Hosts, seasonal occurrence and life cycle of *Rhipicentor nuttalli* (Acari: Ixodidae)

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ABSTRACT

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There are only two species worldwide within the genus *Rhipicentor*, namely *Rhipicentor bicornis* and *Rhipicentor nuttalli* and both occur only in Africa. *Rhipicentor nuttalli* has a widespread distribution in South Africa and the present investigation was initiated to elucidate its host preference, seasonality and life cycle.

Rock elephant shrews, *Elephantulus myurus* were examined for ticks at four localities in the Free State Province, one in Gauteng Province and two in Limpopo Province, South Africa. Cape elephant shrews, *Elephantulus edwardii* were examined at two places in the Western Cape Province, and a single specimen of the bushveld elephant shrew, *Elephantulus intufi* was examined in central Namibia. Small mammals of other species were also examined at two of these localities.

The majority of *E. myurus* at two sites in the Free State, at the locality in Gauteng and both sites in Limpopo Province were infested with larvae and/or nymphs of *R. nuttalli*, while the single *E. edwardii* examined at one site in the Western Cape Province and the single *E. intufi* examined in Namibia were infested with nymphs of this tick. Not one of the other small animals was infested. Although larvae and nymphs of *R. nuttalli* were present on *E. myurus* throughout the year, the former were generally most numerous during the period March to September, and the latter during May to October. The preferred hosts of the adults are domestic dogs, leopards, *Panthera pardus* and South African hedgehogs, *Atelerix frontalis*. Adult females engorged on *Atelerix frontalis* in 16–32 days and, after a preoviposition period of 2–4 days, produced approximately 17000 eggs during the following 60–70 days. The average incubation period of the eggs was 59 days. Larvae engorged on *E. myurus* in 4–10 days and moulted to nymphs 12–20 days later. Nymphs required 11–15 days to engorge on *E. myurus* and moulted to adults 32–47 days later. Allowing 14 days for the exoskeletons and mouthparts of each of the three parasitic stages to harden before they can attach to a host, the life cycle took approximately 214 days to complete in the laboratory. The length of this period, considered in conjunction with the times of maximum seasonal occurrence of the immature stages, indicates that the life cycle probably takes a year to complete in the field.

Keywords: *Atelerix frontalis*, *Elephantulus myurus*, life cycle, preferred hosts, *Rhipicentor nuttalli*, seasonal occurrence

INTRODUCTION

There are only two species worldwide within the genus *Rhipicentor* and the distribution of both of these is restricted to Africa (Theiler 1961, 1962). *Rhipicentor nuttalli* has been recorded in the Eastern and Western Cape Provinces, and the Free State, Gauteng, North-West and Limpopo Provinces, South Africa (Theiler 1961; Du Toit 1993). In Namibia it occurs north of Windhoek, while it is also

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present in Botswana and Zimbabwe (Theiler 1961; Norval & Colborne 1985). The other species, *Rhipicentor bicornis*, is apparently present only in the northern regions of South Africa, while it has been reported in northern Namibia, in Zimbabwe and Zambia, and is widely distributed in Central Africa (Theiler 1961; Walker 1991).

Adult *R. nuttalli* has been collected from domestic dogs and several wild carnivore species as well as from the South African hedgehog, *Atelerix frontalis* and porcupine *Hystrix africaeaustralis* (Theiler 1961; Walker 1991). However, Norval & Colborne (1985) consider the preferred hosts to be leopards, *Panthera pardus*. The hosts of the immature stages were unknown until Du Toit, Fourie & Horak (cited by Du Toit 1993) collected them from rock elephant shrews, *Elephantulus myurus*.

Adult *R. nuttalli* produces a toxin that can cause paralysis in domestic dogs (Perchman 1976; Norval & Colborne 1985), and the present investigation was conducted to ascertain more about this rare, but potentially important tick.

MATERIALS AND METHODS

Hosts

Immature ticks of all species were collected from rock elephant shrews at various localities in South Africa, from Cape elephant shrews, *Elephantulus edwardii* in the Western Cape Province and from a bushveld elephant shrew, *Elephantulus intufi* in central Namibia, and from other small mammals at two of these localities. For the purposes of this communication only the data pertaining to *R. nuttalli* are presented. Data on the hosts of adult *R. nuttalli* were gleaned from the published records of Theiler (1961, 1962), Perchman (1976), Norval & Colborne (1985), Walker (1991) and Horak, Braack, Fourie & Walker (2000), and have been summarized in tabular form.

