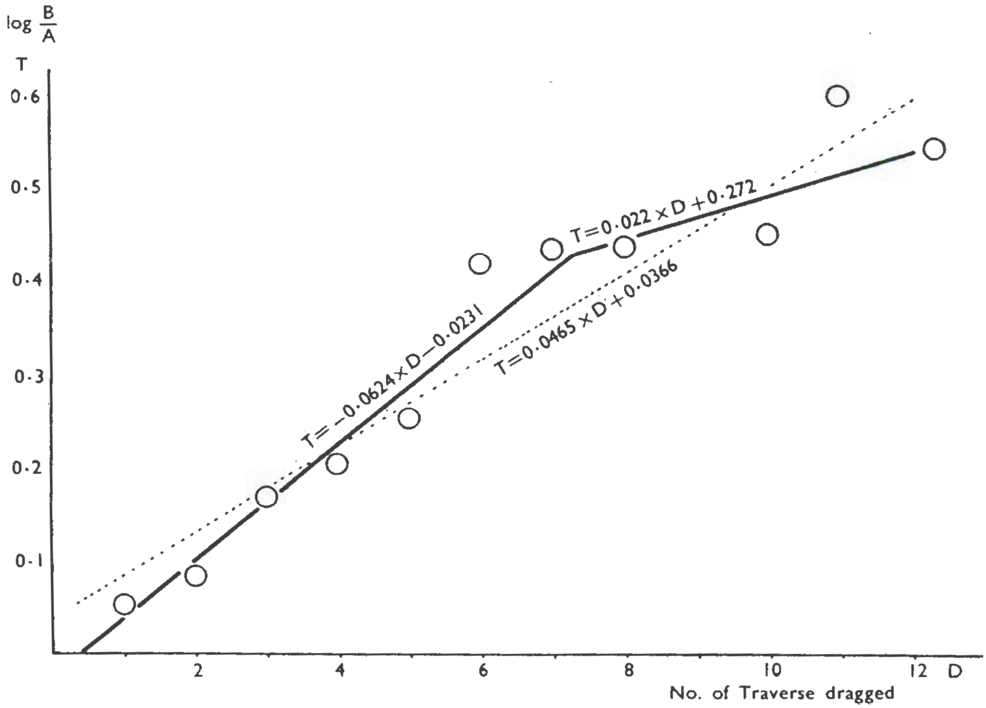
Larval Counts from 12 "Tails" During 12 Drags

Traverse No.	1	2	3	4	5	6	7	8	9	10	11	12	Total
Tail No.													
1	0	0	0	0	2	1	0	0	0	0	0	1	4
2	0	0	0	0	2	0	0	0	0	0	0	0	2
3	0	0	0	0	3	4	0	0	0	0	0	0	7
4	0	0	0	1	6	1	1	0	0	1	0	1	11
5	3	0	0	0	8	1	0	0	0	0	0	2	14
6	1	0	0	0	11	2	1	1	0	0	0	0	16
7	1	1	0	0	6	3	0	0	0	0	0	0	11
8	0	1	0	0	7	1	0	0	0	0	0	0	9
9	0	0	0	1	5	1	0	0	0	0	0	0	7
10	1	0	0	0	0	5	0	0	1	0	1	0	8
11	0	0	0	0	2	0	1	0	0	0	0	2	5
12	5	0	1	0	1	2	0	0	1	2	0	0	12
TOTAL	11	2	1	2	53	21	3	1	2	3	1	6	106

This uniformity could perhaps be attributed to some extent to horizontal movement on the part of the larvae. If this were so one would expect the tick counts from adjacent "tails" to exert an influence upon each other. The statistical analysis of 22 drags reveals, however, that there is no relation between the individual tick counts from neighbouring "tails", each "tail" representing an individual collection. It can be deduced either that the larvae do not move horizontally at all, as is the case with the larvae of *I. ricinus* (Lees & Milne, 1951) or that their horizontal movement is so great that this method of testing cannot reveal it. The explanation of the uniformity of larval distribution of *I. rubicundus* thus remains unknown.

Losses of Larvae During the Course of Dragging.—A certain number of ticks picked up in the course of dragging is usually lost again (Milne, 1943). These losses can be attributed to the abrasive effect of vegetation, stones, etc., on the flannelette strips or "tails", resulting in a varying percentage of the ticks being lost in relation to the distance dragged. If abrasion were the only cause of loss the number of ticks on the apparatus would increase per traverse (provided the ticks were only counted and not picked off) by an ever-decreasing amount and should therefore follow a logarithmic course, i.e. the log of the tick counts after each traverse would fall into a straight line. This would be the case if the ticks were evenly distributed over the area surveyed.

Tick densities, however, vary considerably and the effect of these variations upon the logarithmic progression can be excluded by removing and counting the ticks from the odd numbered "tails" only (A) at the end of each traverse, at the same time leaving and counting the ticks on the even numbered "tails" (B). The figure obtained by dividing B by A would produce the same picture as would be the case in veld with an even tick distribution if counts were made at the end of each traverse without any ticks being removed from the apparatus.



GRAPH 5.—Logarithms of the Number of Larvae on the "B Tails" divided by the Number on the "A Tails" plotted against the Number of Traverses.

The result is shown in Graph 5, which represents the sum of 25 repetitions. The graph shows that only the values of the first eight traverses appear to follow a straight line. Thereafter losses become greater. [The connection of the points by the line showing a break is close to being significantly better statistically than the connection of the points by a straight line (dotted in Graph 5). The sum of the squares of the distances of the points from the line, viz. 0·0018988 in the case of the line showing the break, and 0·003613 in the case of the straight line]. This observation indicates the probability of a second factor being present which causes additional loss of larvae, commencing at a certain time after the beginning of the experiment. Fatigue of the ticks or voluntary detachment could be responsible for this additional loss observed.

F. The Free-Living Tick and its Environment

1. *General Aspects*

Each tick species requires certain specific environmental conditions for its development and survival; some ticks are able to exist under a greater variety of conditions than others, whereas many are considerably restricted by their specific requirements. Temperature, humidity, soil, altitude, aspect of slope and plant coverage all play a direct role in creating microclimatic conditions suitable or unsuitable to each tick species. The factors influencing the distribution of the hosts also indirectly affect the tick. The picture of the general distribution of a tick species can thus be taken to indicate its requirements.

The South African tick survey (Theiler, 1950) shows *I. rubicundus* to be confined to the moister regions of the Karooveld, regions which are hilly or mountainous rather than flat and open, with localities having a distinctive type of Karoo vegetation. The tick is absent in areas with a rainfall below 10 inches per annum.

A study of the distribution of the tick in relation to the veld-types (types of pasture) present in the heavily infested area of the Sneeuberg Range around New Bethesda was undertaken with the object of establishing the conditions necessary for the survival of the tick. Areas in which the tick is present but has rarely or never caused paralysis were examined as well as areas in which tick paralysis is of such regular occurrence that steps for the protection of stock have to be taken every year.

2. *Veld Types*

The veld in the Sneeuberg area offers an endless number of variations. For this survey these variations have been grouped into six types namely:—

(i) Sweet-grass veld, (ii) danthonia veld on slopes, (iii) danthonia veld on flats, (iv) Karoo veld on slopes, (v) Karoo veld on flats, (vi) rhenoster-harpuis veld.

The danthonia and Karoo veld offer different conditions for the tick on the slopes than do those on the flats. Mixtures of these six basic veld-types are plotted on the map (Map 1) in colours.

(i) According to Acocks (1953) sweet-grass veld was the main type present in the area before white settlement. It consists of mixtures of the following species: *Themeda triandra, Tetrachnia* spp.,

FIG. 3.—Sweetgrass Mountain Veld, one year's growth. Note how little shelter is offered by the grass.

Eustachus pespiloides, Heteropogon contortus, Sporobolus fimbriatus, Digitaria arogyrogropta, Eragrostis curvula, E. chloromelas, E. obtusa, Hyparrhenia hirta. The first four species are the more valuable perennial grasses providing good food for stock in winter; the last six species are valuable for summer grazing only, being less palatable when dry. What is significant of this sweet-grass veld is the fact that it can be grazed down completely. Figure 3 shows one year's growth of sweet-grass mountain veld.

(ii) Danthonia or sourveld contains as the main coverage the sour grasses *Danthonia disticha* and *Aristida diffusa.* Some sweet-grasses and karroid shrubs may also be present. Stock only eat *D. disticha* and *A. diffusa* when the grass is still young. Cattle and horses graze them down better than do sheep. Hence, where sheep constitute the main line of farming, as is the case on all the farms surveyed, danthonia veld is inclined to grow out of hand and form a dense mass of old, dried-out, unpalatable material as is shown in Fig. 4. In this stage sheep, unless very hungry, only touch the seed of *D. disticha,* and grazing does not prevent the formation of the compact wiry tufts so characteristic of sour veld. In former times cattle-farming played a bigger role in the area and the *Danthonia disticha* tussocks remained much smaller.

FIG. 4.—Karoo Mountain Veld

During the course of the investigations it was possible to show that the development of young valuable grasses is handicapped by the presence of these masses of *D. disticha*. This indicates that for an improvement of the veld, which can take place by the invasion of good grasses, it is necessary to either remove the tussocks formed by *D. disticha* or to keep them short.

The role played by *A. diffusa* is similar. In the Sneeuberg Range this grass in only eaten by small stock when young and not at all when dry. In other areas of South Africa, however, this grass is fairly well grazed by all stock and is looked upon as valuable (Acocks, pers. comm.).

(iii) Karoo veld contains mixtures of the following plants: *Pentzia incana, P. globosa, Eriocephalus glaber, Ester immericatus, Chrysocoma tenuifolia, Walfrida saxatilis* and the edible grasses, *Eragrostis obtusa, E. lehmanniana, Aristida congesta, Tragus culerioides.* On mountains, *P. globosa* is more prevalent whereas in flat country, *P. incana* plays the bigger rôle. *Ch. tenuifolia* is unpalatable. *P. incana, P. globosa, E. glaber* and *E. immericatus* are well grazed under certain conditions, under other conditions not. The grasses provide good food when young, *A. congesta* is also well grazed when dry after having lost its seed, i.e. in August/September. Fig. 5 shows Karoo veld on a mountain.

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(iv) In rhenoster-harpuis veld the shrubs *Euryops racemosus, Elytriopappus rhinocerotis,* and plants of similar taller habit, form the main coverage. Some *D. disticha,* a few edible grasses and short karroid shrubs may also be present. Only the blossom of *E. racemosus* is eaten by stock, otherwise no food is provided by the typical plants of the rhenoster-harpuis veld type. It is significant, furthermore, that its shrubs grow considerably taller than do the karroid shrubs, reaching two to three feet in height. Fig. 6 shows rhenoster-harpuis veld in flat country in the foreground and on a hill in the background. In flat country the ground is shaded by the vegetation but no masses of plant debris accumulate. On mountains the coverage of the ground is somewhat denser and heaps of leaflets are frequently found accumulated under the plants or between stones.

A mixture of danthonia veld with rhenoster-harpuis veld is frequently met with in the Sneeuberg area. Fig. 7 shows such a veld type.

FIG. 5.—Danthonia Mountain Veld. Note the dense mass of tussocks.

FIG. 6.—Rhenoster-Harpuis Veld.

