THE DEVELOPMENTAL SUCCESS OF AMBLYOMMA HEBRAEUM AND AMBLYOMMA MARMOREUM ON THE LEOPARD TORTOISE, GEOCHELONE PARDALIS

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ABSTRACT

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The success of natural infestations of various life history stages of Amblyomma hebraeum and Amblyomma marmoreum on the leopard tortoise, Geochelone pardalis, was compared. Success was measured by the time taken for ticks to detach, as well as the percentage of ticks engorging and subsequently either moulting to the next life history stage or laying viable eggs. Larvae of A. hebraeum were the only developmental stage not recovered. Nymphae and female A. hebraeum were less successful in moulting or laying eggs than the corresponding stages of A. marmoreum. Nevertheless, 48,7 % of A. hebraeum nymphae moulted, while 1 of 6 females laid viable eggs.

INTRODUCTION

The bont tick, Amblyomma hebraeum, is the main vector of the rickettsia, Cowdria ruminantium, the cause of heartwater in domestic ruminants in South Africa. Amblyomma marmoreum, the South African tortoise tick, can also be infected with this rickettsia provided it attaches to a tortoise that is already infested by experimentally infected A. marmoreum (Oberem, 1987).

Although A. hebraeum is normally a parasite of mammals and, in the case of the immature stages, also of ground-feeding birds (Theiler, 1962; Norval, 1974; Horak & Williams, 1986), it has been found on the angulate tortoise Chersina angulata and the leopard tortoise Geochelone pardalis (Walker & Schulz, 1984). This raises the possibility that tortoises play a role in the epidemiology of heartwater.

In this paper, natural infestations of A. hebraeum and A. marmoreum on the leopard tortoise, G. pardalis, were studied to determine the relative success of both species on this host. Our aim was to ascertain how well A. hebraeum is adapted to tortoises as hosts and hence the importance of tortoises in the epidemiology of heartwater.

MATERIALS AND METHODS

Localities and dates of collection of the 14 tortoises used in this study, with their masses and sexes, are given in Table 1. A single tortoise from the farm Bucklands (33° 05′ S; 26° 41′ E) is included with the 13 from the Thomas Baines Nature Reserve (33° 23′ S; 26° 28′ E), as its infestation level was well within the range of those from Thomas Baines. Climate and vegetation are fairly similar at both localities.

The tortoises were kept in wire cages, 800 mm × 600 mm × 300 mm with a mesh diameter of 22 mm, at the field station of the Tick Research Unit at Rhodes University. Temperature, relative humidity and photoperiod were ambient. These cages were supported over trays containing water approximately 10 mm deep to prevent detached ticks from escaping. The trays were checked at approximately 08h00 and 20h00 daily for ticks which had detached. Tortoises were kept until tick detachment had ceased except for the last 5 animals which were released on 9 July 1986 because of physical deterioration. Food and water were supplied ad libitum.

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TABLE 1 The date of collection, sex, mass and localities of collection of 14 leopard tortoises, Geochelone pardalis

Tortoise	Date of collection	Sex	Mass (kg)	Locality
1 2 3 4 5 6 7 8 9 10 11 12 13 14	1986-2-11 1986-2-14 1986-2-14 1986-2-14 1986-2-14 1986-2-14 1986-2-25 1986-2-25 1986-3-06 1986-3-19 1986-3-24 1986-5-21	FFMFFF MFFFFFFFFFFFFFFFFFFFFFFFFFFFFFF	7,7 8,5 6,0 16,5 12,0 11,5 4,8 9,5 2,4 0,68 13,0 10-15 10-15	Thomas Baines Bucklands Thomas Baines Thomas Baines

Daily minimum and maximum temperatures, rainfall and relative humidity records were supplied by the Hydrographic Research Unit, Rhodes University.

Ticks collected were identified, mass-measured and then placed in 6 mℓ glass vials which were kept in complete darkness at 29 °C and 80 % relative humidity. Vials were checked at 3 day intervals and the ticks were examined for moulting, egg laying or death. The mass of moulted ticks was redetermined and the eggs observed for hatching.

Because of unforeseen circumstances 5 of the 677 A. hebraeum nymphae were not mass-measured and the number of days required to moult was not recorded for 20 nymphae of this species. Six A. marmoreum larvae and 1 A. marmoreum male were not mass-measured and the mass of 6 newly emerged nymphae was not recorded. Because of this, the numbers recorded in the various tables do not always equal those of the detached ticks.

RESULTS

The numbers of each developmental stage of A. hebraeum and A. marmoreum detaching from each tortoise are given in Table 2. No larvae of A. hebraeum were recovered. A. hebraeum nymphae represented the commonest category (64,3%) on 9 of the 14 hosts, while A. marmoreum larvae were commonest (21,4%) on 3 and A. marmoreum males (14,3%) on 2 of the tortoises. Considerable variation in the total burdens of any life history stage occurred between tortoises. Such variation occurred within each month sampled.