Seasonal occurrence

Elephantulus myurus were trapped each month from August 1994 to June 1995 on the farm "Spes Bona" (29°07'S, 26°04'E), in the central Free State Province. They were transported to the laboratory and caged individually at 20 °C to 25 °C and a photoperiod adjusted to that prevailing outside. The cages were placed above collection trays and engorged ticks were collected daily from these trays, and washed in water to remove traces of urine and prevent the growth of fungi. Once all ticks had detached, the rock elephant shrews were returned to their original habitats on the farm "Spes Bona" and released. The following month's trapping commenced a week after this release so that if the same shrews that had just been released were caught again they would have had adequate time to become re-infested with ticks. Despite intensive efforts no elephant shrews were trapped during July 1995. The detached, engorged ticks were maintained at 20 °C and a relative humidity (RH) of approximately 90 % in permanent darkness. Once moulting was complete the various species were identified and counted, and the seasonal occurrence of *R. nuttalli* determined.

Life cycle

Adults

Engorged nymphs were collected from naturally infested elephant shrews and maintained in a cabinet at 20 °C (± 1 °C) and RH > 90 % and a permanently dark photoperiod. The resultant adults were fed on hedgehogs, *A. frontalis*. A male hedgehog was infested with seven male ticks on 17 October 1994 and 2 days later with seven female ticks. This animal was maintained at a constant temperature of 23 (± 0.5 °C) and a photoperiod of 14 h light: 10 h dark. On 19 October 1994 a female hedgehog was infested with seven female ticks, followed 10 days later by seven male ticks. This hedgehog was caged under shelter outdoors where she was exposed to the prevailing climatic conditions. The hedgehogs were kept in cages with mesh floors of which the apertures were large enough to allow detached, engorged female ticks to fall through and thus prevent the hedgehogs from eating them. Double-sided masking tape was applied to the sides of the collection trays positioned below the mesh cage floors to prevent female ticks escaping. The trays were cleaned daily and inspected for ticks.

Engorged female ticks collected from the hedgehogs were placed separately in glass tubes of which both ends were covered with gauze to allow free airflow. One of the four engorged females that laid viable eggs was maintained at 20 °C (± 1 °C), RH > 90 % and a photoperiod of 14 h light: 10 h dark, and the other three at the same temperature and humidity, but in permanent darkness. The ticks were inspected daily to determine the onset of egg-laying, and once this occurred the daily egg production of each female was collected and placed in separate vials. Daily egg production was carefully weighed and converted to eggs per day after the weight of a single egg had been determined. The

conversion efficiency index (CEI) and reproduction efficiency index (REI) of the female ticks were determined (Drummond & Whetstone 1970), where CEI = weight of egg mass (g) / weight of female (g), and REI = number of eggs / weight of female (g).

The eggs were maintained in a cabinet at 20 °C (± 1 °C) and RH > 90% in permanent darkness, and were inspected every second day to determine the length of the incubation period.

Larvae

The larvae that hatched were maintained under the same conditions as the females from which they originated. Three to four weeks after they had hatched the larvae were used to infest rock elephant shrews that were individually kept in plastic cages with wire-mesh lids. During infestation the elephant shrews were placed in a small wire cage and unknown numbers of larvae were placed on their pelage by means of a fine brush. Seven elephant shrews were infested. After infestation the elephant shrews were transferred to plastic cages similar to those they had been held in, but with fine mesh floors so that engorged larvae could fall through into collection trays. Two of the infested elephant shrews were held at 20 °C (± 1 °C) and a photoperiod of 14 h light: 10 h dark, two at the same temperature and a photoperiod of 12 h light: 12 h dark, two at 25 °C (± 1 °C) and a photoperiod of 14 h light: 10 h dark, and one at the same temperature and a photoperiod of 12 h light: 12 h dark. The sides of the collection trays were lined with masking tape to prevent the escape of engorged larvae and the base of the trays with paper towelling to protect the larvae from urine. Detached larvae were collected every 24 h by means of a suction apparatus, and the larvae originating from each elephant shrew were incubated separately at 20 °C (± 1 °C) and RH > 90% in permanent darkness. The larvae were inspected every 24 h to determine the pre-moult and moulting periods.