FIG. 7.—Danthonia-Rhenoster-Harpuis Mountain Veld.

FIG. 8.—*Rhus erosa.*

Taller woody shrubs growing four to six feet high are met with in certain localities. *Rhus erosa* is shown in Fig. 8 as a typical example. It provides no food for stock: masses of debris of dropped leaves accumulate beneath it. It appears to provide shelter, and perhaps also food, for the main intermediate host of the tick, *Pronolagus crassicaudatus* sp. This hare, is more abundant in veld intermingled with *Rhus erosa* than where other or shorter shrubs only are present.

The trees *Acacia karoo* and *Portulacaria efra* are met with in the warmer river valleys, sometimes also on hill slopes where the tick can exist. Their leaves form a very valuable stock food.

(*a*) *Mapping the Occurrence of the Tick*

In mapping a distinction was made between camps in which the tick was found to be present, camps in which the tick was found to be absent and camps in which the presence of the tick could be assumed according to the veld type. Most of the information for this map was obtained from farmers.

When the information was given that the tick was present, this was accepted as correct whenever the camp concerned had veld types which had been established as being suitable for *I. rubicundus*. All but one infested camp, according to its owner, contained veld suitable for the tick and in this one exceptional case the tick species present proved to be *R. capensis*.

The information that the tick was absent was accepted for all camps that included only veld types known to be free of the tick as established in other surveys. When veld suited to the tick was also included in a camp described as tick-free by the owner, it was surveyed by shooting and examining some of the intermediate hosts, i.e. *P. crassicaudatus* or *Elephantulus* spp., and by examining stock or by dragging for immature stages. In all but one case ticks were found to be present. Such an area obviously suitable for the species in which the tick was described as not present and in which it was not found, existed in the southern half of the farm Dorsfontein, the adjacent camps of the farm Seekoegat and a small adjoining area in the south of the farm Kismet. This suggests that the tick has not yet been introduced, and that the veld may only have become suitable for the tick recently. In fact, neighbouring areas are known to have become infested quite recently, e.g. Dorsfontein, northern camp—1956, Koppermyn, southern half—1957, and Rietpoort, southern camp—1957. An infestation of the as yet uninfested but suitable veld on Dorsfontein may, therefore, very probably still take place.

A separate symbol was used in the map indicating that the tick is likely to be present in those instances where it was stated to be absent but where its presence could be assumed on account of the veld type in the camp and on account of an old known established infestation in the neighbouring areas, and where it was not possible to conduct a survey for lack of time.

The survey shows the tick to be present in all types of mountain veld with the exception of sweet-grass mountain veld. In the flats the tick is present in sweet-grass veld when it is invaded by rhenoster-harpuis veld (Waterkrantz, Hartebeesfontein), in Karoo veld invaded by rhenoster-harpuis veld (Klawervlei, Krugerskraal), and in one case in danthonia veld (Gordonville).

The tick is *absent* in the mountains from sweet-grass veld, sweet-grass veld invaded by tropical shrubs such as *Portulacaria afra* and the tree, *Acacia karroo*, (Touwsrivier, Schoonberg), in the flats from sweet-grass veld (Blaauwater, Koloniesplaas), mixtures of sweet-grass and Karoo veld (Oudeland, Penzoy, Tweefontein B, Kwaggasfontein), mixtures of sweet-grass, Karoo and danthonia veld, unless danthonia is very dense (Gordonville) and Karoo veld.

(b) Mapping the Occurrence of Tick Paralysis

In mapping a distinction is made between camps in which paralysis is a regular feature, camps in which the disease occurs but seldom, and in camps in which the tick is present but has never been associated with paralysis.

Wherever a farmer stated that tick-paralysis was regularly experienced, this was accepted as true, its presence was also accepted for camps where stock is foot-dipped every year. Tick paralysis was taken to be an exceptional feature where foot-dipping was only practised in the exceptional years in which tick paralysis had been observed, and in those instances where foot-dipping is never practised but odd animals have been found paralysed.

Tick paralysis was accepted to be absent where, according to the owner, stock had never been found paralysed, even if dipping had been carried out occasionally.

1. *Sweet-grass Veld and its Mixture with Other Veld Types.*—In the mixtures of sweet-grass veld tick paralysis is recorded as being regularly experienced on the farms Groot Hoek, Abbottsbury, Wellwood, Woodcliff, Aasvoëlkranz and Bloemhof East. * The circumstances in all the infected camps on these farms are similar in that the good pasture of sweet-grasses mixed with other plants is far from water and can be reached by stock only after climbing several hundred feet.

   Tick paralysis is also recorded on the map, where it had been a regular experience in the past, in certain camps containing mixtures of sweet-grass veld where the pasture is close to water, namely: Koloniesplaas, two southern camps, Dassiehoogte West and Pienaarsbaken East. The surveys have revealed the presence of the tick but, due to the regular dipping which has been carried out for many years, sheep are protected. It is difficult to say at this stage whether tick paralysis will still occur if dipping ceases, as a considerable improvement of the veld in these camps has occurred within recent years.

   Tick paralysis is recorded as of rare occurrence in camps containing small portions of sweet-grass veld in the neighbourhood of drinking places, regardless as to what other veld types are included in the camps: Damesfontein, southern camps, Oudeland, south-western camp, and Gordonville, two south-western camps.

   In all other cases in which sweet-grass veld alone, or with its mixtures, takes in a greater portion of a camp in the neighbourhood of watering places, tick paralysis is absent, strangely enough even in camps surrounded by an area in which tick paralysis is a regular feature: Hartebeesfontein, Koppermyn, north-eastern and eastern camp; Wellwood, two northern camps; Request, three camps; Highlands B, south-eastern camp and Tweefontein B, south-eastern camp.

2. *Danthonia veld.*—Tick paralysis is experienced regularly in all camps in which danthonia-mountain veld is the main coverage unless sweet-grass veld is found in the neighbourhood of the drinking places. In danthonia veld on the flats (Gordonville), tick paralysis has never occurred.

3. *Karoo-mountain veld.*—Tick paralysis is a regular feature as a rule, in Karoo-danthonia-mountain veld. On some farms, however, it is experienced in exceptional years only. It is also regularly experienced in Karoo-rhenoster-harpuis-mountain veld (Krugerskraal). Tick paralysis is seldom experienced, or is entirely absent, in unmixed Karoo-mountain veld.

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* On the farms De Nek and Vrede, not shown on the map, similar conditions prevail.

4. *Karoo veld on Flats.*—Where larger stretches of flat Karoo veld are included in a tick-infested camp, tick paralysis has been observed in exceptional years on the farms Klawervlei, Winterhoek, Bothashoek, Legkraal, Enslinsrust, Tweefontein A., Ou Tweefontein, Wanganella and Krugerskraal, otherwise it is absent in such camps. On the farm Pienaarsbaken, in a camp with some flat Karoo veld, tick paralysis is of regular occurrence. Here the larger portion of the camp, which is also the nearest to water, consists of poor Karroo-mountain veld invaded by rhenoster-harpuis veld, i.e. good food far from water.

5. *Rhenoster-harpuis veld.*—Tick paralysis is a regular experience in rhenoster-harpuis veld as also in danthonia-rhenoster-harpuis veld.

3. *Tick Densities in Different Types of Veld*

(*a*) *Introduction*

The evidence of historical records as well as that of present observers well acquainted with the problem, points clearly to the fact that *I. rubicundus* is found in certain types of veld only. Sweet-grass-mountain-veld, so long as it is not invaded by shrubs, Karooveld, thorntree-riverveld and cultivated lands are known to be free of the tick, indicating that plant growth obviously influences the presence or absence of the tick

Plants exercise a direct influence upon a tick by protecting it against unsuitable temperatures, solar radiation, wind and drought. They can also exert an influence indirectly by providing food and cover for the hosts (MacLeod, 1939). At this stage it is proposed to deal only with the direct influence of plants.

The problem was approached in three stages.

The first step of the investigation aimed at determining the actual stage of the tick requiring the greatest degree of protection. Secondly, the extent to which the protection required by the most susceptible stage of the tick was provided for by the different plants present in its environment. The third step was the measurement of tick densities in the different veld types encountered within the Sneeuberg Range

(*b*) *Findings in other Countries*

Lees (1946) found that the *Ixodes* species examined by him (*ricinus, hexagonus, casigua*) were more susceptible to adverse environmental conditions than the *Amblyomma, Rhipicephalus, Dermacentor* and *Ornithodoros* species with which he compared them. Lancaster (1955) showed that for the *hatching* of *Amblyomma americanum* larvae a higher degree of relative humidity was required than for the *survival* of the larvae. MacLeod (1934, 1935) found the larvae of *I. ricinus* to be more susceptible to unsuitable environmental conditions than were the nymphs. Koslowski (1953) found *I. ricinus* larvae to be confined to more restricted areas than were the adults. From this it may be deduced that the adults can withstand a less suitable environment better than can the larvae.

High humidity and moderate temperatures are essential for the survival of *I. holocyclus* (Oxer & Ricardo, 1942; Seddon, 1951), *I. ricinus* (Koslowski, 1953; Lachmajerowa, 1952; Lees, 1946; MacLeod, 1934, 1935 a, b), *I. hexagonus* (Arthur, 1951), *Boophilus microplus* (Gelormini, 1948) and *Amblyomma americanum* (Lancaster & McMillan, 1955). Such conditions are created mainly by layers of decaying plant materials (MacLeod, 1939; Milne, 1944 a; Theiler, 1949). The density of *I. ricinus* (Milne, 1944 b), stands in direct relation to the thickness of such layers. For the formation of such humus mats, uneaten parts of plants, shade and humidity are required. It was shown that such plants of low palatability are associated with the presence of the tick (*I. ricinus*). The decisive factor is not the species of plant, but its capacity to form layers of decomposing materials (Arthur, 1948; Evans, 1951 a; MacLeod, 1938; Milne, 1944 a; 1946). In Britain such plants are particularly prevalent where drainage is poor and where the soil moisture favours the formation of "mats" (Arthur, 1948; Evans, 1951 a; Milne, 1944 a). "Good pasture" has been found to be uninfested by *I. ricinus* (Evans, 1951 a; Milne, 1944 a) and improvement of poor pasture reduces the population of the tick (Arthur, 1948; Milne, 1944a; 1948 a).

(c) Changes in the Composition of the Plant Associations in the Sneeuberg

The relationship between mats of decaying plant material and *I. ricinus* seen in Europe is also seen in the Sneeuberg for *I. rubicundus*. Deterioration of the grazing has coincided with an increase in tick densities and a spread of *I. rubicundus* over the past 50 years into areas previously tick-free. This statement is made on the assumption that the information supplied by farmers can be regarded as reliable, and is supported by a considerable amount of evidence.

The picture presented by the veld is one that is never static and changes in the constitution of plant associations are constantly taking place practically everywhere. Plants of little or no feeding value are being replaced by more valuable species in some parts, whereas in others this process is reversed.

According to Acocks (personal communications), all the veld shown in Map 1, consisted originally of sweet-grasses (Type 1). The veld types as found today represent different stages in the process either of deterioration due to overstocking, or stages in the process of reclamation of previously deteriorated pasture due to good field management.

