

# Selected body temperature, metabolic rate and activity pattern of the Australian fossorial skink, *Saiphos equalis*

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Fossorial and nocturnal lizards have limited opportunities to thermoregulate because they do not have access to basking opportunities, which has implications for their thermal physiology and metabolism. We measured substrate temperatures ( $T_s$ ) in the field, and selected body temperatures ( $T_b$ ) and metabolic rates in the laboratory, in fossorial skinks, *Saiphos equalis*, to quantify basic aspects of their thermal and metabolic physiology. *Saiphos equalis* selects relatively cool temperatures over a broad range (approximately 17–24 °C), suggesting that it does not thermoregulate precisely. Individuals of *S. equalis* are active more often at night than during the day. Rate of oxygen consumption was measured at 2 °C intervals from 10–30 °C in adult lizards. Metabolic rate increased as a function of temperature but there was no significant difference in  $\dot{V}O_2$  over the preferred temperature range. Like many other fossorial lizards, *S. equalis* is nocturnal and selects relatively low body temperatures compared to heliothermic lizard species.

*Key words:* metabolism, nocturnal lizard, oxygen consumption, thermoregulation

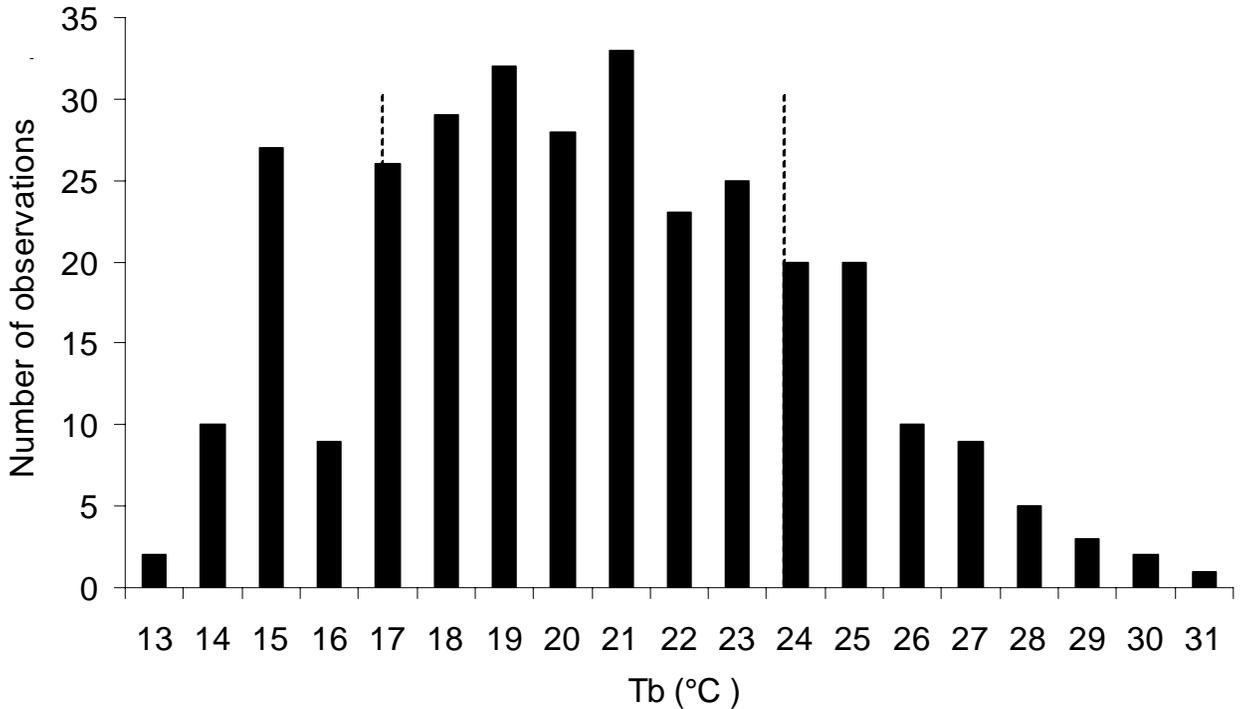
## INTRODUCTION

Temperature regulation by reptiles is a dynamic process in which behavioural and physiological mechanisms determine selection of body temperatures within a narrow range of preferred values (Huey, 1982). Most diurnal lizard species thermoregulate behaviourally by shuttling in and out of the sun or shade and by orienting their bodies positively or negatively to the sun (Greenberg, 1977; Regal & Gans, 1980). The extent of behavioural thermoregulation in lizards may be influenced by physiological states such as ontogenetic stage, feeding or gestation (Gier et al., 1989; Hailey et al., 1987; Mathies & Andrews, 1997; Robert & Thompson, 2000; Rock et al., 2000; Slip & Shine, 1988; Stewart, 1984), as well as the constraints imposed by the thermal environment. Fossorial lizards, in particular, may face thermoregulatory challenges because they generally do not bask and their fossorial habits may preclude them from exploiting the diverse range of thermal microenvironments that are typically available to heliothermic species (Porter et al., 1973; van Damme et al., 1986). Thus, the thermal physiology of fossorial lizards may differ markedly from terrestrial basking species, although detailed comparisons are lacking because data on temperature selection and thermoregulatory behaviour of fossorial species are scarce (Bury & Balgooyen, 1976; Qualls & Shine, 1998).

The three-toed skink, *Saiphos equalis*, is a fossorial lizard that occurs in coastal eastern Australia (Greer, 1989). Because of its secretive fossorial habits, little is known of its thermal biology and ecology. Unlike many species of skinks, *S. equalis* inhabits cool environments under rocks and logs in sandy areas, which probably limits the opportunity to thermoregulate by basking. In the laboratory, *S.*

