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Detachment rhythms of immature *Ixodes rubicundus* from their natural host, the rock elephant shrew *(Elephantulus myurus)*

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ABSTRACT

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Detachment rhythms of immature Karoo paralysis ticks *(Ixodes rubicundus)* from their natural host, the rock elephant shrew *(Elephantulus myurus)*, were investigated under laboratory and natural conditions. Larvae and nymphs detach mainly during the day. Peak detachment always occurred after the commencement of artificial as well as natural light cycles. The detachment of larvae appears to be more synchronous than that of nymphs, with a larger percentage of larvae detaching over a shorter period of time. The detachment rhythms of *I. rubicundus* are strongly correlated with the activity patterns of their hosts. This enhances not only the survival, but also the dispersion and host contact of subsequent stages.

INTRODUCTION

Numerous ethological and physiological characteristics indicate intimate and complex relationships that have evolved between particular tick species and their natural hosts (Hoogstraal 1978). The close species-specific association between ticks and their hosts is also revealed by the detachment rhythms of the ticks after engorgement. The daily detachment times of engorged ticks are both physiologically and ecologically important. Engorged ticks tend to drop in areas where conditions are favourable for their post-engorgement development, and where they are likely to encounter a host (Belozerov 1982; Matuschka, Richter, Fischer & Spielman 1990a).

The existence of a circadian rhythm in the detachment of engorged ticks from a diversity of hosts has been demonstrated by several authors (Amin 1970; George 1971; Rechav 1978; Matuschka *et al.* 1990a, b). Detachment is controlled by endogenous circadian regulation mechanisms which are entrained by exogenous signals (Hadani & Rechav 1970; George 1971; Hadani & Ziv 1974). The endogenous rhythm can be affected by the host's daily physiological and activity rhythms, and this in turn affects the precision of the detachment rhythm (Rechav 1978). This dependence of parasite rhythms on host rhythms is of adaptive importance to host-parasite relationships (Belozerov 1982).

The Karoo paralysis tick *(Ixodes rubicundus)* is a three-host tick confined mainly to hilly or mountainous terrain in localities which have a distinct Karoo vegetation (Theiler 1950; Fourie, Kok & Van Zyl 1991). The

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larvae and nymphs of this tick occur primarily on rock elephant shrews *(Elephantulus myurus)* (Fourie, Horak & Van den Heever 1992) and the adults on wild ungulates (Stampa 1959; Horak, Moolman & Fourie 1987). Such a change in host preference between instars is usually reflected in different detachment rhythms and habitat requirements for post-engorgement development by the various instars (Belozerov 1982).

The purpose of this study was to investigate the detachment rhythms of immature *I. rubicundus* from *E. myurus* and to relate these to particular behavioural characteristics of the host. These data contribute to an understanding of this tick's dispersal and survival within its preferred habitat.

MATERIAL AND METHODS

Experimental animals

Ticks

Engorged female *I. rubicundus* were collected from sheep and cattle in the field during the 3 winter months. These ticks were divided into two groups (A and B), each consisting of eight females.

Elephant shrews

Eight adult rock elephant shrews (four males and four females) were live-trapped in the same locality from which the ticks had been collected, and initially put in separate plastic cages (400 x 400 x 300 mm) with wire-mesh floors. The cages were then placed over water-traps for 2 weeks to allow naturally attached ticks to engorge and detach. These elephant shrews were divided into two groups (A and B), each consisting of two males and two females.

Experimental procedures

Group A

Female ticks belonging to group A were placed individually in sealed containers (± 95 % RH) in a temperature-controlled cabinet at 25 °C in the dark, and allowed to oviposit. After the eggs had hatched, larvae were maintained in the temperature-controlled cabinet at a light cycle of 13L:11D and a temperature of 15 °C (± 90 % RH). Some of the larvae were fed on elephant shrews in a temperature-controlled cabinet at 15 °C, RH of 34 ± 4 % and 13L:11D light cycle. Engorged larvae were maintained at 25 °C (± 95 % RH) in the dark and allowed to moult into nymphs. After moulting, nymphs were maintained at 15 °C (± 90 % RH) and a light cycle of 11L:13D.

Elephant shrews belonging to group A were acclimated for at least a month in an environmental room at 20 °C (± 42 % RH) and a light cycle of 11L:13D. These elephant shrews were then each infested with at least 100 laboratory-reared larvae inside a temperature-controlled cabinet at 15 °C and a light cycle of 13L:11D.

A similar procedure was followed for infestation of the elephant shrews with 50–150 nymphs each. Infestations with laboratory-reared nymphs were done at 15 °C and a light cycle of 11L:13D. During all infestations the elephant shrews were individually housed in plastic cages with wire-mesh floors. The cages were suspended over water-traps into which the detached ticks could fall. The water-filled traps were periodically inspected for the first engorged ticks to detach. Once detached ticks had been found, hourly observations were made during which the ticks were removed from the traps and counted. This procedure continued until all the ticks had detached. Care was taken not to disturb the host animals. Infestation of the elephant shrews took place between 18:00 and 19:00.