The process of deterioration is: sweet-grass veld (Type 1 on the map) to sweet-grass and danthonia veld (Type 2) to danthonia veld (Type 3); thereafter, either danthonia and rhenoster or harpuis (Type 14) to rhenoster-harpuis veld (Type 18) or danthonia and karroid veld (Type 8) to Karoo mountain veld (Type 9). An invasion of danthonia veld by rhenoster or harpuis and karroid plants simultaneously is also possible (Type 15), deteriorating to Karoo mountain-rhenoster or harpuis veld (Type 17). The stages of reclamation go from rhenoster and harpuis veld, frequently by merely removing these shrubs, to danthonia veld (Type 3), to sweet-grass and danthonia veld (Type 2), to sweet-grass veld (Type 1). In the case of false mountain Karoo, top soil is usually lost and frequently *Danthonia* does not come in again. Reclamation starts with invasion by *Aristida diffusa, A. congesta* and related species. These are then invaded by annual sweet-grasses such as *Eragrostis chloromelas, E. lehmanniana* and *E. obtusa*. Perennial sweet-grasses follow thereafter.

Taller shrubs, mainly *Rhus* spp., can invade the veld at any stage. They apparently do not disappear again in the course of reclamation. Hence the combination of *Rhus erosa* and sweet-grass-mountain veld which is sometimes encountered.

In Britain the formation of mats of decomposing plant materials is associated with the presence of *I. ricinus*. Such "mats" are also found in the Sneeuberg range. Whilst in Britain a great variety of plants is capable of forming mats when soil conditions are favourable, in the Sneeuberg only certain plant species are capable of doing so. All such plants are characterised by—

1. providing masses of uneaten plant material,
2. providing shade,
3. providing shelter against the desiccating winds, i.e. providing conditions under which moisture is retained.

It may be inferred that all plants present in the later stages of veld-deterioration, with the exception of certain karroid plants, are capable of forming mats of decomposing material.

The inferences together with the observations of farmers, that the spreading of the tick coincide, generally speaking, with a deterioration of the veld, suggest that special attention be paid to the study of those plant species which form humus layers.

(1) *Initial Investigations*

The reactions of the different stages of the tick to unsuitable environmental conditions were tested in the laboratory as well as under field conditions which were regarded as either partly suited or partly unsuited to the tick. Results were taken at 12 hour intervals in the laboratory and at daily intervals in the field When the survival times exceeded three weeks, field observations thereafter were taken twice a week only.

Samples of unengorged, partly engorged and fully engorged larvae and nymphae were kept in tubes in the laboratory under conditions known to be unsuitable. They died in the following sequence:—

Unengorged and semi-engorged larvae — within a few hours to 2 days;

Fully engorged larvae — 25 days;

Unengorged nymphae — 1 to 3 days;

Semi-engorged nymphae — 3 to 21 days;

Fully engorged nymphae survived for many months.

The actual time of death was not recorded. One moulted but the rest all died.

Unengorged females and males were kept in tubes in the laboratory, under Karoo bushes, under dolorite stones, and within layers of decomposing plant materials under *Rhus erosa*. Males died within three days in the laboratory, females within eight days. Under Karoo bushes males died within three to 21 days and females within seven to 33 days. In *Danthonia disticha* tussocks males survived for four to eight days, females eight to 34 days. In decomposing leaf layers under *Rhus erosa* males survived for 17 to 24 days and females for 24 to 71 days. The experiment under dolorite stones gave results too indefinite to permit of a conclusion being arrived at.

Semi-engorged females survived for periods similar to those of unengorged specimens.

Fully engorged females survived under all the conditions to which they were exposed. The percentage mortality was highest in the laboratory and lowest under *Rhus erosa*, but exact data cannot be given.

Eggs survived well under all experimental conditions. In the laboratory they died after six to eight months, in the Karoo veld within five months. Survival times in leaf mould under *Rhus erosa* cannot be given as hatching occurred after about seven months.

Direct sunlight killed all stages very quickly. Even fully engorged females failed to survive direct sunlight for three successive days.

Up to 100 per cent hatching of larvae was observed when eggs were placed in layers of decomposing plant material under *Rhus erosa*. In *Danthonia disticha* tussocks hatching took place in the first tests only after a snow coverage lasting a few days, whilst two batches which received no snowfall failed to hatch. Larvae failed to hatch in the laboratory unless moisture was specially provided and also in the Stevenson screens in different localities and in Karoo veld or under cover of sandstone where no decomposing plant material was present.

Fully engorged larvae failed to survive to the moulting stage in the laboratory. Out of a batch of six, two moulted to nymphae in a Stevenson screen placed on a southern hill slope. The best moulting was obtained within layers of decomposing plant material under *Rhus erosa*.

Fully engorged nymphae moulted under all the conditions observed, viz.: in the laboratory, in the Stevenson screens on hill slopes and on the flats, and in layers of decomposing plant material under *Rhus erosa*. The moulting percentage, however, was not high under any of these conditions, due most probably to the fact that the nymphae were not fully engorged prior to being collected and placed,

The influence of the type of environment upon the moulting time cannot be determined from the results available.

The results indicate that the most critical stage of the life-cycle of the tick under unsuitable environmental conditions is the hatching of the larvae, and that the larva itself is the most vulnerable. This is not likely to be very different in other years as the two years during which these observations were made represent, according to the weather records, normal years. Only during years with abnormal droughts or heat waves can it be assumed that stages other than larvae may be more affected, provided that these weather conditions occur during a time of the year when larvae are not due to hatch or to be active. Droughts during the spring, the active season of the nymph, have been recorded (Rubidge, 1949) in the years 1884, 1894, 1895, 1900, 1903, 1907, 1912, 1915, 1927, 1945 and 1949. Droughts during the autumn, critical for the larvae, are recorded for the years 1915, 1922 and 1947, only.

As the hatching of larvae is found to take place under certain climatic conditions only, such as those experienced during the normal years, 1954-57, it can be expected to be delayed or prevented during times of extreme drought such as those recorded above.

(2) *Second Series of Investigations*

The second question, namely, the influence of the microclimate provided by certain plants upon the most susceptible stage of the life-cycle of the tick, was investigated in an experimental camp on the farm "Doornberg", 5,000 feet altitude, on a southern slope with doloritic soil, i.e. under conditions ideal for the tick. Inspections were carried out at weekly intervals.

Batches of eggs laid in the laboratory during the spring of 1955 in tubes stoppered with cotton wool were placed under different plants as deeply into the underlying debris (if there was any) as was possible.

It was realised later that the cotton wool plug itself could exercise an shrubs *Elytriopappus rhinocerotis* and *Rhus erosa*. The grasses were tested when initial exposure. Hatching commenced a fortnight after the removal of the plugs. Whether hatching was taking place or not could readily be observed by the presence or absence of egg shells. Larvae remained in the open tubes for a considerable time.

The following plants were tested:—

The grasses *Themeda triandra, Eragrostis curvula, Danthonia disticha,* the shrubs *Elytriopappus rhinocerotis* and *Rhus erosa.* The grasses were tested when in full growth as well as when cut short, the cutting being carried out at regular intervals to simulate grazing. Ticks were also placed under stones partly covered by plants, stones associated with each plant species being selected, the grasses being left uncut, and under stones not covered by plants. The particular stone in this case, the only uncovered one that could be found, had root growth of *Danthonia disticha* beneath it but was not shaded by the plant.

The tubes were placed with the open end downwards in order to prevent rainwater from collecting in them. Four thousand eggs divided between two tubes were placed in each position.

The results are given in Table 9.

These experiments were replicated in 1956-57. The aim was to ascertain how many years of regrowth after cutting would be required by the different grasses in order to provide sufficient shelter for the hatching of larvae. The tubes were placed in position on 16/10/56. Observations were carried out on 25/5/57, by which time the eggs had either hatched or failed to hatch. Results are given in Table 10, the symbols used being the same as in Table 1.

Hatching was good in all positions under *Elytriopappus rhinocerotis* and *Rhus erosa.* Larvae failed to hatch under stones covered by uncut sweet-grasses, in the newly cut grasses, in one year's regrowth of *Danthonia disticha* and in two years regrowth of *E. curvula.* There was also some hatching under the uncovered dolorite stone but the percentage of larvae that hatched was small. Larvae failed to hatch in one year's growth of *Themeda triandra* in 1956, one tube hatched, the other failed to hatch in one year's growth of *Themeda triandra* in 1957. The time that elapsed before hatching or death were observed, appears to bear a direct relationship to the cover provided.

TABLE 9

Eggs placed in Position on 25/1/56

Position	Date																Percentage Hatched
	15·2	22·2	7·3	14·3	21·3	28·3	4·4	11·4	18·4	25·4	2·5	9·5	16·5	23·5	30·5	6·8	
Themeda triandra, uncut..........	—	—	—	—	—	—	—	—	—	—	O						
	—	—	—	—	—	—	—	—	—	—	O						
Themeda triandra, cut............	—	—	—	O													
	—	—	—	—	—	—	O										
Stone covered by uncut *Th. triandra*	—	—	—	—	—	—	—	O									
	—	—	—	—	—	—	—	O									
E. curvula, uncut................	—	—	—	—	—	—	—	—	O								
	—	—	—	—	—	—	—	O									
E. curvula, cut..................	—	—	—	—	—	O											
	—	—	—	—	—	—	O										
D. disticha, uncut...............	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	O	
	—	—	—	—	—	—	—	—	—	X	X	X	X	X	X	X	20
D. disticha, cut.................	—	—	—	—	—	—	—	—	—	—	—	—	—	O			
	—	—	—	—	—	—	—	—	—	—	O						
Stone covered by *Danthonia disticha*	—	—	—	—	—	X	—	—	—	X	X	X	X	X	X		50
	—	—	—	—	—	X	X	X	X								90
Rhus erosa.......................	—	—	—	—	—	—	—	—	—	X	—	—	—	—	X	X	90
	—	—	—	—	—	—	—	—	—	X	—	—	—	—	X	X	90
Stone covered by *Rhus erosa*......	—	—	—	—	—	—	—	—	X	X	X						100
	—	—	—	—	—	—	X	X	X	—	X						95
E. rhinocerotis..................	—	—	—	—	—	—	—	—	X	X	X	X	X				95
	—	—	—	—	—	X	—	—	X	X	X						95
Stone covered by *E. rhinocerotis*...	—	—	—	—	—	—	—	—	—	X	X	X	—	—	X		95
	—	—	—	—	—	—	—	—	—	X	X	X					90
Stone " uncovered ".............	—	—	—	—	—	—	—	O									
	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X	X	90

X = Hatch. O = No hatch.

TABLE 10
Hatching of Larvae in Grasses Newly Cut, 1 and 2 Years After Being Cut

Grass	Newly cut	1 year's growth	2 years' growth
Themeda triandra	O	O X	X X
Eragrostis curvula	O	—	O O
Danthonia disticha	O O	O O	— —
Stone (no grass)	X X	— —	— —

(3) *Third Series of Investigations*

The series of investigations deals with tick densities in limited areas of veld, up to approximately two acres in extent, showing a definite type of plant association.

The basic information on tick densities was obtained by means of the tethering method (Stampa & du Toit, 1957). A more detailed study of the problem, however, was conducted with the dragging method. At first the latter method was attended by a number of difficulties under Karoo conditions.

