

Adam R. Main · C. Michael Bull

The impact of tick parasites on the behaviour of the lizard *Tiliqua rugosa*

Received: 02 March 1999 / Accepted: 07 October 1999

Abstract Populations of the Australian sleepy lizard, *Tiliqua rugosa*, near Mt. Mary, South Australia carry natural infestations of two tick species *Aponomma hydrosauri* and *Amblyomma limbatum*. In field experiments at two sites, 18 km apart, lizards with experimentally increased tick loads had smaller home ranges, moved shorter distances in a day, and were found basking more but moving less often than lizards from which ticks were experimentally removed. The results were consistent for adult lizards in two years, and for sub-adults in a third year. Laboratory trials showed that juvenile lizards that had tick infestations had lower sprint speeds than uninfested siblings, and that adults with tick infestations had less endurance than those that were uninfested. The results contrast with those of a previous survey that showed that lizards with high tick loads had greater body size and remained longer at a site, but indicate that there may be a balance, for lizards, between the fitness advantages in occupying habitats with high-quality resources, and the costs from parasites that also prefer those habitats.

Key words Lizards · Ticks · Home range · Sprint speed · Parasite-host interaction

Introduction

Parasites can influence a range of ecological parameters and behaviour in a population, and have significant impacts on population dynamics (e.g. Hudson et al. 1998; Richards et al. 1999). A common strategy to study the impact of parasites on their host population is to compare the fitness, physiology, or behaviour of host individuals that are naturally infested in the population with

those that are free from parasites. For instance, in lizard populations, individuals with parasites had poorer body condition (Dunlap and Mathies 1993; Sorci and Clobert 1995), reduced social status (Dunlap and Schall 1995), lower reproductive output (Sorci et al. 1996), slower running speed (Oppliger et al. 1996), and poorer competitive ability (Schall 1992) than uninfested individuals. The inference is that parasites have caused these fitness reductions, although not all studies conducted in this way could show that parasites lower the fitness of lizards (Christian and Bedford 1995; Ostfeld et al. 1996).

A problem with the observational approach described above is that, for some independent reason, a subset of the population may have different behaviour or fitness from the rest of the population, and also be more susceptible to parasites. Thus a correlation between parasite presence and fitness that is derived from data from natural infestations does not necessarily imply causation. For instance, Brown et al. (1994) found that helminth-infested mice moved further than helminth-free mice during radio-tracking, but they could not determine whether that behaviour was a consequence of the mice being parasitised or whether a group of more active mice were more likely to become parasitised. Similarly, in lizards, Sorci et al. (1996) pointed out that the correlation they found between haematozoan parasite load and reproductive effort in *Lacerta vivipara* could result either from a direct impact of the parasites on the lizards, or because lizards with different reproductive strategies were differentially susceptible to parasites.

Another way to investigate the impact of parasites on hosts in natural populations is by experimental manipulation of parasite load. A random sample treated, for instance, with reduced parasite load, that then shows improved fitness or altered behaviour relative to non-treated controls, provides strong evidence that parasites are directly influencing the host (Lehmann 1992; Butler and Roper 1996; McKilligan 1996). Some experiments of this kind have still failed to confirm that parasites adversely affect their hosts (Brown et al. 1994; Bloomer et al. 1995).

The Australian sleepy lizard, *Tiliqua rugosa*, is a large, long-lived, herbivorous lizard of the family Scincidae

A.R. Main · C.M. Bull (✉)
School of Biological Sciences, Flinders University,
GPO Box 2100, Adelaide SA 5001, Australia
e-mail: michael.bull@flinders.edu.au
Fax: +61-8-8201-3015

(Bull 1987, 1995; Bull et al. 1993b), which is widely distributed over southern Australia (Cogger 1992). Individual lizards occupy stable home ranges (Bull and Freake 1999) which are broadly overlapping (Bull 1994). Home ranges are similar in size for males and females (Bull and Baghurst 1998).