All developmental stages of A. hebraeum took a longer mean time to detach than the corresponding stages of A. marmoreum. A. hebraeum nymphae remained on the host for as long as 125 days after the capture of the

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TABLE 2 The total tick burdens of 14 leopard tortoises. The numbers of each life history stage are expressed as a percentage () of the total number detaching

	,	Total number of each life history stage detaching								
	Month of collection	Amblyomma hebraeum			Amblyomma marmoreum					
		Nymphae	Males	Females	Larvae	Nymphae	Males	Females	Total	
1	Feb.	81 (80,2)			1 (1,0)	7 (6,9)	10 (9,9)	2 (2,0)	101	
2	Feb.	54 (77,1)	1 (1,4)		1 (1,4)	1 (1,4)	7 (10,0)	6 (8,6)	70	
3	Feb.	16 (43,2)	- \ , , ,		17 (45,9)	l ` ′ ′	3 (8,1)	1 (2,7)	37	
4	Feb.	76 (78,4)	4 (4,1)	1 (1,0)	2 (2,1)		14 (14,4)		97	
5	Feb.	200 (93,5)	1	,	1	2 (0,9)	6 (2,8)	6 (2,8)	214	
6	Feb.	12 (85,7)	1 (7,1)			1 (7,1)			14	
7	Feb.	3 (50,0)	' ' '		1 (16,7)		2 (33,3)		6	
8	Feb.	66 (94,3)		2 (2,9)		2 (2,9)		1	70	
9	Feb.	3 (75,0)					1 (25,0)	1	4	
10	Mar.	3 (16,7)			14 (77,8)	1		1 (5,6)	18	
11	Mar.	136 (41,3)	2 (0,6)	3 (0,9)	167 (50,8)	4 (1,2)	12 (3,6)	5 (1,5)	329	
12	Mar.	4 (11,4)			8 (22,9)	1 (2,9)	16 (45,7)	6 (17,1)	35	
13	May	2 (25,0)	2 (25,0)		1 (12,5)		3 (37,5)		8	
14	May	21 (67,7)			9 (29,0)		1 (3,2)		3	
	Total	677 (65,5)	10 (1,0)	6 (0,6)	221 (21,4)	18 (1,7)	75 (7,3)	27 (2,6)	1034	

TABLE 3 The range and mean number of days to detachment of Amblyomma hebraeum and Amblyomma marmoreum

Species and stage	No. detached	Mean No. of days to detachment + S.E.	Range	
A. hebraeum Nymphae Males Females	677 10 6	40,34 + 0,94 55,60 + 6,77 49,33 + 9,95	1-125 14-92 15-77	
A. marmoreum Larvae Nymphae Males Females	221 17 75 27	35,52 + 1,07 21,17 + 2,84 28,20 + 3,11 27,26 + 3,26	8-104 4-47 1-111 1-73	

host (Table 3). A. marmoreum nymphae required a maximum of 47 days to detach after capture of the host.

In general, A. hebraeum was less successful than A. marmoreum, since a substantially smaller proportion of nymphae moulted (48,7%) and females laid eggs (16,7%) compared with A. marmoreum (94,4% and 37,0% respectively) (Table 4). Moulting success was directly dependent on the mass attained at detachment by the individual nymphae of both species and by larval A.

marmoreum (Table 4). Egg laying did not appear to be related to engorgement mass (Table 4).

The premoult period did not differ between nymphae of these 2 species (Table 5). The single A. hebraeum female that laid eggs did so sooner after detachment than the mean time taken by A. marmoreum females (Table 6). All egg masses were fertile.

The engorged mass attained by A. hebraeum nymphae and females and by A. marmoreum larvae was related to tortoise size (Table 7). Thus tortoises in the 15–20 kg range produced ticks with a higher engorgement mass than any other group, while tortoises of 5 kg or less produced ticks with very low masses. A. hebraeum females attached to tortoises from 5–10 kg in mass reached a greater mass than the other mass groups of tortoises, while tortoises below 5 kg in mass were not as successful as hosts for A. marmoreum larvae as other groups (Table 7).

DISCUSSION

Peak abundance of the parasitic larvae of A. hebraeum occurs between February and May in the eastern Cape Province of South Africa (Rechav, 1982). A study of the free-living larvae of A. hebraeum in the Thomas Baines Nature Reserve showed peak larval abundance in January in heavily bushed habitat and during March in

TABLE 4 A comparison of the moulting or egg laying success of Amblyomma hebraeum and Amblyomma marmoreum. A t test was used to determine the significance of differences between the masses of moulting and non-moulting immatures and between female A. marmoreum laying and not laying eggs