The percentage of larvae that engorged daily was calculated from the total number of larvae that engorged successfully and not from the total number of larvae used for infestation. The percentage of larvae that moulted daily was calculated from the total number of larvae that moulted and not from the total number of engorged larvae incubated.

Nymphs

Nymphs that had moulted from engorged larvae that had been maintained at 20 °C (± 1 °C) and RH > 90 % in permanent darkness were kept for approximately 21 days to ensure hardening of their mouthparts and exoskeleton before they were used for infestation. An elephant shrew was infested with 50 of these nymphs and housed in a plastic cage with a mesh floor with apertures large enough to allow engorged nymphs to fall through into a collection tray. Engorged nymphs were collected from the tray every 24 h and placed in separate vials maintained at 20 °C (± 1 °C) and RH > 80 % in permanent darkness. Engorged nymphs were also collected from naturally infested elephant shrews and incubated at the same temperature in permanent darkness at RH ± 90 %. The nymphs were inspected daily to determine the length of the pre-moult and moulting periods.

RESULTS

Hosts

The animals and the localities at which they were examined and the numbers of immature *R. nuttalli* collected are summarized in Table 1. Immature ticks were collected from *E. myurus* at two localities in the central Free State Province, the Pretoria district in Gauteng Province, and two localities in the Limpopo Province. Nymphs were collected from the single *E. edwardii* examined in the Clanwilliam District, Western Cape Province and the single *E. intufi* examined near Erongo in central Namibia. None of the other small mammals examined were infested with *R. nuttalli*.

The hosts from which adult *R. nuttalli* has been collected in southern Africa are listed in Table 2. The most frequently infested animals were domestic dogs, hedgehogs and leopards.

Seasonal occurrence

The seasonal occurrence of the immature stages of *R. nuttalli* on rock elephant shrews is graphically illustrated in Fig. 1. With the possible exception of July, when no elephant shrews were captured, larvae and nymphs were present throughout the year. The former life stage was generally most numerous during the period March to September and the latter during May to October.

Life cycle

Adults

Female ticks required 16–32 days to engorge on hedgehogs. All seven females placed on the male

TABLE 1 Hosts of the immature stages of *Rhipicentor nuttalli*

Locality, year of collection and host species	Number examined	No. of *R. nuttalli* collected			Prevalence % (No. infested)
		Larvae	Nymphs	Total	
Free State Province					
"Preezfontein"* (29°50'S, 25°23'E), 1985–1989; "Slangfontein"* (30°08'S, 25°24'E), 1985					
Elephantulus myurus	137	0	0	0	0
Aethomys namaquensis	321	0	0	0	0
Saccostomys campestris	10	0	0	0	0
"Moreson" (28°48'S, 27°13'E), 1992					
Elephantulus myurus	23	147	70	217	95.6 (22)
"Langberg" (29°36'S, 25°28'E), 1992					
Elephantulus myurus	54	0	0	0	0
"Spes Bona" (29°07'S, 26°04'E), 1989/90; 1994/95					
Elephantulus myurus	72	361	261	622	75 (54)
Gauteng Province					
Pretoria District (25°45'S, 28°12'E), 1985					
Elephantulus myurus	11	161	69	230	63.6 (7)
Limpopo Province					
Mapungubwe (22°12'S, 29°21'E), 1985					
Elephantulus myurus	3	1	4	5	100 (3)
Pafuri (23°27'S, 31°19'E), 1984–1987					
Elephantulus myurus	3	14	44	58	100 (3)
Aethomys chrysophilus	8	0	0	0	0
Aethomys namaquensis	2	0	0	0	0
Saccostomys campestris	3	0	0	0	0
Western Cape Province					
Clanwilliam District (32°11'S, 18°54'E), 2001					
Elephantulus edwardii	1	0	7	7	100 (1)
"Gifberg" (31°47'S, 18°40'E), 1989; 1992					
Elephantulus edwardii	66	0	0	0	0
Namibia					
Erongo Wilderness Lodge (21°27'S, 15°52'E), 2001					
Elephantulus intufi	1	0	3	3	100 (1)

* Adapted from Fourie, Horak & Van Heerden (1992)

hedgehog engorged successfully, but only three produced viable eggs. Only two of the seven females on the female hedgehog engorged successfully and only one of these produced viable eggs. The four females that produced viable eggs had required an average of 22.5 days to engorge. Egg laying began 2–4 days after detachment and continued for 58–71 days. It reached a peak 7–17 days after commencement (Fig. 2a) with more than 80 % of eggs produced by day 30. Although the tempo of egg laying was slightly slower when the ticks were kept in permanent darkness it did not differ significantly from that of a tick kept at a photoperiod of 14 h light: 10 h dark (Fig. 2b).

