

# Basking is affected by season and influences oxygen consumption in desert-living striped mice

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## Abstract

Small mammals that inhabit arid and temporally unproductive environments use several methods to conserve energy. Here, we investigate the energetic role of sun basking in striped mice *Rhabdomys pumilio* from the Succulent Karoo desert in South Africa. We observed mice in front of their nests for 140 h and recorded the time they spent basking during the non-breeding (dry) and the breeding (wet) seasons. We measured temperature changes in model mice to provide an indication of the heat that can be absorbed from the sun. Finally, we measured the oxygen consumption ( $\dot{V}O_2$ ) of mice at their basking sites in the field both in the sun and in the shade. This was accomplished using a portable respirometry system with a metabolism chamber, which could be placed in and out of the sun. Observations showed that mice basked more often during the non-breeding than during the breeding season. During the former season, mice spent an average of  $11.9 \pm 1.1$  min (SE) in the morning and  $5.5 \pm 0.5$  min in the afternoon per day basking. Within the metabolism chamber,  $\dot{V}O_2$  decreased when the animal was in the sunshine compared with the shade. This effect occurred independent of the ambient temperature ( $T_a$ ), indicating that a significant amount of radiant energy was absorbed from the sun. Basking may be an alternative to other energy-acquisition behaviours, such as foraging, which might be particularly useful at times when food is scarce.

## Introduction

Small mammals that inhabit arid environments and encounter reduced amounts of both water and food as well as extremes of temperature commonly adopt special strategies to use available energy. For example, the round-eared elephant shrew *Macroscelides proboscideus* enters into torpor during cold nights when food is restricted (Lovegrove, Lawes & Rosenburgh, 1999). Common behavioural strategies include avoiding extremes of heat and cold by remaining in dens and burrows (du Plessis, Kerley & Winter, 1992) and using solar heat by basking (Mzilikazi, Lovegrove & Ribble, 2002; Geiser & Drury, 2003; McKechnie & Wolf, 2004).

Deserts are often characterized by an abundance of available heat in the form of solar radiation. This energy source is clearly used by ectotherms such as reptiles, which derive exogenous heat from the sun to maintain operative body temperatures ( $T_b$ 's) (Christian & Bedford, 1995; Bauwens, Hertz & Castilla, 1996). In contrast, small mammals predominantly use endogenous reserves to maintain  $T_b$  (Haim & Izhaki, 1993; Scantlebury *et al.*, 2002). Although

sun basking has been observed in a few mammals, its importance remains poorly understood. The striped-faced dunnart *Sminthopsis macroura* derives a significant amount of heat from basking in order to arouse from torpor, which may reduce the energy demands of arousal by over 60% (Geiser & Drury, 2003). Elephant shrews *Elephantulus myurus* may similarly derive energetic benefits through basking during arousal (Mzilikazi *et al.*, 2002) and rock hyraxes *Procavia capensis* through maintenance of  $T_b$  (Brown & Downs, 2007). Thus, basking may provide an important source of heat in some mammals, especially for those inhabiting arid and food-limited environments (Geiser, Goodship & Pavey, 2002; Geiser *et al.*, 2004; Brown & Downs, 2005, 2007; Schwaibold & Pillay, 2006; Pavey & Geiser, 2008; Warnecke, Turner & Geiser, 2008).

The striped mouse *Rhabdomys pumilio* from the Succulent Karoo desert of South Africa is a 40–80 g diurnal, group-living rodent (Schradin & Pillay, 2004, 2005a). Groups have one territory and one nest that they defend against mice from other groups (Schradin, 2004). In the morning, mice emerge from their nest and bask together in the sun for

