

# Field observations of extended locomotor activity at sub-optimal body temperatures in a diurnal heliothermic lizard (*Tiliqua rugosa*)

Gregory D. Kerr\* and C. Michael Bull

School of Biological Sciences, Flinders University, Adelaide, Australia

(Accepted 17 March 2004)

## Abstract

The behavioural response of the sleepy lizard *Tiliqua rugosa* to an extended drought was examined in spring and summer 2002. Observations of the behaviour and use of microhabitat by radio-tagged lizards for spring in 2000–2002 showed that the lizards in 2002 suffered decreased body mass and increased mortality, were less active, showed reduced mating behaviour and increased use of burrows when compared with the more normal wetter years of 2000 and 2001. The lizards lost significant mass owing to dehydration and starvation. An ‘onboard’ data logger recorded lizard stride frequency and body temperature continuously for 4 months on 11 lizards during the drought of 2002. The normally diurnal heliothermic sleepy lizards responded to rare rainfall events during the drought whenever they occurred, day or night, by emerging from burrows or other shelters for extended periods of activity with sub-optimal body temperatures as low as 8.5 °C. They moved more often, and with higher stride frequencies during periods of rain than during dry periods, both overnight and during the day. As a consequence of this extended activity under physiological stress, the lizards were able to respond to naturally occurring transient opportunities for food and water that would not have been available if they were only active at optimal body temperatures. In an area where freestanding water is rarely available, the lizards were able to access limited water by licking substrate. They also gained water and perhaps nutrition by consuming the temporarily rehydrated thalli of the free-living terrestrial cyanobacterium *Nostoc commune*. Such behaviour enabled lizards to regain much of the mass lost before the rainfall and probably enabled many lizards to survive until more normal food sources became available. These rare events may have a significant effect on the shaping of the sleepy lizards phenotypic capacities outside routine day-to-day activities.

**Key words:** lizard, *Tiliqua rugosa*, rainfall, locomotor activity, *Nostoc commune*, hypothermia

## INTRODUCTION

This paper describes a situation where lizards showed voluntary activity in temperatures well below their normal optimal body temperature. As ectotherms, the activity of lizards is normally limited by dynamic temporal and spatial changes in the physical environment (Huey, 1982). Lizards that thermoregulate tend to be active in the field with body temperatures within a definable range (Hertz, Huey & Garland, 1988; Diaz, 1994) that they effectively control using behavioural means (Bauwens, Hertz & Castilla, 1996; Bauwens, Castilla & Mouton, 1999). There is no single body temperature that is best for every ecological situation (Stevenson, Peterson & Tsuji, 1985) as different physiological and behavioural processes may have different optimal temperatures. Active lizards in the field maintain body temperatures that allow maximal

locomotor performance, but they rarely use that capacity (Van Berkum, Huey & Adams, 1986; Hertz *et al.*, 1988). The rare use of locomotor capacity is analogous to the principle of excessive construction (Gans, 1979). This principle suggests that maintenance of excessive structural and physiological abilities, despite having an energetic cost, has evolved to compensate for the occurrence of rare events that are critical for an animal’s survival (such as threats from predators).

A disadvantage of ectothermy is that individuals cannot always achieve their optimal temperature. At sub-optimal body temperatures, temperature-dependent metabolic support systems strongly limit the behavioural capacities of lizards (Bennett, 1980). For instance, relative locomotor performance decreases with lower body temperature (Bennett, 1980; Huey, 1983; Van Berkum, Huey & Adams, 1986). Often, lizards have low body temperatures at times or in climatic conditions when they are inactive in a refuge (Huey, 1982). However, lizards in temperate zones are sometimes active when their

\*All correspondence to: Greg Kerr.  
E-mail: greg.kerr@flinders.edu.au

body temperatures are sub-optimal for locomotion. Some emerge to bask at low body temperatures, a time when they may be particularly vulnerable to predation (Huey, 1982). This paper describes the Australian sleepy lizard *Tiliqua rugosa* under conditions of food and water stress, emerging to move around and feed with sub-optimal body temperatures when food and water became available for short periods of time.

Our observations followed an extended drought in spring and summer 2002, at our field study site at Mt Mary in South Australia. They provide an insight into rare events that require relatively high levels of endurance at low body temperatures to ensure survival. Small activity-loggers placed on individual lizards measured stride frequency and body temperature every 2 min (Kerr, Bull & Cottrell, 2004) and provided continuous field data on actual lizard movement patterns over the spring–summer period. During the drought there were extended periods without rain when the lizards lost significant mass owing to dehydration and starvation. A few overnight rainfalls provided a transient water source that seemed critical to individual survival. To gain access to briefly available resources, most lizards had to move, sometimes at night, from refuge burrows to the surface. They were then active for extended periods with low body temperatures in physiologically demanding conditions.

The sleepy lizard is a large (snout–vent length (SVL) mean 30 cm), long-lived (Bull, 1995), mainly herbivorous (Henle, 1990; Dubas & Bull, 1991) skink from temperate regions of Australia. It is a posturing heliotherm (Warburg, 1965; Spellerberg, 1972) and is usually diurnally active only when body temperatures are high (Firth & Belan, 1998). The mean body temperature of field-caught active lizards of this species has been reported as 33–35 °C (Light *et al.*, 1966; Wilson, 1974; MacMillen, Augee & Ellis, 1989; Firth & Belan, 1998), with a trend for body temperatures to be slightly higher in the summer than the early spring. Body temperatures of inactive sleepy lizards in winter conform to ambient temperatures (Firth & Belan, 1998). Even in spring when ambient temperatures allow sleepy lizards to achieve optimal temperatures over extended periods, they are rarely active for > 3 h per day (Bull, 1995). The locomotor and energetic capacities of the sleepy lizard describe a relatively slow lizard with limited stamina (John-Alder, Garland & Bennett, 1986). Maximum aerobic scope (MAS) occurs within 1 °C of preferred body temperature (32.6 °C) (Wilson, 1974). This parameter measures the capacity of aerobic metabolism to supply energy for locomotion. At a body temperature of 20 °C, when sleepy lizards will normally emerge to bask, they attain 53% of MAS (Wilson, 1974). At 10 °C sleepy lizards have an average maximum heart rate of 10 beats/min (compared with 100 beats/min at 32 °C) and attain 20% of MAS (Wilson, 1974). At their critical minimum temperature of 4.5 °C (Spellerberg, 1972), sleepy lizards are unable to sustain coordinated movement.