In a semi-arid site near Mt. Mary, South Australia, sleepy lizards are naturally infested with two tick species, *Aponomma hydrosauri* and *Amblyomma limbatum* (Bull and Burzacott 1993; Chilton and Bull 1996; Dawes-Gromadzki and Bull 1997). In an 8-year study, Bull and Burzacott (1993) found median values of 1–6 ticks per host, with 32 lizards (of the 3416 captures) having over 100 ticks. In that study they reported that the number of years a lizard stayed in its home range was either not correlated, or was positively correlated with tick load. They also reported that lizards with high tick loads tended to be larger, and mated pairs of lizards had more ticks than unpaired lizards (Bull and Burzacott 1993). This could be explained if the fittest lizards, and those most likely to gain mates, lived in parts of the study area where tick densities were highest, and if less fit lizards lived in areas where they were less likely to encounter ticks. Bull and Burzacott (1993) pointed out that this would make it difficult to determine, from direct observation, whether the ticks had any negative impact on their host lizards.

Ticks should decrease sleepy lizard fitness. Ticks are known to have adverse effects on populations of amphibians (Lampo and Bayliss 1996), other lizard species (Dunlap and Mathies 1993), birds (McKilligan 1996; Hudson et al. 1998) and mammals (Addison et al. 1994; Fourie et al. 1992). They consume host blood, and may cause anaemia (Hair et al. 1992; Wikelski 1999). Ticks commonly transmit blood parasites that can have adverse effects on their lizard hosts (Wozniak et al. 1996; Eisen and Schall 1997; Oppliger and Clobert 1997). In the sleepy lizard, a haemogregarine blood parasite, *Hemolivia mariae*, is transmitted to lizards by both tick species at Mt. Mary (Smallridge and Paperna 1997).

This paper describes experiments conducted in the field and in the laboratory, where the tick load on sleepy lizards was experimentally manipulated, to investigate whether ticks have a negative impact on their lizard hosts. Our hypothesis was that lizards with experimentally increased tick loads would behave differently from lizards with reduced tick loads. Specifically, we predicted that lizards with experimentally imposed high tick loads would have reduced movement and smaller home range areas than lizards with experimentally reduced tick loads in the field, and would show less vigorous activity in the laboratory.

Materials and methods

Field work

The field study was conducted from 1995 to 1997, at two semi-arid sites (site A 85 ha; site B 50 ha) 18 km apart. They were in

homogeneous chenopod bushland, previously described by Bull et al. (1998), 10 km east of the Winters study area (33°55'S, 139°20'E) near Mt. Mary, South Australia. The chenopod bluebush, *Maireana sedifolia*, was the dominant large plant and provided shelter for the lizards and unattached ticks. The lizards fed mainly on berries from bushes, and flowers of annual plants and weeds. During the study annual plants at both sites were grazed by sheep, but site B was less heavily grazed. Bluebush density at each site was estimated by counting the number of individual plants encountered along six 200×2 m transects.

We worked in spring and early summer (late August to mid-December) in each of the three study years. This is the period when sleepy lizards are most active. It is too cold in winter, and too hot and dry after mid-summer for extensive lizard activity (Bull et al. 1991; Bull 1995). In August and September 1995, we tagged 30 adult lizards at site A, and 29 at site B with 20 g, 12×9 mm, single stage radio transmitters (Sirtrak), representing 2–3% of the mass of the lizard. Radios were attached to the dorsal surface of the tail using surgical adhesive tape. In 1996, 36 lizards retained their radios from the previous year and we radio tagged other adults as we located them from late August to make a total of 26 at site A and 30 at site B. Juvenile lizards are harder to locate in the field (Bull 1995; Bull and Baghurst 1998). In June 1997 we released 50 laboratory reared juvenile (3 month old) and sub-adult (15 month old) lizards with attached radios, to the field sites. By August there had been heavy predation from foxes and feral cats, particularly at site A, and no juveniles survived there. In September 1997 the 21 remaining sub-adults were all at site B.

At the start of each season, radio-tagged lizards at each site were randomly divided into two groups. One group, the low-tick treatment, had all naturally occurring ticks removed on three occasions over the 1995 season, on four occasions over the 1996 season, and on eight occasions over the 1997 season. In the other group, the high-tick treatment, natural tick attachments were left. In addition 50 larvae of *Aponomma hydrosauri* were attached to each lizard in this group on each of three occasions in 1995, 50 larvae and 5 nymphs were attached on each of four occasions in 1996, and 20 nymphs were attached on each of four occasions in 1997. These infestation levels were in the upper range of tick numbers that naturally infested hosts over 8 years in the previous study in the same area (Bull and Burzacott 1993). We chose only to manipulate the densities of *Aponomma hydrosauri* because it was easier to raise large numbers of this species. In the Mt. Mary region *Amblyomma limbatum* and *Aponomma hydrosauri* reach comparable levels of infestation (Bull and Burzacott 1993). Because tick densities vary substantially among years (Bull and Burzacott 1993) we expected background tick levels to be different in each year.