several minutes before leaving to forage alone (Schradin, 2006). In the afternoon, mice again congregate outside their nest and bask in the sun before retiring for the night. Striped mice expend increased amounts of energy on thermoregulation when the ambient temperature ( $T_a$ ) is low (Scantlebury *et al.*, 2006). In addition, they do not enter torpor and their  $T_b$  is the lowest in the morning (Haim, van Aarde & Zisapel, 1998). Thus, one might hypothesize that they may derive a useful amount of heat when they bask in the sun, which can presumably serve to reduce energy expenditure (Geiser & Pavey, 2007; Warnecke *et al.*, 2008). Here, we provide information on the following: (1) the time spent basking in front of their nest during the non-breeding season; (2) the frequency of basking across both the non-breeding and the breeding seasons; (3) temperature changes in model mice at natural basking sites when they are placed in and out of the sun; (4) oxygen consumption of mice inside a respirometry chamber placed at a natural basking site both in the sun and in the shade. Thus, we determine whether a reduction in energy expenditure exists independent of  $T_a$  as a result of the radiant heat they receive while in the sun. We do not aim to measure the resting metabolic rate values *per se* but the changes in oxygen consumption ( $\dot{V}O_2$ ) due to differences in incident radiation in the natural environment.

## Materials and methods

### Study site and animals

The study was conducted in the Goegap Nature Reserve near Springbok in the Northern Cape Province, South Africa (29°41'56"S, 18°1'60"E). The area is arid and experiences a winter rainfall, with an average annual precipitation of 160 mm (Rösch, 2001). Minimum night-time and maximum daytime temperatures at the field site are -1.5 and 24 °C during the (wet) breeding season and 4 and 40 °C during the (dry) non-breeding season (C. Schradin, unpubl. data). The vegetation type is classified as Succulent Karoo (Cowling, Esler & Rundel, 1999). Trapping and marking of striped mice has been described previously (Schradin & Pillay, 2004).

### Measurement of the time spent basking in front of nests

We undertook 187 observations (103 in the morning and 84 in the afternoon) of 68 randomly chosen focal individuals from the end of January to the end of May in 2005. Fifty-one individuals were observed 103 times during mornings. Forty-eight individuals were observed 84 times during afternoons. Each observation lasted 45 min (a period during which mice normally leave the nest site to forage). If mice remained for longer at their nest, observations continued until the focal animal had left the nest (Schradin & Pillay, 2004, 2005b). The total observation time was 140 h. Fifty per cent (36 out of 72) of the individuals were observed several times. For analysis, mean values were taken for each individual to avoid pseudoreplication. Thirty-two indivi-

duals were observed during both morning and afternoon sessions, enabling paired comparisons. Mice were observed from a distance of 5–10 m and were habituated to the presence of observers (Schradin, 2006). Observations occurred during the non-breeding season because that is when mice are observed to bask the most. We argued previously that basking is likely to be energetically more important during this season because food is more plentiful during the breeding season (Schradin *et al.*, 2007).

Basking events were recorded when a mouse left the shade or the inside of the shrub to sit still in the sun without showing any other activity, such as feeding or social interaction. Basking was an actively chosen behaviour, in which the mouse sought solar radiation, which subsequently put it at risk from predation (Schradin *et al.*, 2007; C. Schradin, pers. obs.). For analysis purposes, we recorded the times spent basking as remaining inactive for periods of longer than 5 s. The total time spent basking by each focal mouse was measured using a stopwatch that was started when the mouse moved into the sun and stopped during the periods it disappeared into the shade or into a shrub, but started again once the individual resumed basking. We did not collect data on individual periods of time that mice moved into and out of the sun during a morning or an afternoon session but the mean total basking times for morning and afternoon sessions for each animal.

### Focal observations during the day

Focal observations were performed to obtain information on the frequency of sun basking while foraging. Seven males were observed during the non-breeding season (August 2003) and 13 during the breeding season (September/October 2003). Observations were part of a study on male reproductive strategies (Schradin, 2006). Observations occurred during the main activity periods, which were during the mornings (just after mice left their nest) and the afternoons (3 h before the expected time that mice return to their nest: Schradin *et al.*, 2007) but not during the hottest times of the day when mice are usually hidden in shrubs (Schradin, 2006). Morning observations started at the nest and evening observations always ended at the nest. Thus, data were collected both 'at the nest' and 'away from the nest'. A total of 20 observations (3 h each) were made in the morning (five during the non-breeding season and 15 during the breeding season) and 20 (3 h each) in the afternoon (three during the non-breeding season and 17 during the breeding season). Individuals were equipped with radio-collars (2g, MD-2C transmitters, Holohil Systems Ltd., Carp, ON, Canada) and were followed at a distance of 5–10 m while their behaviour was observed (with the help of 10 × 25 binoculars) (Schradin, 2006). We recorded whether the mouse had been basking during the previous minute (+/0 sampling). For each observation, the proportion of records spent basking was calculated and arcsine transformed before analysis (Zar, 1984). Times spent in the nest at the start of morning observations or at the end of afternoon observations were excluded from analysis.

