

## **HOST AND TICK RELATIONSHIPS: A REVIEW \***

Author: ARTHUR, DON. R.

Source: Journal of Wildlife Diseases, 9(1) : 74-84

Published By: Wildlife Disease Association

URL: <https://doi.org/10.7589/0090-3558-9.1.74>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## HOST AND TICK RELATIONSHIPS: A REVIEW\*

DON. R. ARTHUR, Tick Research Unit, Rhodes University, Grahamstown, South Africa

**Abstract:** Our knowledge, at all levels of information, on the relationships of ticks with wild fauna is sparse. There is a need for greater understanding of these facets if we are to understand the transmission of disease to wild vertebrates. The following levels of information required are outlined: (a) the behaviour of the ticks on the host before feeding, (b) the feeding process, (c) the host reaction at the level of tissue response, (d) parasite induced resistance mechanisms of the host to repeated tick infestation, (e) the temporal occurrence of ticks, (f) the regulating factors controlling tick populations, (g) the population dynamics of the host and (h) the susceptibility of hosts to trans-species transmitted pathogens.

### INTRODUCTION

The range of interactions between ticks and their hosts is varied and the activities of these arthropods during the process of obtaining their meal may subject the host to minimal inconvenience, acute irritation, or cause it to suffer severely from blood loss or from the effects of toxins introduced during feeding. Superimposed on one or more of these interactions is the possible transmission during feeding of a wide range of disease agents, many of which probably remain to be categorized. In attempting to assess the complex phenomenon of tick - host - disease relationships, information at a number of different levels is required.

### BEHAVIOUR OF TICKS BEFORE FEEDING

Having obtained access to the hosts the initial behaviour of adult ticks is determined by the completion, or otherwise, of spermatogenesis in the preceding nymphal stages. In *Ixodes* ticks, for example, the formation of the spermatozoa is evident before the engorged nymph drops off. Consequently fertilization of the female by the male can be effected without delay, either on or off the host, and does not necessarily involve feeding by the male. In nymphs of *Amblyomma*,

*Rhipicephalus*, *Haemaphysalis* and *Dermacentor*, destined to become males, spermatogenesis proceeds only as far as the formation of primary spermatocytes. Here the completion of spermatogenesis is dependent on the males acquiring a blood meal. In some tick species the males are known to seek the attached females but in others, such as the bont tick (*Amblyomma hebraeum*), the females are attracted to the males. The nature of the attractant has not been satisfactorily determined. Berger *et al*<sup>4</sup> have indicated that the chemical properties of the active substance is a weak acid, possibly a phenol. Moreover, they report that the pheromone is contained in the female and that the male of *Amblyomma maculatum* is attracted to the female. In the same tick species Gladney<sup>10</sup> noted that the females are attracted to the males. Under these circumstances the females do not usually start to feed until fertilization has been effected, although they may probe and remain temporarily attached for up to 24 hours (unpublished data. — A. Norval). Complete engorgement is never achieved under these circumstances. Observations by Whitnall *et al.*<sup>30</sup> also demonstrate that over periods of up to 6 months the male bont ticks increase their numbers cumulatively on the host and may, at any one time, be 4 to 5 times as numerous as females. The individual male

\* Presented at the 2nd International Conference on Wildlife Disease, University of Sussex, England, July 18-22, 1971.

bont tick is capable of inseminating a large number of females, and after each mating the female is capable of feeding and producing viable offspring. Whilst the bont tick is recognized as a serious problem on cattle in the south-eastern Cape region of South Africa it is also known to occur on such wild antelopes as the kudu. There is no reason to believe that this behavioural pattern differs on wild hosts. Much remains to be explored on the pre-feeding behaviour of all stages of the tick when they have obtained access to the host. Thus, immature stages may colonize one part of the body and adults another, in particular the "choice" of the ears of hares and rabbits by the larvae and nymphs of the red-legged tick *Rhipicephalus evertsi* and of the perianal regions by its adults is a case in point.