On tick sampling days, all lizards were collected in the afternoon into individual calico bags, and transported 10 km to the field research station. There, all ticks attached to lizards were counted, and removed if the lizard was from the low-tick group. On tick attachment days, high-tick lizards were then held overnight, sealed in their bags with attaching ticks, on a 27°C heat pad. Over 90% of ticks had attached to their hosts by the following morning. Low-tick lizards were held in similar conditions but without additional ticks. Next morning all lizards were released at their site of capture.

Tick loads per lizard, averaged over all sampling days in a year, and measured before tick attachment or removal, are shown in Table 1. They reflect maximum loads attained for the low-tick group, because those ticks were then taken off. They reflect minimum loads for the high-tick group, because new ticks were about to be attached. Thus the actual difference in the mean tick load per lizard between the two experimental groups was greater over much of the study than the table suggests. Nevertheless real differences in tick loads were sustained up to the time of the next manipulation.

Because of their larger size, adult female ticks engorge more, and probably have a higher impact on host lizards than do nymphs. Similarly nymphs would be expected to affect host lizards more than larvae. Adult male ticks do not engorge on the lizard hosts and would only have a small effect.

Table 1 The mean number of each life stage of *Aponomma hydrosauri* ticks (SE) attached to each lizard in the high- and low-tick groups averaged over all sampling occasions from counts on each occasion before experimental tick removal or tick attachment

Lizard treatment group	Number of lizards	Density of attached ticks			
		Larval ticks	Nymphal ticks	Male ticks	Female ticks
Adults 1995					
High tick	30	21.5 (3.9)	2.9 (0.9)	2.1 (0.3)	0.2 (0.1)
Low tick	29	6.0 (2.4)	0.4 (0.2)	0.4 (0.1)	0.1 (0.0)
Adults 1996					
High tick	28	7.4 (0.8)	2.6 (0.3)	0.4 (0.1)	0.2 (0.0)
Low tick	28	0.8 (0.2)	0.4 (0.1)	0.0 (0.0)	0.1 (0.1)
Sub-adults 1997					
High tick	10	1.6 (0.5)	4.1 (0.8)	0.8 (0.2)	1.2 (0.3)
Low tick	11	1.4 (0.4)	0.3 (0.1)	0.2 (0.1)	0.2 (0.1)

Each site was mapped, and bushes at 30–50 m intervals were marked with flagging tape for easy location of any position within the site. We located radio tagged lizards relative to these reference points with a three-element YAGI antenna at least once per day on 4–7 days per week during most weeks of the study period each year. In 1995 the 59 adults were each located an average 18.2 (SE 0.4; range 10–22) times. In 1996 the 56 adults were each located an average 46.2 (SE 1.5; range 14–61) times. In 1997 the 21 sub-adults were each located an average 69.1 (SE 3.4; range 22–82) times. We usually avoided extended behavioural observation or locating lizards more regularly in a day because observer presence interrupted normal activity, and caused lizards to retreat into refuges for very long periods (Bull et al. 1993a). In each year the mean number of observations did not differ between low-tick and high-tick treatments (1995, $t_{57}=0.79$; $P=0.43$, 1996, $t_{54}=0.57$; $P=0.57$, 1997, $t_{19}=0.24$; $P=0.81$). At the time of each location we recorded whether or not the lizard was in a refuge, and if it was out whether it was basking, moving or feeding.

Minimum convex polygon estimates of the home range area for each lizard were derived using Ranges V software (Kenward and Hodder 1996). We used the central 80% of locations to derive the home range area, because, in this species, home range estimates can be substantially inflated by occasional records of excursions out of the normal occupied area (Bull and Baghurst 1998; Bull and Freaque 1999).

In 1996 and 1997 we recorded additional information about daily movement patterns by attaching 3.1-g spools, containing 250 m of cotton thread, to the backs of lizards. As each lizard moved, it left a cotton thread track of where it had been. Spools were attached in the morning before activity had commenced, and tracks were recorded on the evening of the same day. In 1996, 56 tracks were recorded from 39 of the radio-tagged adult lizards. In 1997, 35 tracks were recorded from the 21 sub-adult lizards.