The cloth fabric flag as mainly used in other countries failed to pick up any of the stages of *I. rubicundus* during preliminary trials, due to its riding over the bushes and the coarse vegetation, and thus failing to come into contact with the ticks situated at lower levels. This difficulty was overcome by modifying the apparatus as previously described.

British investigators (Milne, 1943) secured counts for comparing the densities of adults and nymphs of *Ixodes ricinus* by dragging. Larval counts of this species were of little value as the larvae attach to the flag in clusters. It is easier to avoid errors by gauging results with nymphs and adults, as these larger stages are more easily spotted on the sheet than are the larvae.

Most of the present work on *Ixodes rubicundus* was done with larvae for three reasons:—

1. It was proved to be possible to work with larval counts, as the larvae do not form clusters.
2. Even the improved apparatus failed to pick up nymphae and adults effectively.
3. Larval counts serve as a more sensitive index of the influence of veld-type upon the tick in that the hatching of the larva is the most critical stage of the life-cycle.

All the areas on which these investigations were made were heavily infested or were adjacent to known infested veld.

TABLE 11

Influence of Veld Type upon Larval Density

Veld Type	No. of Repetitions		*Rhus erosa* present: Average No. of Larvae per Drag		*Rhus erosa* absent: Average No. of Larvae per Drag		No. of Repetitions
Sweet-grass	30		3·37	AV XX Chi X	0·075 0·0 0·16 0·076		48 8 8 40
		Chi X				AV XX Chi X	
Sweet-grass Danthonia	15 20		20·39 15·92	Chi X	2·33		29
		AV XX				Chi X	
Danthonia	25		27·5*		6·72 7·98		10 4
		AV XX					
	12 13		13·2 † 6·41†	AV XX			
		AV XX					
	20 12		61·4 35·7	AV XX		AV O Chi O	
		Chi X					
Danthonia-Rhenoster	42		5·27	AV O Chi O	4·35 4·45 3·92		4 18 22
						Chi X Chi X	
Rhenoster-Harpuis					1·33 2·46	AV(X) Chi O	33 13
Danthonia-Karoo					3·47* 21·22	Chi O	40 10
Karoo					3·27*		

* = gradual slope
† = Rhus scattered
AV = Analysis of Variance
Chi = Chi-square test

O = not significant
(X) = significant to 95%
X = significant to 99%
XX = significant to 99·9 %

The results of the investigations conducted in 1957 are shown in Table 11. They are arranged in accordance with the stages in which sweet-grass veld deteriorates under bad management. Dragging was carried out on six (in a few cases five) evenings at fortnightly intervals. The average tick counts per drag are given in Table 11 together with the number of repetitions in each locality. Where veld-types under one heading differ in minor respects from one another, individual figures for each variation are given. The significance of the differences between the groups has been tested by the " Analysis of Variance " and by the " Chi-square-test ". The statistical analyses are shown in Table 11 on the lines connecting the squares with the figures for each veld-type. The minor variations within each veld-type have not been considered in the statistical analysis.

The table shows that in veld without *Rhus erosa* the tick density is very low in sweet-grass mountain veld. It is, however, significantly higher in sweet-grass danthonia veld and again significantly higher in danthonia veld. No significant difference between the tick density of danthonia veld and danthonia rhenoster veld is apparent, but the density in rhenoster harpuis veld is lower than in danthonia or danthonia rhenoster veld. A marked variation is met with in danthonia Karoo veld whereas no difference between the tick densities of the latter and of danthonia veld can be indicated. In Karoo mountain veld the tick density is somewhat lower than in danthonia veld, but only a 95 per cent significance is found for the difference by the method of " Analysis of Variance " and no significance is shown by the " Chi-square-test ".

TABLE 12

Adult Counts in Different Veld-Types

	Rhus erosa present		*Rhus erosa* absent	
Veld Type	*No. of Repetitions*	*Average Count*	*Average Count*	*No. of Repetitions*
Sweet-grass	18	1·05	0·375	24
		AV O	Chi X	
Danthonia........	21	3·38		
	12	3·67		
Danthonia-Rhenoster.........			4·43	7
			AV O	
Rhenoster-Harpuis...........			1·33	6

(Symbols similar to those used in Table 11).

The tick densities in the veld-types with *Rhus erosa* show a similar tendency. The figures for danthonia veld with *Rhus erosa* have been subdivided according to the density of this shrub, and one figure on a very steep slope was treated separately.

The tick densities in each veld-type with *Rhus erosa* in all cases are significantly higher than the tick density of the corresponding veld-type without *Rhus erosa*.

Table 12 gives the counts of adult ticks in those localities which carried no stock during the survey work. Everywhere else adult counts were very small. These counts were made on Corduroy pants worn by the workers during the larval surveys. Corduroy material picks up adults very well but not larvae. The figures show that the adult counts are influenced very little by the type of veld, thus confirming the result of the initial investigation. It was shown during the course of these surveys that the fully engorged nymph can survive practically everywhere and moult to an adult, which in its turn also survives fairly well under conditions unsuitable for the larva.

Larval counts made during 1956 support the evidence presented in Table 11. They were obtained by a somewhat different technique. During 1957 dragging was carried out in a marked field, each drag being 50 meters long. In 1956 the area was not marked and dragging occupied 10 minutes per drag. Figures for 1956 should therefore be considered as less accurate. The results are given in Table 13.

TABLE 13

Larval Counts in Different Veld-Types in 1956

Veld Types Compared	Average A	Average B	Significance	
			AV	Chi
Sweet-grass A: Sweet-grass danthonia rhenoster B........	0·5	10·31	—	X
Sweet-grass danthonia, short A: long B................	1·14	10·31	—	O
Karoo danthonia A: Karoo Danthonia *Rhus erosa* B....	17·22	13·54	—	O
Karoo danthonia A: Karoo B........................	17·22	0·714	O	O
Karoo A: Karoo rhenoster B (both very steep slopes).....	6·5	26·0	(X)	—
Karoo, sloping a: Steep A: Very steep B.......... a 0·148	0·714	6·5	XX	X
Karoo rhenoster, sloping A: Steep B..................	4·6	26·0	O	O
Rhenoster harpuis A: Rhenoster harpuis-*Rhus erosa* B...	6·0	23·13	O	O

Presence of Ticks in the Flats

Surveying by means of the tethering method (Stampa & du Toit, 1957) as also by dragging shows that all stages of *I. rubicundus* are absent from flats covered by Karoo, sweet-grass veld or mixtures of the two. On a flat area of veld covered by a Karoo-danthonia-rhenoster-harpuis-mixture odd larvae and nymphae were found as was also the case in one instance of danthonia veld on flats at an altitude of 6,000 feet. A few larvae have also been found on the edges of eroded gulleys covered by a danthonia-rhenoster-harpuis vegetation. The harvest was always very small, however, and no significant differences between tick counts in eroded gulleys and on the flats with similar vegetation could be found.

G. THE ECOLOGY OF THE TICK

Influence of Farm Management Upon the Presence of Tick Paralysis

It has been shown in Section F that certain plant associations are more suitable for the Karoo Paralysis Tick, *I. rubicundus*, than are others. It was also pointed out that the plant associations encountered in the Sneeuberg Range are not stable but are inclined to change their composition with time. These alterations are due to the type of veld management applied, namely:—

1. Time of the year at which the veld is grazed and the duration of the grazing period.
2. Number of stock kept in relation to the quality of the pasture.
3. Type of stock kept.
4. Special treatment such as removing the shrubs, flooding level veld or burning the veld.

Alterations of the veld-types can be expected to lead to changes in the microclimate produced by the plants themselves, the microclimate in its turn influencing the incidence of the tick.

The tick can also be expected to be influenced directly by certain methods of farm management such as dipping of the stock, keeping stock out of the infested veld during the active period of the tick and by resting or burning the veld.

(*a*) *Alteration of the Plant Associations*

The different degrees of veld stocking, which may lead either to improvement or deterioration, cannot be dealt with in this article. It is of interest, however, to note the time taken to bring about the change from one stage in veld-type to the next in the course of deterioration or of reclamation.

The observation has been made that harpuis veld (*Euryops racemosus*) has not reverted to danthonia harpuis veld within a period of 25 years even when stock was excluded entirely (Tweefontein B, Map 1). Reclamation of such veld requires special treatment. Rhenoster veld (*Elytriopappus rhinocerotis*) presents less of a problem, as this plant species is eliminated at times by certain specific diseases (Waterkrantz, Eureka, Map 1).

Danthonia-rhenoster-harpuis veld can be changed into danthonia veld rapidly by removal of the shrubs. The cost of such removal is estimated by farmers at from 20 to 50 per cent of the value of the veld, i.e. too high to recommend it as a general practice. Where *D. disticha* is dense in danthonia-rhenoster-harpuis veld, veld fires can bring about a fair control of the shrubs (Gordonville south, Highlands B.) but little or no control of the shrubs is achieved by veld fires where grass is scarce (Gordonville, northwest, Highlands B, south, and Wintershoek, west).

An alteration of danthonia veld with a little sweet-grass to sweet-grass-danthonia veld within four years, during which good veld management was practised, has been observed after an accidental fire on the farm Gordonville during the course of these investigations.

An experiment with weed-killers indicated that *Rhus erosa* can be controlled by 2-4-5-T. The control of other *Rhus* species is more difficult, however, and accurate dosages of the weed-killer have still to be determined.

Alteration of the veld-type in two different directions is illustrated in two adjoining camps of the farms Lucerne and Tweefontein B. (fig. 1). According to the information available both camps were similar 25 years previously, when Tweefontein was bought by the present owner. Today Lucerne has a rhenoster-harpuis veld and Tweefontein a sweet-grass veld with some danthonia and some rhenoster-harpuis invasion. Tick paralysis is regularly experienced on Lucerne and has not occurred during the last 10 years on Tweefontein.

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(b) Dipping

The chances of controlling *I. rubicundus* by dipping appear to be very good, for the following reasons:—

1. a very high grade and long lasting residual killing effect can be achieved with some of the modern insecticides by foot-dipping woolled sheep;
2. the alternative hosts of the tick never appear to be as numerous as is the case with other tick species.

In spite of this, however, no area is known from which *I. rubicundus* has been eradicated by dipping. In how far the density of *I. rubicundus* is brought down by dipping stock regularly was investigated by a series of three experiments. The effect of the dipping was assessed by the number of larvae (found by dragging) in veld grazed during the preceding season by *regularly dipped* sheep as against the larval counts in veld of a similar type grazed during the previous season by *undipped* stock (Table 14).

TABLE 14

Average Number of Larvae Found in Veld Grazed by Dipped Sheep During the Preceding Season as Against Similar Veld Grazed by Undipped Sheep

	Camps 1 and 2	Camps 3 and 4	Camps 5 and 6
Grazed by undipped stock....................	1·13	1·57	1·43
Grazed by dipped stock.......................	0·05	0·67	0·26
Significance (Chi-square-test)..................	X	X	X

The table shows a significantly smaller number of larvae in all three camps grazed during the previous season by dipped sheep as against the controls, but complete control of the tick has not been achieved. Antelope species, which are the hosts next in importance to domestic stock were not present in anv of the camps. Only females which engorged on hares or carnivora could account for the larvae found in the dipped camps but an odd female that had succeeded in reaching full engorgement on the dipped sheep is a possibility that must not be lost sight of.

