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Prevalence and intensity of the blood parasite *Hemolivia mariae* in a field population of the skink *Tiliqua rugosa*

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Abstract The impacts of virulent parasites on humans or domestic animals are well documented. Less is known of the impact of parasites in natural host-parasite associations. A population of the Australian sleepy lizard *Tiliqua rugosa* is infected with the blood microparasite *Hemolivia mariae*, which is transmitted by the ectoparasitic tick *Amblyomma limbatum*. In most infected lizards a very small proportion, usually < 1%, of red blood cells are infected. A study of the prevalence of the microparasite in the field population found no difference either over 5 years of study or among times within a lizard activity season. Juvenile and sub-adult lizards and larger adults were less frequently infected with *H. mariae* than were other adults. In sub-adults this was related to a lower level of tick infestation. In adults, male and female lizards were equally frequently infected with *H. mariae*, but the presence or absence of ticks was not predictive of infection. The lizards' body condition was measured as the residual of the regression of log snout-vent length against log body mass. In female lizards the body condition was not affected by infection. In males the body condition declined over the sampling period each year, probably as a result of mate attendance. The body condition was poorer in male lizards with *H. mariae* infection than in uninfected males. Possible explanations for the associations of microparasites and host lizards are discussed.

Introduction

The effect of microparasites on their host populations is best documented for those virulent parasite species that cause epidemic outbreaks of disease, especially if they affect humans or their domestic animals. Infections of less virulent microparasite species that are persistent and endemic in natural populations have received less attention (Anderson 1995). Description of their impact is important for an understanding of the potential role of microparasites in host population dynamics and ecology. Often the first step in understanding how a microparasite interacts with its host and persists in a population is determination of the natural levels of prevalence and intensity of a parasitic infection among individuals within the host population. Prevalence and intensity can vary with host size (Blower and Roughgarden 1988), age (Earle et al. 1992), sex (Fedynich and Rhodes 1995; Schall 1986), or reproductive effort (Korpimaki et al. 1993, 1995; Norris et al. 1994). Extrinsic factors such as the geographical region (Merila et al. 1995; Super and van Riper 1995) and the season or year (Earle et al. 1992; Weatherhead and Bennett 1992) can also influence microparasite levels. The effect of any given intensity of parasitism on an individual host may also vary with changes in environmental conditions that can alter the ability of the host to meet the cost of being parasitised (Weatherhead et al. 1995).

This paper considers a population of the Australian sleepy lizard *Tiliqua rugosa* and the prevalence and intensity of natural infections of the blood microparasite *Hemolivia mariae*. *T. rugosa* is a large skink with a high rate of adult survival; a long life in individuals, perhaps as long as 50 years (Bull 1995); and stable home-range conformations (Bull and Freake 1999). The lizards display a low degree of annual fecundity and there is high mortality among juveniles (Bull 1995).

The blood parasite *H. mariae* (Smallridge and Paperna 1997) is a haemogregarine in the family Karyolysidae from the sub-order Adeleiorina of the apicomplexans (Barta 1999). It has an indirect life cycle involving definitive invertebrate hosts; the ticks *Amblyomma limbatum* and *Aponomma hydrosauri*; and an intermediate vertebrate host, the sleepy lizard *T. rugosa*. The parasite is ingested by ticks when they engorge on

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blood from infected lizards. It reproduces sexually within the tick gut to produce oocysts and then asexually to produce infective sporocysts containing sporozoites (Smallridge and Paperna 1997). The infection is transmitted to the vertebrate host when lizards ingest infected ticks (Smallridge and Bull 1999). The parasites undergo further asexual division in various lizard organs and then invade lizard erythrocytes, in which they persist for over 12 months (Smallridge 1998a, b).

Of the two tick species, *A. limbatum* is more susceptible than *A. hydrosauri* to infection with *H. mariae*, and it transmits the blood parasite more effectively (Smallridge and Bull 1999). *H. mariae* is more common in lizards in which *A. limbatum* occurs (Smallridge 1998a). Near Mount Mary in South Australia there is a parapatric boundary between the two tick species (Chilton and Bull 1996; Smyth 1973), and this paper examines the prevalence and intensity of *H. mariae* infections in the sleepy-lizard population on the *A. limbatum* side of the boundary.