*equalis* spends most of its time at the cool end of enclosures and is observed on the substrate surface at night (Wu, unpublished observations). Its cool temperature preference differs from many other skink species, which maintain relatively high and constant body temperatures of approximately 32–34 °C, despite wide variations in ambient temperature (Bennett & Huey, 1990; Hertz & Huey, 1993), but is similar to nocturnal terrestrial lizards, which maintain low body temperature while active. The reproductive biology of *S. equalis* is of interest because, although the species is oviparous, it has the unusual capacity to retain eggs until embryonic development is complete (Smith & Shine, 1997). As embryonic development in lizards is temperature dependent (Muth, 1980), embryos incubated at cool maternal body temperatures develop more slowly than embryos incubated at warm temperatures (Huey, 1982; Shine, 1983; Rock et al., 2000). Gravid or pregnant females of lizard species that typically maintain relatively cool body temperatures may thermoregulate at higher body temperatures compared to non-gravid females, presumably to enhance the developmental rate of embryos retained *in utero* (Andrews et al., 1997; Daut & Andrews, 1993; Werner, 1990). Because *S. equalis* inhabits relatively cool thermal environments, it is of particular interest for evaluating the effect of reproductive condition on thermoregulatory behaviour.

Temperature has a marked effect on metabolism. Studies of metabolism are important in physiological ecology because they identify potential energetic constraints that operate on individual organisms and provide mechanistic explanations for large-scale ecological and evolutionary patterns (Litzgus & Hopkins, 2003; Secor & Nagy, 1994; Zaiden, 2003). Reptiles generally have a metabolic rate that is an exponential function of ambient temperature



**Fig. 1.** Frequency distributions of selected body temperatures ( $T_b$ ) of *Saiphos equalis* in a thermal gradient. Superimposed on the figure is the central 50% of the mean  $T_b$  (dashed vertical lines).

(Aleskiuk, 1971; Murrish & Vance, 1968). However, a departure from strict thermal dependence occurs in several surface-active reptiles with a decreasing  $Q_{10}$  with increasing temperature near preferred body temperature (e.g. *Thamnophis sirtalis*, *Sphenodon punctatus*; Aleksiuk, 1971; Bennett & Dawson, 1976; Cartland & Grimmond, 1994). Nevertheless, investigations of this pattern in fossorial lizards are scarce.

The ecological characteristics of *Saiphos equalis* make it an ideal species to address our aims, which are to determine: 1) the preferred (selected) body temperatures ( $T_b$ ) of *S. equalis*; 2) whether reproductive condition affects thermoregulatory behaviour and temperature selection, 3) whether *S. equalis* is diurnal or nocturnal, and 4) whether *S. equalis* has a low metabolic rate that is independent of temperature within the preferred body temperature range.

