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Basking behaviour in relation to energy use and food availability in one of the smallest marsupials

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ABSTRACT

Although several mammals have been observed to bask in the sun, little is known about this behaviour or its energetic consequences. We investigated the importance of basking behaviour for one of the smallest marsupials, *Planigale gilesi* (9 g). Metabolic rates of captive planigales (n = 6) exposed to simulated natural conditions with access to a radiant heat source were measured. Basking behaviour as a function of food availability was quantified using a video camera installed within the planigales' home cages (n = 7). All planigales basked during respirometry measurements, reducing resting energy expenditure by 58% at an ambient temperature of 15 °C, which reflects conditions in their nesting sites in the wild during winter. Basking behaviour in home cages was displayed by all but one planigale; food withdrawal either triggered basking or it caused a significant increase in basking duration. Our study demonstrates the effectiveness of basking for reducing energy expenditure in one of the smallest marsupials, supporting recent findings on the importance of behavioural thermoregulation in small mammals in general.

1. Introduction

Basking behaviour in mammals has been observed in numerous species and has fascinated researchers for many decades. Almost a century ago, Goodwin [1] described striped chipmunks *Tamias striatus lysteri*: "On bright sunny days after rain many of them could be seen basking in the warm sun". The diversity of animals observed basking in the wild is high, and includes representatives from the orders Hyracoidea [2,3], Artiodactyla [4], Rodentia [5–9] and Dasyuromorphia [10–12]. All of these species live in arid and semi-arid habitats, suggesting that, as one might predict, basking is associated with sunny habitats.

As basking is employed by a large number of different mammalian species, it is of interest to examine the underlying motivation. Rodents are often observed basking in groups, so it may serve a social function [13]. However, the main reason for basking behaviour appears to be the positive impact that radiant heat gain has on animals' thermal energetics [2]. Early laboratory studies demonstrate that hairless mice eagerly press a lever in order to gain access to radiant heat, and that this behaviour increases with decreasing ambient temperature (T_a) [14]. Free-range studies similarly describe an increase in basking duration at times when food is scarce and T_a is low, as for example shown for the rock hyrax *Procavia capensis* [15]. The antelope ground squirrel *Ammospermophilus leucurus* lowers its body temperature (T_b) at night by about 6 °C, and it was estimated that basking accounts for 20% of the energy required for the elevation of T_b in the morning [16]. In the false antechinus *Pseudantechinus macdonnellensis* an increase in basking duration is associated with decreased food availability [17]. All these studies suggest a close link between basking and energy requirements.

While many studies have identified a correlation between energy shortages and increased basking duration, few have quantified the direct effects that basking has on the energy expenditure of mammals. The small marsupial stripe-faced dunnart *Sminthopsis macroura* (15–25 g), which basks in the wild [12], reduced normothermic energy requirements by up to 76% when exposed to radiant heat in the laboratory [18]. Similarly, the closely related fat-tailed dunnart *S. crassicaudata* (10–20 g), which also employs basking in the wild [19], was shown to actively move under a heat source during metabolic measurements with comparable energy savings [20].

Recently, basking has also been observed in combination with mammalian heterothermy. Heterothermic mammals are able to enter torpor, a state of controlled reduction of T_b and metabolic rate (MR). The use of torpor results in enormous energy savings [21] and is likely to be a key factor contributing to the success of many mammals in arid Australia [22], if not for the long-term survival of small mammals in general [23]. Therefore, the combination of basking and torpor appears highly advantageous to further enhance energetic savings. The South African elephant shrew *Elephantulus myurus* is assumed to employ basking during arousal from torpor, based on correlations between T_b and blackbody temperature [24]. Direct observations of torpid animals gaining access to solar radiation at the end of a torpor bout are rare and

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currently restricted to dasyurid marsupials [10,19]. However, the increasing number of heterothermic species observed basking in recent years suggests that basking in combination with torpor may be widespread among small heterotherms [25].

The smallest mammal known to bask is a member of the marsupial genus *Planigale*, which contains five species restricted to Australia and New Guinea. The Giles' planigale *Planigale gilesi* (6–15 g) is insectivorous and has a dorso-ventrally flattened, darkly-furred body (Plate 1). It is distributed in parts of Australia's arid and semi-arid zones, where it inhabits deep cracks formed in dry clay soil [26]. Basking has been reported for captive individuals [27,28]; however, it was only recently that this species was observed basking in the wild both during normothermia and during arousal from torpor [29]. Planigales were observed emerging from deep soil cracks to bask with a T_b of 13.8 °C, which is remarkably low for a mammal showing coordinated movements. While the thermal energetics of Giles' planigale have previously been investigated [30], no information is available regarding the effect of basking on its energy expenditure, and basking behaviour in relation to food availability has not been examined at all.