In the Karoo paralysis ticks, *Ixodes rubicundus*, the immature stages are rarely found parasitizing domestic stock, although adults do. The larvae and nymphs are most abundant on the elephant shrew (*Elephantulus capensis karroensis*), and the Cape hare *Pronolagus rupestris saundersiae*. Exceptionally are females found on other wild fauna. The reasons for ticks having sites of predilection, either on the same or different hosts, as well as different hosts for different tick stages remain to be solved.

#### THE FEEDING PROCESS

Having acquired a site for feeding, the next level of information relates to the activities of ticks in attaching themselves to hosts, together with the method of obtaining nutriment from their tissues and the method of detachment at the appropriate time after feeding. This involves overcoming the non-specific defences of the skin and, provided the other tissues are not completely intractable, feeding can commence.

Ticks fall into two morphological groups, the argasid, or soft ticks, and the ixodid, or hard ticks, the former being characterized by feeding for short times and the latter feeding and remaining attached to the hosts for several days to complete engorgement. In both groups the initial process of overcoming the

non-specific skin barrier is by the sweeping and cutting motions of the cheliceral digits. This is accompanied by alternative thrusting movements of the chelicerae effecting penetration through the stratum corneum. Inoculation of salivary secretions into the lesion follows, but the question of their activity and function in host-parasite-disease relationships is not entirely clear in ticks nor in some other arthropods. Thus, anticoagulins, which were thought to be essential for mosquito feeding, are absent in as many species as those which possess them,<sup>5</sup> whilst Lester and Lloyd<sup>12</sup> showed that, though there is an anticoagulin present in tsetse fly saliva, feeding can be successfully carried out after cutting the salivary duct, without causing any host allergic responses. In the rapidly feeding argasid ticks, there is evidence that the salivary secretion contains a potent anticoagulin and a proteolytic enzyme. In such species as *Ornithodoros savignyi* there is also a toxin of some potency, all of which suggests a destructive action on host tissues. Ixodid ticks, on the other hand, show some variation in the composition of their salivary secretions. Some, for example *Hyalomma asiaticum*, and *Ixodes ricinus*, have salivary components which prevent blood clotting, others, e.g. *Dermacentor andersoni* and *Boophilus microplus*, lack discernible anticoagulins. The secretion of a 'cement' from the salivary glands of all genera of hard ticks, with the possible exception of some species of *Ixodes*, appears to be a major function of the salivary glands. This is released as a latex-like secretion which, on hardening, anchors the penetrant mouth parts. In tick genera (e.g., *Amblyomma*, *Hyalomma* and *Aponomma*) which insert their long mouth parts completely into the dermal tissues, the mouth parts are enveloped by cement, with little or no superficial deposition on the skin surface. In *Dermacentor*, *Boophilus* and *Rhipicephalus*, the cement is largely superficial and the mouth parts do not penetrate the dermis. In the genus *Haemaphysalis* the inserted mouth parts come to lie just beyond the epidermis and the cement is predominantly on the surface. No cement is produced by the glands of such species as *I. ricinus*, and the mouth parts are

inserted deeply into the skin tissues, where they are probably held *in situ* by transformed host tissues, in much the same way as fine reticulin fibrils succeed tissue damage inflicted by parasitic flatworms. Around the mouth parts of this species in the dermis there is an abundance of collagen, suggesting that secure attachment is not due solely to aggregation of fibres, but that there may be active synthesis of collagen. Fibroblasts are generally believed to be responsible for secreting collagen but these are noticeably absent from around the mouth parts. Collagen is, however, a highly polymerized and relatively insoluble substance and, enzymes in the salivary secretion of *I. ricinus* may polymerize the collagen precursors in the skin.

It seems reasonable to postulate in ixodid genera, with deeply inserted mouthparts and supported by cement, that circumferential attachment is secure and that any rigorous host tissue destruction by salivary enzymes will take place at the tip of the hypostome. On the other hand, superficially attaching species are unlikely to have powerful digestive enzymes, for this would imperil their attachment. Accordingly such species must inflict tissue damage by more subtle specific means. The progressively more superficial insertion of the mouth parts diminishes the tissue irritation and places the more highly vascularized outer layers of the dermis beneath the mouth parts. In *Dermacentor andersoni* the initial feeding of blood appears to take place after a short period of attachment and is probably due to mechanical injury to the capillaries in the path of the chelicerae producing a blood pool.<sup>9</sup> Suffusion of red and white cells, due to diapedesis as a result of irritants in the tick saliva may supplement this. The flow of blood occurs only after extensive damage to the tissue, which Gregson thinks is likely to be due to proteolytic and diabrotic tick secretions rupturing capillary walls. This view does not appear to be consistent with the remarks of Tatchell<sup>28</sup> who states that the saliva of this species "has no anticoagulin or indeed any discernible active constituents although it does have antigenic properties". During the first hours of attachment normal blood forms the major