During our study an extended dry period over spring and summer 2002 resulted in the sleepy lizard population at Mt Mary becoming stressed as a result of dehydration and starvation. Under these conditions it was found that they respond to naturally occurring opportunities for food and

**Table 1.** Records of rainfall at Bunday Bore during August–December 2002

Date	Rainfall (mm)
4 Aug	2.3
7 Sep	0.8
16 Sep	4.9
3 Oct	0.1
23–24 Oct	1.1
2 Nov	0.1
11 Nov	0.1
23–26 Nov	9.5
6 Dec	3.5
31 Dec	2.5

water at extremely low body temperatures. The unusually dry conditions of 2002 and the rare rainfall events are described. The declining condition and reduced activity of lizards in this season, and their ability to restore rapidly some of that condition following rain are documented. Enhanced activity during and following rain in conditions normally expected to be sub-optimal for lizard activity are also documented.

## MATERIALS AND METHODS

The study site (33°55'S, 139°21'E) was a 50 ha plot within the previously described Mt Mary study area (Kerr, Bull & Burzacott, 2003) about 5 km south of the Bunday Bore Homestead in the mid-north of South Australia. The habitat is semi-arid chenopod shrubland dominated by the bluebush *Maireana sedifolia*. Mean rainfall from 1970 to 1997 at Bunday Bore Station was 287 mm/year. In 2000 and 2001 rainfall at Bunday Bore Station was 227 mm and 224 mm. The area has an average 101 mm of rain in August–December, which normally sustains growth of the annual plants that the lizards feed on over that period. These warm months of spring and early summer are the period of maximum activity of sleepy lizards in this area. As the hot dry summers progress, most annual vegetation dries off, and becomes unavailable as lizard food by mid-December in most years.

To explore whether lizards behaved differently under extreme stress, the requirements for unusual behaviour were first established. 2002 was an unusually dry year with only 81 mm rainfall at Bunday Bore and only 25 mm during August–December. There were only 7 rain events yielding 0.1 mm or more of rainfall recorded over that 5-month period (Table 1), and there were long dry spells between them.

By 15 October 2002, no living annual plants could be found in the study site, and subsequent rain events produced no new flush of growth to provide food for the lizards. One potential food species in the area did respond, however, to rainfall even after prolonged dry spells. This was the free-living terrestrial chlorophyllic cyanobacterium *Nostoc commune* (Vaucher). *Nostoc commune* has a worldwide distribution and exhibits oxygenic photosynthesis and nitrogen fixation (Dodds, Gudder & Mollenhauer, 1995). Macroscopic colonies of

this cyanobacterium can remain desiccated for years, and can fully recover metabolic activity soon after rehydration with liquid water. Although most *Nostoc* species produce a variety of toxins, they may represent an important source of nutrients and water for animals that can consume them, particularly where free-standing water is scarce (Dodds *et al.*, 1995). The use of this food source during drought by sleepy lizards, and any modifications of their behaviour to take advantage of the brief availability of hydrated *Nostoc* following rain was investigated.

To achieve this, account was taken of all possible rainfall events at the study site, which is located in a rain shadow area to the east of the northern Mt Lofty Ranges. As a consequence, rainfall in this area is generally sporadic in location and highly variable in quantity, often within short distances. Thus rainfall at the study site may not have been recorded at Bunday Bore Station 5 km to the north. The Commonwealth Bureau of Meteorology analysis chart archive was used to determine the timing of movement of cold fronts and low pressure systems and any corresponding rainfall events across the general study area using the 6-hourly mean sea level pressure analyses charts for the Australian region (<http://www.bom.gov.au/nmoc/MSL/>). These data were used in combination with daily rainfall records from Sutherlands (27 km SSW of the study site), 4- to 6-hourly rainfall records from Eudunda (36 km SW of the study site) and daily rainfall records from Bunday Bore Station homestead (5 km N of the study site) to identify the timing of all rainfall events and possible rainfall events in the overall region during 16 August 2002 to 26 December 2002.

Rainfall events at the study site were then categorized as:

- definite rain*, when rainfall was known to have occurred at the study site or nearby;
- possible rain*, when rainfall was recorded at one of the weather stations but was not evident at the study site and could not be verified;
- definite dry*, days on which rain did not fall.

These categories were subsequently used when lizard movement patterns were analysed.

### Stress from drought in 2002

Lizard condition and behaviour in the dry season in 2002 were compared with the 2 prior but more normal years to determine if the drought conditions seemed to stress the lizards. Two indicators of stress were used: reduced body mass and changes in behaviour. The data used came from radio-tagged adult lizards that were monitored over 3 field seasons; August–December 2000 (30 lizards), 2001 (30 lizards) and 2002 (50 lizards). A 3.6 g radio transmitter (Sirtrack, New Zealand) was attached to the lateral surface of the tail of each lizard with surgical adhesive tape, and the lizards were located over the season using a TR-4 receiver (Teletonics, AZ, U.S.A.) with a 3-element Yagi antenna. Each lizard was normally located and weighed once per fortnight, except in 2002 when some lizards were

down wombat burrows for long periods of time and were inaccessible.

To examine the impact of drought on lizard mass, changes in mass were investigated as the season progressed in 2001 (the normal year), and 2002 (the drought year). For 9 lizards, data on average mass were obtained for each month from August to December in both years. All data were normally distributed. Repeated measures ANOVA was used to compare the average monthly weights among years, with both month and year as within-subject factors. The conservative Greenhouse-Geisser method was used to adjust for violation of sphericity in this and all subsequent repeated-measures analyses. It was expected that an indication of unusual stress in 2002 would be detected through a significant interaction between month and year in the analysis.

The second set of indicators of stress was drawn from observations of behaviour on up to 7 locations of each lizard over 4 days each week in each of the 3 field seasons, 2000–2002. First, the proportion of observations in a month when an individual lizard was active when observed in 2001 and 2002 was recorded. Lizards were considered to be active if they were found either moving, or stationary but stretched out (Kerr, Bull & Burzacott, 2003). Only lizards curled up, usually under some shelter, or located within a rabbit or wombat burrow, were classed as inactive (Kerr *et al.*, 2003). Data were obtained for 19 lizards on the proportion of observations in which lizards were active for each month from September to November in each year (mean number of observations per lizard per month = 13.0, SE = 5.6). All datasets were normally distributed. A repeated-measure ANOVA was used to compare the arcsine-transformed (Zar, 1999) proportions of observations in which lizards were active, among months and years. It was expected that more inactivity among lizards in the drought year would be recorded if drought caused stress.