	Species and life history stage	No. detached (% of total)	Mean mass (mg) + S.E.	t value	Significance
A. hebraeum:	Nymphae —moulted —unmoulted Males Females —laying —not laying	672 327 (48,7) 345 (51,3) 10 6 1 (16,7) 5 (83,3)	19,60 + 0,64 30,95 + 0,70 8,84 + 0,64 16,94 + 2,49 294,60 + 169,71 904,30 + 0 172,66 + 144,57	t = 23,38	P<0,001
A. marmoreum:	Larvae —moulted —unmoulted Nymphae	215 135 (62,8) 80 (37,2) 18	$\begin{array}{c} 2,20 + 0,06 \\ 2,61 + 0,05 \\ 1,51 + 0,11 \\ 83,51 + 9,73 \end{array}$	t = 8,99	P<0,001
	moulted —unmoulted Males Females —laying —not laying	17 (94,4) 1 (5,6) 74 27 10 (37,0)	88,33 + 8,97 1,50 + 0 52,42 + 2,42 1,752,25 + 237,86 2,238,68 + 272,04	t = 2,28 $t = 1,62$	P<0,05

TABLE 5 Mean premoult period for Amblyomma hebraeum nymphae and Amblyomma marmoreum larvae and nymphae

Species and developmental stage	No. moulting	Days to moult (mean) (+ S.E.)		
A. hebraeum nymphae	307	20,93 + (0,22)		
A. marmoreum larvae nymphae	141 17	16,97 + (0,31) 21,00 + (0,90)		

TABLE 6 Mean preoviposition period for female Amblyomma hebraeum and female Amblyomma marmoreum

Species	No. laying	Days to lay eggs (mean) (+ S.E.)
A. hebraeum	1	12,00
A. marmoreum	10	46,20 + (7,07)

TABLE 7 A comparison of the masses of Amblyomma hebraeum and Amblyomma marmoreum on tortoises of various sizes

The mean masses (in mg) of ticks on tortoises of various mass classes (in kg)						A 1 i				
Tortoise mass	nass 0,0-5,0 (3)		5,1-10,0 (4)		10,1–15,0 (5)		15,1–20,0 (2)		Analysis of variance	
Species and developmental stage	No.	Mean + S.E.	No.	Mean + S.E.	No.	Mean + S.E.	No.	Mean + S.E.	F. ratio	Significance
A. heb.: N M F	9	0,93 + 0,20	216 1 2	16,39 + 1,25 18,10 + 0 827,05 + 77,25	366 5 3	19,65 + 0,75 15,38 + 4,41 18,67 + 9,10	81 4 1	29,20 + 1,61 18,60 + 3,45 57,50 + 0	17,18 0,16 102,67	<0,001 n.s. <0,01
A. mar.: L N M F	$\frac{15}{3}$	1,37 + 0,34 	19 10 20 9	2,72 + 0,26 85,85 + 15,88 54,64 + 5,11 1875,60 + 368,04	171 7 22 11	2,17 + 0,07 85,93 + 10,43 48,30 + 4,15 2021,52 + 374,79	10 1 29 6	2,87 + 0,12 43,10 + 0 53,78 + 4,20 1360,12 + 568,60	8,22 0,48 0,09 1,06	<0,001 n.s. n.s. n.s.

No. = Number of ticks detached

grassland (Petney & Horak, 1987). As tortoises were collected in this reserve during the period of peak larval abundance, it seems probable that the absence of infestation on these animals indicates their unsuitability as hosts for A. hebraeum larvae. This observation is independent of the size of the tortoise. This finding is significant as it precludes the possibility of the life cycle of A. hebraeum being completed on G. pardalis in that other hosts are required by the larval stage.

Both nymphae and female A. hebraeum proved less successful parasites of the tortoise than the corresponding life history stages of A. marmoreum. This is not surprising as adult A. hebraeum is usually classed as a tick with a preference for large mammalian hosts, the nymphae also occur on these hosts and on ground-feeding birds (Theiler, 1962; Hoogstraal & Aeschlimann, 1982; Horak, MacIvor, Petney & De Vos, 1987). Nevertheless, this study clearly shows that almost half the A. hebraeum nymphae collected from the leopard tortoise moulted successfully and, although the proportion of females laying eggs was low, 1 did succeed in producing viable offspring. By contrast, adult A. marmoreum occur almost exclusively on large reptiles (Theiler, 1962; Hoogstraal & Aeschlimann, 1982). Although the nymphae also commonly use reptiles, they have a wider host range which includes mammals and birds (Theiler, 1962; Horak et al., 1987). If the passage of C. ruminantium through the tortoise from infected adults or nymphae of either species to nymphae of either species is possible, then tortoises could form part of a tangential cycle in the epidemiology of heartwater.

These results should be qualified by the observation that the Thomas Baines Nature Reserve has a very high stocking density which leads to a correspondingly high density of *A. hebraeum*. Also, tick densities are usually considerably lower on farms where acaricidal treatment is practised, as *A. hebraeum* attaching to domestic stock are removed from the population (Petney & Horak, 1987).

Although the possibility exists that heartwater is carried by tortoises, and is subsequently transferred to ticks

and hence to domestic stock, the importance of such a cycle remains to be evaluated.

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