## MATERIAL AND METHODS

*Saiphos equalis* (14 males, 9 non-gravid females, 5 gravid females, 5 juveniles) were collected at Forsyth Park (33°50'S, 151°13'E) and Poulton Park (33°58'S, 151°05'E) in Sydney, Australia from September to December 2007. Individuals were sexed in the field, placed in cloth bags and transported to the University of Sydney. Lizards were housed individually in plastic containers (150 mm × 80 mm × 50 mm) in an animal facility. Each container was provided with approximately 10 mm of moist potting mix (Brunnings Easy Wetta Coir-Peat Brick, Bentleigh, Australia) and a piece of ceramic tile as a hide for the lizards. The containers were heated at one end using heat tape to allow individuals to thermoregulate. Temperatures inside

the containers ranged from approximately 23 to 35 °C during the day and decreased to approximately 20 °C during the night. Lizards were maintained under a photoperiod of 12:12 h light:dark. Each lizard was fed two crickets (*Acheta domestica*) dusted with vitamin mineral supplement three times a week and supplied with water daily.

Lizards were collected beneath rocks during the day and their field body temperatures ( $T_b$ ) were estimated indirectly by measuring the temperature of the substrate beneath the rock where the lizard was captured. As *S. equalis* is relatively small (mean  $3.8 \pm 0.1$  g), body temperatures rapidly come to equilibrium with the surrounding soil (Daut & Andrews, 1993; Kearney & Predavec, 2000). Substrate temperatures ( $T_s$ ) were measured using an infrared thermometer (Model C-600M, Linear Laboratories, Los Altos, California, USA). Selected body temperatures ( $T_b$ ) were measured in laboratory thermal gradients using a thermocouple thermometer (Digitech QM-1600, Hounslow, UK). The thermocouple thermometer was calibrated by using a temperature controlled water bath (Julabo Labortechnik GMBH D-77960 Seelabach, Germany) and the infrared thermometer was calibrated against the thermocouple thermometer.

The thermal gradients consisted of three rectangular runways (each 960 mm × 250 mm). The bottoms of the gradients were covered with approximately 10 mm of potting mix for the lizards to bury themselves. The gradients were housed in a temperature-controlled chamber, and ceramic heat bulbs were suspended at different heights along each runway to produce a linear temperature gradient ranging from 10 to 40°C. The gradients were insulated with Styrofoam to minimize temperature fluctuations in

**Table 1.** Central 50% mean selected temperature (MST; °C), field body temperature ( $T_s$ ), maximum selected body temperature ( $T_{bmax}$ ) and minimum selected body temperature ( $T_{bmin}$ ) for different sex and age classes of *Saiphos equalis*. (Mean values are presented  $\pm$  SE.)

Sex-age classes	Central 50% MST (°C)	$T_s$ (°C)	$T_{bmax}$ (°C)	$T_{bmin}$ (°C)
Males ( $n=14$ )	20.8 $\pm$ 0.5	16.3 $\pm$ 0.4	26.1 $\pm$ 0.7	16.1 $\pm$ 0.5
Non-gravid females ( $n=9$ )	19.5 $\pm$ 1.2	16.7 $\pm$ 0.7	25.4 $\pm$ 1.1	16.2 $\pm$ 0.9
Gravid females ( $n=5$ )	22.1 $\pm$ 0.8	19.7 $\pm$ 1.3	27.3 $\pm$ 0.8	16.0 $\pm$ 0.4
Juveniles ( $n=5$ )	19.8 $\pm$ 1.1	16.4 $\pm$ 0.7	25.8 $\pm$ 1.2	16.0 $\pm$ 0.9

the gradient. Temperatures were monitored using iButtons (Dallas Semiconductor, Texas, USA) evenly distributed along the length of each runway.