Second, the proportion of lizards forming pairs in each month in each of the 3 field seasons, 2000–2002 was recorded. Sleepy lizards are monogamous both within and between years. In September and October of each year they form pairs and remain in close contact for an average of 6–8 weeks (Bull, McNally & Dubas, 1991; Bull, Cooper & Baghurst, 1998) before mating in late October or early November (Bull, McNally *et al.*, 1991). A pair was defined as a male and female within 0.5 m of each other (Bull, 1988; Bull, McNally *et al.*, 1991; Bull, Bedford & Schulz, 1993). Data were obtained for 21 lizards on the proportion of observations in which lizards were paired for each month from September to November in each year (mean number of observations per lizard per month = 14.7, SE = 0.5). All datasets were normally distributed. A repeated-measure ANOVA was used to compare the arcsine-transformed proportions of observations in which lizards were paired, among months and years. Less pairing among lizards was expected to be recorded in the drought year if drought caused stress.

The number of observations of lizards in burrows each month, over 3 seasons, 2000–2002 were also recorded. Data were obtained for 19 lizards on the proportion of observations (mean observations per lizard

per month = 15.0, SE = 7.2) in which the microhabitat that the lizards occupied was underground for each month from September to November in the 3 years. Again a repeated-measure ANOVA was used to compare arcsine-transformed proportions of observations down burrows, among months and years.

## Response to rain in 2002

### *Changes in mass and burrow use following a rainfall event*

Repeat measures of mass were obtained in the week before and the week after rainfall for 17 lizards when it rained on 23–26 November 2002 (9.5 mm), and for 14 lizards when it also rained on 20–21 February 2003 (55 mm). Lizard masses were compared either side of these high-rainfall events using paired *t*-tests. The underlying distributions of differences in all pairwise comparisons were normal. Our interest was how lizard mass changed immediately following rainfall events. Any mass gain was attributed to the uptake of water or the consumption of food that became available with the onset of rain.

For the November rainfall event, proportions of observations in which lizards were using burrows in the 2 weeks before and the 2 weeks following the rainfall event were also compared. Arcsine-transformed proportions of observations down burrows were compared either side of this high rainfall event using a paired *t*-test.

### *Movement patterns associated with rainfall events*

Stride frequency was used to compare daytime and nighttime activity of lizards during dry periods and rainfall events in 2002. Any modifications of the behaviour of lizards in response to water and food becoming available with rain were examined.

Stride frequency was monitored continuously for 10 individual radio-tagged lizards from 16 August to 26 December 2002 using lightweight (11.8 g) activity-loggers (Kerr *et al.*, 2004). The combined mass of the radio-transmitter and activity-logger represented 2.9% body mass of an average lizard. The loggers measured  $27.5 \times 27.5 \times 12.0$  mm, and were attached with surgical adhesive tape to the dorsal surface of the tail. They recorded the body surface temperature of the lizard under the logger (highly correlated with internal body temperature; Chilton & Bull, 1992) every 2 min, and the number of strides taken by the lizard over the previous 2 min (Kerr *et al.*, 2004).

One tagged lizard with an activity-logger attached was struck by a car and died in October. It was replaced in the survey, so most analyses used data from 11 lizards.

The average number of strides/2 min for each lizard was used to test whether lizard activity differed during definite rain and definite dry periods. To avoid bias from observer disturbance, all activity data for 1 h following any approach by a researcher were omitted.

Each 24 h period was divided into day (06:00–19:59) and night (20:00–05:59). Data were considered from

8 days and 10 nights when there was definite rain, and 124 days and 105 nights when it was definitely dry. Periods of possible rain when it may or may not have rained at the study site were omitted.

Natural log-transformed average stride frequency/2 min for each lizard ( $n = 11$ ) were calculated for each time (day or night) and weather (rain or dry) category. For each lizard, movement was also defined as when 1 or more strides were taken in a 2-min interval, and the arcsine-transformed average proportion of 2-min intervals in which movement occurred for each lizard ( $n = 11$ ) were determined for each time and weather category.

Repeated-measures ANOVA were used on each of these parameters to investigate the influence of the within-subjects factors, time and weather, on lizard activity.

## Body temperature and movement

Data were then analysed to examine whether lizards were likely to be active at cooler body temperatures in rain periods than in dry periods. Whether each lizard was stationary or moving was determined for each 2-min interval. Surface body temperature was averaged for each lizard ( $n = 11$ ) for each movement category (stationary or moving), for each weather category (rain or dry) and for each time category (day or night). Data were normalized by a natural log-transformation. A repeated-measure ANOVA was used to compare average body temperature with time, weather and movement as within-subject factors.

## Food consumption associated with rainfall events

Sleepy lizards retain recently consumed food in their mouths (Bull & Pamula, 1998). Radio-tracked lizards that were active were briefly held and their mouths examined for food on 1859 occasions during 2000–2002. On 544 of these occasions, lizards were found to have food in their mouths. In 28 lizards more than 1 type of food was in the mouth and in 63 lizards the food type could not be identified. In all other lizards, the single food type in the mouth was recorded.

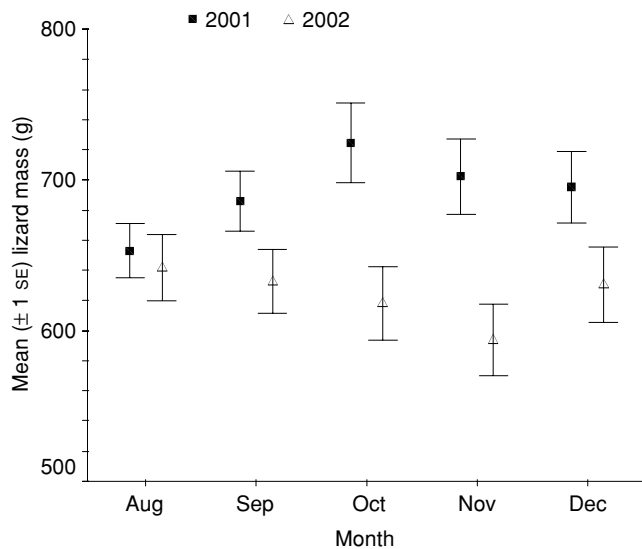
Additional lizards were sampled by random encounter captures along road transects around the study area on 1 day/week for 15 weeks in spring 2002. Two of these days (16 September and 25 November) coincided with rainfall events. The food in the mouth of each lizard was identified.

Both sets of dietary data were analysed to determine whether any changes occurred at the time of rain.

## Response of *Nostoc thalli* to hydration

To determine the volume of water held following hydration with rain, 10 *Nostoc commune* thalli were used. The hydrated thalli were collected from the field and then left to dry for up to 33 months. They were each weighed,





**Fig. 1.** Change in (mean  $\pm$  SE) lizard *Tiliqua rugosa* mass (g) from August to December for the 2001 and 2002 field seasons.  $n = 9$ .

rehydrated by immersion in distilled water for 60 min, then reweighed to determine water uptake.

## RESULTS

### Stress from drought in 2002

Of the 50 lizards radio-tracked in spring and summer 2002, 10 died from natural causes before the end of the year. This compares with one (out of 30) in 2001 and none (out of 30) in 2000, and represents a significant increase in mortality ( $\chi^2 = 10.19$ ; d.f. = 1,  $P < 0.01$ ).