## Heating of copper models at basking sites

To determine the impact of being in the sun compared with the shade, we constructed model animals (Bakken *et al.*, 1981). These consisted of copper tubes (15 mm diameter, 2 mm thick), which were covered with skins of striped mice. We placed two copper models at each of the nine natural basking sites inside shrubs – one in the shade and the other in the sun. Nine experiments were conducted in November 2004 and 10 in March 2005. These occurred at natural basking sites for 15 min in the morning in March and for 30 min in November (representing seasonal differences in the duration of basking: Schradin *et al.*, 2007). Ten mouse skins were used; no skin was used more than once in the shade or in the sun to avoid any possible bias as a result of differences between the skins. Temperatures were measured using a Conrad Electronics GmbH (Hamburg, Germany) maximum/minimum thermometer ( $\pm 0.1^\circ\text{C}$ ) that simultaneously measured the temperature of two sensors. One sensor was suspended in the middle of the copper model and the other was placed outside the model in the open air (measuring  $T_a$ ). The model temperature,  $T_m$ , thus approximated the average temperatures of the top, sides and bottom of the model mouse.  $T_m$  and  $T_a$  were measured both in the shade and in the sun.

## Oxygen consumption

Metabolic measurements were performed during the non-breeding season (February and March 2005) when food availability was low, the habitat was dry and mice showed the highest frequency and duration of basking. Measurements were conducted in the field at the basking sites of eight different mouse groups using one individual male from each group (mean body mass  $52.5 \pm 4.6$  g). Animals were trapped in the afternoon and kept outdoors at the research station overnight in a cage ( $45 \times 30 \times 30$  cm), which was provided with hay and tissue paper as bedding and nesting material, as well as with 4 g of seed mix for food and with water *ad libitum*. In an attempt to reduce the unfamiliarity experienced during the metabolic measurement, cages contained a Perspex chamber identical to the experimental one so that the animal could become accustomed to the chamber. The following day, animals were taken to the field, to a site at which they had been observed previously to bask (some 200 m away from the field laboratory). Measurements of  $\dot{V}O_2$  and  $T_a$  were performed during the following four periods:

1. Before sunrise; the mouse was placed in the respirometry chamber to allow it to settle and become accustomed to the chamber (*c.* 06:00–06:30 hours).
2. After sunrise; the mouse was exposed to natural shaded light when the field site was surrounded by hills (*c.* 06:30–07:00 hours).
3. When the sun rose above the hills; the respirometry chamber was exposed to the rays of the sun (*c.* 07:00–07:30 hours).
4. After the experimenter shaded the chamber with a cloth, which was positioned *c.* 50 cm away from the chamber so

that air could freely circulate around the chamber (*c.* 07:30–08:00 hours).