Lizards were fasted for 48 h before being placed in the gradients to ensure that they were post-absorptive (Robert & Thompson, 2000). At 1600 on the day after fasting, a single lizard was placed into each of three runways and allowed to equilibrate for 20 h (Daut & Andrews, 1993). After equilibration, the position and temperature of each lizard were measured every 60 min over 10 h. Body temperature was measured by placing a thermocouple under the lizard at the midpoint of the body (Daut & Andrews, 1993; Gregory, 1980). Measurements of body temperatures appeared not to disturb lizards or to alter their behaviour. To test whether *S. equalis* is primarily nocturnal or diurnal, the frequency that lizards were observed out on the surface of the substrate during the day (1300–1500) and night (2000–2200) was recorded during the temperature selection trials. Observations were made hourly along with the  $T_b$ . Lizards were considered surface active if at least their head was visible protruding from the surface of the substrate.

Resting metabolic rates of adult male and non-gravid female *S. equalis* (body mass >2.0 g) were measured outside the breeding season as rates of oxygen consumption ( $\dot{V}O_2$ ) at eleven discrete temperatures from 10 to 30 °C, 2 °C apart (10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30 °C). This temperature range encompasses the minimum and maximum that *S. equalis* actively selected in the thermal gradient, together with the annual average air temperature range (8–30 °C) in Sydney. Lizards ( $n=28$ ) were fasted for 48 h prior to measurement of  $\dot{V}O_2$  to ensure a post-absorptive state (Robert & Thompson, 2000; Iglesias et al., 2003). Three or four different lizards were allocated to each temperature treatment. Most lizards were only used once, but seven were used at two different temperatures and two were used at three temperatures after a minimum of a week between tests. Lizards were conditioned for 2 h at their treatment temperature twice before the test to familiarize them with the experimental environment (Hare et al., 2004, 2006). Measurements were conducted during the day

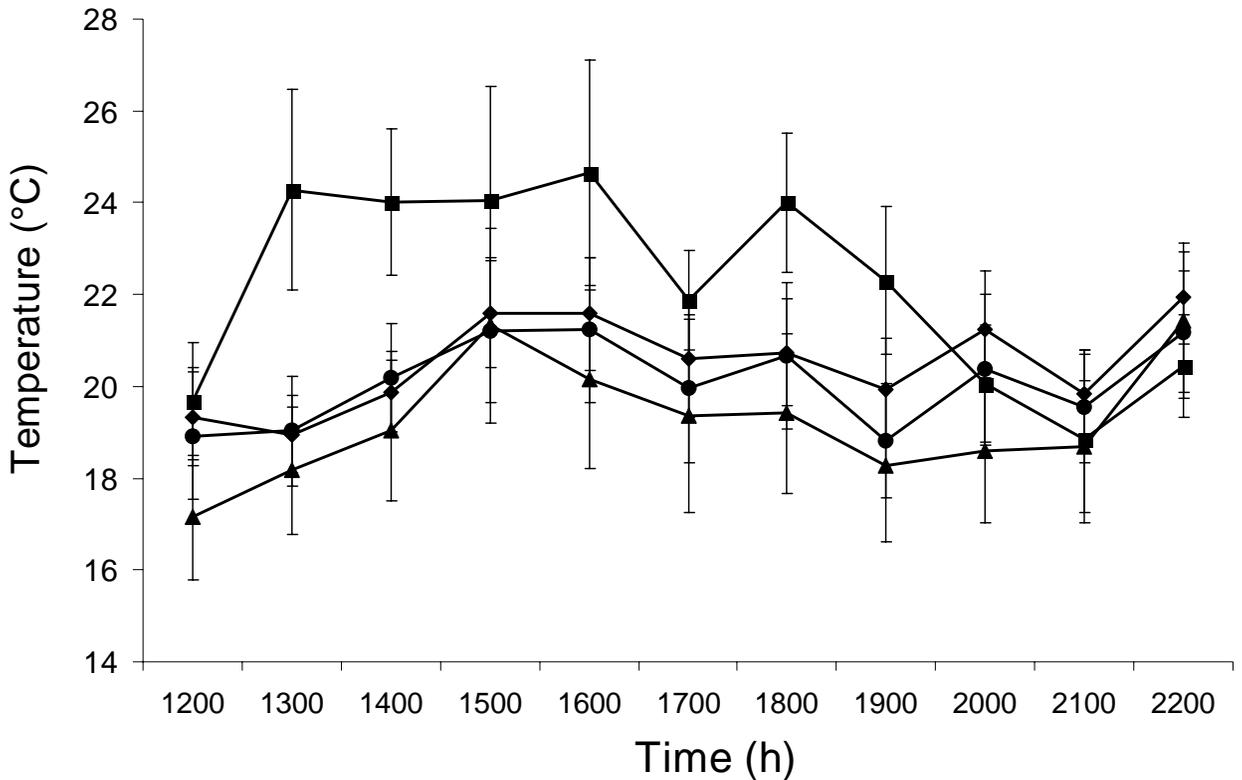
(0900–1100), which is the non-active period for *S. equalis*, to obtain a standard metabolic rate. Lizards were allowed to settle in a 170 mm long plastic chamber in a controlled constant temperature incubator for 30 min at each test temperature for equilibration prior to measurement (Cartland & Grimmond, 1994). The chamber was connected to an Oxzilla II oxygen analyser, with sub-samplers used to control a constant flow rate of 3.0 ml min<sup>-1</sup>. A soap bubble flow-through system was used to calibrate the flow controller (Long & Ireland, 1985). A reference (blank) chamber was included within the incubator to monitor the baseline oxygen concentrations. Chambers were shielded from the incubator lights with cardboard to maintain low light intensity, as the animals are fossorial. Measurement of  $\dot{V}O_2$  in the reference chamber was taken at the beginning and end of each  $\dot{V}O_2$  measurement. Lizards were weighed after each test. Data were recorded and analysed using Sable System Software and the mean mass-specific  $\dot{V}O_2$  (ml O<sub>2</sub>g<sup>-1</sup>h<sup>-1</sup>) was calculated from a minimum of 5 min of steady state oxygen consumption (Hare et al., 2006).