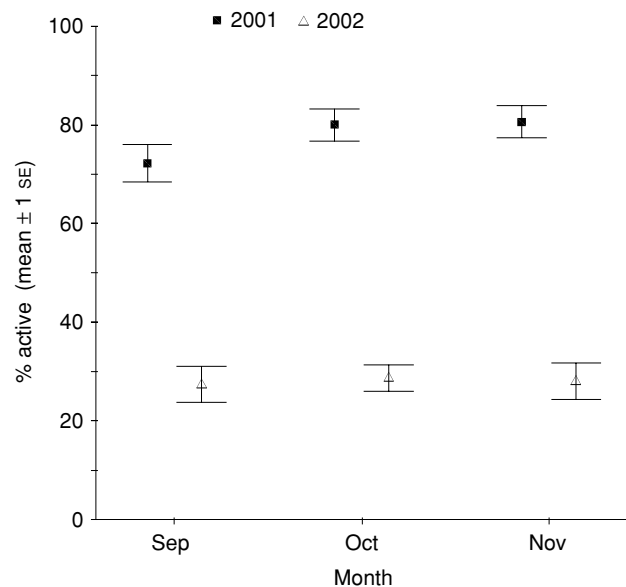
Sleepy lizards normally undergo ecdysis, shedding their external skin layer once a year during December–March. This process may be restricted by water availability (Shea, 1980). In 2002–2003 only seven of 30 lizards had shed their skin by the end of April 2003.

### Changes in mass between seasons

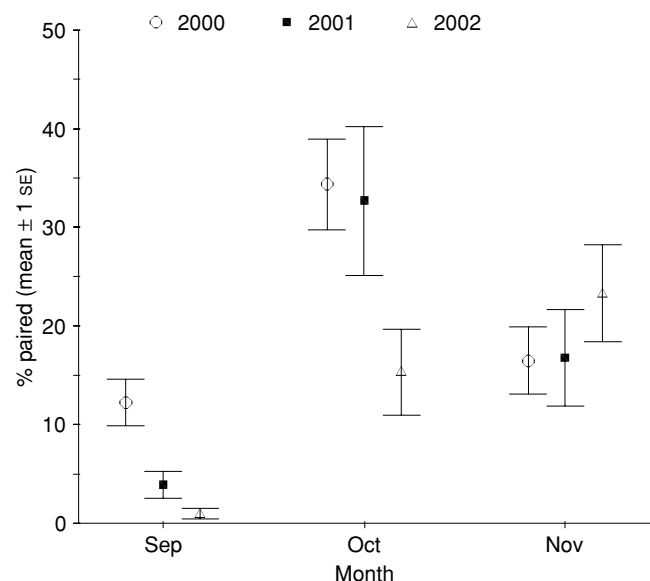
The repeated-measure ANOVA showed that lizard mass varied significantly between both months ( $F_{2,0,16.1} = 4.78$ ,  $P = 0.023$ ) and years ( $F_{1,8} = 23.19$ ,  $P = 0.001$ ). The same lizards were significantly lighter in 2002 than in 2001. There was also a significant interaction between month and year ( $F_{4,32} = 14.61$ ,  $P < 0.001$ ). In August of both years, average lizard mass was approximately equal (Fig. 1). In 2001 the lizards steadily gained mass in September and October, but in 2002 they steadily lost mass over the same period.

### Changes in activity levels, pairing behaviour and microhabitat use

The repeated-measure ANOVA showed that the proportion of lizards observed active in 2002 was significantly lower than in 2001 ( $F_{1,18} = 352.9$ ,  $P < 0.001$ ) (Fig. 2). There was



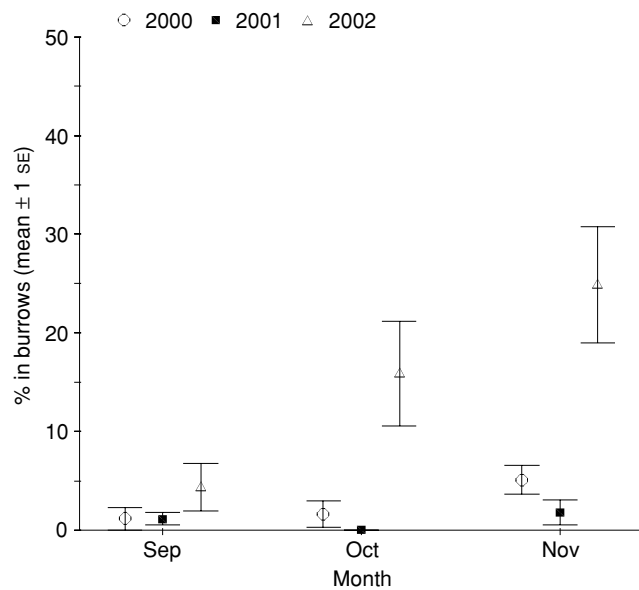
**Fig. 2.** Proportion of observations (mean  $\pm$  SE) on which lizards *Tiliqua rugosa* were found active in each month of 2001 and 2002.  $n = 19$ .



**Fig. 3.** Proportion of observations (mean  $\pm$  SE) on which lizards *Tiliqua rugosa* were found paired in each month of 2000, 2001 and 2002.  $n = 21$ .

no significant effect of month ( $F_{2,36} = 1.32$ ,  $P = 0.279$ ) and no significant interaction effect between month and year ( $F_{2,36} = 0.45$ ,  $P = 0.249$ ).

The proportion of lizards forming pairs (Fig. 3) varied significantly among years ( $F_{2,40} = 3.97$ ,  $P = 0.027$ ) and there was a significant effect of month ( $F_{2,40} = 28.21$ ,  $P < 0.001$ ). Lizards were found in pairs more frequently in October than in September or November. They formed pairs less frequently in 2002 than in 2000 or 2001. The significant interaction effect between month and year ( $F_{2,50,50.1} = 4.25$ ,  $P = 0.013$ ) reflected the normal peak of



**Fig. 4.** Proportion of observations (mean  $\pm$  SE) on which lizards *Tiliqua rugosa* were found in burrows each month of 2000, 2001 and 2002.  $n = 19$ .

pairing behaviour in October of 2000 and 2001, relative to the consistently low levels of pairing in 2002.

The proportion of lizards in burrows (Fig. 4) varied significantly among years ( $F_{2,36} = 14.71$ ,  $P < 0.001$ ) and

there was a significant effect of month ( $F_{1,47,26.4} = 34.74$ ,  $P < 0.001$ ). Lizards used burrows more frequently later in spring than earlier, and more frequently in 2002 than in 2000 or 2001. The significant interaction effect between month and year ( $F_{4,72} = 3.31$ ,  $P = 0.015$ ) showed the proportion occupying burrows increased more in late spring 2002 than in either 2000 or 2001.