The female kept at 14 h light: 10 h dark laid 16 882 eggs, whereas the average production of the three females kept in permanent darkness was 17 068 eggs.

The CEI varied between 66 % and 69 % and REI between 12 950 and 13 740 eggs per g body weight (Table 3).

TABLE 2 Hosts of adult *Rhipicentor nuttalli*

Hosts	Number of records
Domestic animals	
Dogs	22
Donkeys	1
Cattle	Number not stated
Wild animals	
South African hedgehog, *Atelerix frontalis*	9
Black-backed jackal, *Canis mesomelas*	1
Cheetah, *Acinonyx jubatus*	1
African wild cat, *Felis lybica*	1
"Wild cat"	4
Lion, *Panthera leo*	1
Leopard, *Panthera pardus*	12
Brown hyaena, *Parahyaena brunnea*	4
"Hyaena"	2
"Genet", *Genetta* sp.	1
Eland, *Taurotragus oryx*	1
South African porcupine, *Hystrix africaeaustralis*	3

TABLE 3 Average number of eggs produced, conversion efficiency index and reproduction efficiency index of female *Rhipicentor nuttalli*

Number of females	Temperature	Photoperiod	Average weight of females	Average weight of egg mass	Average number of eggs	CEI	REI
1	20 °C	14 h light: 10 h dark	1.22871 g	0.854245 g	16 882	0.69	13 740
3	20 °C	Permanent darkness	1.31801 g	0.869938 g	17 068	0.66	12 950

CEI = conversion efficiency index (g eggs/g female)
REI = reproduction efficiency index (no. of eggs/g female)

TABLE 4 Length of the life cycle of *Rhipicentor nuttalli* in the laboratory

Activity	Period in days	Average or peak (days)
Female engorgement	16–32	22 (on *A.frontalis*)
Pre-oviposition	2–4	3
Egg laying	58–71	15
Eclosion	59	59
Hardening of exoskeleton	14	14
Larval engorgement	4–10	6 (on *E. myurus*)
Larval moulting	12–20	14
Hardening of exoskeleton	14	14
Nymphal engorgement	11–15	13 (on *E. myurus*)
Nymphal moulting	32–47	40
Hardening of exoskeleton	14	14
Total		214 days

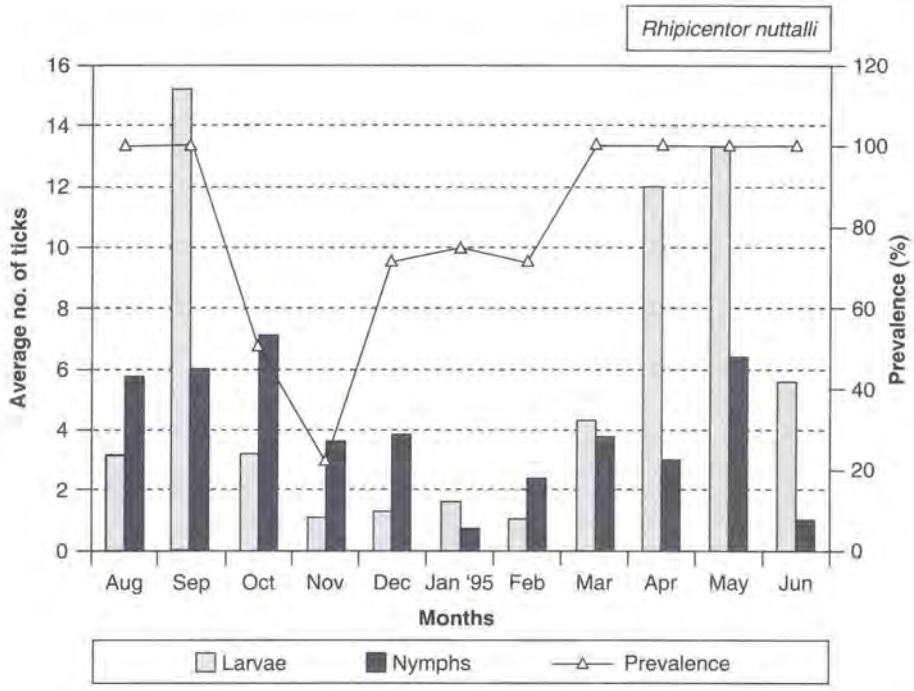

FIG. 1 The seasonal occurrence of the immature stages of *Rhipicentor nuttalli* on rock elephant shrews in the Free State Province

Eggs

Eggs hatched after an average incubation period of 59 days.