part of the blood meal of *D. andersoni*,<sup>9</sup> although there appears to be a need for a subtle mixture of blood and salivary fluid together, perhaps with tissue fluid, for the initiation of feeding. On the basis of spectrophotometric analysis of gut contents at varying intervals of tick feeding, Sutton and Arthur<sup>22</sup> have demonstrated that females of *I. ricinus* ingest nutrients other than blood at early periods of feeding, and there may be ingestion of significant amounts of other tissue fluids during engorgement.

In *Boophilus microplus*, specific vascular damage results from the saliva of the tick, whereas tissue damage is caused by the host response — an hypothesis based on the finding that collagen destruction beneath the mouth parts was preceded by an intense infiltration of neutrophils. Induction of a leukopenia by administration of nitrogen mustard to dogs, parasitized by *Rhipicephalus sanguineus*, substantiates this concept, for in the skin of such animals, polymorphonuclear leucocytes were rare but heavy infiltrations around the trophi characterized untreated tick-infested hosts. The latter, too, towards the time of full engorgement, had well established cavities beneath the mouth parts due to destruction of the collagen. Whereas in treated dogs, cavities were either absent or insignificant and dermal collagen appeared to be unaffected.

#### HOST REACTION

The third level of information required relates to the host reaction both at the level of tissue response and, after primary exposure, to the parasite-acquired resistance mechanisms of the host. In most cases, acquired resistance is immunological, at least in part. The successful host-parasite relationship is therefore one where the innate resistance and the immune responses of the hosts interact to control, but not to overcome, the challenge of the parasite.

Some ticks such as *Ixodes ricinus* can parasitize lizards as well as a very wide range of mammals and birds; others are very much more restricted in their choice of hosts. These limitations of host selection may in part be determined by ecological associations or by a more real,

restrictive host specificity. *I. trianguliceps*, a parasite of small British rodents, is indicative of this situation but the exact blood intake is reduced as a result of repetitive feeding, are considerably lower (c 40-54%) when compared with age

#### TEMPORAL AND NUMERICAL OCCURRENCE OF TICKS

The fourth level of information required is the temporal and numerical occurrence of ticks on their hosts in relation to disease transmission. Most of the information on this aspect of the subject refers to infestation of domestic stock. One of the most carefully studied ticks in terms of distribution and detailed ecology is the three-host species, *Ixodes ricinus* L. In Great Britain its host relationships on domestic stock has been examined by MacLeod,<sup>13,14,15</sup> Milne,<sup>10,17,18,19</sup> Edwards and Arthur<sup>6</sup> and Evans.<sup>7</sup> The results indicate that these ticks generally have bimodal peaks of activity in the spring and in the autumn, or in some districts a single summer peak. *Ixodes ricinus* is catholic in its choice of hosts<sup>18,19</sup> but details of its ecology in relation to wildlife remain largely unexplored. So that its role as a vector of wild life diseases is unknown. Of British ticks habitually associated with wild animals, the biology of *I. hexagonus* Leach, the hedgehog tick, has been investigated under laboratory conditions by Arthur,<sup>1</sup> as also has its life history based on the seasonal incidence of ticks on hedgehogs. Here, too, there is evidence for bimodal seasonal activity.