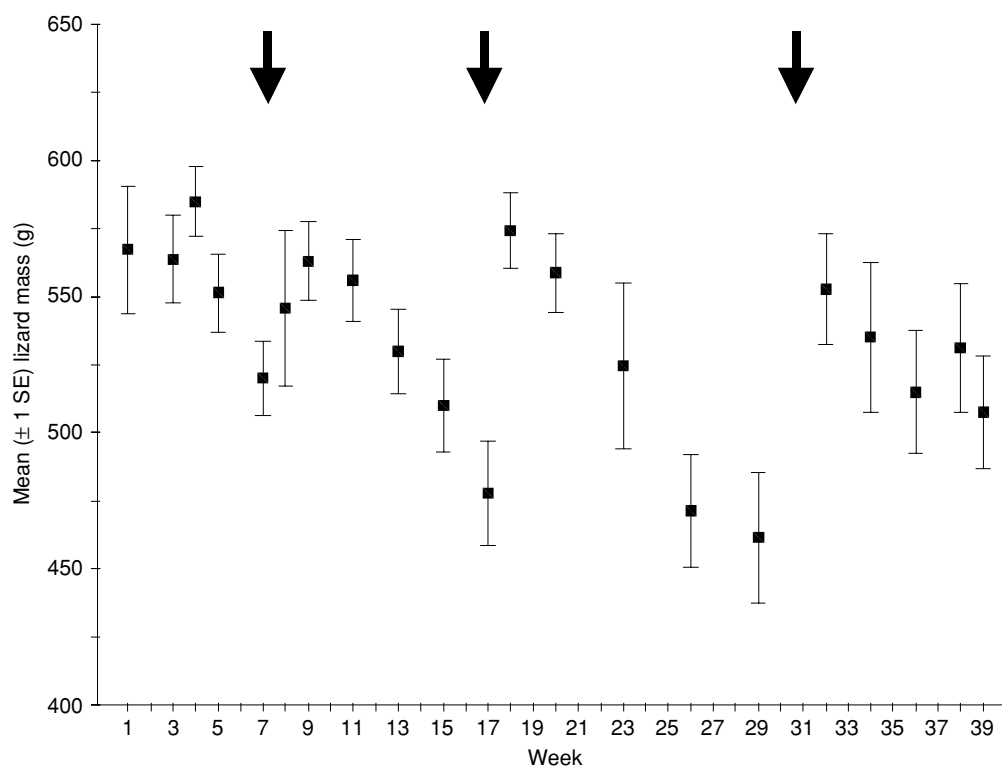
All three indicators of decreased activity, decreased pair formation and increased use of burrows in 2002 relative to previous years, imply higher stress for the lizards in 2002.

### Response to rain in 2002

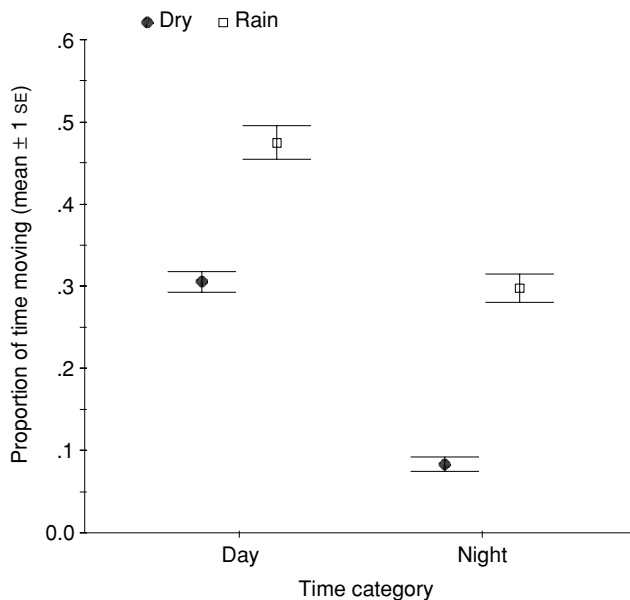
#### *Changes in mass and burrow use following a rainfall event*

Rainfall led to an immediate and significant increase in lizard mass in both November 2002 (paired  $t$ -test:  $t_{16} = 8.61$ ,  $P < 0.001$ ) and February 2003 (paired  $t$ -test:  $t_{13} = 5.61$ ,  $P < 0.001$ ) (Fig. 5). No new green food became immediately available for lizards after rain. Observed weight gains may have resulted from direct uptake of water or from consumption of hydrated *Nostoc*.

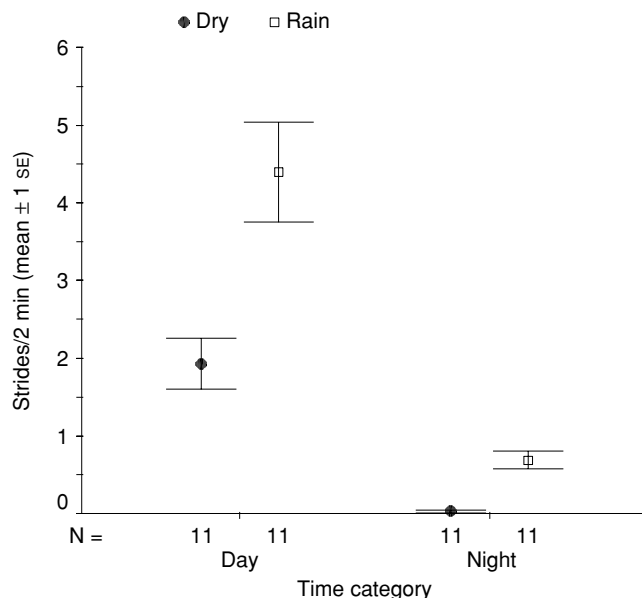
In November 2002 there was a significantly lower proportion of observations of lizards in burrows in the 2 weeks following rain (mean = 0.7%, SE = 0.5%) than in the 2 weeks before rain (mean = 17.3%, SE = 3.6%) (paired  $t$ -test:  $t_{44} = 5.09$ ,  $P < 0.001$ ).



**Fig. 5.** Change in (mean  $\pm$  SE) lizard *Tiliqua rugosa* mass (g) over 39 weeks from 29 July 2002 to 27 April 2003. Arrows, timing of three main rainfall events (15 September 2002, 23–25 November 2002, 19–21 February 2003).  $n$  varies between 10 and 20 depending on proportion of lizards occupying burrows in a week.