Larvae

The larvae used for artificial infestation of the elephant shrews attached mainly around the tail base. The greatest percentage of larvae engorged and detached 5–6 days after infestation irrespective of the photoperiod (Fig. 3).

Most larvae moulted to nymphs between 12 and 19 days after they had detached from elephant shrews (Fig. 4), and 71.5 % of the 225 larvae that had engorged moulted successfully.

Nymphs

Only 17 of the 50 flat nymphs used to infest an elephant shrew engorged successfully, with engorgement and detachment taking place between 11 and 15 days after infestation (Fig. 5). The average weight of an engorged nymph was 0.03188 g.

The 17 engorged nymphs originating from the artificially infested elephant shrew moulted to adults 32–37 days after engorgement, while those detaching from naturally infested elephant shrews and incubated at a slightly higher RH moulted to adults between 37 and 47 days (Fig. 6).

DISCUSSION

Hosts

The large numbers of rock elephant shrews infested with immature ticks confirm the observation of Du Toit, Fourie & Horak (cited by Du Toit 1993) that these animals serve as hosts for these life stages of *R. nuttalli*. The collection of nymphs from both *E. edwardii* and *E. intufi* would seem to indicate that these animals, and possibly other species of *Elephantulus* too, are suitable hosts for immature *R. nuttalli*, particularly in those regions in which *E. myurus* does not occur.

Norval & Colborne (1985) state that although *R. nuttalli* is colloquially known in South Africa as the hedgehog tick, their findings in Zimbabwe indicate that the adults are principally parasites of leopards and that the tick's distribution is restricted to the rocky habitats in which leopards normally occur. It thus seems logical to us that the immature stages, if they do not infest leopards, would infest some other host animal with a preference for rocky habitats. The present results confirm this supposition because both *E. myurus* and *E. edwardii* prefer rocky habitats as signified by the inclusion of the word "rock" in their colloquial names (Skinner & Smithers 1990).