Our study aimed to investigate the importance of basking for Giles' planigale by exposing captive animals to simulated natural conditions. Metabolic measurements were specifically designed to examine energy expenditure during basking, and animals were provided with access to radiant heat in their home cages to monitor the effect of food withdrawal on basking duration. Based on findings for closely related species, we hypothesise that Giles' planigale employs basking in the laboratory to achieve substantial reductions in energy expenditure, and that basking duration increases with a shortage of food energy.

2. Methods

2.1. Animals

Eight planigales were captured in Kinchega National Park (32°30′ S, 142°20′E) in April 2007 and transported to the University of New England, Armidale, where they were kept in separate cages at $T_a = 20 \pm 1$ °C under a 12:12 LD light regime (lights on at 06:00). They were fed with a mixture of lean minced meat, hard-boiled eggs and dog kibble [31], and mealworms; water was freely available. MR measurements took place in November 2007 and behavioural observations during August and September 2007. The mean body mass was 9.3 ± 1.4 g.

Plate 1. A *Planigale gilesi* in its natural habitat; note the dorso-ventrally flattened skull and body.

2.2. Respirometry

To obtain MR under standard and basking conditions, we used three different experimental approaches: (1) We measured MR at $T_a = 15$ °C and 20 °C for about 6 h during the planigales' inactive phase (09:00 to 15:00) to obtain resting MR (RMR). To investigate MR during basking, planigales were exposed to simulated natural conditions for 23 h with 5 h radiant heat access, based on environmental data collected in the field [29]: (2) At constant $T_a = 15$ °C (simulating conditions deep in soil cracks) and (3) at a T_a cycle with an amplitude of 15.4–30.9 °C (simulating conditions closer to the surface). Measurements lasted from about 18:00 to 17:00 the following day with access to a radiant heat lamp (details see below) from 09:00 to 14:00, corresponding to the time when sun reached soil crack openings in the field.

An open-flow respirometry system (FOX Field oxygen analysis system, Sable Systems) was used to measure MR as VO_2. Outside air was dried (using $CaSO_4$) and pumped (Optima A-807) into the animal's chamber. The flow rate was 400 ml min^{-1} (Omega FMA-5606), of which a sub-sample of 150 ml min^{-1} was analysed for O_2. The O_2 analyser was connected to a computer via a serial port and the flow meter readings were interfaced via a 14 bit A/D converter. Values were calculated and stored on a personal computer using a custom-written Visual Basic V6 program (G. Körtner). Concurrent measurements of MR and T_a were alternated with a reference channel and the differential was used to calculate VO_2, thereby correcting for a possible drift. For calculations of MR [according to Equation 3a, 32], a respiratory quotient of 0.85 was assumed. Prior to measurements, the O_2 analyser was calibrated [33] against high purity compressed Nitrogen (BOC GASES) and a calibration gas ($O_2 = 19.9 \pm 0.03\%$ in Nitrogen, BOC GASES). The flow meter was calibrated using a custom made bubble meter [34]. T_b was measured using a digital thermometer (Omega HH-71T) connected to a thermocouple wire which was inserted 1 cm into the cloaca immediately following the RMR measurements.

The respirometry chamber (V = 480 ml) was made from a 20 cm long Perspex tube sealed with rubber stoppers and was placed horizontally on a plastic rack inside a temperature-controlled cabinet. It was connected to tubing on either side that allowed air to flow through the entire chamber. For the basking experiment we covered half of the chamber with black plastic to provide animals with a choice between the sheltered side of the chamber and the exposed side that allowed access to radiant heat. A basking lamp (50 W SunGlo, ExoTerra) was placed at a distance of 25 cm away from the chamber at a 45° angle, resulting in a light intensity inside the chamber of 3800 lx [for details see 20]. We measured T_a within the animal chamber via a thermocouple, which regulated T_a by duty-cycling between the fridge and a 50 W ceramic heat lamp using a custom-written program Visual Basic V6 program (G. Körtner). Therefore, the system was able to compensate for heat produced by the basking lamp. T_a was measured at both ends of the chamber to ensure that no thermal gradient existed. The high flow rate prevented an increase in T_a inside the chamber due to the lamp, which was controlled by measuring the difference in T_a between incoming air and outgoing air, which remained <1 °C during all measurements. Furthermore, the T_a inside the chamber and the temperature of the internal chamber surface on which the planigales sat to bask were within 0.1 °C of each other (Infrared thermometer, Sein Electronics SE-100), which means that animals did not absorb heat from the chamber surface. To allow for the calculation of mass-specific MRs, planigales were weighed before and after each experiment and a linear decrease in body mass was assumed.