The metabolic chamber ( $1610\text{ cm}^3$ ) was a clear Perspex cylinder that allowed the animal inside to be exposed to the solar radiation that was not absorbed by the chamber wall. We recorded the  $T_a$ 's approximately every 2 min both inside the respirometry chamber and in dry incurrent air using a digital thermometer (THERMO-tech digital, Conrad Electronics GmbH) to obtain measures of chamber temperature and  $T_a$ , respectively.  $\dot{V}O_2$  was measured using an open-circuit respirometry system (Depocas & Hart, 1957). Dried air (silica gel) was pumped into the chamber at  $800\text{ mL min}^{-1}$ . The air was dried again after exiting the chamber. At this flow rate, a change in the behaviour of the mouse could be detected rapidly (*c.* 20 s) in the output of the analyser. The wind speed in the chamber was *c.*  $10\text{ cm min}^{-1}$ , which was similar to that experienced at ground level by foraging rodents (Geiger, 1957; Chappell & Holsclaw, 1984). Airflow was controlled using a flow regulator (F900, Applied Electrochemistry, AEI Technologies Inc., Naperville, IL, USA) placed upstream of the chamber. Measurements of  $\dot{V}O_2$  were performed using a portable oxygen analyser (S-2A Applied Electrochemistry, AEI Technologies Inc.). The analyser and the pump were connected to a car battery (90 A h), which was next to the nest of a mouse group so that the metabolic chamber could be placed in a known basking site. Measurements of oxygen concentration were performed before the animal was placed in the chamber and after the animal was removed to account for any drift in the analyser. The analyser was calibrated to an upper value (20.95%  $O_2$ ) before the measurement of each animal and to a lower value (0%  $O_2$  in  $N_2$  gas, AFROX, South Africa) before all measurements.

To measure illuminance, the exposure value ( $EV$ ) was determined directly in front of the chamber at a distance of 10 cm using a Universal exposure meter (Sangamo Weston Ltd., Enfield, UK).  $EV$  is logarithmically related to illuminance ( $lux$ ) by the equation:  $lux = a \times 2^{EV}$ , where  $a$  is a constant depending on the light spectrum and physical characteristics of the detecting device and method. Because of the optical properties of the Perspex, light intensity within the measurement chamber is reduced according to a transmission factor  $t$ . Hence, the exposure value we measured was related to the actual illuminance in the chamber as:  $EV = \log_2(lux) - \log_2(t) - \log_2(a)$ .

We assume that  $a$  and  $t$  were constant under our experimental conditions so that  $EV$  is a logarithmic measure of illuminance. The behaviour of the mouse was noted at all times, and measurements of  $EV$  and  $\dot{V}O_2$  were performed approximately every 2 min. The research was approved by the animal ethics committee of the University of the Witwatersrand, South Africa.

## Statistical analyses

Data were analysed using SAS (version 8.2) in linear models (multiple regression, ANCOVA). Residuals were accepted as being normally distributed when both

Kolmogoroff–Smirnov and Shapiro–Wilk statistics yielded  $P > 0.05$ . Effects were tested using type III (simultaneous) modelling, that is each effect was corrected for all other effects in multiple-effects models. Parameter estimates (regression coefficients and means) are given as estimate  $\pm$  standard error (SE); effects were considered significant for  $P < 0.05$ . Paired and two-sample *t*-tests were used as indicated in ‘Results’. To examine whether copper models increased in  $T_m$  due to radiation (independent of  $T_a$ ), we performed an analysis of covariance with  $T_m$  as the dependent variable, shading as the categorical effect (shaded/exposed) and  $T_a$  as the covariate. We used *EV* (a measure of energy per unit area:  $W m^{-2}$ ) for the regression of metabolic rate on illuminance. As heating of the body is proportional to volume, the dependence of heat transfer on illuminance follows some function to the power of  $2/3$ , which can be modelled using a logarithmic relationship. The fit of the regression model was high and residuals were normal, as shown in the ‘Results’ section.

A general linear mixed model (proc MIXED) was fitted with  $\dot{V}O_2$  as the response variable and  $T_a$  and *EV* as fixed effects, thus accounting for the possible confounding effect of  $T_a$ . The intercept and the two slopes were considered to vary randomly among individuals because of the potential influence of body composition and other uncontrolled variables affecting the metabolic rate. Hence, intercept and slope parameters were entered into the model as random coefficients for the individual animals. This procedure calculates the overall fixed-effect regression from a set of random regression coefficients, and hence the error degrees of freedom is the number of individuals minus one (i.e. seven). In addition,  $\dot{V}O_2$ ,  $T_a$  and *EV* signals were analysed as time series (Stata 10.0) to determine whether data were predictable over time. Stationarity and cointegration among signals were examined using the Dickey–Fuller test.