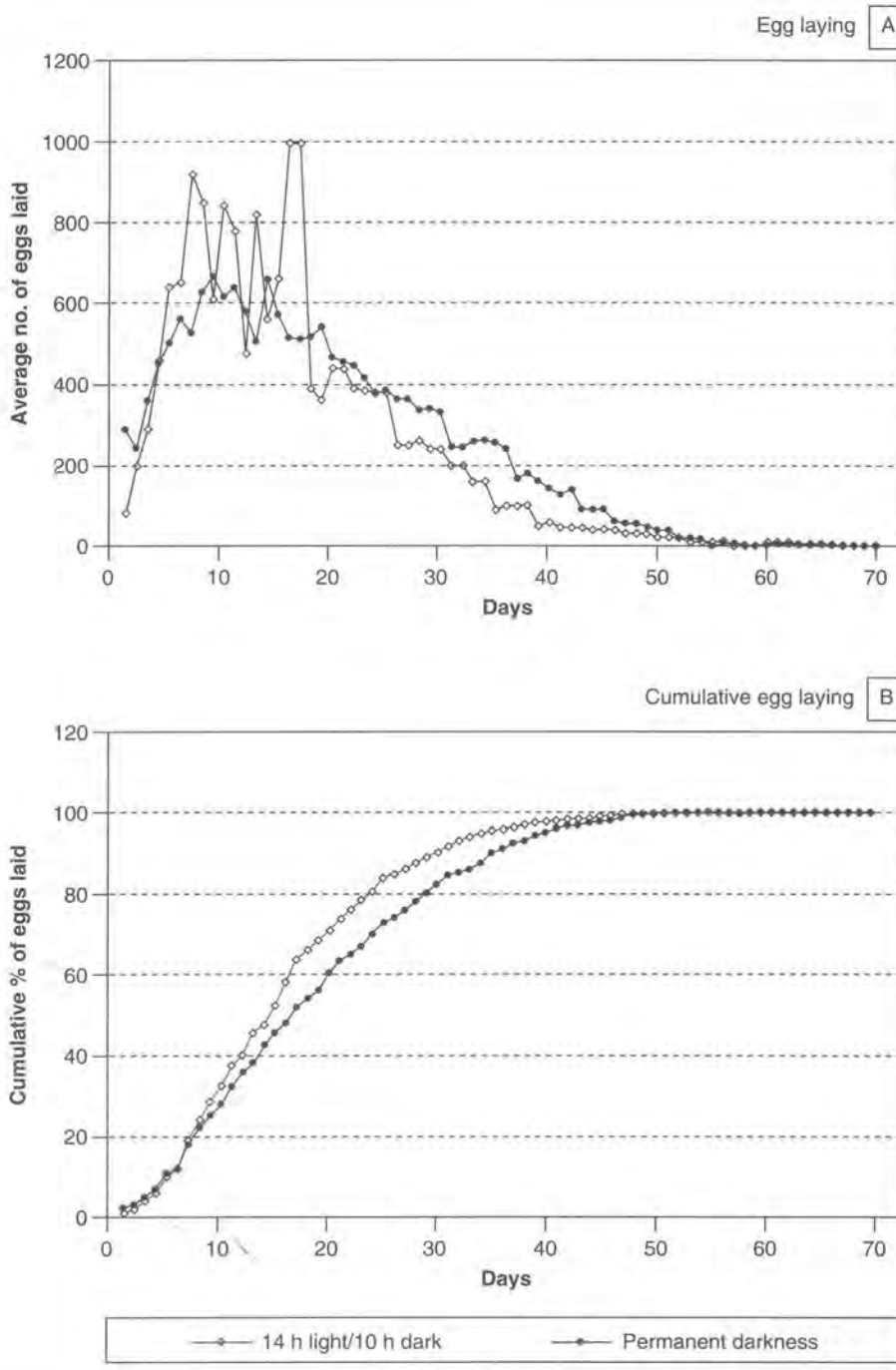

FIG. 2 Egg laying (A) and cumulative egg laying (B) of *Rhipicentor nuttalli* females at 20°C and RH ± 90 %, one female at a photoperiod of 14 h light: 10 h dark and three in permanent darkness

An interesting and perhaps significant finding is that in the Free State *E. myurus* is the host of preference for the immature stages of three ticks capable of inducing paralysis in their adult stage. These are *Ixodes rubicundus*, the Karoo paralysis tick that is responsible for massive annual mortalities of sheep within its distribution region (Spickett & Heyne 1988), *Rhipicephalus warburtoni*, the brown paralysis tick that has been incriminated as inducing paralysis in goat kids in the Free State (Walker, Keirans & Horak 2000), and *R. nuttalli* that can cause paralysis in dogs (Perchman 1976; Norval &