(c) Resting of Veld

Similar experiments have been conducted whereby veld not grazed at all during the previous tick season has been compared with veld grazed by undipped stock. Veld-types were not uniform in the two areas compared, however, as the role played by the veld-type was underestimated when the ekperiment was commenced. The results show considerable variation, in two experiments many more ticks being found in the rested camp than in the grazed one, and in the third more in the grazed camp than in the rested camp.

Considering, however, that the highest larval counts ever made were found in camps which had carried no stock at all during the previous season, it could be assumed that the direct influence of pasture-resting upon the tick population must be negligible.

This led to the further assumption that hares play a greater rôle as hosts of the imagines in rested camps than they do when other hosts are available. Tick counts on one southern bush hare, *Lepus saxatilis albaniensis* and two Cape red hares, *Pronolagus rupestris saundersiae*, shot in rested camps, supported this assumption. Twelve females were collected off the bush hare and two and five off the red hares respectively. The total number of female ticks found previously on these host species was fourteen on ten bush hares and nine on seventy-six red hares examined, i.e. an average of 0·22 and 0·027 females per animal, excluding the three hares mentioned above.

(d) Burning of the Veld

In the earlier days, burning of the grass after winter, was practised regularly in the Sneeuberg Range, as is the custom in other parts of South Africa. It has the advantage that the young shoots of the grasses are more easily accessible to stock after the fire has removed the old dried material. Young shoots appear after little or no spring rainfall and a certain quantity of food can thus be provided for stock by burning veld early in spring, i.e. at a time of the year when food is otherwise very scarce.

Another observation which induced farmers to burn the veld in former years was that after fire, sheep feed readily on the new growth of the less palatable grasses such as *D. disticha*, which provides little food when mature.

However, grasses cannot withstand burning and grazing in areas with a low rainfall and a cool climate. Young grass is easily eradicated by stock, particularly by sheep. The final outcome of veld fires and grazing of recently burnt veld was the destruction of the grass coverage, the invasion by shrubs and the loss of precious top soil. This policy has now been abandoned.

However, the observation has been made recently that the fire itself was not the cause of the damage to the veld but rather the subsequent grazing. Veld can even be improved by fire if it is rested for a certain time thereafter for reseeding, and farmers are considering its controlled use again.

As far as the tick is concerned veld fires can be expected to cause a considerable decrease in its numbers by direct destruction or indirectly by removing the masses of dead material forming the suitable microclimate. A further indirect effect upon the tick paralysis problem, which can be expected from correctly applied veld fires is the provision of more food for the stock in all those veld-types dominated by *D. disticha*, as this grass is readily grazed shortly after fires. The provision of food not far from drinking places is regarded as a factor preventing the development of tick paralysis.

In January 1953 an accidental veld fire occurred on the farm Gordonville in danthonia mountain veld, badly infested with *I. rubicundus* and where regular trouble with tick paralysis was being experienced. The tick density was investigated in this veld $2\frac{1}{2}$, $3\frac{1}{2}$ and $4\frac{1}{2}$ years after the fire.

Two-and-a-half years after the fire one male was found by means of the tethering method as against 146 adults on the controls in the unburnt veld. Larvae were entirely absent. Three-and-a-half years after the fire dragging revealed 1·14 larvae per drag in the burnt veld as against 4·0 larvae in the unburnt veld. The difference between the larval counts in the burnt as against the unburnt veld was found to be significant even $4\frac{1}{2}$ years after the fire. The burnt veld had improved, however, in the meantime from danthonia veld to sweet-grass danthonia veld whereas the control unburnt veld was unchanged, i.e. the difference of larval density could not necessarily be attributed to the direct effect of the fire.

Although sheep grazing on the veld burnt $4\frac{1}{2}$ years previously were not dipped, not a single case of tick paralysis had occrured amongst them. The incidence of paralysis was exceptionally severe amongst stock grazing in the unburnt camps on the same farm.

On Gordonville the veld had been stocked lightly and only after a total rainfall of five inches had fallen after the fire, was stocking commenced. The effect upon the tick may have been even more pronounced if, after a period of complete rest, more stock had been introduced for shorter periods separated by longer spells of resting. By applying such a system *D. disticha* would have been kept shorter than by the grazing method applied, as is demonstrated elsewhere by carefully controlled experiments.

H. The Control of I. rubicundus on Woolled Sheep by Foot-Dipping with Remarks on the Control of Hyalomma sp. and Rhipicephalus evertsi.

Up to the present dipping is practically the only way in which *I. rubicundus* is controlled and stock protected against tick paralysis. So far the tick has not developed resistance to any of the insecticides tested and is readily killed by all compounds that are effective against other tick species, such as Arsenic, DDT, BHC, Toxaphene, Aldrin, Dieldrin, PE 101 and Diazinon.

1. *Work of Other Investigators*

For the control of *I. rubicundus* on sheep Van Rensburg & Silcock (1927) recommended the use of arsenic in a foot- or walk-through type of bath. They stated that complete immersion was not required as the ticks are attached to the legs, the lower abdomen and the lower parts of the neck only. McHardy (pers. comm.) compared arsenic with some of the modern insecticides and found that considerable residual protection could be obtained with some compounds. BHC at 125 p.p.m. gamma in combination with 0·16 per cent arsenite of soda was found by him to prevent engorgement of all ticks up to four to six weeks after dipping.

It is noteworthy that complete protection was obtained by McHardy even on the hairy parts of the legs, the lower thorax and loins where a considerable number of ticks normally engorges on undipped sheep, as has been shown in Section C, although insecticidal residues can only be expected to be retained for a certain length of time in the fleece. Thus the control of *I. rubicundus* is not nearly as difficult as is the control of *I. ricinus*. Jolly, Stones, Page & Brander (1953) found that only a transitory residual effect is obtained with the use of the newer insecticides against *I. ricinus*. They explain their findings by the statement that *I. ricinus* is able to reach its site of attachment without crawling through the wool, i.e. without coming into contact with residues of insecticide in the fleece. *I. rubicundus* behaves differently and always crawls through the wool to its place of attachment with the exception of those ticks that attach themselves to the bare parts of the head, as has been shown (Section D). The control of *I. rubicundus* differs thus from that of *I. ricinus* as a considerable percentage of the latter species is found attached to the head (Evans, 1951). Furthermore the bulk of *I. rubicundus* females attach themselves to the woolled parts of the sheep's body where continuous contact with the insecticide in the fleece occurs during the whole period of engorgement; the ticks attached to the bare regions find less suitable conditions for engorgement as has emerged from these studies. *I. ricinus*, on the other hand, shows a preference for the bare regions which accounts for the greater difficulties experienced in the control of this species by means of insecticides with residual effect.

McHardy (pers. comm.) found also that some insecticides, although giving a good initial kill, were disappointing in their residual effect, i.e. DDT and Toxaphene. He found that Dieldrin, although disappointing in its initial killing capacity, gave a very durable protection against the ticks when used at a concentration somewhat higher than that necessary for BHC, namely 0·1 per cent a.i. or even higher.

A comparison between these results and the findings on the protection of sheep against blowfly strike shows some points of similarity. BHC and Dieldrin afford a very durable degree of protection against blowflies, the former at any rate in clean wool (du Toit & Fiedler, 1953). DDT and Toxaphene, on the other hand, are considerably less effective and du Toit & Fiedler (1953), Stampa, Fiedler & du Toit (1958) were able to show that three factors govern the period of protection against blowfly strike produced by any compound in clean wool, namely: (1) the specific efficacy of the compound against the maggots, as judged by the lowest dilution effecting a kill in the nutritional medium; (2) the ability of the insecticide to diffuse along the wool fibre; (3) the quantity of active ingredient applied per sheep.

Field experiments confirmed these findings but revealed that under field conditions soiling of the wool and the number of blowflies present (fly-population-pressure), constitute additional influences affecting the period of protection against blowfly strike (Stampa, Fiedler & du Toit, 1958).

The information obtained from McHardy's work on the protection of sheep against *I. rubicundus* indicates that the specific efficacy of the compounds against the ticks and their ability to diffuse along wool fibres may well be equally decisive.

Whether the number of ticks present influences the period of protection is not known for *I. rubicundus*. Jolly, Stones, Page & Brander (1953) found such an effect in the case of *I. ricinus*. Their findings suggest that similar field experiments be carried out for *I. rubicundus* and in order to exclude the possible influence of tick-population pressure, should this exist, sheep under test for different insecticides should run together in a single flock.

Fiedler (pers. comm.) immersed engorged larvae of *I. rubicundus* in different concentrations of DDT, BHC, Dieldrin and Diazinon under laboratory conditions, in order to determine the specific efficacy of these compounds against this tick. The results were somewhat difficult to read due to technical difficulties associated with the small size of the larvae. He concluded, however, that Gamma BHC effects a kill at about one-quarter the concentration of the other compounds.

The aim of the present investigation was:—

1. To determine whether (*a*) the specific efficacy of various insecticides against the tick as found by laboratory methods, (*b*) the ability possessed by the insecticides to diffuse along wool fibres to skin level as demonstrated by du Toit and Fiedler (1953) and (*c*) the quantity of insecticide applied per sheep, influence the length of the period of protection against *I. rubicundus* as has been found in the case of blowflies.

2. To attempt to find by what means a protection of longer duration against *I. rubicundus* could be achieved.

3. To test whether a residual killing effect could also be obtained on woolled sheep against other ticks of importance in the Karoo.

2. *The Specific Efficacy of BHC and Dieldrin*

A repetition of Fiedler's experiment appeared desirable, using those stages of the tick on which the effect of the insecticide could be observed more accurately. Semi-engorged females collected off sheep, which have acquired an immunity to the full engorgement of the tick (Stampa & du Toit, 1957) survive well under laboratory conditions and are very suitable for laboratory tests.

Technique

Ten semi-engorged female ticks collected from sheep in tick-infested pastures were placed in a glass specimen tube, 1″ × $2\frac{1}{2}$″. About 2–5 c.c. of the wash to be tested was poured into the tube which was corked and, while held horizontally, approximately 60 shaking movements were made for one minute. The cork was replaced by a piece of muslin drawn over the open end and the wash poured out while agitation was continued. The ticks were transferred from the muslin to filter paper in a Petri dish. If some clung together they were separated. The result was read after 24 and 48 hours, the following key being used:—

(*a*) Number apparently not affected × 0
(*b*) Number affected capable of slight movement × 1
(*c*) Number incapable of forward movement but alive × 3
(*d*) Number Dead × 5

If all the ticks were killed the figure obtained would be 10 × 5 = 50.

The result is given in Table 15.

TABLE 15

The Effect on Semi-engorged Female I. rubicundus *of* in vitro *Immersion in Various Concentrations of BHC and Dieldrin*

Insecticide	Conc. p.p.m.	Average of 4 Repetitions 24 hours after Dipping	Average of 4 Repetitions 48 hours after Dipping
BHC	4	19·5	23·0
BHC	16	29·0	31·5
BHC	64	36·0	39·0
BHC	250	35·5	39·5
Dieldrin	16	4·5	9·5
Dieldrin	64	5·5	12·75
Dieldrin	250	9·25	17·5
Dieldrin	1000	11·0	25·25
Dieldrin	4000	16·75	28·5

BHC kills the tick more rapidly than does Dieldrin and in fact, the observation time of 48 hours after immersion is too short in the case of Dieldrin, which produces results, therefore, somewhat lower than those of BHC. The table indicates, furthermore, that 16 p.p.m. BHC and 64 p.p.m. Dieldrin might be the concentrations just effecting a kill. There was a considerable degree of variation which may have to be attributed to the fact that ticks of varying stages of engorgement were used. A second test was conducted, therefore, with BHC at 16 p.p.m. and Dieldrin at 64 p.p.m., using ticks selected according to the stage of engorgement. The results are given in Table 16.

