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The impact of tick load on the fitness of their lizard hosts

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Abstract. A survey was conducted of natural populations of the sleepy lizard *Tiliqua rugosa* in South Australia to determine whether infestation by ectoparasitic ticks reduced their fitness. Between 1982 and 1990, 2183 captures of 824 individual lizards were made in an area where they were infested by the tick *Aponomma hydrosauri*, and 3668 captures of 586 individual lizards were made in an area where they were infested with the tick *Amblyomma limbatum*. Lizards with high tick loads in one year tended to have high loads the next year. Longevity of lizards in the study was either not correlated with tick load, or positively correlated. Size achieved was greater amongst lizards with greatest tick load, and lizards in mating pairs had higher tick loads than those never found in pairs. The data do not support the hypothesis that tick load diminishes host fitness.

Key words: Tick – Reptile – Ectoparasite – Infestation – Parasite-host interaction

Parasites have traditionally been considered as equivalent to predators in their impact on victim populations. However, recent studies show parasites have more subtle and multifaceted influences on their host populations. While a predator kills it prey, a parasite may kill its host (sooner or later), or may have only a minor, almost undetectable impact on host viability (Munger and Karasov 1989; Dobson et al. 1992). Non-lethal parasites can alter host fecundity (Hudson 1986; Jaenike 1992), physiology (Schall et al. 1982), competitive ability (Park 1948), behaviour (Moore 1983), social dominance (Schall and Houle 1992), ability to attract mates (Hamilton and Zuk 1982), and mating system (Read 1991). Parasites can even advantage hosts, by making intermediate hosts more available as prey (Lafferty 1992), or by reducing more the fitness of a co-infested competitor species (Jaenike 1992). Parasitic interactions can have profound implications at other trophic levels (Grenfell 1992).

This paper examines the influence of ectoparasitic ticks on their reptile hosts. *Aponomma hydrosauri* and *Amblyomma limbatum* are tick species which commonly infest the sleepy lizard *Tiliqua rugosa* in South Australia (Bull et al. 1981). The sleepy lizard is a large (adult weight 500–800 g; snout-vent length 28–32 cm) viviparous skink. Ticks might adversely affect their lizard hosts in at least two ways.

1. Ticks remove blood and may induce anaemia. An adult female tick engorges up to 0.5 g (Chilton and Bull 1993). If blood makes up about 7% of a lizard body weight (Prosser and Brown 1965), then a 500-g lizard will lose 1.4% of its blood for each engorging female. For the 2.9% of lizards with four or more females attached (Bull et al. 1989) this blood loss may be significant.

2. Ticks may transmit blood parasites. In field populations a *Rickettsia*-like blood cell inclusion is found in some lizards (50/10,000 cells average). We are currently attempting to determine if it is transmitted by ticks. Blood parasites may reduce lizard fitness (Schall et al. 1982).

We used host survey data over 9 years to determine the fitness consequences for host lizards of infestation by ticks.

Materials and methods

The study was conducted from 1982 to 1990 at the Mt. Mary study site in mid-North South Australia, previously described by Petney and Bull (1984). The area contains a parapatric boundary between the two tick species, *Aponomma hydrosauri* in the south and *Amblyomma limbatum* in the north (Bull et al. 1981, 1989; Bull 1991). Both ticks infest the same host, the sleepy lizard *Tiliqua rugosa*.

Sleepy lizards were captured during spring and early summer of each year by random encounter along two road transects. South of the boundary, on an 18.3-km transect, there were 2183 captures of 824 different individual lizards between 1982 and 1990. These lizards were only infested with *Aponomma hydrosauri*. North of the boundary, on an 8.2-km transect, there were 3668 captures of 586

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different individual lizards between 1983 and 1990. These were only infested with *Amblyomma limbatum*. The two transects were 4.8 km apart at their closest points.

In spring some lizards form monogamous pairs over several weeks (Bull 1987, 1988, 1990). Lizards were recorded as paired or single at each capture. Each captured lizard was individually marked by toe clip. Its sex, weight and snout-vent length were determined, and the number of attached ticks was recorded. It was released at point of capture within 10 min.