Laboratory studies

We conducted two experiments in the laboratory to further test predictions that ticks adversely affect the movement performance of sleepy lizards.

Laboratory sprint speeds

Ten litters, each made up of two juvenile lizards, were born in the laboratory in March 1996. Each litter was divided so that one juvenile was left uninfested and the second was infested with *Aponomma hydrosauri* larvae. Tick attachments were performed as in the field experiments. At 4-week intervals from April to June, each lizard in the infested group was exposed to 200 tick larvae. There was an average 88% attachment rate. Larvae were observed to engorge and detach from their lizard hosts in the period between attachments, but rates were not recorded. In previous

studies Bull et al. (1989) showed that *A. hydrosauri* larvae took an average 19–25 days to engorge and detach in the laboratory.

All infested lizards were kept separate from uninfested lizards. Lizards were housed as non-sibling pairs in 30×75×35 cm glass tanks, in a 25°C room with a 12:12 h photoperiod. A 60-W globe suspended 20 cm above the floor of one end of each tank produced a 30–37°C gradient when it was turned on from 0900 to 1700 hours each day. An inverted square 4-l container provided shelter. Water was continuously available, and lizards were fed three times each week (Main and Bull 1996).

Each lizard was tested for sprint speed in five trials between May and August 1996. Each trial for a lizard was completed between 1200 and 1700 hours on one day, and there was a period of at least 2 weeks between trials. Lizards basked under a 150-W heat lamp before each trial, and were only used when their body temperature exceeded 30°C. The preferred body temperature for *Tiliqua rugosa* when active is 32–34°C (Bennett and John-Alder 1986; Licht et al. 1996), although at Mt. Mary they have been observed active with cloacal temperatures of 19–35°C (Chilton and Bull 1992).

A 2.4-m wooden running track (base 20 cm wide, walls 20 cm high), was marked at 50-cm intervals. The lizard was placed at the start of the track and prompted to run by tapping its tail. If it stopped in the track it was prompted to run again. On some occasions the lizard completed 2 m of the track and the time taken to cover that distance was used to calculate its sprint speed. On other occasions the lizard stopped in mid-track and refused to proceed. Such lizards normally flattened the body and the mouth gaped in a defensive posture. Data from those incomplete runs were not included. In the five trials, each lizard completed two to five 2-m runs, and the average sprint speed for each lizard from its completed runs was used in the analysis. We used paired *t*-tests to compare the speeds of infested and uninfested siblings. Siblings did not differ in growth rate as a result of being infected or uninfected, nor did they differ significantly in size at the time of any trial (Main 1998).

Laboratory endurance trials

Twenty adult female lizards were collected from the field site in December 1996 and housed in individual glass tanks as above. They were maintained free of ticks for 6 months. Then in June 1997, 200 larval *A. hydrosauri* were attached to each of ten lizards. Those ticks engorged on host blood and began to detach 20 days after initial attachment. The remaining ten lizards were kept free of ticks.

Each lizard was tested twice. Trials were conducted with half the lizards in each treatment group on day 12 and then day 26 after tick attachment, and with the others on day 18 and then day 33 after tick attachment. Prior to a trial, a lizard was allowed to bask under a heat lamp for 20–30 min and to raise its body temperature above 30°C.

Table 2 Mean home range size (ha) (80% of minimum convex polygon) of high- and low-tick group adult lizards at each site (1995 and 1996 combined), and for sub-adults in 1997

Treatment group	Site A		Site B	
	<i>n</i>	Home range area (SE)	<i>n</i>	Home range area (SE)
Adults 1995/1996				
High tick	15	1.37 (0.19)	22	0.63 (0.13)
Low tick	14	1.65 (0.37)	24	1.01 (0.23)
Sub-adults 1997				
High tick			10	0.97 (0.39)
Low tick			11	2.76 (1.17)

Table 3 Mean (SE) percentage of observations of each lizard in various behaviours when located by radio-tracking