**Fig. 6.** Proportion (mean  $\pm$  SE) of 2-min intervals in which movement occurred for each lizard *Tiliqua rugosa* ( $n = 11$ ) for each time category (day 06:00–19:59; night 20:00–05:59) for each weather category (rain or dry). Movement is defined as when one or more strides were taken in a 2-min interval.



**Fig. 7.** Mean ( $\pm$  SE) stride frequency (strides/2 min) for each lizard *Tiliqua rugosa* ( $n = 11$ ) for each time category (day 06:00–19:59; night 20:00–05:59) for each weather category (rain or dry).

#### Movement patterns associated with rainfall events

In 2002, sleepy lizards on average moved significantly more often (Fig. 6), and at a significantly higher stride frequency (Fig. 7) during periods with rain than they did during dry weather in both day and night (Table 2). Night-time activity was always significantly lower than daytime activity (Table 2), but there was a significant interaction

**Table 2.** Results of repeated-measures ANOVA analyses comparing activity parameters (natural log-transformed stride frequency and arcsine-transformed proportion of time moving) for lizards at different times of the day (day or night) in different weather conditions (rain or dry).  $n = 11$  lizards

Factor	d.f.	Stride frequency		Proportion of time moving	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Time of day (T)	1, 10	131.4	< 0.001	197.9	< 0.001
Weather (W)	1, 10	60.9	< 0.001	115.1	< 0.001
T $\times$ D	1, 10	2.3	0.163	5.8	0.035

**Table 3.** Results of repeated-measures ANOVA analyses comparing natural-log transformed average body temperature for sleepy lizard movement (moving or stationary) at different times of the day (day or night) in different weather conditions (rain or dry).  $n = 11$  lizards

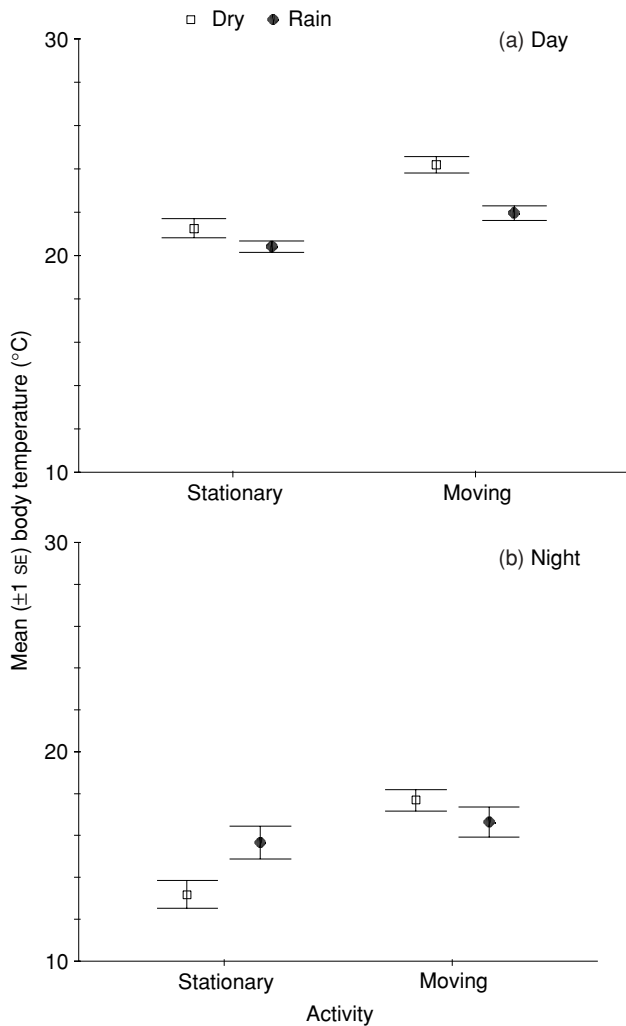
Factor	d.f.	Body temperature	
		<i>F</i>	<i>P</i>
Time (T)	1, 10	140	< 0.001
Weather (W)	1, 10	0.26	0.623
Movement (M)	1, 10	106	< 0.001
T $\times$ W	1, 10	26.5	< 0.001
T $\times$ M	1, 10	20.6	< 0.001
W $\times$ M	1, 10	39.7	< 0.001
T $\times$ W $\times$ M	1, 10	60.7	< 0.001

effect between time and weather for the proportion of 2-min time blocks in which lizards were moving. The response, to increase activity during rain periods, was greater at night than in the day (Fig. 6).

#### Body temperature and movement

There was no significant effect of weather on the overall average body temperature of sleepy lizards (Table 3). However lizards had significantly higher body temperatures in the day than at night and when moving than when stationary (Table 3, Fig. 8).

There was a highly significant three-way interaction between time, weather and movement. Even though body temperatures were on average lower at night, lizards when moving were warmer than when stationary. But, the difference in body temperature between stationary and moving lizards was greater at night than during the day in dry weather. This was not evident during wet weather. The larger difference between day and night lizard body temperatures on dry days than on rain days is expected from ambient conditions. Rain days, with cloud cover, led to cooler days and warmer nights. During the day, lizards moved at lower body temperatures in rain periods (mean = 22.0 °C, SE = 0.34) than in dry periods (mean = 24.2 °C, SE = 0.38). But this difference was not as marked at night (rain: mean = 16.7 °C, SE = 0.72; dry mean = 17.7 °C, SE = 0.52). On wet nights lizards moved often and their body temperatures were on average only



**Fig. 8.** Mean ( $\pm$  SE) lizard *Tilapia rugosa* body temperature ( $^{\circ}$ C) for each level of activity (stationary or moving) for each weather category (rain or dry) for each time category: (a, day; b, night) between 16 August and 26 December 2002. Movement is defined as when one or more strides were taken in a 2-min interval.  $n = 11$  lizards.

slightly warmer when moving than when stationary. In contrast, sleepy lizards moved infrequently on dry nights and when they did move their average body temperature was markedly higher than when they were stationary.

The tendency for lizards to move at low body temperatures on nights with rain, and to be more active on days of rain or immediately following rain is illustrated by records from 3 days around one rainfall event on 15–16 September (Fig. 9).

#### Food consumption associated with rainfall events

Sleepy lizards fed predominantly (87% of observations of radio-tracked lizards with food in their mouths) on flowers and fruit of native and exotic annual plant species. The composition of this diet varied between and within seasons depending on what species were flowering.

*Nostoc commune*, usually multiple thalli in each lizard's mouth, made up 10.4% of all observations of lizards with food in their mouths. Only hydrated thalli of *Nostoc* were observed. On a day after rain, one lizard was observed searching for and eating *Nostoc* with its neck strongly arched, snout pointing at an angle  $\sim 40^{\circ}$  to the substrate, and with frequent tongue flicking of the ground.