Group B

Female ticks belonging to group B were individually put into 10-mℓ glass vials plugged with cotton-wool, and allowed to oviposit. These vials were placed in the field inside a glass box which was buried in the soil to a depth level with its transparent lid. A shade net prevented direct solar radiation entering the box. The RH within the container was maintained above 86 % by means of a saturated salt solution (KH_2PO_4) (Young 1967). Larvae were maintained in the glass box in the field, still with the salt solution, but otherwise under naturally fluctuating climatic conditions. Some of the larvae were fed on caged elephant shrews kept under natural conditions in the field during May and June. These are the months during which larvae are normally active (Fourie *et al*. 1992). Engorged larvae were returned to the glass box in the field and allowed to moult to nymphs. These nymphs were also kept in the glass box in the field.

The remaining four elephant shrews belonging to group B were released into a fenced area (10 x 8 m) in the field to expose them to naturally fluctuating climatic conditions. These elephant shrews were infested with an equal number (*c*. 100) of larvae kept under similar natural conditions. The larvae were about 2–3 weeks old at the commencement of the experiments, which took place during May and June. The natural photoperiod on 30 May was 10,5L:13,5D (sunrise to sunset). Infestation of the partially free-ranging elephant shrews with nymphs took place during August and September, the months during which *I. rubicundus* nymphs are naturally active in the field (Fourie *et al.* 1992). The photoperiod for 30 August was 11,5L:12,5D (sunset to sunset). Infestation methodology and observations made on detached ticks were similar to those described for group A.

RESULTS

Larvae and nymphs detached from the hosts over periods of 2 and 3 d, respectively. As there were no significant differences in the patterns of tick detachment between the individuals or sexes belonging to each group (ANOVA, P > 0,05) the data for each group were pooled. Data for the larvae and nymphs from *E. myurus* kept under artificial (group A) and natural (group B) climatic conditions are graphically illustrated in Fig. 1 and 2.

Larvae detached mainly during the day (93,6 and 73,9 % for artificial and natural photoperiods, respectively). Peak detachment occurred 2 h after the commencement of the artificial as well as the natural light cycles at 07:00 and 09:00, respectively. The pattern of both groups' detachment rhythms was similar, although the detachment peaks were 2 h apart.

Detachment of nymphs also took place during the day, but over longer periods than the larvae (Fig. 2). Peak periods of detachment from the elephant shrews in groups A and B were recorded around 7:00 and 8:00, i.e. 1 and 1,5 h, respectively, after commencement of the artificial and natural light cycles. In group B a second peak of detachment was recorded at 17:00, at dusk.

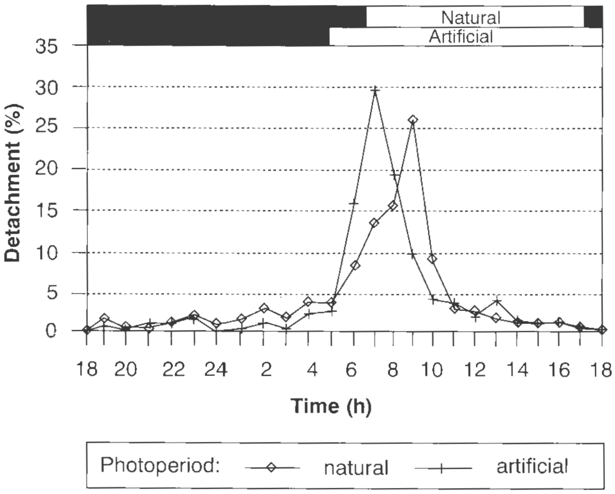

FIG. 1 Detachment rhythms of *Ixodes rubicundus* larvae from *Elephantulus myurus* under artificial and natural conditions (bars at the top of the figure represent the natural [10,5L:13,5D] and artificial [13,0L:11,0D] photoperiods)

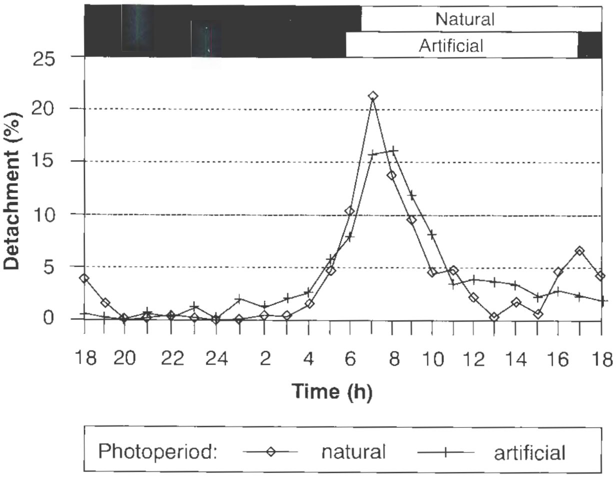

FIG. 2 Detachment rhythms of *Ixodes rubicundus* nymphs from *Elephantulus myurus* under artificial and natural conditions (bars at the top of the figure represent the natural [11,5L:12,5D] and artificial [11,0L:13,0D] photoperiods)

The detachment of larvae appeared to be more synchronous than that of nymphs, with a larger percentage of ticks detaching in a shorter period of time. Between 07:00 and 11:00 67,3 % larvae and 54,7 % nymphs detached.