Cotton and Watts<sup>9</sup> and Young<sup>27</sup> have made contributions to our knowledge of *I. trianguliceps* Birula. Their observations, as well as our own at the King's College Rogate Field Station, are not dissimilar to those of Vysotskaya<sup>28</sup> in Russia and Lachmayer<sup>11</sup> in Poland. For a number of reasons *Ixodes trianguliceps* is a useful model for monitoring tick load and seasonal activity on wild fauna. It has a restricted host range, being found in Britain on the voles *Microtus agrestis*, *Clethrionomys glareolus*, the shrews *Sorex minutus* and *S. araneus* and the rodents *Apodemus sylvaticus* and *Micromys minutus*. The larvae, nymphs and females of this tick occur on all these hosts. All hosts are reported to be infected with piroplasms. All these hosts can be captured alive, examined for ticks, released and recaptured. It is also a potentially interesting species for analyzing and interpreting the role of ticks in the transmission of babesias, and might even give

an insight into the transmission of arboviruses.

Fully engorged females of *I. trianguliceps* lay over 1000 eggs each, and the minimum quantity of blood required before any egg laying proceeds is 25-30 mg.<sup>3</sup> The fully engorged female thus has an egg laying potential not unlike that of *I. ricinus*. But the number of larvae and succeeding instars found on the hosts cannot be correlated with this high egg yield (Table 1). These data are open to criticism on the grounds that sample sizes were inadequate, and that capture-recapture methods of marked individuals were not used. These refinements have been introduced into work in progress at the King's College Rogate Field Station. As an indication of these results we found that — in preliminary work by Sarah Randolph — of 108 *A. sylvaticus* examined 50 per cent have been infested at one time or another. The measure of infestation is still relatively low (Table 2) but is significantly higher than indicated by the average infestation loads cited in Table 1. The period covered in Randolph's survey does in some measure overlap with the peak periods quoted by the other workers but it is obviously necessary to continue these investigations over a much longer period of time before reaching any positive conclusions.

In terms of larval populations, the results presented in Table 1 compare with an average of four *I. ricinus* larvae on shrews, voles and mice on pastures infested with this species in the North of England.<sup>19</sup> However, *I. ricinus* is a species living in open pastures whereas *I. trianguliceps* is presumed to be a nest-inhabiting species. The likelihood would thus be that hosts would pick up *I. trianguliceps* ticks on each occasion when they returned along well established runs to their nests.

The discrepancy between the potential yields of larvae from the large egg masses laid by each female, and the actual numbers of larvae affixing to hosts might be due to (i) a high mortality of larvae within or during emergence from the egg mass, (ii) that successful hatching is followed by a failure of larvae to find hosts, (iii) that having attached on certain areas of the body they are removed

TABLE 1. Average infestation per host of *I. trianguliceps* at peak times of occurrence

Species	Larvae			Nymphs			Females		
	Average Infestation	Peak Months	Author	Average Infestation	Peak Months	Author	Average Infestation	Peak Months	Author
<i>Clethrionomys glareolus</i>	0.7	June	Young (27)	0.35	July	Young (27)	0.3	July	Young (27)
	1.4	October					0.01	October	
	0.5 on ♀	June	Cotton and	0.5 on ♀	July	Cotton and	0.12	April	Cotton and
	2.5 on ♂		Watts (6)	1.25 on ♂	June	Watts (6)	0.09	October	Watts (6)
	1.2 on ♀	October							
	2.6 on ♂								
<i>Apodemus sylvaticus</i>	1.17	April	Young (27)	0.5	July	Young (27)	0.1	June	Young (27)
	1.6	October					0.2	September	
<i>Microtus agrestis</i>	0.57	April	Young (27)	0.4	August	Young (27)	0.05	May	Young (27)
	0.55	October							
Range of small mammals (Russia)	3.8	June	Visotskaya	1.0	August	Visotskaya	0.5	April	Visotskaya
	2.5	October	(25)			(25)	0.66	July	(11)
Range of small mammals (Poland)	3.66	April	Lachmajer	0.85	June	Lachmajer	0.66	April	Lachmajer
	2.53	October	(11)			(11)	0.28	July	(11)

TABLE 2. *Ixodes trianguliceps* populations on *Apodemus sylvaticus* at King's College Rogate