## Results

Basking was easy to observe as mice adopted a particular squat posture, with piloerected fur (Walsberg, 1988), and

often presented one flank to the incident sunlight. The time spent basking was much shorter in striped mice than in animals such as rock hyraxes *P. capensis* that bask in ‘safer places’ for periods of *c.* 1–2 h (Estes, 1991; Brown & Downs, 2005). One reason for this could be that striped mice are extremely vigilant, and thus their basking activities may be readily interrupted by environmental stimuli. Striped mice were frequently disturbed by Karoo scrub-robins *Cercotrichas coryphoeus* that forage on the ground. While these birds are not dangerous to striped mice, they are similar in body size to Fiscal shrikes *Lanius collaris* that do prey on striped mice (C. Schradin, pers. obs.). When disturbed, striped mice rapidly sought the safety of the shrub they were next to, leading to an apparently short basking bout. However, when the threat disappeared, they resumed basking, often in the identical location as before. Undisturbed basking bouts were sometimes in excess of 10 min.

### Time spent basking in front of nests

During the non-breeding season, mice spent  $11.5 \pm 1.1$  min basking in the morning in front of their nests ( $n = 51$  individuals) (range = 0.3–29.2 min) before leaving to forage. In the afternoon, mice basked for  $5.3 \pm 0.6$  min ( $n = 48$  individuals) at their nest before withdrawing for the night. Controlling for individual differences by using data for 32 individuals for which morning and afternoon observations were available, mice basked for significantly longer times in the morning than in the afternoon (paired  $t_{31} = 6.22$ ,  $P < 0.0001$ ).

### Focal observations during the day

In total, mice basked more often during the non-breeding season than during the breeding season ( $t_{18} = 2.65$ ,  $P < 0.02$ ; Table 1). Mice also basked significantly more often in front of their nest during the non-breeding than during the breeding season ( $t_{18} = 2.92$ ;  $P < 0.01$ ). However, when mice were followed while they foraged away from their nest during the day, no seasonal difference in the frequency they spent basking was detected ( $t_{18} = 0.76$ ,  $P > 0.4$ ). During the

**Table 1** Mean percentage of scans (180 one-minute scans within 3-h periods) ( $\pm$  SE) that male mice spent basking during the non-breeding season ( $n = 7$ ) and the breeding season ( $n = 13$ ) both in front of and away from the nest

	Non-breeding season	Breeding season
Total basking (morning)	$25.6 \pm 7.6\%$ (0.0–41.5%)	$2.4 \pm 1.2\%$ (0.0–11.7%)
Basking in front of nest (morning)	$25.1 \pm 7.6\%$ (0.0–41.5%)	$0.5 \pm 0.3\%$ (0.0–2.7%)
Basking away from nest (morning)	$0.5 \pm 0.5\%$ (0.0–2.7%)	$2.0 \pm 1.1\%$ (0.0–11.7%)
Total basking (afternoon)	$6.6 \pm 4.6\%$ (0.6–15.6%)	$4.6 \pm 1.8\%$ (0.0–20.3%)
Basking in front of nest (afternoon)	$0.2 \pm 0.2\%$ (0.0–0.6%)	$1.5 \pm 1.2\%$ (0.0–15.4%)
Basking away from nest (afternoon)	$6.4 \pm 4.7\%$ (0.0–15.6%)	$3.5 \pm 1.3\%$ (0.0–13.3%)

Ranges are presented in parentheses.

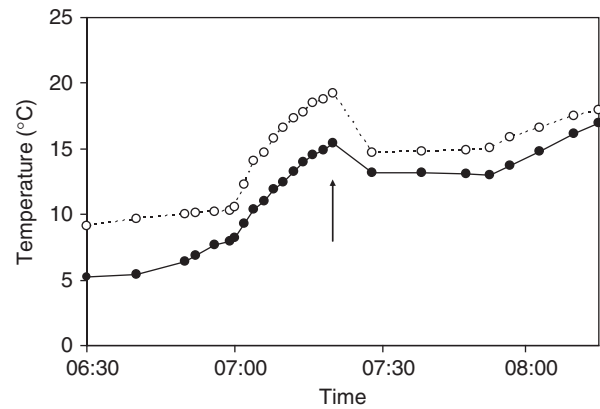
non-breeding season, mice tended to bask more frequently in front of their nest than away from it (paired  $t_6 = 2.16$ ,  $P = 0.07$ ) but not during the breeding season ( $t_{12} = 1.51$ ,  $P = 0.16$ ).