DISCUSSION

The detachment time of *I. rubicundus* larvae from *E. myurus* coincides largely with the period that the hosts are inactive, basking in the sun on top of boulders or in other areas (e.g. under trees) exposed to direct solar radiation (Du Toit 1993). In the central and southern Orange Free State dense grass tufts are commonly found at the base of such boulders and these tufts should provide favourable microhabitats for tick survival. Nymphs should detach in similar places to the larvae but, because of their longer detachment period, also in other places during the host's crepuscular period of activity (Du Toit 1993). Consequently, engorged nymphs will be more widely spread within the home ranges of the elephant shrews. Since the occurrence of adult *I. rubicundus* is directly related to the localities at which engorged nymphs detach, and because the lateral movements of *Ixodes* nymphs are limited (Milne 1950), the ecological significance is two-fold. Firstly, the wider dispersal of engorged nymphs compared with larvae will enhance contact between the following adults and their preferred host, the mountain reedbuck (*Redunca fulvorufula*). Secondly, since these ticks copulate mainly off-host (L.J. Fourie, unpublished data 1992), scattering will increase the chances that the progeny of different females will mate.

When detachment rhythms are considered, a distinction must be made between the parasites of pasture animals and of those animals which make use of nests. Diurnal detachment rhythms, which parallel the diurnal activity rhythms of pasture animals, are common for many ixodid ticks (Belozerov 1982). In nest-dwelling animals, tick detachment rhythms may be either diurnal or nocturnal, depending on the time of day during which the hosts are active (Belozerov 1982). The result of this synchronization is that engorged ticks detach within the sheltering places of their hosts and thereby increase the probability that the following instar will find a suitable host. This phenomenon is enhanced by the fact that most immature ticks tend to detach from their hosts over a remarkably short period of time, regardless of the time of attachment (Matuschka *et al.* 1990a, b). The current study supports this view.

Although *Elephantulus* spp. are considered to be the chief natural hosts of immature *I. rubicundus* (Fourie *et al.* 1992), large numbers of immature ticks also occur on other species, including red rock rabbits (*Pronolagus rupestris*) and caracal (*Felis caracal*) (Horak *et al.* 1987). Red rock rabbits are nocturnal and excavate nests at the base of shrubs (Skinner & Smithers 1990). Diurnal detachment rhythms of *I. rubicundus* larvae and nymphs from red rock rabbits would enhance their chances both of survival, since the nests are protected by shrubs against direct solar radiation, and of finding a host. No nests or nest-building behaviour has been recorded for *E. myurus*, either in nature or in the laboratory (Tripp 1972). However, the activity patterns of caracal (Stuart 1982; Skinner & Smithers, 1990) make it possible for larvae and nymphs to detach in the caracal's protected lairs. A proportion of the nymphs detaching from caracals should also be scattered over a wide area since these animals are known to have extensive home ranges (Skinner & Smithers 1990). This could contribute towards the spread of *I. rubicundus* into uninfested areas.

Various factors are thought to be involved in the regulation of tick-detachment rhythms. Factors in the host's blood as well as the physiological state of the host, have been implicated (Amin 1970; Nelson, Bell, Clifford & Keirans 1977). Amin (1970) suggested that the detachment rhythm of immature *Dermacentor variabilis* is stimulated by the adrenal cycle of the host which, in turn, is synchronized by external light/dark cycles. George (1971) stated that detachment patterns of *Haemaphysalis leporispalustris* are regulated by circadian rhythms in the tick, but might also be affected by patterns of host activity or feeding. Similar suggestions have been made by Hadani & Rechav (1970), Hadani & Ziv (1974) and Rechav (1978). Matuschka *et al.* (1990a, b) claimed that factors associated with periods of host inactivity seemed to stimulate immature *Ixodes ricinus* to detach.

Ixodes ricinus generally engorge and detach diurnally from nocturnally active mice (Graff, Mermod & Aeschlimann 1978, cited by Matuschka *et al.* 1990a). Although immature *I. ricinus* detach from nocturnally active hedgehogs when these hosts are resting, they also detach diurnally from squirrels active during the day (Matuschka *et al.* 1990a). *Ixodes hexagonus* feeding on dogs detach during periods of prolonged sleep (Matuschka *et al.* 1990b). Similar results have been obtained for *Ixodes dammini*, which detach during the late afternoon while their main rodent host is sleeping (Mather & Spielman 1986).

In contrast, the detachment of *D. variabilis* occurs at the onset of their host's period of greatest activity (Amin 1970). This is consistent with the morning detachment tendencies of *I. ricinus* from avian and reptilian hosts which are also most active at this time (Matuschka *et al.* 1990a).

The detachment rhythms of *I. rubicundus* from rock elephant shrews suggest that photoperiod is the controlling factor. The extent to which these detachment rhythms can be modified by host activity should be elucidated by specifically designed experiments.

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