TABLE 16

In vitro *Immersion of Female* I. rubicundus *in Different Stages of Engorgement in BHC and Dieldrin at* 16 *and* 64 *p.p.m., Respectively*

	24 hours after Immersion					48 hours after Immersion				
	Dead (d)	K.D. (c)	Aff. (b)	Unaff. (a)	Key Fig.	Dead (d)	K.D. (c)	Aff. (b)	Unaff. (a)	Key Fig.
I. BHC 16 p.p.m. Selected Ticks										
Commencing engorgement (2 replications)	10	0	0	0	50	10	0	0	0	50
Slightly engorged.........	1	9	0	0	32	2	8	0	0	34
Semi-engorged (2 replications)	0	6	4	0	21	1	9	0	0	31
	0	5	5	0		0	10	0	0	
Fully engorged...........	1	9	0	0	32	1	9	0	0	32
II. Dieldrin 64 p.p.m. Selected Ticks										
Commencing engorgement	0	1	2	7	5	5	5	0	0	40
Slightly engorged (2 replications)	0	0	0	10	0	1	7	2	0	16·5
	0	0	0	10		0	0	5	5	
Semi-engorged (2 replications)	0	0	0	10	0	0	0	0	10	0
	0	0	0	10		0	0	0	10	
Fully engorged...........	0	0	0	10	0	0	0	0	10	0

The less engorged the female tick the greater is the effect of the insecticide. When compared at 48 hours after immersion, which is not quite fair in the case of Dieldrin, BHC appears to be more than four times as effective as Dieldrin.

3. *The Ability of the Insecticide to Diffuse Along the Wool Fibres*

Whether the ability of the insecticide to diffuse along the wool fibres is also of importance for the duration of protection against *I. rubicundus* as is the case with protection against blowflies, can only be ascertained from field experiments, as no laboratory method is known by which this could be assessed. Toxaphene, which possesses poor qualities of diffusion in wool and BHC which diffuses well (du Toit & Fiedler, 1953) were selected for comparative purposes.

The results confirm the findings of McHardy. Toxaphene was excellent in its initial killing capacity but gave only partial protection against *I. rubicundus* two weeks after dipping and no protection at all six weeks after dipping. BHC was disappointing at the strength used (125 p.p.m.) so far as initial kill was concerned but gave complete protection two weeks after dipping and partial protection six weeks after dipping. The results obtained by McHardy (personal communication) were similar as also were those in which he compared DDT with BHC.

It may be concluded thus that the ability of an insecticide to diffuse along wool fibres is important for the protection of woolled sheep against *I. rubicundus*.

4. *Duration of Protection in Relation to the Quantity of Active Ingredient Deposited per Fleece*

Stampa, Fiedler & du Toit (1958) were able to show that the duration of the period during which the clean fleece is protected against blowfly strike depends, under laboratory conditions, on the quantity of insecticide deposited. It appeared desirable to ascertain whether this applied in the case of *I. rubicundus.*

(*a*) *Residual Effects Against* I. rubicundus

A series of foot-dipping experiments was conducted with gamma BHC as the active ingredient. The depth of the dipwash in the tank was 18 inches in all cases.

One year-old wethers carrying six months of wool at the time of the trial were used as experimental animals. The amount of gamma BHC deposited per sheep was estimated from the amount of wash removed, the concentration in the tank at the beginning of dipping and the drop in concentration during the course of dipping being ascertained by chemical analysis. Each experimental group consisted of 10 sheep, 10 sheep were also left as untreated controls.

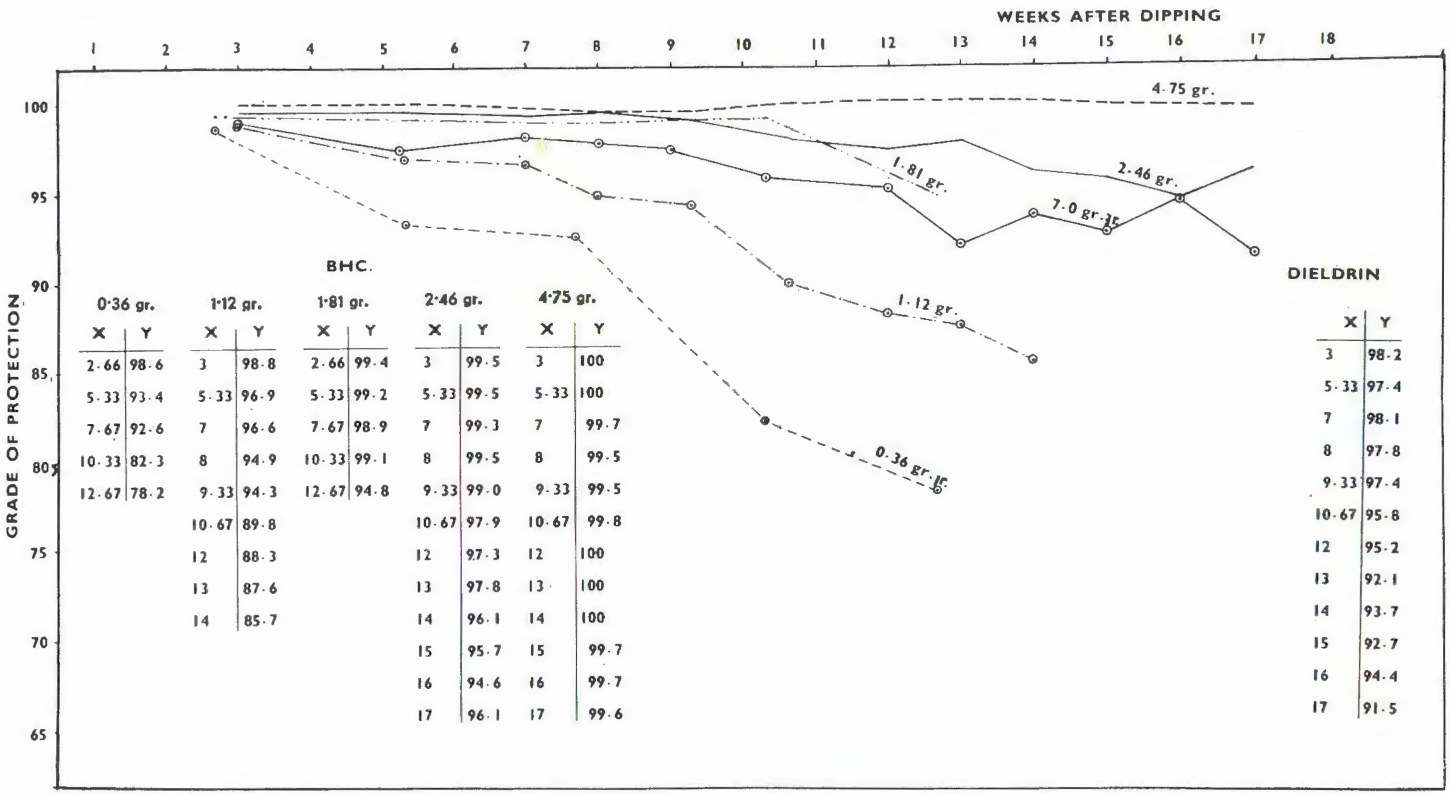
Two groups with their controls had to be kept on the one farm, the other groups with the controls on another farm. The tick incidence on the two farms was similar but became higher on one farm during the 17th and 18th week after dipping.

As 10 sheep alone could be expected to bring about only a very small drop in the concentration in the tank and this could not be estimated accurately enough by chemical analysis, 70 additional sheep were dipped after each experimental group before measuring the tank level and taking the sample for analysis. One-eighth of the quantity removed by the total 80 sheep is given in the following table as the quantity removed per experimental group. Due to a mistake in conducting one of the experiments it was impossible to give the accurate quantity removed for two of the groups. Only the approximate figures, less than 20·0 gm. and more than 40·0 gm. can be given. It appears from the results that the actual amount removed by the first of these groups must have been approximately 12·5 gm. in which case that for the second group must have been 47·5 gm. as the two groups together removed 60·0 gm.

The following formulations were used at the concentrations given:—

Group 1. Wettable Powder, low depletion rate	125 p.p.m.
Group 2. Wettable Powder, low depletion rate	212 p.p.m.
Group 3. Emulsion, very high depletion rate	70 p.p.m.
Group 4. Emulsion, high depletion rate	160 p.p.m.
Group 5. Wettable Powder, high depletion rate	215 p.p.m.
Group 6. Emulsion, very high depletion rate	154 p.p.m.

The results are given in Table 17 and Graph 6. The protection achieved with 7·0 gm. Dieldrin per sheep is also given in Table 17 for comparison. The sheep were not controlled during the first two weeks.



BHC.

0·36 gr.

X	Y
2·66	98·6
5·33	93·4
7·67	92·6
10·33	82·3
12·67	78·2

1·12 gr.

X	Y
3	98·8
5·33	96·9
7	96·6
8	94·9
9·33	94·3
10·67	89·8
12	88·3
13	87·6
14	85·7

1·81 gr.

X	Y
2·66	99·4
5·33	99·2
7·67	98·9
10·33	99·1
12·67	94·8

2·46 gr.

X	Y
3	99·5
5·33	99·5
7	99·3
8	99·5
9·33	99·0
10·67	97·9
12	97·3
13	97·8
14	96·1
15	95·7
16	94·6
17	96·1

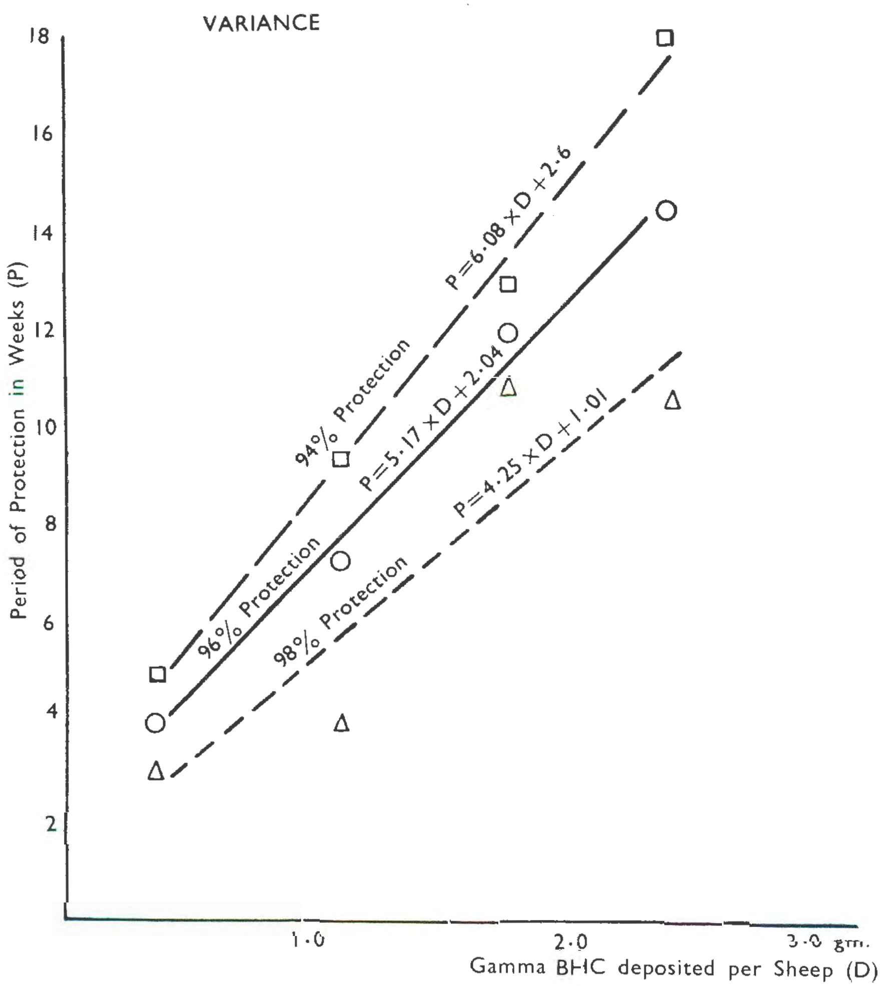
4·75 gr.