The effect of reproductive and age classes (male, gravid female, non-gravid female, and juvenile) on  $T_s$ ,  $T_b$ , maximum selected body temperature ( $T_{bmax}$ ) and minimum selected body temperature ( $T_{bmin}$ ) was analysed using a one-way repeated measures ANOVA. The sphericity assumption for repeated measures ANOVAs was satisfied using Mauchly's Test of Sphericity (all  $P_s > 0.05$ ). The effect of time period (day versus night) on lizard activity was analysed using a  $\chi^2$  test. As each metabolic data point was taken to be independent, the effect of temperature on metabolic rate of adult *S. equalis* was analysed using one-way ANOVA. For all ANOVAs, post-hoc pairwise comparisons were made using a Tukey's honestly significant difference test. Data are reported as mean  $\pm$  SE unless otherwise noted, and probability values less than 0.05 were considered statistically significant. All statistical analyses were performed using SPSS statistical package version 15.0 (SPSS Inc. Illinois, USA).

## RESULTS

Selected  $T_b$  of *S. equalis* in the thermal gradients and  $T_s$  in the field ranged from 13 to 31 °C and 15 to 24 °C respectively (Fig. 1). Mean selected body temperature (MST) in the thermal gradient of non reproductive adult *S. equalis* was 20.6 $\pm$ 0.5 °C ( $n=28$ ) and was similar to juvenile  $T_b$  (19.8 $\pm$ 1.1 °C,  $n=5$ ) (Table 1). Mean  $T_b$  from 1200 to 2200 ranged from 15.7 to 26.1 °C (Fig. 2). There was no overall statistically significant difference in  $T_s$ ,  $T_b$ ,  $T_{bmax}$  or  $T_{bmin}$  ( $P > 0.05$ ) among reproductive or age classes. Gravid females, however, had higher  $T_b$  during the early afternoon at 1400 compared to non-gravid females ( $F_{1,13}=5.454$ ,  $P < 0.05$ ) (Fig. 2). Individuals were more active during the night than the day ( $\chi^2=30.5$ ,  $df=1$ ,  $n=72$ ,  $P < 0.01$ ). Approximately 75% of surface activity was observed during the night.