There were two specific aims of the study. The first was to describe the general population biology of *H. mariae* in sleepy lizards under field conditions. The second was to determine whether specific sub-populations of lizards were more at risk for infection than others. Both aims are fundamental first stages in the acquisition of an understanding of the ecological interactions in this natural host-microparasite system.

Materials and methods

The study site (33°55′S, 139°15′E) is in semi-arid chenopod shrubland near Mount Mary, South Australia, where most sleepy-lizard activity occurs in spring and early summer. Lizards were captured along gravel roads in the study site from August until December in each of the 5 years 1992–1995 and 1998. Data were recorded on 97 days, corresponding to 10–36 days per year. Sampling was representative of the population of lizards. For instance, it is unlikely that infected lizards were easier to catch because the slow gait of these reptiles meant that each lizard seen could be captured.

Each captured lizard was individually marked by toe-clipping, sexed, weighed, and measured for its snout-vent length (SVL). The life stages of any attached ticks were recorded, and a smear was made on a microscope slide from blood taken either from the caudal vein or from a toe-nail clip. The lizard was then released at the point of capture. Blood smears were air-dried. In the laboratory the smears were fixed in absolute methanol for 5 min and then stained in Giemsa (pH 7.0) for 15 min before their examination for *Hemolivia mariae*.

There were 830 captures of 567 individual lizards. Data from these captures were used to determine any changes in the prevalence or intensity of *H. mariae* infection among years and among sampling months within years. Data obtained from the 567 individual lizards were used to examine whether any group of lizards showed higher prevalence or intensity of *H. mariae* infection or whether *H. mariae* infection was associated with tick infestation or with any reduction in the body condition of the host lizards. When lizards were captured more than once during the study period, only the first capture record was used in the analysis. Host records were grouped into three size categories: juveniles (SVL <20 cm), sub-adults (SVL 20–23.5 cm), and adults (SVL ≥ 24 cm). In comparisons of male and female lizards, only adults were considered.

Non-normal data were either log-transformed or analysed with non-parametric tests. Parasite prevalence was estimated as the percentage of infected lizards (Margolis et al. 1982). Prevalence was compared among different groups of lizards using contingency-table analysis of the actual numbers of lizards recorded as infected and non-infected. Whenever $n < 200$, the tests were adjusted for small sample sizes using Williams correction (Krebs 1989).

Parasite intensity was estimated for each infected host as the percentage of infected red blood cells found in approximately 10,000 cells scanned at 1000× magnification. In previous laboratory studies, estimates of infection intensity from a lizard had been similar, whether the blood was sampled from the caudal vein or from a toe-nail clip (Smallridge 1998a). Intensity was compared among groups of lizards using Mann-Whitney *U*-tests.

The lizards' body condition was calculated separately for each sex as the residual of the regression of log SVL on log body mass (Christian and Bedford 1995; Dunlap and Mathies 1993) and infected and non-infected lizards were compared. In this lizard species, tail loss does not occur and, thus, did not need to be considered.

Results

Temporal trends and overall population data

The prevalence and intensity of infection of *Tiliqua rugosa* by *Hemolivia mariae* did not change either among years or among sampling months (Table 1). In the surveyed population, 66 of 567 individual sleepy lizards (11.5%) were detected as being infected with *H. mariae*. The intensity of *H. mariae* infection ranged from $<0.01\%$ (only 1 infected cell in more than 10,000 erythrocytes examined) to 2.5%. Among the infected lizards, 28 showed an infection intensity of 0.01% or less, 22 displayed an intensity of 0.01%–0.1%, 11 exhibited an intensity of 0.1–1.0% and 5 showed an intensity of $>1.0\%$.

Host size and sex

The prevalence of infection was significantly higher in adults (12.8%) than in sub-adults and juveniles (1.6%; $G = 9.641$, $df = 1$, $P < 0.05$, Table 2). No significant difference (NS) was found in the prevalence of infection between female and male adult lizards ($G = 0.910$, $df = 1$, NS, Table 2).