### Heating up of copper models at natural basking sites

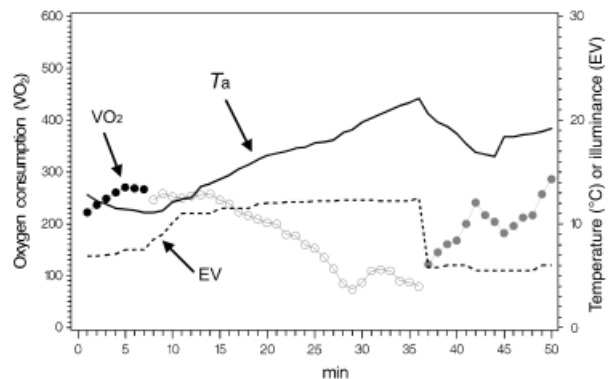
Across both seasons,  $T_m$  increased with  $T_a$  ( $F_{1,37} = 140.76$ ,  $P < 0.0001$ ). At any given  $T_a$ ,  $T_m$  was  $5.3^\circ\text{C}$  higher when the model was placed in the sun compared with when it was placed in the shade ( $F_{1,37} = 48.23$ ,  $P < 0.0001$ ). Additionally, across both seasons,  $T_m$  in the shade was significantly greater than  $T_a$  in the shade ( $17.2 \pm 1.1$  vs.  $15.8 \pm 1.2^\circ\text{C}$ , paired  $t_{18} = 7.5$ ,  $P < 0.0001$ ), as was  $T_m$  in the sun compared with  $T_a$  in the sun ( $22.5 \pm 1.3$  vs.  $17.3 \pm 1.3^\circ\text{C}$ ,  $t_{18} = 6.80$ ,  $P < 0.001$ ). During the winter,  $T_m$  in the shade was significantly greater than  $T_a$  in the shade ( $13.0 \pm 1.0^\circ\text{C}$  vs.  $11.4 \pm 1.0^\circ\text{C}$ ,  $t_8 = 9.95$ ,  $P < 0.001$ ); likewise,  $T_m$  in the sun was significantly greater than  $T_a$  in the sun ( $19.7 \pm 1.5^\circ\text{C}$  vs.  $13.2 \pm 1.2^\circ\text{C}$ ,  $t_9 = 7.73$ ,  $P < 0.001$ ). During the summer,  $T_m$  in the shade was significantly greater than  $T_a$  in the shade ( $20.9 \pm 0.9^\circ\text{C}$  vs.  $19.8 \pm 1.0^\circ\text{C}$ ,  $t_9 = 3.69$ ,  $P = 0.005$ ), and  $T_m$  in the sun was greater than  $T_a$  in the sun ( $25.0 \pm 1.7^\circ\text{C}$  vs.  $20.9 \pm 1.4^\circ\text{C}$ ,  $t_9 = 3.49$ ,  $P = 0.007$ ).