Host no.	L = larva; N = nymph; ♀ = female;						
	27-29.7.71	10-12.8.71	24-26.8.71	7-9.9.71	22-24.9.71	5-7.10.71	19-21.10.71
30	1N	o	—	—	—	—	1L
33	1L	6L + 1N	6L	3L	3L + 2 ♀	9L + 1 ♀	12L, 1N 1 ♀ + 1 ♂
34	2N	—	10L	1L	—	—	—
36		o	2L	2L	3L	2L + 1 ♀	12L + 1 ♀
37		1L	o	o	3L	5L + 1 ♀	—
40		6L	1L + 1N	3L, 1N, 1 ♀	2L	5L, 1 ♀, 1 ♂	5L
41		o	o	o	—	—	—
42			1N	2L	—	—	—
43			o	o	—	—	—
44				o	—	—	o
45				o	1L	4L + 1 ♀	o
46				1N	o	1L	2L
47				1 ♀	1L, 1 ♂, 2 ♀	—	—
51					5L	4L + 1L	—
53					1L	2L	—
54					o	5L	—
56						o	o
57						1L	6L
58						4L	2L + 1L
61							3L
62							2L + 1L
63							1L + 1L
64							2L
67							1L
69							4L
72							6L
73							—
74							—
75							—
76							—
77							—
78							—
79							—
81							—
83							—
84							—
87							—
88							—
87							—
89							—
107							—
108							—
90							—
91							—
93							—
94							—
95							—
85							—
100							—
97							—
98							—
99							—
101							—
106							—

\*Data collected by Sarah Randolph



## Field Station.\*

♂ = male; L = dead larva; o = no ticks; — = host not recaptured

Host no.	2-4.11.71	17-19.11.71	30.11-2.12.71	14-16.12.71	29-31.12.71	11-13.1.72	25-27.1.72
30	—	—	—	4L			
33							
34							
36							
37							
40							
41							
42							
43							
44	6L						
45	—	1L	—	12L	1L		
46	1L	14L	2L + 1L	3L + 1L	5L	2L	2L
47							
51							
53							
54							
56	—	1L	1L	—	1L	o	o
57	15L + 1 ♀	12L					
58	2L						
61	4L						
62	3L	1L + 1L	8L	8L	5L	o	o
63	—	2L	—	1L	o	o	o
64	—	9L					
67	—	3L					
69	7L	15L	5L	8L	4L + 1L	o	
72	o	2L					
73	1L	3L	3L	1L + 1L	—	1L	o
74	2L	—	—	9L	o	1L	o
75		5L	—	2L	—	1L	o
76		5L	—	6L	2L	1L	1L + 1 ♀
77		o	—	1L	—	1L	o
78		15L, 1N, 1 ♀	6L	3L	2L	2L	1L
79		1L	—	—	o	o	o
81		5L	—	1L	o	1L	o
83		3L + 1L	—	2L	1L	o	o
84		8L	6L	9L	—	o	3L
87		o	—	o	2L	o	
88			2L	o	4L + 1L	o	1L
87			5L	1L	o	o	o
89			1L	1L	—	3L	1L
90			3L	4L	o	1L	
91			9L + 1L	o	o	o	
93			4L	o			
94			o	o	1L	o	o
95				o	2L	2L	
85		9L	—	—	—	—	o
100				o	1L	o	
97				2L	—	1L	1L
98					2L	1L	2L
99					1L	o	o
101					o	o	1L
106						1L	o
107						o	o
108						o	o

by the host, (iv) that gorged stages drop off and are rapidly consumed by their hosts, and (v) that there is a resistance response by the host which militates against either full engorgement or successful feeding. Considering each of these possibilities in turn, there is no evidence, on the basis of laboratory investigations, that there is a high mortality of larvae on hatching. A 100% R.H. within the temperature range of 10-26° C they survive for 36-89 days, whilst nymphs survived even longer at lower humidities. The animals normally acting as hosts for *I. trianguliceps* all use extensive burrow and runway systems, even though in such animals as *M. agrestis* the nests may be above ground. Most of the ticks thus far detected have been found in the nests and these have been, usually, unfed stages. Fully fed engorged females have been recorded most often in the burrow systems and, in the absence of egg clumps in the nest, it seems probably that this is the location for oviposition. Under these conditions, the emerging larvae may become widely dispersed along the burrow system and the smaller the host body, the less will be the front available for attachment, by any stage of the parasite.