Treatment group	<i>n</i>	In refuge	Out moving	Out basking	Out feeding
Adults 1995					
High tick	30	54.5 (3.1)	21.4 (2.7)	21.8 (2.5)	2.3 (0.6)
Low tick	27	53.4 (3.0)	22.7 (2.0)	19.2 (2.0)	4.6 (1.3)
Adults 1996					
High tick	28	71.0 (2.1)	6.4 (0.9)*	20.5 (1.4)*	1.9 (0.4)
Low tick	28	73.2 (1.8)	11.8 (1.8)*	14.4 (1.4)*	1.8 (0.6)
Sub-adults 1997					
High tick	10	84.6 (4.1)	5.0 (1.8)	10.4 (3.1)	0.0 (0.0)
Low tick	11	84.0 (1.9)	5.9 (1.1)	9.2 (1.7)	0.9 (0.5)

*Statistically significant difference between high-tick and low-tick treatments

Endurance was tested on a 2.8-m-long×0.8-m-wide rubber based treadmill, rotating at 0.28 m s⁻¹. Each lizard was placed on the moving treadmill and then induced to keep moving by prodding the tail with a piece of wooden dowelling. The time was recorded from the start of the trial until the lizard refused to continue moving. All lizards ran in the first trial but two refused to start in the second.

Results

Field sites

Bluebush densities averaged 11.5 (SE 2.9) individual plants per 200 m transect at site A and 29.8 (SE 2.0) at site B. These values were significantly different ($t_{10}=5.25$; $P<0.001$). The northern site (A) had a lower density of bluebush.

Lizard home ranges

Table 2 shows the mean home range areas for lizards as measured by the 80% minimum convex polygon method. For adults, average areas per year were used for individuals tracked in both years. Thus in the analysis, each individual lizard was only considered once. A three-way ANOVA examined the effects on adult home range area of sex, infestation treatment and site. Home ranges for males (1.10 ha; SE 0.18) and females (1.08 ha; SE 0.16) were similar, but among all adults, high-tick lizards had significantly smaller home ranges (0.93 ha; SE 0.12) than low-tick lizards (1.25 ha; SE 0.20) ($F_{1,67}=8.36$; $P=0.005$). There was also a larger mean home range at

site A (1.51 ha; SE 0.20) than at site B (0.83 ha; SE 0.14) ($F_{1,67}=16.88$; $P<0.001$), and significant interaction terms involving site. For sub-adults in 1997, the mean home range of low-tick lizards was not statistically different from that of high-tick lizards ($F_{1,19}=1.95$; $P=0.18$).

Observations of behaviour

Data for the behaviour of lizards when they were encountered during radio tracking, are presented in Table 3. For adults in 1996, high-tick lizards were observed basking significantly more frequently than low-tick lizards ($F_{1,48}=5.23$; $P=0.027$), and high-tick lizards were observed moving significantly less frequently than low-tick lizards ($F_{1,48}=7.56$; $P=0.008$). There was no significant effect of site or of lizard sex for either of these behavioural parameters. Although the same trends were shown in the observations from adults in 1995 and sub-adults in 1997, there were no other significant results. Sub-adults tended to be found active less often than adults, although the effect of varying the sampling procedure in different years cannot be eliminated as an explanation.

Cotton spooling of daily paths

There were 56 cases in 1996 where the path of an adult lizard was tracked by cotton spooling. The minimum distance moved in a day was 15 m, and in six cases the lizards moved beyond the full 250 m of the spool. In the analysis, those six lizards were counted as having moved 250 m, but because total distances were not known, the

Table 4 Mean length (m) of daily path of high- and low-tick groups: adult lizards at each site in 1996, and sub-adults that moved in 1997, as measured by the length of cotton laid out from a spool on the lizard back

Treatment group	Site A		Site B	
	<i>n</i>	Path length (SE)	<i>n</i>	Path length (SE)
Adults 1996				
High tick	16	122.1 (17.0)*	14	101.3 (15.7)
Low tick	12	189.6 (17.1)*	14	105.1 (18.1)
Sub-adults 1997				
High tick			7	60.1 (19.8)*
Low tick			7	141.3 (31.3)*

*Statistically significant difference between high-tick and low-tick treatments

data were analysed by non-parametric Mann-Whitney tests. Table 4 shows the average distances of paths by high and low-tick adult lizards at each site. Lizards had significantly longer paths in a day at site A than site B (Mann-Whitney $U=243$; $P=0.015$). At site A high-tick lizards had significantly shorter paths than low-tick lizards (Mann-Whitney $U=44.5$; $P=0.017$).