### Oxygen consumption, ambient temperature and illuminance

During the experiments, nights were cool during the non-breeding season and temperatures of  $4^\circ\text{C}$  were not uncommon (M. Scantlebury, unpubl. data). For measurements of  $\dot{V}\text{O}_2$ ,  $T_a$  measured in the chamber was always higher than the  $T_a$  measured outside. Temperatures in the shade were  $15.4 \pm 1.7^\circ\text{C}$  in the chamber and  $13.3 \pm 1.90^\circ\text{C}$  outside (paired  $t_7 = 7.86$ ,  $P < 0.0001$ ); temperatures in the sun were  $18.8 \pm 1.2^\circ\text{C}$  in the chamber and  $17.1 \pm 1.4^\circ\text{C}$  outside ( $t_7 = 2.8$ ,  $P < 0.03$ ) (Fig. 1). The random coefficients model fitted well, because an analysis of residuals did not reveal deviations from normality and the coefficient of determination ( $R^2$ ) was 86%.  $\dot{V}\text{O}_2$  decreased as illuminance ( $EV$ ) and  $T_a$  (inside the chamber) increased after sunrise (Fig. 2).  $\dot{V}\text{O}_2$  increased again when the chamber was shaded from the sun.  $\dot{V}\text{O}_2$  values for the four measurement periods (before sunrise, after sunrise when the sun was shaded by the hills, when the sun rose above the hills and when the chamber was shaded by a cloth) were  $6.28 \pm 1.18$ ,  $5.51 \pm 1.02$ ,  $3.59 \pm 1.05$  and  $3.72 \pm 1.12 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , respectively. These values do not take into account the effect of  $T_a$ , which was rising as the day was progressing, reducing the apparent differences in  $\dot{V}\text{O}_2$  between periods 3 and 4.  $\dot{V}\text{O}_2$  values that take into account the effects of  $T_a$  are shown in Fig. 3. The multiple regressions of  $\dot{V}\text{O}_2$  on  $T_a$  and  $EV$  were significant ( $b_T = 22.06 \pm 4.76$ ,  $t_7 = 4.50$ ,  $P < 0.003$  and  $b_{EV} = 8.34 \pm 1.86$ ,  $t_7 = 4.63$ ,  $P < 0.003$ , respectively), indicating that both  $T_a$  and  $EV$  affected  $\dot{V}\text{O}_2$ , and yielded the following



**Figure 1** Chamber temperature (open symbols, dotted line) and outside temperature (closed symbols, solid line) from c. 06:30 hours until 08:30 hours. The arrow indicates the time when the chamber was shaded by a cloth.

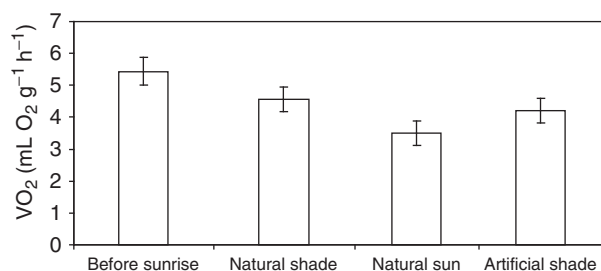


**Figure 2** Oxygen consumption ( $\dot{V}\text{O}_2$ ,  $\text{mL O}_2 \text{ h}^{-1}$ ) in relation to the ambient temperature ( $T_a$ ,  $^\circ\text{C}$ , solid line) and the associated differences in light intensity ( $EV$ , broken line) against time for a focal mouse.  $\dot{V}\text{O}_2$  was measured at natural basking sites approximately every 2 min, firstly in natural shade before the sun started shining on the nest (black symbols), then in the sun while 'basking' (open symbols) and finally under artificial shade (grey symbols).  $\dot{V}\text{O}_2$  decreased when mice were exposed to solar radiation and then increased again when placed in the shade.

fixed estimate:

$$\dot{V}\text{O}_2 (\text{mL O}_2/\text{h}) = 798.84 - 8.34 \pm 1.86 EV - 22.06 \pm 4.76 T_a (^\circ\text{C}) \quad (1)$$

Residuals from the Dickey–Fuller test for stationarity and cointegration of data signals showed significant non-stationarity ( $Z(t) = -4.14$ ,  $P < 0.01$ ;  $-3.63$ ,  $P < 0.01$  and  $-8.28$ ,  $P < 0.01$  for  $\dot{V}\text{O}_2$ ,  $EV$  and  $T_a$ , respectively). Hence, cointegration was not supported and data were unsuitable for time-series analysis modelling.