It has been established by Milne<sup>19</sup> that gorged *I. ricinus* are eaten by voles, by Arthur<sup>1</sup> that fed *I. hexagonus* are eaten by hedgehogs, and Young<sup>27</sup> has shown the same to be true in wild and laboratory animals. It is also clear that sites of predilection for feeding by ticks on small mammals are the ears (90-95%), the head (3-7%) and, much more rarely, on the bare parts of the scrotum. Here there would seem to be an active deticking process, whereby excrescences caused by the bodies of ticks are removed and possibly consumed.

It has often been observed that stages of *I. trianguliceps* failed to feed to repletion, but remained attached to their natural hosts and died *in situ*. This may be symptomatic of an acquired resistance by the host, but until our work has proceeded further it is not possible to make a valid judgment. What is clear, however, is that there are factors regulating the reproductive potential of ticks, but without minimizing their parasitic challenge,

and this in turn will maintain arthropod borne pathogenic infections in a state of stable equilibrium.

#### TRANSFER OF TICKS AND PATHOGENS BETWEEN HOSTS

The transfer of ectoparasites between different host species has an important bearing on the epidemiology of vector transmitted diseases and in three-host ticks, such as *I. trianguliceps*, pathogen transfer must be either trans-stadial or trans-ovarial. On the evidence available, the transfer of piroplasms by this species is trans-stadial, although the eating of fully fed ticks from an infected host by an uninfected host can also result in infection, as shown by Young.<sup>27</sup>

Pathogen dissemination by ticks between different host species naturally requires that the hosts overlap in their distribution, or that they use common facilities, such as burrows. This may be due to seasonal changes influencing the choice of the animals' habits. Or it may be to the overlapping of biotopes on the borders of woodland, scrub and hedgerow. Trapping in an experimental area showed that in the autumn *C. glareolus* and *A. sylvaticus* used runways in the same area and sometimes the same burrows. *M. agrestis* was dominant in grassland, although overlapping with *C. glareolus* and *A. sylvaticus*, where scrub impinged on it. *S. araneus* overlapped with all three. In the winter the specificity of biotopes was no longer apparent. *Apodemus sylvaticus* had moved into the grassland and was using the burrows of *Microtus*, which had disappeared. *Sorex* had disappeared from the area, too, whilst *C. glareolus* was restricted to the scrubland. By the following May all these animals had returned to their pre-winter biotopes. Southern<sup>21</sup> has shown that these migrations by small mammals are normal, so that within any one natural habitat there is a turn-over of different host species, according to the season. By these means different groups of mammals can pick up infected ticks, particularly if the latter are active throughout the year, as appears to be so in *I. trianguliceps*.

Hitherto adequate attention has not been given to the incidence of ticks on wild hosts, to the population dynamics of the hosts in relation to their ectoparasitic infestations nor to the frequency of piroplasms in natural populations. We know little on the continuous abiotic parameters in nests, burrows and runways of known tick infested animals, for these will determine the survival and activity of the unfed ticks and of their contained pathogens. Of equal importance from the point of view of disease transmission is the

need to ascertain the nature of the resistance response of the host to tick attack, and to determine the level at which it occurs. It is also important to know whether all the small mammals, from which ticks have been recorded, are true maintenance species of piroplasms, specific viruses and rickettsiae. For it seems reasonable to consider that the only true maintenance hosts for these pathogens are those in which pathogens can circulate adequately in concentration and duration to infect ticks.