Both *Aponomma hydrosauri* and *Amblyomma limbatum* are three-host ticks. Larvae, nymphs and adults attach separately to hosts. Adult males do not engorge, but remain many months on hosts waiting to mate with females (Andrews and Bull 1980). All other stages engorge on host blood, then detach, either to moult to the next stage or to lay eggs. In this study, tick load was considered either as the total number of attached ticks of all stages on a host, or the total of feeding stages (i.e. all ticks minus males). For host individuals captured several times in a year, the maximum recorded load for that year was used in all analyses. Analyses using mean recorded load per year gave similar results.

We analysed the data to determine relationships between tick load and lizard fitness. We used three parameters of lizard fitness. None could be measured directly, and the indirect measures all have potential noise, and may only detect strong effects.

1. Survival. This was deduced from longevity in the study, which was determined for all lizards captured in each year as the maximum number of years over which a lizard was subsequently recaptured. *Tiliqua rugosa* has a life span of over 10 years and tends to remain in the same home range area (Bull 1987). Failure to recapture a lizard could mean the lizard had died, dispersed or evaded further capture.
2. Growth. This could not be measured directly because most captures were of adults which grow little between years. However adult size is variable and may indicate growth to adulthood.
3. Reproduction. Females produce clutches of live young in autumn after several months of inactivity when they are very hard to find. An indirect measure of reproductive success is the frequency of recordings in male/female pairs in the spring when lizards pair up for 4–6 weeks before mating. Radio-tracking results show that a proportion of individuals do not pair (Bull unpubl. data), and these are assumed to be reproductively unsuccessful.

Results

Table 1 shows the mean and median tick loads per lizard on the two transects in each year. Many hosts have very few attached ticks; 50% of all hosts had six or fewer ticks and two or fewer feeding-stage ticks. Some hosts were heavily infested. On the *Aponomma hydrosauri* transect 48 hosts had 50 or more attached ticks, and 22 had 100 or more. On the *Amblyomma limbatum* transect 30 hosts had 50 or more ticks, and 10 had 100 or more. Male and female lizards did not differ significantly in mean tick loads (*Aponomma hydrosauri* transect: males 7.79 (SE 1.10), females 8.03 (SE 1.06); *Amblyomma limbatum* transect: males 7.33 (SE 1.29), females 8.38 (SE 1.64)).

From all lizards captured in one year, we selected the subset of lizards which were subsequently recaptured in the following year. Spearman rank correlations (Table 2) showed strong positive relationships between tick loads on individual lizards in consecutive years. Lizards heavily infested in one year tended to be heavily infested in the next year.

Table 3 shows, for each lizard captured in a year, the relationship between its maximum recorded tick load that year and its subsequent longevity in the study. Neither tick species showed any significant negative correlations. For *Amblyomma limbatum* there were significant positive correlations in four years. Lizards with higher tick loads persisted longer in the study.

Table 1. The mean (SE) and median tick loads for each year on individual lizards on the *Aponomma hydrosauri* and *Amblyomma limbatum* transects

Year	*n*	Ticks per host					
		All ticks			Feeding ticks		
		Mean	SE	Median	Mean	SE	Median
Aponomma hydrosauri							
1982	48	1.56	0.28	1	0.31	0.12	0
1983	133	4.43	1.30	2	3.09	1.29	0
1984	114	7.34	1.38	2	6.25	1.34	1
1985	154	5.44	1.13	2	3.95	1.12	0
1986	156	8.08	1.08	3	6.37	1.06	1
1987	232	14.15	2.59	4	12.36	2.57	2
1988	263	8.30	1.22	4	6.32	1.20	2
1989	320	7.97	1.93	3	6.11	1.92	1
1990	182	20.56	6.27	4	18.52	6.26	2
Amblyomma limbatum							
1983	58	6.78	0.80	6	2.62	0.69	1
1984	219	6.90	0.99	5	3.62	0.96	1
1985	216	9.67	1.28	6	6.71	1.27	2
1986	253	8.22	0.84	5	5.09	0.81	2
1987	270	14.10	7.42	5	11.24	7.42	2
1988	286	9.02	1.00	5	6.02	0.96	2
1989	242	7.91	1.01	5	4.74	0.97	1
1990	270	7.02	1.06	4	4.32	1.04	2