Sub-adult lizards were spooled on 35 occasions in 1997. Only 7 out of 19 high-tick lizards, and 7 out of 16 low-tick lizards moved at all on the day they were spooled. The proportion that moved was not significantly different between the two groups ($\chi^2=0.17$). When only the seven cases in each group that did move were considered (Table 4), high-tick lizards had significantly shorter paths than low-tick lizards (Mann-Whitney $U=9.0$; $P=0.048$).

Laboratory sprint speeds

Although the lizards grew from a mean 115 g to 150 g over the 4 months during which the trials were run, the date of trial did not have a significant effect on sprint speed ($F_{4,69}=0.30$; $P=0.88$). Infested lizards completed an average 3.9 (SE 0.41) runs from their five trials. Clean lizards completed an average 3.5 (SE 0.37) runs. In a paired t -test comparing infested and clean siblings from each litter, mean number of completed runs did not differ ($t_9=0.74$; $P=0.48$). However in a paired t -test comparing mean sprint speed of infested and clean siblings from each litter, infested lizards were significantly slower (0.19 m s^{-1} ; SE 0.02) than clean lizards (0.25 m s^{-1} ; SE 0.02) ($t_9=2.86$; $P=0.019$).

Laboratory endurance trials

For the 18 female lizards that ran in both trials the mean endurance time was the same in the first trial (4.27 min; SE 0.82) as in the second (3.40 min; SE 0.60) (paired t -test: $t_{17}=0.76$; $P=0.46$). Subsequent analysis used the average endurance time for each lizard over the trials it ran. The ten tick-infested females had a significantly shorter endurance time (2.47 min; SE 0.54) than the uninfested females (5.15 min; SE 0.86) ($t_{18}=2.62$; $P=0.017$).

Discussion

Field experiments

The experimental manipulation, of removing or adding ticks to lizards, led to the successful maintenance of distinctly different tick loads on the two experimental groups in the field. There was some individual variation among lizards in the behavioural parameters measured, for instance in home range areas and distance moved. However male and female lizards did not differ in home range area. Previous reports have also suggested the two sexes maintain similar-sized home ranges in this species (Bull and Baghurst 1998; Bull and Freake 1999). There were significant differences in lizard home range area between the two study sites, even though they were of similar habitat and only 18 km apart. At site A, lizards had larger home ranges and moved longer distances in a day. A possible explanation is that site A had a lower density of blue bush refuges and was more heavily grazed by sheep, so these herbivorous lizards may have had to move further each day to find adequate plant food resources.

The main result from the field was the demonstration of a significant effect of the experimental manipulation. The level of tick infestation significantly influenced several measured parameters of lizard behaviour. Lizards in the high-tick treatment had significantly smaller average home range areas than lizards in the low-tick treatment. Also, during random, radio-tracking locations in 1996, a significantly higher proportion of high-tick lizards than low-tick lizards were found basking, and a significantly higher proportion of low-tick lizards than high-tick lizards were found walking. While these once-a-day observations do not represent the entire behavioural profile of a lizard, they indicate overall behavioural differences between the two groups. Those differences were also reflected in the measured distance moved per day. In both sub-adults and adults, the daily path was significantly shorter for high-tick than for low-tick lizards.

The behavioural differences reported above indicate reduced activity in lizards with experimentally enhanced tick loads. Experimental tick densities were equivalent to the upper levels recorded on lizards in natural field populations. With those tick loads lizards had significantly lower movement and home range area than lightly infested lizards.

Laboratory studies

The laboratory studies support the conclusion that high tick loads reduce lizard movement in the field. Sleepy lizards that had ticks attached had slower sprint speeds, and lower endurance than lizards without ticks.

Other lizard studies have shown a number of factors can influence sprint speed and endurance. Some are fixed attributes of the individual such as limb dimensions (Bauwens et al. 1995), genotype (Sorci et al. 1995; Cullum 1997) or sex (Dohm et al. 1998). Other variable factors can cause temporal shifts in lizard performance. For instance, sprint speed and endurance can be affected by willingness to run, by temperature (Mautz et al. 1992; Smith 1997), by the lizard's previous social environment, or the hormone levels induced by that environment (John-Alder et al. 1996), or by recency of the last meal (Martin 1996). The sprint speed of juvenile lizards can be influenced by the feeding rate of their mother (Sorci and Clobert 1997). A few studies have examined the impact of parasites on lizard sprinting and endurance. In *Lacerta*, high parasite load in female lizards actually enhances sprint speed in their daughters (Sorci et al. 1994), and Schall et al. (1982) found locomotory performance of *Sceloporus* was inhibited by infection with malaria.