X	Y
3	100
5·33	100
7	99·7
8	99·5
9·33	99·5
10·67	99·8
12	100
13	100
14	100
15	99·7
16	99·7
17	99·6

DIELDRIN

X	Y
3	98·2
5·33	97·4
7	98·1
8	97·8
9·33	97·4
10·67	95·8
12	95·2
13	92·1
14	93·7
15	92·7
16	94·4
17	91·5

GRAPH 6.—Degree of Protection of Sheep against *Ixodes rubicundus* by different Quantities of Gamma BHC and Dieldrin in the Fleece. (The lines connect the average Values of each of three successive Observations.)



GRAPH 7.—Period of Protection against *Ixodes rubicundus* by different Quantities of BHC, when 94, 96 or 98 per cent of the Degree of Protection terminates the Period of Protection.

In Graph 7 the duration of protection is plotted against the quantity of Gamma BHC deposited per sheep when 98, 96 or 94 per cent of the degree of protection is taken to terminate the period of protection. The graph shows a straight relation between the quantity of BHC applied and the period of protection, i.e. the period of protection against *I. rubicundus* depends on the quantity of insecticide deposited per sheep.

There is no correlation between period of protection and concentration in the tank unless the quantity deposited is dependent on the concentration exclusively. A very durable protection results with a deposit of 4·75 gm. Gamma BHC per sheep when the sheep carry six months wool and when they are dipped in a walk-through bath 18 inches deep.

TABLE 17

Degree of Protection of Sheep Against I. rubicundus *by Deposits of Different Quantities of Gamma BHC and Dieldrin in the Fleece*

$$\text{Degree of Protection} = 100 - \frac{\text{(No. of Ticks on dipped sheep)}}{\text{(No. of Ticks on Controls)}} \times 100.$$

Week after Dipping	Quantity of Gamma BHC deposited per Sheep						Dieldrin
	0·36 gm.	1·12 gm.	less than 2 gm.	1·81 gm.	2·46 gm.	more than 4 gm.	7 gm.
1	—	—	—	—	—	—	—
2	—	(a)	(a)	—	(a)	(a)	(a)
3	98·98	—	—	98·98	—	—	—
4	—	96·83	96·83	—	100·00	100·00	96·83
5	96·83	—	—	99·30	—	—	—
6	—	99·47	96·98	—	98·40	100·00	—
7	—	94·33	96·45	—	100·00	100·00	—
8	85·10	95·95	97·69	99·40	99·49	99·22	98·80
9	—	94·41	94·97	—	98·88	99·44	96·90
10	95·91	—	—	97·96	—	—	—
11	—	92·57	89·84	—	98·29	100·00	96·57
12	—	82·27	88·96	—	96·45	100·00	93·97
13	66·00	89·90	86·53	100·00	96·97	100·00	94·95
14	—	90·70	83·72	—	100·00	100·00	87·47
15	72·73	76·47	80·36	91·17	91·17	100·00	98·53
16	—	—	—	—	96·03	99·22	92·19
17	—	—	—	—	96·70	99·84	92·41
18	—	—	—	—	95·57	99·68	89·87

(*a*) second farm

Messrs K.O.P. very kindly supplied the BHC materials and Messrs Cooper & Nephews the Dieldrin.

The curve of protection, resulting from a deposit of 7·0 gm. Dieldrin per sheep, in Graph 6 falls between the curves for protection by 1·12 and 2·46 gm. Gamma BHC. By interpolating the Dieldrin curve between the two adjacent BHC curves it may be deduced that 1·65 gm. of BHC per sheep would give the same protection as 7·0 gm. Dieldrin (4·24 times the quantity). The expectation based on the laboratory dipping experiment is, therefore, confirmed and it can be stated, that the specific efficacy of the insecticide as found by the laboratory immersion technique described above gives an indication as to what degree of protection can be expected from such a compound in a field experiment, provided it possesses the necessary properties of being able to diffuse along the wool fibres.

(*b*) *Residual Effects Against* Hyalomma spp. *and* Rhipicephalus evertsi.

Considerable losses are suffered annually by farmers over extensive areas of the Karoo due to the bites of ticks of the genus *Hyalomma* and of *Rhipicephalus evertsi*. The question as to whether a residual killing effect against these ticks can also be achieved by BHC has been investigated during the course of these experiments.

These two tick species behave somewhat differently from *I. rubicundus*. They are, as a rule, only found attached to the bare parts of the body and it is believed that they reach their sites of attachment without having to crawl through the wool. It can be assumed, therefore, that a residual killing effect as effective as in the case of *I. rubicundus* cannot be anticipated.

A dipping experiment was conducted on the farm Riverdale which was particularly heavily infested with these two species. A BHC emulsion dip with a low rate of depletion was compared with one having a high rate of depletion at the same concentration. Two groups of 10 sheep each were dipped and another 10 left untreated as controls. The results are given in Table 18.

TABLE 18

Degree of Protection Against Hyalomma *spp. and* R. evertsi *by a High as Against a Low Depletion Rate Emulsion*

I. *Hyalomma spp.*

Weeks after treatment	1	2	3	4	Average
High depletion rate	93·66	83·25	79·20	93·25	87·34
Low depletion rate	41·58	61·25	64·53	69·26	59·15

II *Rhipicephalus evertsi*

Weeks after treatment	1	2	3	4	Average
High depletion rate	100·00	78·00	89·00	80·50	86·90
Low depletion rate	74·60	0·00	11·00	44·20	32·40

Result.—The result is in accordance with what was to be expected. An incomplete degree of protection only was achieved. The protection given by the high depletion rate emulsion is greater than that of the low depletion rate emulsion, i.e. the higher BHC deposit in the fleece in the former case produced better protection. A breakdown of the protection could not be observed within the four weeks during which the observations were made.

Experience gained in the Application of the Foot- or Walk-through Bath for Sheep

A. Immersion

Although *I. rubicundus* females have been found attached to adult sheep as high up as 21 inches above the ground, foot-dipping at a tank level of 18 inches gives a complete residual effect against the tick. Where, however, emphasis is laid upon the killing of the tick attached to the sheep at the time of immersion, the tank should be filled to a depth of 22 inches. Immersion of the heads, although more difficult when foot-bathing sheep than in full immersion dipping is essential in order to obtain a residue of the insecticide in the wool of head and neck. It is easier and safer to do the immersion of the heads by hand than with the help of a dipping-stick or crook.

B. Replenishment

Van Rensburg and Silcock (1927) recommend replenishment of the foot-bath during the process of dipping in order to maintain the tank level. This is today practised everywhere in the areas infested by the paralysis tick and must be regarded as essential in order to maintain uniformity of application and efficiency. The method could be improved however, by introducing a floating gauge connected with a scale which would make possible the continuous reading of the bath level during operations and the replenishment which would make allowance both for the wash removed as well as for the fluid returned from the sheep while draining.

C. The Effect of the Insecticide

It has been noted that dipping materials which have been condemned as ineffective by some stock owners, if correctly used, were found to be very satisfactory. In some instances it was possible to trace the fault to incorrect dipping technique, such as incorrect measurements of tank capacities and the use of too low a concentration, etc. Frequently, however, the farmer judged protection to have broken down because he saw ticks on the sheep or because he found a single tick attached to one out of 10 sheep. None of the modern insecticides kills ticks instantly, therefore free ticks on the fleece and newly attached females do not necessarily indicate a breakdown in the protection. It is also obvious that a single engorged tick need not necessarily be indicative of the end of protection. Such odd ticks are usually affected by the insecticide and are incapable of causing paralysis. Based upon the present investigations it is believed that a degree of protection of 96 per cent or less indicates the breakdown of protection; that is to say, that during the main tick season four or more females, showing signs of engorgement, would be required on the 10 treated sheep to signify the cessation of the protection.

I. Discussion and Recommendations

1. *Discussion*

The host list shows the immature stages to be present on *Menotyphla, Lagomorpha* and to a lesser extent on *Canidae*. Other *Carnivora,* the *Rodentia* and the wild *Ruminantia* are found to be free of immature stages. The adults are found on all *Carnivora, Artiodactyla* and on *Lagomorpha.* Domestic animals serve as the main hosts of the adult tick; small numbers of immature stages were found on sheep occasionally.

The *I. rubicundus* female prefers the woolled parts of the sheep to the bare ones as sites of attachment and is found in small numbers only on the bare parts of the head. In this respect she behaves differently from *I. ricinus.* The chance to reach full engorgement is better for the females attached to the woolled parts than for those attached to bare regions; the time required to reach full engorgement, however, is longer for those females attached to the woolled parts than for those attached to bare parts. An influence of active movement of the sheep on the time required by the tick for reaching full engorgement has not been found.

Two distinct stages of engorgement are recognised when the ticks are attached to sheep which have not remained in tick-infested areas for a long time and when the temperature remains between 8° and 15° C. A slow increase of size suggesting the condition described as a "local immunity" of the host, is observed when the female is attached to a sheep which was exposed to tick infestation for a considerable time. The chance of reaching full engorgement decreases in such cases

When checked at daily intervals 283 of 797 females were never observed to be in copulation and yet they reached full engorgement. Copulation could have taken place, however, before attachment or for a short period between the observation times. Thirty-one females were found in copulation for two periods with an interval between. Copulation on the first to third day of attachment tends to shorten the engorgement period, but exceptions have been observed.

The surveying of tick densities by grazing sheep in paddocks and by examination at intervals, has been modified to the tethering method, which is more suited to Karoo conditions. A modification was also necessary in the case of the dragging method. An improved apparatus was found suitable for surveying for larvae, which presents in the case of *I. rubicundus* a number of advantages. Larvae were found to be very evenly distributed in the field. An explanation for this observation has not been found.

The loss of larvae from the apparatus during the course of dragging is attributed to the abrasive effect of vegetation and stones. A certain time after the beginning of dragging additional losses are observed which are attributable to fatigue or to voluntary detachment of the ticks.