Significantly more adult lizards (73.3%) than juveniles and sub-adults (26.2%) were found to be infested with ticks ($G = 28.962$, $df = 1$, $P < 0.05$). Equivalent proportions of adult female (77.3%) and adult male lizards (69.8%) were infested with ticks ($G = 3.121$, $df = 1$, NS, Table 2). Among adult lizards the prevalence of *H. mariae* did not differ significantly between the 382 tick-infested lizards (13.9%) and the 124 lizards without ticks (9.7%; $G = 1.554$, $df = 1$, NS).

The prevalence of *H. mariae* differed significantly among five adult size classes (Table 3, $G = 11.370$, $df = 4$, $P < 0.05$). As male and female lizards have the same average SVL (Bull and Pamula 1996), the corresponding data were pooled for this analysis. The

Table 1 The prevalence of infection of *Tiliqua rugosa* by *Hemolivia mariae* as determined in each year of the study and then in each month, with data being pooled across years. Because August and December were not sampled in each year, for this analysis we combined data from August and September and pooled data from November and December. Also shown are the mean infection intensities detected among infected lizards during each sampling period. Contingency-table analyses were used to compare prevalence, and Kruskal-Wallis tests were applied to compare infection intensity

	Total lizards	Number infected	Prevalence (%)	Mean infection intensity (%)	Intensity range
1992	46	5	10.9	0.77	0.01–2.00
1993	241	33	13.7	0.22	0.01–2.50
1994	137	13	9.5	0.06	0.01–0.40
1995	191	22	11.5	0.20	0.01–1.58
1998	215	22	10.3	0.10	0.01–0.71
Chi-squared			1.97; NS	5.96; $P = 0.20$	
Aug–Sept	219	20	9.1	0.15	0.01–1.38
Oct	280	34	12.1	0.29	0.01–2.50
Nov–Dec	331	41	12.4	0.12	0.01–2.00
Chi-squared			1.59; NS	3.64; $P = 0.16$	

Table 2 Number of lizards sampled in each of four categories of development and the prevalence of infection with *H. mariae*. Also shown is the percentage of lizards in each category found with ticks attached. Lizards were classified as juveniles when their SVL was <20 cm, as sub-adults when their SVL was 20–23.5 cm, and as adults when their SVL was >24 cm

	Number of lizards	Number infected with *H. mariae*	Prevalence of *H. mariae* (%)	% With ticks
Juveniles	28	0	0.0	21.4
Sub-adults	33	1	3.0	30.3
Adult females	238	27	11.3	77.3
Adult males	268	38	14.2	69.8

Table 3 Total number of adult lizards captured in each of five size categories and the proportion of those adult lizards found to be infected with *H. mariae*. Also shown are the numbers of tick-infested adult lizards in each size class, the proportion of those found to be infected with *H. mariae*, and the mean infection intensity determined among infected lizards

Lizard SVL (cm)	All lizards		Tick-infested lizards		Mean (SE) *H. mariae* intensity in infected lizards (%)
	n	% Infected	*n*	% Infected	
24–25.5	22	27.3	12	50.0	0.37 (0.230)
26–27.5	42	19.0	34	23.5	0.05 (0.028)
28–29.5	124	16.9	98	18.4	0.33 (0.153)
30–31.5	230	10.9	175	9.7	0.14 (0.082)
32–35.0	88	5.7	63	6.3	0.11 (0.097)

prevalence of *H. mariae* decreased with increasing adult lizard size (Table 3). The proportion of adult lizards infested with ticks did not differ significantly among those size classes ($G = 6.884$, $df = 4$, NS). However, the influence of tick infestation differed. In the smallest size class (24.0–25.5 cm SVL), 50% of 12 lizards with ticks had *H. mariae* infections, whereas none of the 10 lizards without ticks was infected ($G = 5.068$, $df = 1$, $P < 0.05$). No significant difference in the prevalence of *H. mariae* infection was found between lizards with ticks and those without ticks for any other size class of adult lizards.

The mean infection intensity of infected adult lizards did not differ significantly among the five adult size classes (Table 3, Mann-Whitney U-test, $z = 1.311$, $P = 0.190$). Among all infected adults, females displayed a significantly higher mean infection intensity (0.35%) than did males (0.11%; Mann-Whitney U-test, $z = 323$, $P = 0.008$).