The present study found that parasites, ticks in this case, reduce sprint speed and endurance in their host sleepy lizards. The results further confirm the adverse impact of ticks. Sprinting is often used by lizards to escape predators (Hertz et al. 1988). Sleepy lizards have relatively few predators as adults (Bull 1995; Bull and Pamula 1998) and their body is not designed for fast running (John-Alder et al. 1986). Nevertheless juvenile sleepy lizards are eaten by snakes (Bull and Baghurst 1998), cats and foxes (Main 1998), and a slower sprint speed may reduce their chance of escape to a close refuge. Endurance is probably a more relevant attribute for adult lizards with daily moves often exceeding 200 m. If tick load reduces endurance, it could also reduce the capacity of a lizard to move around a large home range. The laboratory results contribute to understanding why the field lizards with high tick loads had smaller home ranges.

In passing it is worth comparing our laboratory measures of sprint speed and endurance with those derived for the same species by John-Alder et al. (1986). They reported an average maximum sprint speed of 2.7 km h⁻¹. Our lizards ran slower than that, perhaps because they were juveniles with shorter legs. Also our lizards, in both years, were confined for months in glass tanks and may have lost the condition of field lizards. This could explain why their endurance was also much less than the 23 min reported by John-Alder et al. (1986). Despite these differences, the comparison of infected and uninfected lizards from our experiments remains relevant.

Summary

Both laboratory and field experiments showed that the effects of tick infestation can reduce the activity of sleepy

lizards. The sprint speed and endurance of lizards in the laboratory were reduced, and some field measures of daily movement and home range size were smaller for lizards with high-tick loads. Tick induced activity changes could reduce fitness, because lower movement may lead to fewer opportunities to sample or use resource patches or suitable refuges. In the more heavily grazed field site A, where blue bush refuges were scarcer, lizards had larger home ranges. If home ranges expand in response to reduced resources, parasites that force smaller home ranges could reduce lizard fitness. In sleepy lizards there are overlapping home ranges (Bull 1994), so parasites are unlikely to have a direct influence on territory ownership.

This study found reduced lizard activity following high tick infestation, which would probably reduce lizard fitness. Some of the observed behavioural changes may reflect compensation. Thus, if having a high tick load diminishes sprint speed and endurance, the lizards may bask more and move less to reduce their exposure to predators, and to reduce the need to run fast to avoid them. Nevertheless the results contrast with the previously reported result from surveys of the same population (Bull and Burzacott 1993). In that survey, lizards with high natural tick loads tended to have greater longevity in the population, larger body mass, and greater chance of having a mate than lizards with fewer ticks. Bull and Burzacott (1993) suggested there was spatial heterogeneity in the habitat, and that some places were good lizard habitat but also good tick habitat. In those places, the lizards were fitter, perhaps because of more resources, allowing them to grow bigger, stay longer and gain more mating opportunities. However, they suggested ticks were also fitter there, perhaps because the refuge microhabitats allow greater off-host survival. This could explain the association between successful lizards and high tick load.

The field survey (Bull and Burzacott 1993) suggested that lizards which gain fitness from choosing good habitat may also gain high tick loads from that habitat. The results of the present study show that those high tick loads have fitness costs for the lizards. Thus for the lizards there are costs from tick parasites to balance the benefits of a high-quality habitat. Under the present conditions at Mt. Mary, where tick loads are relatively low (Bull and Burzacott 1993), the balance may favour staying in areas favourable to ticks, because those areas are also good for the lizards. In other regions, where tick densities are higher, the disadvantage from tick parasites may override any advantage from high-quality habitat. This interaction between habitat quality for hosts and parasite prevalence, parallels the more visible interactions in many species between resources and risk from predators. In many other studies predators have been shown to influence the habitat use of prey species profoundly (Dickman 1992; Brabrand and Faafeng 1993; Walls 1995). Parasites may have a similar impact on habitat use of hosts.

Acknowledgements This research was supported by a grant from the Australian Research Council. We are grateful to the land holders in the study area who continued to allow generous access to their properties, particularly the Eberhardt, Jaensch, Rowett, Kleinig and Phillips families.

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