**Figure 3** Mean oxygen consumption ( $\dot{V}O_2$ , mL O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) values corrected for ambient temperature for time periods: (1) before sunrise, within the respirometry chamber (c. 06:00–06:30 hours) (before sunrise); (2) after sunrise, when exposed to the natural shaded light (c. 06:30–07:00 hours) (natural shade); (3) when the respirometry chamber was exposed to the sun (c. 07:00–07:30 hours) (natural sun); (4) after the experimenter shaded the chamber with a cloth (c. 07:30–08:00 hours) (artificial shade). Values were calculated using the mean residual for each of the periods added to the grand mean across all periods. Error bars denote standard errors.

## Discussion

In desert environments, animals are exposed to harsh conditions such as extremes of  $T_a$  and restrictions in free water and food. In these habitats, solar energy often provides an abundant source of heat during the day (Brown & Downs, 2007). Basking is a conspicuous behaviour of striped mice inhabiting the Succulent Karoo. Basking might allow mice to gain heat from the environment and assist with energy requirements for thermoregulation. However, basking is presumably associated with some risk, such as an increased possibility of predation (Brown & Downs, 2005). Hence, striped mice might not be expected to bask without some benefit. In support of this notion, we found that striped mice basked four times as much during the non-breeding season when food was scarce than during the breeding season when food was more plentiful (Schradin *et al.*, 2007). Indeed, the non-breeding season is clearly energetically costly as striped mice may lose 12% of their body mass (Schradin & Pillay, 2005a).

In the model mice, a significant increase in temperature above  $T_a$  occurred when the model was exposed to the sun. Even though  $T_m$  was higher than  $T_a$  both in the shade and in the sun, the difference in temperature was much higher in the sun. Presumably, this was due to absorption of radiant energy on the relatively dark skin of mice (Hamilton & Heppner, 1967). This absorption occurred in incident sunlight and in reflected light when mice piloerect their fur (Schradin *et al.*, 2007). The fact that mice can obtain energy from solar radiation is consistent with the decreases in  $\dot{V}O_2$  of individual mice observed in the current study when the metabolic chamber was placed in the sun. While we did not measure core  $T_b$  in striped mice, solar energy may help maintain  $T_b$ . Consequently, mice would be able to save energy by reducing endogenous heat production (e.g. Shanas *et al.*, 2002; Brown & Downs, 2005, 2007). When striped mice were maintained in the laboratory at a  $T_a$  of 25 °C, the

lowest  $T_b$  values recorded within the  $T_b$  daily rhythm envelope occurred in the early morning (Haim *et al.*, 1998). Hence, striped mice may benefit the most from an external heat source in the morning after they leave their nests. In fact, data from observations in front of the nest indicate that animals basked up to 50% longer in the mornings (c. 12 min) than in the afternoons (c. 5 min). It is worthwhile noting that mice may be exposed to solar radiation not only while basking but also while foraging during the day. However, in practice, mice always prefer cover, and if they do venture into the sun (e.g. to eat a piece of vegetation), they rapidly return to the cover (Schradin, 2006).

Interestingly, desert-originating striped mice have a lower mean  $T_b$  than those from mesic grasslands (35.3 and 36.9 °C, respectively) (Haim & Fairall, 1986). Thus, an overall reduction of  $T_b$ , combined with the use of passive heating, could decrease energy requirements in the desert, which might be particularly useful in an animal inhabiting a water- and energy-restricted habitat (e.g. Shanas *et al.*, 2002, 2003). Striped mice remain motionless in sheltered sunny places while basking and do not bask on cloudy days (C. Schradin unpubl. data). This suggests that basking occurs predominantly to save energy, rather than for other reasons (such as behavioural or territorial interactions). Moreover, mice appear to bask in sheltered areas where the absorbance of solar radiation is not hampered by wind and air convection (e.g. Boyer, 1965; de Jong, 1976).

This study shows that striped mice use basking as an active behavioural strategy (see also Schradin *et al.*, 2007), and by absorbing solar radiation, they can reduce  $\dot{V}O_2$ . Basking may, therefore, be important in minimizing energy expenditure, which is useful at a time of year when food resources are limited. More generally, this work presents further evidence that mammals may make substantial use of behavioural thermoregulation through basking, as has been suggested only recently (Geiser & Drury, 2003).

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