Where a lizard was captured more than once in a year, only its maximum tick load was included

Table 2. Spearman rank correlations of tick loads on individual lizards in consecutive years, for lizards captured in consecutive years

Year 1	Year 2	*n*	All ticks		Feeding ticks	
Aponomma hydrosauri						
1982	1983	18	0.78	***	0.18	N.S.
1983	1984	38	0.45	**	0.06	N.S.
1984	1985	41	0.58	***	0.13	N.S.
1985	1986	52	0.67	***	0.42	***
1986	1987	66	0.56	***	0.42	***
1987	1988	97	0.59	***	0.46	***
1988	1989	119	0.66	***	0.39	***
1989	1990	83	0.52	***	0.28	**
Amblyomma limbatum						
1983	1984	36	0.51	***	0.25	N.S.
1984	1985	127	0.32	***	0.07	N.S.
1985	1986	141	0.41	***	0.25	***
1986	1987	156	0.57	***	0.33	***
1987	1988	159	0.61	***	0.39	***
1988	1989	163	0.48	***	0.32	***
1989	1990	142	0.32	***	0.21	**

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; N.S. = not significant

Table 3. Mean longevity in the study (years) for all hosts caught in a year, and spearman rank correlations of tick load in a year and subsequent longevity

Year	*n*	Mean (SE) Longevity	Spearman rank correlations			
			All ticks		Feeding ticks	
Aponomma hydrosauri						
1982	48	3.69 (0.49)	−0.04	N.S.	−0.09	N.S.
1983	133	3.42 (0.26)	−0.01	N.S.	−0.03	N.S.
1984	114	3.14 (0.23)	−0.04	N.S.	0.02	N.S.
1985	154	2.63 (0.16)	0.11	N.S.	0.01	N.S.
1986	156	2.06 (0.13)	0.06	N.S.	0.05	N.S.
1987	232	1.32 (0.08)	−0.01	N.S.	0.00	N.S.
1988	263	0.69 (0.05)	−0.03	N.S.	−0.07	N.S.
1989	320	0.26 (0.03)	0.11	*	0.09	N.S.
Amblyomma limbatum						
1983	50	4.60 (0.37)	−0.09	N.S.	−0.06	N.S.
1984	200	4.14 (0.16)	0.08	N.S.	0.12	*
1985	204	3.44 (0.13)	0.06	N.S.	0.03	N.S.
1986	236	2.69 (0.10)	0.07	N.S.	0.03	N.S.
1987	251	1.94 (0.08)	0.16	**	0.12	*
1988	272	1.27 (0.05)	0.20	***	0.17	**
1989	226	0.63 (0.03)	0.21	***	0.19	**

Symbols as in Table 2

Table 4. Spearman rank correlations of maximum tick load in first year of capture (T1) or maximum tick load over whole study (T2) against maximum size achieved in the study, for each host lizard

		Spearman Rank Correlations			
		All ticks		Feeding ticks	
Aponomma hydrosauri $n = 824$					
T1	Weight	0.13	***	0.02	N.S.
	Length	0.14	***	0.02	N.S.
T2	Weight	0.36	***	0.30	***
	Length	0.33	***	0.28	***
Amblyomma limbatum $n = 586$					
T1	Weight	0.34	***	0.13	***
	Length	0.35	***	0.15	***
T2	Weight	0.47	***	0.39	***
	Length	0.46	***	0.38	***

Symbols as in Table 2

Tick load, whether measured as the maximum in the first year the host was captured, or as the maximum recorded over the whole study period, was positively correlated with host body size, on both transects (Table 4). Larger lizards tended to have more ticks attached.