Temperature has a significant effect on metabolic rate in *S. equalis* ( $F_{10,38}=18.96$ ,  $P < 0.05$ ; Fig. 3) with a  $Q_{10}$  over the whole range of about 2.0. Multiple comparisons, however, show that metabolic rate does not vary significantly with increasing temperatures from 18 to 26 °C ( $P > 0.05$ ), a



**Fig. 2.** Relationship of hourly  $T_b$  ( $\pm$ SE) of male, non-gravid and gravid female, and juvenile *Saiphos equalis* in a thermal gradient. Squares represent gravid females, diamonds males, circles non-gravid females and triangles juveniles.

range that is similar to the preferred  $T_b$  range (17–24 °C) of *S. equalis* (Fig. 1).  $\dot{V}O_2$  does increase exponentially with temperature, however, over the whole range from 10 to 30 °C ( $R^2=0.6025$ ) (Fig. 3). Metabolic rate at 20 °C is significantly higher than at 10 °C, 12 °C and 16 °C ( $P<0.05$ ).

## DISCUSSION

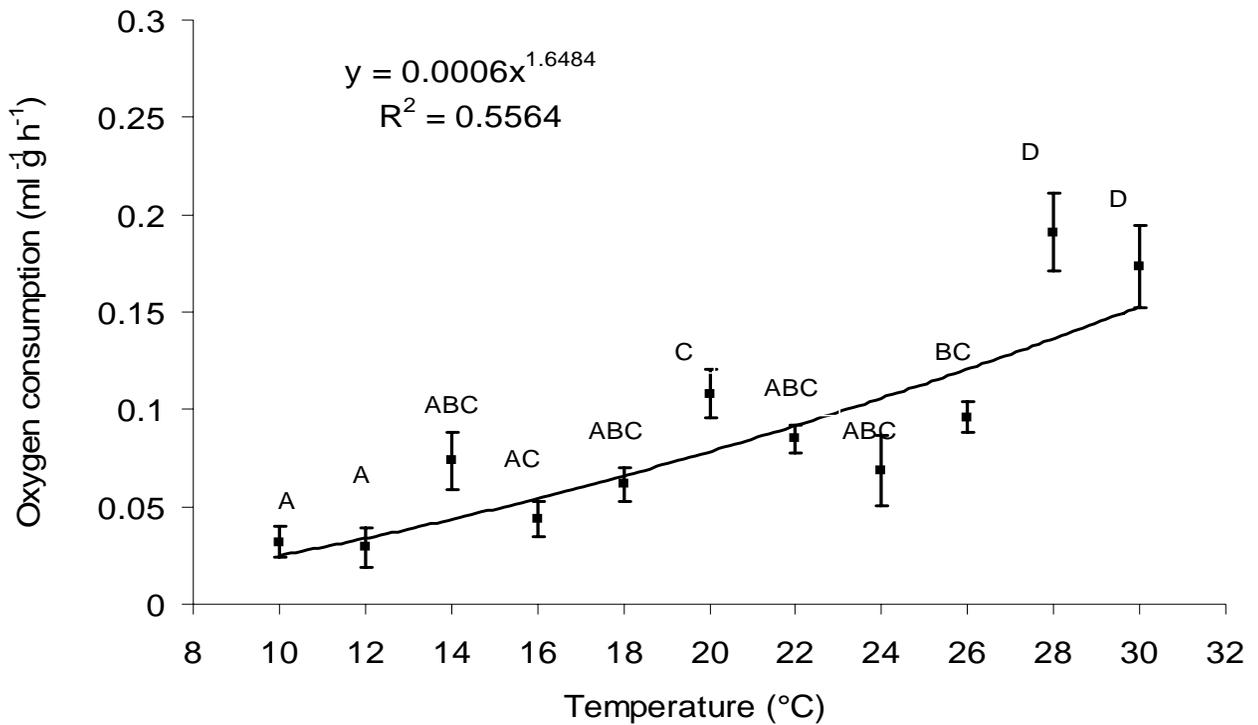
### Thermal biology

Much of our knowledge of lizard thermophysiology is based on diurnal heliothermic species, which typically maintain relatively high body temperatures within a narrow range. Thermoregulatory behaviour in reptiles, however, forms a continuum ranging from precise thermoregulation to thermoconformity where  $T_b$  varies with ambient temperature (Hertz & Huey, 1993; Huey, 1982). *Saiphos equalis* actively selects a broad range of relatively cool temperatures (approximately 17–24 °C) in laboratory thermal gradients compared to the potential range of ambient temperatures (10–40 °C) available. This thermoregulatory pattern is typical of many nocturnal lizards, which normally maintain  $T_b$  in the range from 20 to 30 °C during activity (Avery, 1982; Dial, 1978; Hitchcock & McBrayer, 2006; Nagy & Knight, 1989). For example, two nocturnal gecko species have upper and lower set-point body temperatures ranging from 23.6 to 26.0 °C (*Christinus marmoratus*) and 26.4 to 29.4 °C (*Hemidactylus turcicus*), which are considerably lower than those of most diurnal heliothermic species, which

generally maintain set-point temperatures from 31.0 to 33.0 °C (Kearney & Predavec, 2000). The relatively low temperatures preferred by *S. equalis* are consistent with nocturnal activity and its distribution in cool, shady environments. *Saiphos equalis* is sometimes observed beneath sun-warmed rocks during the day, a behaviour that also occurs in other fossorial and nocturnal lizard species (e.g. *Pachydactylus bibron*, *Lerista bougainvilli*; Nagy & Knight, 1989; Qualls & Shine, 1998). These observations suggest that *S. equalis*, and possibly other nocturnal ectotherms, thermoregulate behaviourally during the day when higher and more heterogeneous thermal environments are available (Hitchcock & McBrayer, 2006; Kearney & Predavec, 2000).