#### LITERATURE CITED

1. ARTHUR, D. R. 1951. The bionomics of *Ixodes hexagonus* Leach in Britain. *Parasitology*. 41: 82-90.
2. ARTHUR, D. R., and J. LONDT. 1972. The immature stages and metamorphic changes of *Boophilus decoloratus* (Koch 1844). In press. *J. ent. Soc. Sth. Afr.*
3. ARTHUR, D. R., and K. SNOW. 1967. The implications of size as shown in *Hyalomma anatolicum anatolicum* (Ixododidae: Ixodidae). *Wiad. Parazyt.* 13: 497-509.
4. BERGER, R. S., J. C. DUKES, and Y. S. CHOW. 1971. Demonstration of a sex pheromone in three species of hard ticks. *J. med. Ent.* 8: 84-86.
5. CLEMENT, A. N. 1963. *The Physiology of Mosquitoes*. pp. 1-393. London, Pergamon Press.
6. COTTON, M. J., and C. H. S. WATTS. 1967. The ecology of the tick *Ixodes trianguliceps* Birula (Arachnida: Acarina: Ixodoidea). *Parasitology*. 57: 525-532.
7. EVANS, G. O. 1951. The seasonal incidence of *Ixodes ricinus* on cattle in mid-Wales. *Bull. ent. Res.* 41: 459-468.
8. EDWARDS, E. E., and D. R. ARTHUR. 1947. The seasonal activity of the tick *Ixodes ricinus* L. in Wales. *Parasitology*. 38: 72-85.
9. GREGSON, J. D. 1967. Observations on the movements of fluids in the vicinity of the mouth parts of naturally feeding *Dermacentor andersoni*. *Parasitology*. 57: 1-8.
10. GLADNEY, W. J. 1971. Mate seeking by female *Amblyomma maculatum* (Acarina: Ixodidae) on a bovine. *Nature*. 232: 401-402.
11. LACHMAJER, J. 1962. The ecology of the tick *Ixodes trianguliceps* Bir. *Bull. Inst. Mar. Med. Gdansk*. 13: 149-160.
12. LESTER, H. M. O., and L. LLOYD. 1928. Notes on the process of digestion in tsetse flies. *Bull. ent. Res.* 19: 39-60.
13. MACLEOD, J. 1932. The bionomics of *Ixodes ricinus* L., the sheep tick of Scotland. *Parasitology*. 24: 382-400.
14. MACLEOD, J. 1934. The part played by alternative hosts in maintaining the tick populations of hill pastures. *J. anim. Ecol.* 3: 161-164.
15. MACLEOD, J. 1939. The seasonal and annual incidence of the sheep tick, *Ixodes ricinus* L., in Britain. *Bull. ent. Res.* 30: 103-118.
16. MILNE, A. 1945. The ecology of the sheep tick, *Ixodes ricinus* L. Host availability and seasonal activity. *Parasitology*. 36: 153-157.

17. MILNE, A. 1947. The ecology of the sheep tick, *Ixodes ricinus* L. Some further aspects of activity, seasonal and diurnal. *Parasitology*. 38: 27-33.
18. MILNE, A. 1949. The ecology of the sheep tick, *Ixodes ricinus* L. Host relationships of the ticks. Part 1. Review of previous work in Britain. *Parasitology*. 39: 167-172.
19. MILNE, A. 1949. The ecology of the sheep tick *Ixodes ricinus* L. Host relationships of the tick. Part 2. Observations on hill and moorland grazings in northern England. *Parasitology*. 39: 173-197.
20. STAMPA, S. 1959. Tick paralysis in the Karoo areas of South Africa. *Onderstepoort J. vet. Res.* 28: 169-227.
21. SOUTHERN, H. N. 1964. *Handbook of British Mammals*. Blackwell. Oxford.
22. SUTTON, E., and D. R. ARTHUR. 1962. Tick feeding in relation to disease transmission. In: Arthur, D. R. (Ed.) *Aspects of Disease Transmission by Ticks*. pp. 223-52. Symp. zool. Soc. Lond., No. 6.
23. TATCHELL, R. 1969. Host parasite interactions and the feeding of blood sucking arthropods. *Parasitology*. 53: 93-104.
24. TRAGER, W. 1939. Acquired immunity to ticks. *J. Parasit.* 25: 57-81.
25. VYSOTSKAYA, S. O. 1951. On the biology of *Ixodes trianguliceps* Bir. *Parazit. Sborn. Zool. Inst. Akad. Nauk SSR*. 13: 105-110.
26. WHITNALL, A. B. M., W. M. McHARDY, G. B. WHITEHEAD, and F. MEERHOLZ. 1951. Some observations on the control of the bont tick *Amblyomma hebraeum* Koch. *Bull. ent. Res.* 41: 577-591.
27. YOUNG, A. S. 1970. Investigations on the epidemiology of blood parasites of small mammals with reference to piroplasms. Ph.D. Thesis. University of London.

Received for publication April 25, 1972

---