Host body condition

The body mass of male and female adult lizards was compared by analysis of covariance using SVL as a covariate. There was a significant positive correlation between body mass and SVL ($F_{[1,502]} = 870.450$, $P < 0.001$) and a significant interaction between sex and SVL ($F_{[1,502]} = 15.681$, $P < 0.001$). Females were significantly heavier than males of equivalent SVL. The body condition of each individual host (the residual of the regression between log SVL and log body mass) was therefore calculated separately for each sex.

Lizards were sampled when they were most active, from August to December of each year. Females maintained an equivalent condition over this period, and their body condition was not correlated with the sampling date ($r = 0.047$, $P = 0.471$, $n = 238$). Analysis of variance (ANOVA) showed no significant effect of the presence or absence of *H. mariae* infection ($F_{[1,235]} = 0.004$, $P = 0.948$) on the female body condition.

The male body condition was negatively correlated with the sampling date ($r = -0.197$, $P = 0.001$, $n = 268$), indicating a loss of condition over the season. An analysis of covariance for male body condition using the sampling date as the covariate showed a significant effect of *H. mariae* infection ($F_{[1,264]} = 7.069$, $P = 0.008$). Overall, males lost condition over the spring, and males infected with *H. mariae* were in significantly poorer condition than were uninfected males (Fig. 1).

The body conditions of the 27 infected females and the 38 infected males were not correlated with the *H. mariae* infection intensity (females: $r_s = -0.100$, $P = 0.621$, NS; males: $r_s = 0.161$, $P = 0.333$, NS).

Discussion

Temporal trends

There was no detectable change in the prevalence of infection of sleepy lizards with *Hemolivia mariae* over

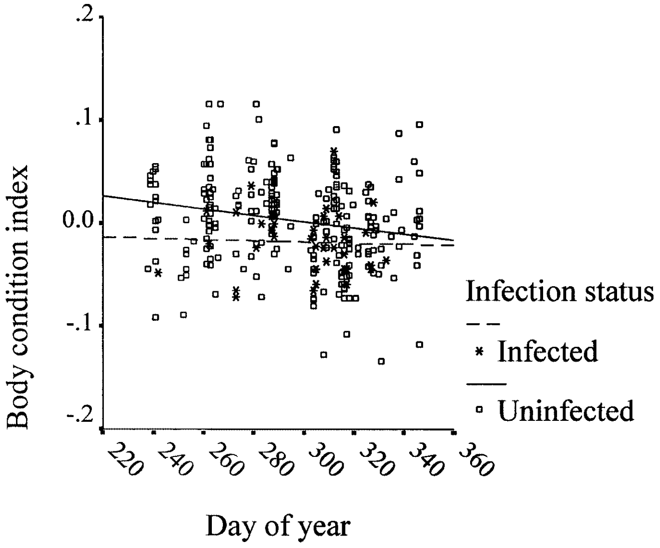

Fig. 1 Relationship between the body condition of male lizards (the residual of the regression between log SVL and log body mass) and the day of the year on which the lizards were sampled

the course of the study. The prevalence probably remains stable within a year because of the long period over which an initial infection can be detected. The intensity of infection also remained similar across the sampling period. Ticks are available throughout the season for ingestion, and new infections, leading to initially high intensity levels, probably happen regularly across a season rather than at a particular time. The consistency of prevalence and intensity across years may reflect the stability of the interaction in this population of lizards.

Host sex and size

In the field sample taken over 5 years, juveniles and sub-adults were almost never found to be infected with *H. mariae*. Studies of blood protozoa of birds have often reported an opposite trend involving a higher degree of prevalence in juveniles than in adults (Fedynich et al. 1993; Weatherhead and Bennett 1992; Work and Rameyer 1996). Those birds may experience substantial exposure to the microparasites or their vectors early in life, or they may develop an immunity to infection later in life. Also the nestlings of many bird species, being confined to their nests, are more exposed than adults to the nest-dwelling ectoparasites (Barton et al. 1996; Feare and Gill 1997) that vector the microparasites (Bennett et al. 1992; Hunter et al. 1997). In these cases, younger birds would have been exposed more recently than older birds.