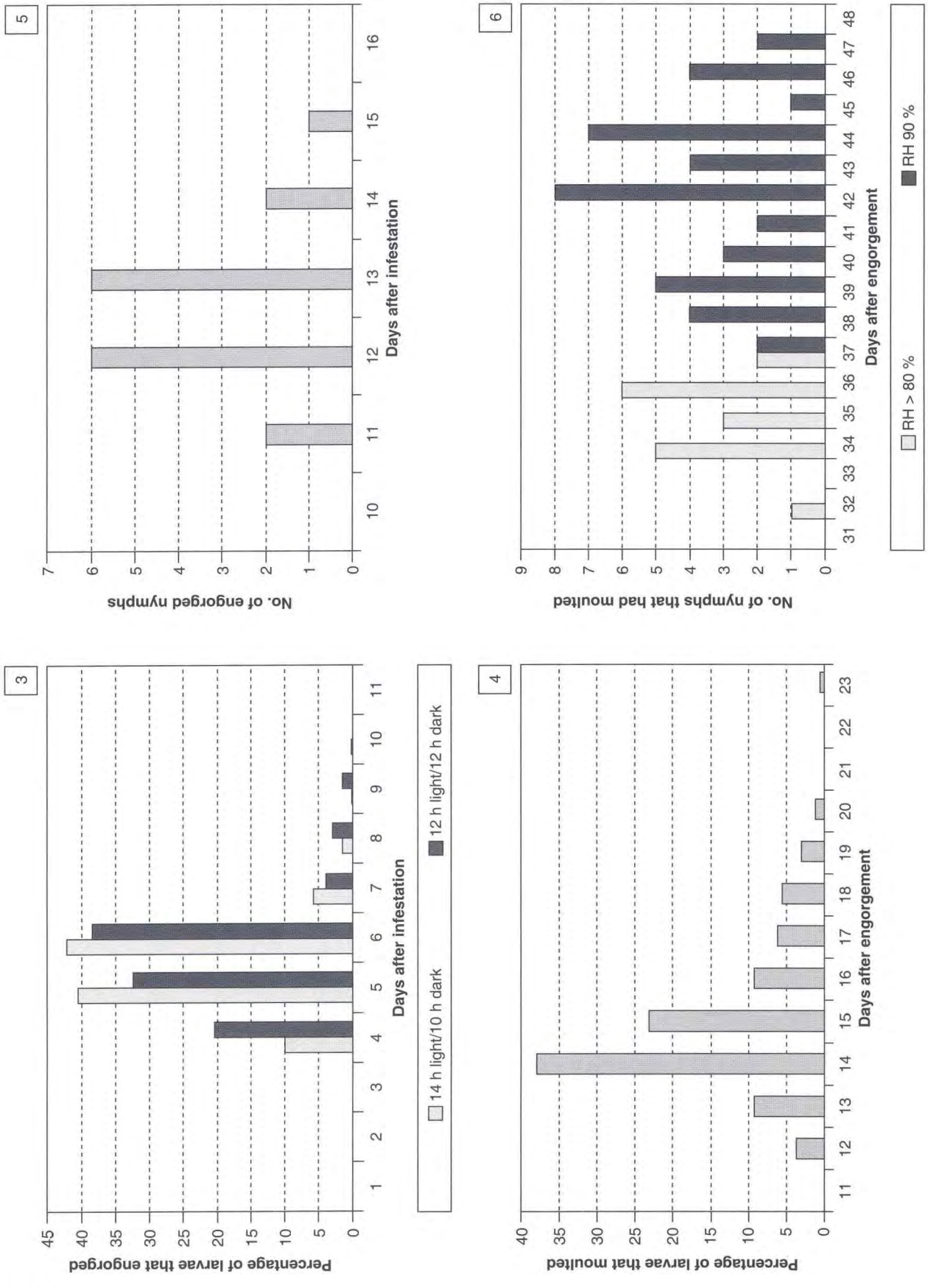
5
No. of engorged nymphs
Days after infestation
6
No. of nymphs that had moulted
Days after engorgement
RH > 80 %
RH 90 %
3
Percentage of larvae that engorged
Days after infestation
14 h light/10 h dark
12 h light/12 h dark
4
Percentage of larvae that moulted
Days after engorgement

FIG. 3 Engorgement of *Rhipicentor nuttalli* larvae on rock elephant shrews kept at 20 °C to 25 °C and a photoperiod of either 14 h light: 10 h dark, or 12 h light: 12 h dark

FIG. 4 Moulting period of *Rhipicentor nuttalli* larvae to nymphs at 20 °C and RH > 90 % in permanent darkness

FIG. 5 Engorgement of *Rhipicentor nuttalli* nymphs on a rock elephant shrew kept at 20 °C and a photoperiod of 14 h light: 12 h dark

FIG. 6 Moulting period of engorged *Rhipicentor nuttalli* nymphs collected from an artificially or from naturally infested rock elephant shrews and kept at 20 °C in permanent darkness at RH > 80 % or RH ± 90 % respectively

Colborne 1985). Within their overall distribution ranges all these ticks prefer rocky habitats.

In addition to the immature stages of *R. nuttalli* and those of the above-mentioned two ticks, the majority of *E. myurus*, examined from September to February on the farm "Spes Bona" in the seasonal occurrence survey, were infested with the immature stages of *Rhipicephalus arnoldi*. The adults of this tick are parasites of Smith's red rock rabbit, *Pronolagus rupestris* (Walker *et al.* 2000). Interspecific competition for attachment sites on the elephant shrews by these four species may have adversely affected the burdens of each.

Seasonal occurrence

Although immature ticks were present on *E. myurus* throughout the year, the majority of larvae were collected from late summer to early spring and nymphs from autumn to spring (Fig. 1). According to Theiler (1962) adult ticks are common on dogs in the Clanwilliam District in the Western Cape Province and in the Omaruru District, Namibia during late summer. In Gauteng and the Free State Provinces adult ticks were collected from a leopard, a brown hyaena and a black-backed jackal in September 1990, October 1993 and December 1994 respectively. In Zimbabwe, however, Norval & Colborne (1985) found that adult ticks were present on hosts during all months of the year.