Among all adult lizards in the sampled populations there were significantly more ticks on lizards found at least once in a pair than on lizards never found in a pair, on both transects (Table 5). Reproductively more successful lizards have more ticks. When only resident lizards were considered, those that persisted in the population record for 3, 4 or 5 years, lizards with *Aponomma hydrosauri* still showed significantly higher tick loads on paired than single lizards in the 3- and 5-year groups. Lizards with *Amblyomma limbatum* showed no relationship (Table 5).

Discussion

The data from our surveys show variation in levels of tick infestation, but strong positive correlations between tick infestation levels on individuals in consecutive years.

Table 5. Mean maximum tick load (SE) for lizards found in a pair at least once (P), and for lizards never found in a pair (S)

Years		*n*	All ticks				Feeding ticks			
			Mean	(SE)	*F*		Mean	(SE)	*F*	
Aponomma hydrosauri										
All	S	532	8.4	(1.0)	93.4	***	7.1	(1.0)	84.3	***
	P	293	25.1	(4.7)			22.9	(4.6)		
3	S	28	7.8	(1.7)	5.0	*	6.2	(1.6)	3.4	N.S.
	P	30	15.8	(3.3)			12.7	(3.2)		
4	S	17	29.8	(13.1)	0.2	N.S.	28.0	(13.1)	0.3	N.S.
	P	35	20.7	(6.9)			18.9	(7.0)		
5	S	14	5.9	(1.4)	3.8	N.S.	4.0	(1.5)	6.5	*
	P	34	16.4	(3.2)			14.3	(3.2)		
Amblyomma limbatum										
All	S	348	10.1	(1.3)	96.5	***	7.6	(1.3)	97.5	***
	P	238	25.6	(8.5)			21.5	(8.5)		
3	S	35	23.4	(8.9)	0.0	N.S.	20.8	(8.9)	0.1	N.S.
	P	16	21.3	(12.1)			17.3	(12.2)		
4	S	20	10.4	(2.0)	1.4	N.S.	7.0	(2.0)	1.9	N.S.
	P	27	17.3	(6.2)			13.7	(6.2)		
5	S	16	19.4	(6.6)	0.7	N.S.	15.9	(6.3)	0.5	N.S.
	P	30	80.9	(66.3)			76.9	(66.3)		

The results of ANOVAs comparing the tick loads (data $\log_{10}$ transformed) of lizards in the two groups are shown. Data are presented for the whole sample, and then for subsets of lizard found to persist for specific numbers of years

Many lizards have low infestation levels, but some remain heavily infested over several years.

Spatial variation in reptile tick densities has been reported previously (Bull 1978a; Bull et al. 1989). This may result from variability in either the quality of the microhabitat where ticks wait for hosts, or the density of hosts. *Tiliqua rugosa* can occupy the same small home range for many years (Bull 1978b, 1987). Lizards in a region of high tick density will remain there over consecutive years, and will continue to pick up high infestation loads. Our data give no evidence that hosts develop resistance to tick infestation.

We exploited the variability in infestation level between lizards to examine the consequences of high infestation level for lizard fitness. In this paper three indirect measures of fitness were used.

Longevity in the study

Longevity in the study was used as a measure of survival. It is an inaccurate measure because the study was shorter than the life span of some individuals, and because absence from the records does not necessarily imply death. Missing individuals may have dispersed or avoided capture. Nevertheless, reduced survival should be reflected in lower values of longevity.

There were no cases where heavy tick infestation was associated with significantly reduced longevity in the study. We did not consider juveniles. For the young, born in late summer, heavy infestation early in life may adversely affect survival. Our sampling in spring and early summer would not detect any mortality in their first 8 months. For adult lizards we found no evidence that ticks reduce survival in field populations.

In fact, for lizards with *Amblyomma limbatum,* high tick load was consistently and significantly associated with increased longevity in the study. There are at least four possible explanations of this.