Sleepy lizards acquire ticks when they share refuges or use a refuge in which ticks have detached from a previous occupant. Young sleepy lizards spend no time in nests and do not physically associate with their parents or siblings (Bull and Baghurst 1998); hence, they acquire fewer ticks and experience a relatively lower degree of exposure to *H. mariae*. A higher proportion of adult lizards have ticks, probably because they associate more with other adults, particularly during the 6- to 8-week pairing period each spring (Bull 1988) when pairs of lizards frequently share refuges (Bull et al. 1998). A previous survey has shown that lizards in pairs have higher numbers of attached ticks than do unpaired lizards (Bull and Burzacott 1993). Associated with higher tick numbers is a greater chance of encountering and eating an infected tick and becoming infected with *H. mariae*.

Among the adult lizards in this study there was a decline in the prevalence of *H. mariae* infection with increasing lizard size. The proportion of lizards infested with ticks did not alter among the size classes, but in the smallest size class, tick-infested adults were more likely to be infected with *H. mariae*. The smallest adults are probably younger (Bull 1995), and this pattern may reflect the importance of tick exposure for initial infection by *H. mariae*. Young lizards found to be free of ticks may not yet have been exposed to tick infestation, whereas larger and older lizards may previously have experienced ticks, even if they are not currently infested. Larger lizards without ticks could have become infected with *H. mariae* during previous tick exposure.

There are two possible explanations as to why larger and older adults show a low prevalence of *H. mariae* infection. One is that on repeated exposure, lizards become resistant to the microparasite or can more quickly reduce the parasite intensity to undetectable levels. For instance, they could inhibit the acute phase of parasite reproduction, leading to lower levels of peak infection, or they could increase erythrocyte turnover, shortening the period during which they are chronically infected. The second is that if infection reduces survival in susceptible individuals, only the more resistant proportion of the population survives to become large adults. Both explanations require further testing.

Host body condition

The body condition of female lizards remained constant over the activity season and was not affected by the presence or intensity of *H. mariae* infection. Male lizards declined in body condition over the activity season. In spring, male *Tiliqua rugosa* establish and maintain monogamous partnerships with females (Bull 1988; Bull et al. 1998), probably in response to rising levels of testosterone. Testosterone stimulates aggression and physical activity in male lizards of other species and may reduce food intake (Marler and Moore 1988; Moore and Marler 1987). In *T. rugosa*, paired males follow their partners closely and are less likely to be found feeding than are unpaired males (Bull and Pamula 1998). Pairing, activities associated with partner defence (Bull and Pamula 1998, 1996), and reduced food intake could all explain the observed decline in the body condition of adult males over the season.

In addition, *H. mariae* infection is associated with a poorer body condition in male lizards. *H. mariae* infection may cause a decline in body condition, for instance, by altering metabolic rates. Schall (1986) found that *Chemidophorus arubensis* lizards showed significantly higher oxygen consumption at rest when infected with haemogregarines. In his sample, 60% of lizards displayed an infection intensity of $<0.01\%$ and there was no evidence for any loss of host erythrocytes or any alteration in haemoglobin concentration. Haemogregarines also influenced the oxygen consumption at rest, the percentage of immature red blood cells and the haemoglobin content in another lizard, *Lacerta vivipara* (Oppliger et al. 1996). In that study the average parasite intensity was 2–4%. The body condition of infected male sleepy lizards may be reduced if *H. mariae* infection increases the host's rate of metabolism.

A second explanation for the association between *H. mariae* infection and a poor body condition in males may be that lizards whose body condition has worsened for some independent reason become more susceptible to infection by *H. mariae*. The nutritional status can influence the capacity of an individual to mount an immune response to infection (Cooper et al. 1985). Alternatively, both susceptibility to infection and the body condition may be controlled by some other factor such as an increase in levels of testosterone. Enhanced testosterone values can decrease the body condition of free-living male lizards (Marler and Moore 1988; Moore and Marler 1987) and lead to increased susceptibility to ectoparasites (Salvador et al. 1996) or haemogregarines (Veiga et al. 1998).

The results of this field survey provide the foundations for some hypotheses about the dynamics of this natural haemogregarine-tick/lizard system.

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