*Nostoc* was found in the mouths of lizards on 17 out of 190 days on which lizards were tracked and was strongly associated with rainfall events (84% of 57 observations within 24 h of verified rain). On nine rain days, an average 88.9% (SE = 5.2) of feeding lizards were observed to have ingested *Nostoc*.

During the road surveys in 2002, *Nostoc* was recorded in the mouths of sleepy lizards only on the two rainfall days. On 16 September some green plant material was still available along road verges for the lizards and *Nostoc* was found in mouths of 46% of 26 feeding lizards. By 25 November green plant material was sparsely distributed along road verges and 81% of feeding lizards had *Nostoc* in their mouths.

#### Response of *Nostoc* thalli to hydration

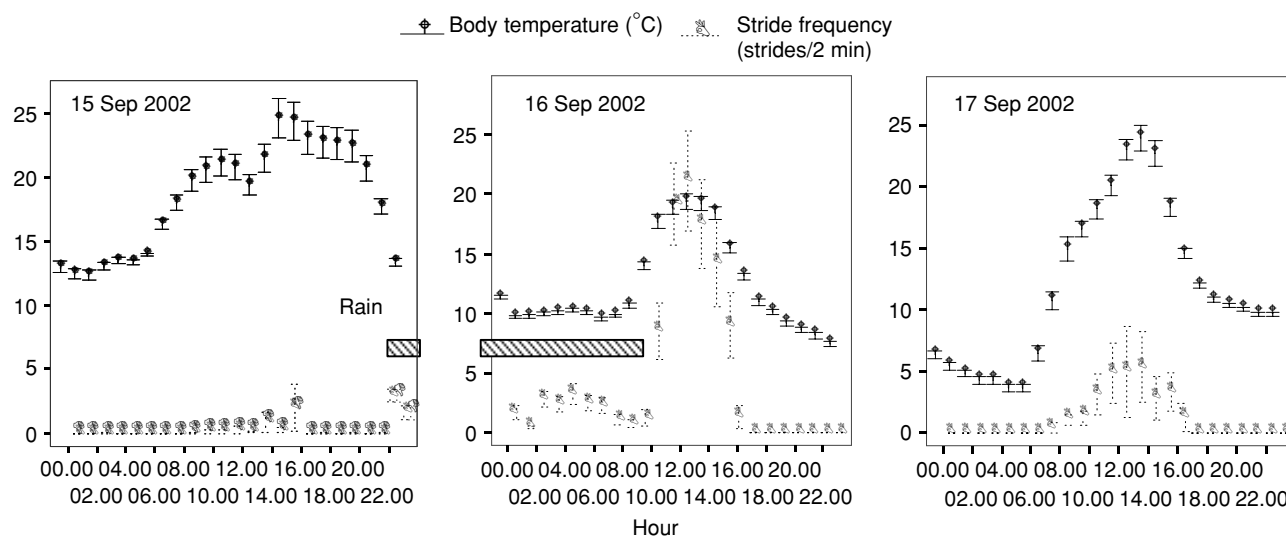
Individual thalli with a dry mass ranging from 0.006 to 0.032 g increased mass on hydration by an average of 472%, with water constituting an average of 74% of their rehydrated mass. Within 2 days, in the laboratory, the thalli had dried out again.

#### DISCUSSION

The extreme drought of 2002 resulted in sleepy lizards suffering decreased body mass and increased mortality, presumably from lack of food (and associated water). The high physiological stress levels induced by the drought were associated with changes in behaviour, such as decreased levels of activity and pair formation and increased use of burrows, when compared with behaviour in previous years with higher rainfall. Stamps (1976) reported similar low levels of activity in the lizard *Anolis aeneus* during extended drought periods.

During rainfall, *Nostoc commune* rapidly hydrates. In an area where rainfall events can be brief and there is little freestanding water available, the opportunity to obtain water from the substrate is limited. Under such circumstances *Nostoc* thalli are consumed by lizards and may provide an important source of water and possibly nutrition for 1 or 2 days beyond the rainfall event. Consumption of water directly from the substrate, and indirectly through *Nostoc* resulted in a significant and rapid increase in lizard body mass. In the drought conditions of 2002, these rainfall events provided an important transient resource, probably enabling many lizards to survive until normal food sources became available again. The question as to whether *Nostoc* only provides water or provides nutrition as well, requires further investigation.





**Fig. 9.** Mean ( $\pm$  SE) lizard *Tiliqua rugosa* stride frequency (strides/2 min) and mean ( $\pm$  SE) body temperature ( $^{\circ}$ C) each h for the 3 days spanning a rainfall event from  $\sim$ 22:00 15 September 2002 to  $\sim$ 09:00 16 September 2002.  $n = 10$  lizards. Error bars, mean  $\pm 1$  SE.

*Nostoc* is exploited extensively by the sleepy lizards when available. But this resource is available only for a brief period following rain on days that are usually overcast and relatively cold. During such days there is little chance for lizards to bask in order to achieve normal optimal body temperatures. If the rainfall event occurs overnight, the body temperatures of lizards are restricted to ambient temperatures.

Despite these strictures, sleepy lizards responded to rainfall events whenever they occurred in the day or night by emerging from burrows or other shelters for extended periods of activity, usually with sub-optimal body temperatures. During the colder overnight rainfall events they were active at body temperatures in the range  $8.5\text{--}17^{\circ}\text{C}$ , which strongly compromised both their physiological and behavioural responses.

The ability of lizards to respond effectively under such conditions and to obtain sufficient water and possibly nutrition has strong implications for the survival of individuals. The ability to survive an extended period without water and nutrients will depend greatly on the lizard's ability to obtain sufficient resources in the brief window of time when they are available.

Long-term studies of sleepy lizards in the Mt Mary area using both road surveys and radio-tags have indicated that sleepy lizards normally confine their activity to conditions when they can achieve high body temperatures (Firth & Belan, 1998). However, in the drought year of 2002, they responded with relatively high levels of activity in sub-optimal conditions while under high levels of physiological stress. This allowed lizards to obtain the nutrients and water necessary to survive extended periods of deprivation. These resources would not have been available to lizards that were only active at optimal body temperatures. This may be analogous to the principle of excessive construction as proposed by Gans (1979) and further expanded upon by Hertz *et al.* (1988).

The behavioural response of emerging from deep within burrows, in sub-optimal conditions, at the start of rainfall events, seems to be adaptive because the transient resources of water on substrate and *Nostoc* must be obtained while available. The ability to respond to these rare but highly selective events may be critical for the survival of an individual sleepy lizard. Such rare events may produce significant impetus in the shaping of the phenotypic capacities of sleepy lizards outside routine day-to-day activities. As relative locomotor performance is correlated across body temperatures in lizards (Bennett, 1980) then activity at low body temperatures may lead to a capability for very high levels of locomotor performance at body temperatures operative in normal field conditions in the sleepy lizard.