### Reproductive thermophysiology

Gravid females have higher  $T_b$  between 1300 and 1400 compared to non-gravid females, suggesting that they may thermoregulate at higher  $T_b$  during the day than during the night. The pattern is, however, likely to reflect a diel cycle where gravid females elevate  $T_b$  during the day while warmer temperatures are available, but experience a decrease in  $T_b$  when foraging at night and have limited availability to thermoregulate. Nocturnal lizards like *S. equalis* grow faster when provided with a diurnal heat source (Autumn & deNardo, 1995). Diurnal thermoregulatory behaviour of gravid females may also influence developmental rates of embryos, since *S. equalis* retains



**Fig. 3.** Rate of oxygen consumption ( $\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$ ) (mean  $\pm$  SE) as a function of temperature for adult *Saiphos equalis*. Means with different letters differ at  $P < 0.05$ .

eggs until embryos have completed more than three-quarters of their development (Smith & Shine, 1997). The relationship between embryonic development and temperature in *S. equalis* is, however, currently unknown. Additional studies using larger sample sizes are required to test the conclusion that gravid females select higher body temperatures during the day than non-gravid females.

#### Effect of temperature on metabolic rate

For adult *S. equalis*, the increase in metabolic rate as a function of  $T_b$  and overall  $\dot{Q}_{10}$  of approximately two is typical of many diurnal lizard species (Bennett, 1982). The rate of oxygen consumption in *S. equalis*, however, does not vary significantly from 18 to 26 °C (Fig. 3), suggesting that metabolic rate may be independent of temperature over the preferred range of  $T_b$  selected in the laboratory (Fig. 1). Thus, the marked increase in  $\dot{V}\text{O}_2$  (and hence  $\dot{Q}_{10}$  values) at 12 °C and 28 °C may indicate threshold temperatures at which temperature-dependent shifts in cellular physiology occur.

Many nocturnal lizards (e.g. *Anarbylus switaki*) have the capacity to maintain relatively high metabolic rates at low  $T_b$  (Putnam & Murphy, 1982). Relatively high metabolic rate at low temperatures may result from the increased capacity to generate energy at cool temperatures, resulting in a reduced thermal sensitivity within the preferred  $T_b$  range (Davies & Bennett, 1981). The capacity to remain active over a broad range of cool temperatures may be an adaptation to nocturnal activity by optimizing their metabolic rate at low ambient temperatures. The fre-

quent coexistence of fossorial lifestyle and nocturnality, as in *S. equalis*, may be a consequence of the limited range of thermal environments available in both circumstances and the physiological adaptations required to exploit this habitat.

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