A geographical survey over a limited area in the Sneeuberg range reveals that the presence of the tick can be correlated with certain plant associations. Tick paralysis is found in all veld (pasture) types which provide little palatable food and in camps where good food is only available at a distance from drinking places. This observation indicates that the necessity for the stock to walk long distances may play a rôle in the development of tick paralysis. An experiment described by Stampa & du Toit (1957) supports this assumption. In this experiment it was shown that sheep which were restricted in their movements by being tethered to stakes never developed paralysis whilst free-running controls and sheep chased for a certain distance every day did develop tick paralysis.

The larva of *I. rubicundus* has been found to be the stage most susceptible to unsuitable environmental conditions, as was anticipated from the findings of other investigators working with other ticks. Eggs were found to hatch in layers of decomposing plant-parts under such plant species which are not eaten by stock. They failed to hatch in the shelter offered by grasses kept short.

Hatching was also observed under stones; but a considerable rootgrowth of the lesser palatable grasses was found under the stone under which eggs were placed. Stones can be accepted as not playing a rôle in the protection of the tick, as eggs failed to hatch under stones covered by more palatable grasses and as ticks were found to be absent from sweet-grass mountain veld with an abundance of dolorite as well as sand stones; it may also be mentioned that no stage of the tick was ever found under a stone.

Surveys for larvae in localities exposed to natural infestation with the tick revealed a very low incidence of ticks in sweet-grass mountain veld. It is assumed that the tick would not be able to complete its life-cycle in such localities during years having less favourable weather conditions than during those in which the surveys were conducted.

If the information given by Acocks (pers. comm) is correct, viz. that sweet-grass mountain veld, when badly treated, deteriorates to sweet-grass danthonia, danthonia, danthonia rhenoster harpuis, and to rhenoster harpuis mountain veld, then the tick incidence can be expected to rise during the first two stages and thereafter to drop, though only slightly, during the latter two stages. When deterioration from danthonia to Karoo mountain veld takes place, the picture is similar. If any one of these veld types is invaded by *Rhus erosa* (Fig. 8), and possibly also by other *Rhus* spp., environmental conditions for the tick are improved. During the stages of veld reclamation tick densities can be expected to increase to start with in the case of rhenoster harpuis and Karoo mountain veld, and to decrease thereafter when edible grass species which are well grazed become more prominent. This decrease of the tick density can be overshadowed if an increase of *R. erosa* takes place. A significant difference of tick densities in veld where *R. erosa* is scattered as opposed to veld where it is dense has been shown.

Veld improvement, usually encouraged by the reduction of stock numbers, may lead to an increase of the tick population in that grasses of lower palatability are eaten to a lesser extent. Such grasses, in the presence of smaller numbers of stock are now able to produce masses of decaying materials and thus create conditions suitable for the tick.

In Karoo mountain veld tick populations are increased when veld becomes invaded by shrubs of the rhenoster harpuis type.

Alterations of plant associations are shown to be possible, in certain cases within a few years, but difficulties are met with when shrubs of the rhenoster harpuis veld dominate the picture. The control of *Rhus erosa* is possible with weed-killers. Veld-fires are seen to be capable of causing a quick improvement of the veld, if correctly applied, but to cause a considerable deterioration if the burnt veld is stocked after the fire. Tick numbers are decreased by regular dipping of sheep; a complete eradication of the tick has, however, not been observed. Absence of stock from tick-infested veld is shown to have no influence upon the tick density. It is concluded, from the observation that certain hare species carry more adult ticks in resting veld than is normally the case and that hares may serve as hosts when stock is absent.

The findings of other investigators indicate that a complete residual killing effect against *I. rubicundus* is achievable with BHC and Dieldrin by foot-dipping sheep. A comparison of the behaviour of the tick on sheep as against the behaviour of *I. ricinus* gives an explanation why such a complete residual killing effect can be achieved against *I. rubicundus* and not against *I. ricinus*. A similarity is found between the problem of the protection of sheep against *I. ricinus* and the protection of sheep against blowfly strike. The specific killing capacity of the insecticide as found by laboratory methods, the ability to diffuse along the wool fibres, and the quantity applied are shown to be of importance for the period of protection achieved against *I. rubicundus* as well as against blowfly strike.

Field experiments showed that a very long-lasting protection against *I. rubicundus* is attainable with BHC and Dieldrin, the latter being required at approximately four times the amount of the former per sheep. The period of protection stands in relation to the quantity of active ingredient applied.

A field experiment against *Rhipicephalus evertsi* and *Hyalomma* spp. shows that a high degree of residual protection of sheep can be achieved with BHC against these tick species, but not an absolute one.

2. *Recommendations for the Control of* Ixodes rubicundus

(i) Sour-grass Veld

An improvement in the quality of tick-infested veld, aiming at its complete reclamation to sweet-grass veld, can be expected to bring about a solution of the tick paralysis problem in two ways—

(*a*) by providing more abundant grazing for the stock and obviating the necessity of excessive walking in order to obtain the necessary food;

(*b*) by giving stock a chance of grazing down the grasses once a year and thereby creating conditions unsuitable for tick survival.

Any method of field management which has as its object the close cropping of grasses, particularly the less palatable species, can be recommended, provided time is allowed for annual palatable grasses to set seed, e.g.

(*a*) To graze more stock for shorter periods in tick-infested pastures.

(*b*) To increase the cattle population as cattle tend to graze down the less palatable grasses more effectively.

(*c*) To burn veld which has been allowed to grow out of hand and to control grazing thereafter.

(ii) Rhenoster harpuis Veld

The invasion of grasses into this type of veld should be encouraged, the aim being to control the shrubs by burning after a certain density of grass has been established. Removal of the shrubs, even if this is only done in strips or patches, and the establishment of grasses by sowing seed, may be necessary in certain localities. The tick density can be expected to rise during the initial stages of reclamation of this veld-type after which it will decrease rapidly as the sweetgrass pasture becomes more stabilised.

(iii) Karoo Mountain Veld

The encouragement of grass-invasion is also recommended in this veld-type. As is the case with danthonia-rhenoster veld, tick densities must be expected to rise initially.

(iv) Rhus erosa

The eradication of this tall shrub should be encouraged and the experimental study of the most economical way in which this may be achieved is desirable. In how far other *Rhus* spp. should be eradicated for purposes of tick control, also requires further investigation. In those localities where *Rhus* spp. provide the only shelter available to stock consideration should be given to the planting of suitable species of trees.

Dipping

Formulations of Gamma BHC and Dieldrin which deposit a uniform amount of the active ingredient in the fleeces throughout the course of dipping can be recommended for the control of *I. rubicundus*. The depletion rate of the dipwash selected should not be too low. A replenishment during the process of foot-dipping is required in any case in order to maintain the required depth of wash. At the same concentration of wash in the dipping tank a greater quantity of active ingredient can be deposited per sheep by a formulation with a high depletion rate than by one having a low depletion rate. On the other hand, very high concentrations of dipwash should be avoided as they may cause toxic effects. No specific recommendation regarding the most suitable formulation for foot-dipping sheep can be made at this stage.

SUMMARY

1. Four forms of tick paralysis in South Africa may be distinguished, which differ as regards the clinical picture and are associated with four distinct tick species.

2. The literature dealing with tick paralysis in South Africa is briefly reviewed.

3. The seasonal occurrence of the adults, nymphae and larvae of *I. rubicundus* is given.

4. The adult is both nocturnal and diurnal and it is possible to demonstrate a peak in diurnal activity between 10 a.m. and 2 p.m.

5. The immature stages are exclusively nocturnal.

6. The influence of temperature upon larval activity is demonstrated graphically.

7. A host list is given which shows that the *Menotyphla* and *Lagomorpha* play the main rôle as hosts of the immature stages. The *Artiodactyla* constitute the main hosts of the adult tick amongst the wild animals. The tick is not found on birds.

8. The attachment sites of the adult stages on adult sheep and lambs are given and the chances of reaching full engorgement on the different regions of the body of the sheep are discussed. The preferential sites for *I. rubicundus* and *I. ricinus* are compared and the differences in habit of these two species on sheep described.

9. The time required by the female to reach full engorgement in different situations on the bodies of sheep is given.

10. The stages of engorgement normally observed are described and exceptions to this rule are discussed.

11. The percentage of females that fail to reach full engorgement on sheep is shown to increase with the time the sheep spends in tick-infested veld.

12. The influence of copulation upon the rate of engorgement is discussed.

13. The use of tethered sheep in tick-infested veld as a means of tick survey is discussed.

14. An improvement on the standard technique of dragging for ticks, for use in the Karoo shrub, is described.

15. The attraction of different materials to *I. rubicundus* tested by the dragging technique in the field has been investigated.

16. Seven species of ticks found during the course of dragging are noted.

17. The uniformity of distribution of *I. rubicundus* larvae in the field is discussed.

18. The factors responsible for the losses of ticks from the apparatus during the course of dragging are demonstrated graphically and discussed.

19. A map showing the distribution of *I. rubicundus* and the occurrence of tick paralysis in relation to veld (pasture) types in a selected area in the Sneeuberg Range is included.

20. The ecological investigations of overseas workers on other tick species are reviewed briefly for comparison with the findings relating to *I. rubicundus* in South Africa.

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21. An association between tick incidence and deterioration of pasture in the case of *I. rubicundus* is found to follow a pattern similar to that of *I. ricinus* in Britain.

22. The hatching and survival of the larvae of *I. rubicundus* are shown to represent phases of the life-cycle more susceptible to unsuitable environment than any other stage.

23. Experimental studies on the hatching and survival of eggs placed in decaying plant material under certain shrubs and rank grasses are described and compared with the differences observed when grasses are not allowed to become rank.

24. Significant differences in tick densities are shown to occur in different naturally-infested veld types. Sweet-grass mountain veld, constituting the original coverage of all mountains in the area under investigation, is not suited to the completion of the life-cycle of the tick.

25. The rôle played by *Rhus erosa* in the creation of suitable environmental conditions for the tick is pointed out.

26. The time required for bringing about an alteration in the existing plant associations by applying different methods of pasture management is discussed.

27. The influence of the regular dipping of sheep upon the incidence of *I. rubicundus* is demonstrated.

28. The exclusion of sheep from tick-infested camps during the active season of *I. rubicundus* is shown to have no effect upon the incidence of the tick.

29. The influence of veld fires upon the tick is pointed out.

30. The recommendations of other investigators for the control of *I. rubicundus* by dipping are compared with the application of dipping to the control of *I. ricinus*.

31. The specific efficacy of insecticides against the tick as found by a laboratory method, the ability of the insecticide to diffuse along the wool fibres and the quantity of insecticide deposited in the fleece rather than the concentration of the wash in the dipping tank, are shown to be the decisive factors governing the period of protection obtained against *I. rubicundus*.

32. BHC is shown to be capable of protecting woolled sheep against *I. rubicundus* for a period exceeding 18 weeks when 4·75 gm. of the gamma isomer is deposited per sheep.

33. Dieldrin is shown to protect woolled sheep for approximately 11 weeks when 7 gm. of the active ingredient is deposited per sheep.

34. The protection of sheep against *Rhipicephalus evertsi* and *Hyalomma* spp. by BHC has been tested.

35. The experience gained in the application of the foot- or walk-through-bath for sheep is given.

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