Life cycle

The length of the life cycle of *R. nuttalli* in the laboratory is summarized in Table 4. Forty-two days have been added to this cycle to accommodate the 14 days each required for the hardening of the exoskeleton and mouthparts of the newly hatched larvae, and newly moulted nymphs and adults respectively to enable each of these life stages to successfully attach to a host.

The total length of the life cycle in the laboratory was 214 days. This length, coupled with the separate peaks of seasonal occurrence of the three developmental stages of the tick on its rock elephant shrew and domestic dog hosts makes it unlikely that more than one life cycle will be completed annually in the field in South Africa.

The engorgement period (16–32 days) of female ticks on artificially infested hedgehogs in this study is considerably longer than that of other ixodid ticks on their preferred mammal hosts. A possible reason for this prolonged period is competition for space. Only a small area dorsal to the tail of the hedgehog was used for attachment, and males, unengorged, and particularly engorged female *R. nuttalli*, are large ticks and hence the number of ticks used to infest the hedgehogs could have been excessive. This attachment site has two advantages for the ticks in that they are protected from the hedgehog's sharp spines and also from predation by the hedgehog. When one of the hedgehogs died approximately 5 months after it had been infested male ticks were still present on it. This phenomenon might be an adaptation to an arid environment in which host-finding and hence mate-finding success is poor. The adult segment of the life cycle should be repeated on domestic dogs or another suitable carnivore host to confirm the duration of engorgement of female ticks and length of attachment of males.

As signified by their weight (> 1.2 g) engorged females are very large and also lay particularly large numbers of eggs, an indication of an adaptation to an unfavourable environment. Another species of which the engorged females are particularly large (> 2.0 g) and egg production exceeds 15 000 is *Amblyomma hebraeum* (Norval 1974a, b). *Amblyomma hebraeum* is a tick that maximises its survival options. The adults have particularly long mouthparts making them difficult to detach and hence unattractive to predation by oxpeckers (*Buphagus* spp.) (Bezuidenhout & Stutterheim 1980). The males can remain attached for months and mate with several females (Norval 1974a), and the

females lay large numbers of eggs within a macro-environment that is generally favourable for their survival, while the resultant larvae possibly have a wider host range than any other ixodid tick in South Africa (Horak, MacIvor, Petney & De Vos 1987). The large number of eggs and larvae produced by *R. nuttalli* are probably a counter to the extremely narrow host preference range of its immature stages and hence the chances of encountering such a host within the rocky environment preferred by rock elephant shrews.

Not only was total egg production high, but so too were the CEI and the REI of the females. The CEI exceeded 0.65 indicating an effective conversion of female body weight to eggs and the REI exceeded 12900, signifying that a particularly large number of eggs were produced per g of female weight. Ticks with a CEI exceeding 0.60 are *A. hebraeum* (Norval 1977), *Amblyomma limbatum* (Chilton & Bull 1993) and *Hyalomma dromedarii* (Hagras & Khalil 1988), while those with a REI exceeding 12 000 are *Hyalomma truncatum* (Linthicum, Logan, Kondig, Gordon & Bailey 1991), *Ixodes rubicundus* (Van der Lingen 1995) and *Ixodes trianguliceps* (Randolph 1975). However, the mean total egg production of *H. trucatum* was only 6 701, that of *I. rubicundus* between 2805 and 3777, and that of *I. trianguliceps* between 1 169 and 1 746, compared to the more than 16 000 eggs produced by *R. nuttalli*.

The pre-oviposition period of 2–4 days and the period of 59 days for eclosion of the larvae are slightly shorter and at least 18 days longer respectively than the pre-oviposition period of 6–8 days and 35–41 days for larvae to hatch recorded for *R. nuttalli* by Theiler (1961).

Only 17 engorged nymphs were harvested from the elephant shrew artificially infested with 50 flat nymphs. This low recovery could have been due to predation of several of the nymphs by the elephant shrew. All these nymphs moulted, however, and the resultant adults all seemed to be viable.

Arthropods are preferred food items for both *A. frontalis* and *E. myurus* (Skinner & Smithers 1990) and hence life cycle studies with ticks or other ectoparasites on these animals must be performed with circumspection lest the parasite itself becomes the victim of predation.

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