It is probable that this flexible behavioural response to unpredictable rainfall events during extensive drought has evolved allowing this species to persist in the semi-arid regions of Australia where droughts frequently occur.

### Acknowledgements

We thank Ron and Leona Clark for giving us access to their land and use of the homestead at Bunday Bore Station, and Geoff Cottrell for ongoing maintenance of the data loggers. Karin Hegetschweiler, Zeta Steen, Des Sinnott and Ron Reid helped with field observations. Thanks to David Catcheside and Monika Ehling-Schulz for confirming identification of *Nostoc commune*. The study was conducted according to the guidelines of the Flinders University Animal Welfare Committee in compliance with the Australian Code of Practice for the use of animals for scientific purposes. Research was funded by the Australian Research Council and The Nature Foundation.

## REFERENCES

- Bauwens, D., Castilla, A. M. & Mouton, P. L. F. N. (1999). Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard (*Cordylus macropholis*). *J. Zool. (Lond.)* **249**: 11–18.
- Bauwens, D., Hertz, P. E. & Castilla, A. M. (1996). Thermoregulation in a lacertid lizard: the relative contributions of distinctive behavioural mechanisms. *Ecology* **77**: 1818–1830.
- Bennett, A. F. (1980). The thermal dependence of lizard behaviour. *Anim. Behav.* **28**: 752–762.
- Bull, C. M. (1988). Mate fidelity in an Australian lizard *Trachydosaurus rugosus*. *Behav. Ecol. Sociobiol.* **23**: 45–49.
- Bull, C. M. (1995). Population ecology of the sleepy lizard, *Tiliqua rugosa*, at Mt Mary, South Australia. *Aust. J. Ecol.* **20**: 393–402.
- Bull, C. M., Bedford, G. S. & Schulz, B. A. (1993). How do sleepy lizards find each other? *Herpetologica* **49**: 294–300.
- Bull, C. M., Cooper, S. J. B. & Baghurst, B. C. (1998). Social monogamy and the extra-pair fertilization in an Australian lizard, *Tiliqua rugosa*. *Behav. Ecol. Sociobiol.* **44**: 63–72.
- Bull, C. M., McNally, A. & Dubas, G. (1991). Asynchronous seasonal activity and male and female sleepy lizards, *Tiliqua rugosa*. *J. Herpetol.* **25**: 436–441.
- Bull, C. M. & Pamula, Y. (1998). Enhanced vigilance in monogamous pairs of the lizard, *Tiliqua rugosa*. *Behav. Ecol.* **9**: 452–455.
- Chilton, N. B. & Bull, C. M. (1992). The on-host temperature environment for two Australian reptile ticks. *Aust. J. Zool.* **40**: 583–592.
- Diaz, J. A. (1994). Field thermoregulatory behaviour in the Western Canadian lizard *Gallotia galloti*. *J. Herpetol.* **28**: 325–333.
- Dodds, W. K., Gudder, D. A. & Mollenhauer, D. (1995). The ecology of *Nostoc*. *J. Phycol.* **31**: 2–18.
- Dubas, G. & Bull, C. M. (1991). Diet choice and food availability in the omnivorous lizard, *Trachydosaurus rugosus*. *Wildl. Res.* **18**: 147–155.
- Firth, B. T. & Belan, I. (1998). Daily and seasonal rhythms in selected body temperature in the Australian lizard *Tiliqua rugosa* (Scincidae): field and laboratory observations. *Physiol. Zool.* **71**: 303–311.
- Gans, C. (1979). Momentarily excessive construction as the basis for protoadaptation. *Evolution* **33**: 227–233.
- Henle, K. (1990). Notes on the population ecology of the large herbivorous lizard, *Trachydosaurus rugosus*, in arid Australia. *J. Herpetol.* **24**: 100–103.
- Hertz, P. E., Huey, R. B. & Garland, T. Jr (1988). Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? In *Energetics and animal behaviour*, **28**: 927–938. Nashville, TN: American Zoologist.
- Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In *Physiology C: physiological ecology* **12**: 25–91. Gans, C. & Pough, F. H. (Eds). London: Academic Press.
- Huey, R. B. (Ed.) (1983). *Natural variation in body temperature and physiological performance in a lizard (Anolis cristatellus)*. Cambridge, MA: Museum of Comparative Zoology, Harvard University.
- John-Alder, H. B., Garland, T. & Bennett, A. F. (1986). Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingle-back lizard (*Trachydosaurus rugosus*). *Physiol. Zool.* **59**: 523–531.
- Kerr, G. D., Bull, C. M. & Burzacott, D. (2003). Refuge sites used by the scincid lizard *Tiliqua rugosa*. *Aust. Ecol.* **28**: 152–161.
- Kerr, G. D., Bull, C. M. & Cottrell, G. R. (2004). Use of an 'on board' datalogger to determine lizard activity patterns, body temperature and microhabitat use for extended periods in the field. *Wildl. Res.* **31**: 171–176.
- Light, P., Dawson, W. R., Shoemaker, V. H. & Main, A. R. (1966). Observations on the thermal relations of Western Australian lizards. *Copeia* **1**: 97–110.
- MacMillen, R. E., Augee, M. L. & Ellis, B. A. (1989). Thermal ecology and diet of some xerophilous lizards from western New South Wales. *J. arid Environ.* **16**: 193–201.
- Shea, G. M. (1980). Notes on ecdysis in *Tiliqua rugosa* (Gray). *Herpetofauna* **12**: 32–33.
- Spellerberg, I. F. (1972). Temperature tolerances of southeast Australian reptiles examined in relation to reptile thermoregulatory behaviour and distribution. *Oecologia (Berl.)* **9**: 23–46.
- Stamps, J. A. (1976). Rainfall, activity and social behaviour in the lizard, *Anolis aeneus*. *Anim. Behav.* **24**: 603–608.
- Stevenson, R. D., Peterson, C. R. & Tsuji, J. S. (1985). The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiol. Zool.* **58**: 46–57.
- Van Berkum, F. H., Huey, R. B. & Adams, B. A. (1986). Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* **59**: 464–472.
- Warburg, M. R. (1965). The influence of ambient temperature and humidity on the body temperature and water loss from two Australian lizards, *Tiliqua rugosa* (Gray) (Scincidae) and *Amphibolurus barbarus* Cuvier (Agamidae). *Aust. J. Zool.* **13**: 331–350.
- Wilson, K. J. (1974). The relationship of oxygen supply for activity to body temperature in four species of lizards. *Copeia* **1974**: 920–934.
- Zar, J. H. (1999). *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice-Hall.