1. An unlikely interpretation is that ticks benefit lizards.
2. Infested lizards may behave differently, to be more easily captured. Reduced sprint speed or agility is unlikely to be important, because these lizards are large and slow and captures are certain following sighting. However if high tick load induced extra activity, it would increase the chance of encounter and bias the longevity records in favour of highly infested hosts.
3. If tick load varies over a season then activity differences between individuals could bias both tick load scores and apparent longevity, in the same direction. An active lizard will be caught more often (and thus be more likely to be recorded as long-lived), and will be more likely to be caught when tick densities peak in the season (and thus will be recorded with a higher tick load). Analysis with average tick loads rather than peak tick loads, which should reduce that bias, gives the same conclusions.
4. More probably the association can be explained by the social organisation of *Tiliqua rugosa.* A successful individual in an established home range will regularly revisit well-protected refuges. In these refuges, ticks waiting for hosts will be advantaged by the sheltered microclimate and frequent host visits, and tick populations will be high. Thus established resident lizards will both persist in the capture record and maintain high infestation levels.

Growth

Rapid growth would be advantageous in juvenile lizards to reduce predation risk. Among adults large size is an advantage. Large males maintain more stable pair bonds (Bull 1990), and larger females produce larger offspring (Bull et al. 1993). Lizard growth may be slowed by tick infestation.

Growth was not measured directly in our study. Very few juveniles were recaptured. Most lizards had achieved adult size when first captured, and grew little over subsequent captures. Instead we took the maximum size achieved by each lizard over the study to reflect its growth over life. Since tick loads on an individual correlate between years, we used the maximum tick load recorded as a measure of overall tick load experienced. If ticks retard growth we predicted lizards with greater loads would be smaller.

The data for adults in our survey showed the opposite. Lizards with more ticks were larger. Again it is unlikely that ticks benefit lizard growth. If lizards grow large because they are in good home ranges, at the same time they will be exposed to more unfed ticks.

Reproductive success

During the 5-month gestation period (Bull 1987; Bull et al 1993), female *Tiliqua rugosa* are inactive and secretive (Bull 1987). Scoring reproduction is difficult. Again we used an indirect measure, whether or not lizards were found in pairs in spring.

This species forms monogamous male-female pairs for up to eight weeks in spring before copulation (Bull 1987, 1988, 1990; Bull et al. 1991, 1993). Some individuals do not pair or reproduce (pers. obs.). In our surveys, lizards never found in pairs may be amongst this unsuccessful group.

If ticks inhibit host reproduction we predicted that lizards never found in pairs would have higher tick loads. Again the opposite trend was found, probably reflecting the fact that lizards established in good-quality home ranges are both most likely to successfully pair, and most likely to maintain high tick densities. Itinerant or juvenile lizards may influence the analysis, being neither familiar enough with the area to expose themselves to ticks in the good refuges, nor established enough to form pairs. If these lizards are excluded, by only considering individuals which have persisted in the study for 3, 4 or 5 years, the trends are the same, but not as strong. There are still cases of significantly lower tick loads on lizards which were never found paired.

Although the three measures of lizard fitness are indirect none gave evidence that high tick loads had any adverse impact on lizard fitness in field conditions. This study has relied on a survey of a natural population. It follows many others where the impact of parasites on natural host populations is inferred from the frequency distribution of parasites on a sample of hosts (Pacala and Dobson 1988), or by comparing the performance of hosts with naturally variable levels of infestation (Hausfater et al. 1990). Sometimes the results of these surveys are counterintuitive in that the most heavily infested individuals are socially dominant (Hausfater and Watson 1976; Ressel and Schall 1989), or as fit as less-infested individuals (Hausfater et al. 1990). It is difficult to separate out the effect of parasite load when activities associated with dominance increase exposure to parasites, or when enhanced mating activity reduces resistance to infestation (Folstead and Karter 1992). Experimental manipulation will be required to determine whether a higher parasite load on socially dominant individuals masks any detrimental effects of the parasites.

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