2.3. Behavioural studies

To investigate the basking behaviour of undisturbed planigales, their home cages (50 × 32 × 25 cm) were divided into two equally-sized compartments by a cardboard divider containing a small hole at the base, which allowed unimpeded movement between cage sides. One compartment contained the nest box, food bowl, water bottle and cage enrichment, while the other side was empty and without shelter provided (herein "Side E"). The basking lamp (as above) was installed directly above the wire mesh cage lid, radiating only into Side E, and was automatically switched on daily between 09:00 and 16:00. Activity patterns were recorded using passive infrared motion detectors mounted on top of both cage compartments and connected to a data logger (E.S.U.), which stored the number of movements over 3-min periods.

The area under the basking lamp was filmed using a small video camera (Swann Global) and recorded onto a video cassette tape (Toshiba VCR) from 08:30 to 16:30. The time spent in Side E was monitored, as well as the time actually spent basking. A planigale was defined as 'basking' when it positioned itself directly under the lamp with its body flattened to maximise the surface area exposed to radiation and remained in that position for more than 30 s. Each animal was monitored for seven consecutive days; food was withheld for two non-consecutive nights within this period to test for the effect of food restriction on basking duration.

2.4. Data analysis

Data are presented as mean ± standard deviation. 'n' denotes the number of individuals, 'N' the number of observations. Analysis of variance (ANOVA) and Student's t-tests were performed to test for differences in means. The relationship between T_a and MR was investigated using linear regressions. For behavioural analyses nocturnal activity was defined as the sum of activity recorded between lights off (18:00) and lights on (06:00). Respirometry measurements were terminated if individuals were too restless for 23-h measurements, resulting in variations in 'n'. All analyses were conducted using *StatistiXL* v1.7 for Microsoft Excel.

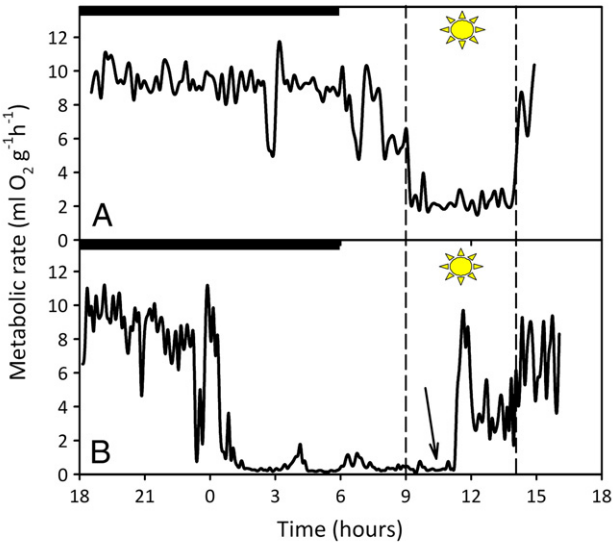

Fig. 1. Metabolic rate (solid line) for two representative *P. gilesi* at $T_a = 15$ °C with access to a radiant heat lamp between 09:00 and 14:00 (dashed vertical lines and sun symbol). The individual that remained normothermic (A) moved under the basking lamp immediately after it was switched on and thereby reduced MR; the torpid animal (B) moved under the lamp at 10:48 (arrow). Both animals remained under the lamp for most of the time until it was switched off (see text for details).

3. Results

3.1. Respirometry

The mean RMR ($RMR_{non\text{-}bask}$) of normothermic planigales (1) was 5.22 ± 0.71 ml $O_2\,g^{-1}\,h^{-1}$ at $T_a = 15$ °C and 3.48 ± 0.13 ml $O_2\,g^{-1}\,h^{-1}$ at 20 °C (n = 6). During the 24 h-exposure to 15 °C with access to radiant heat (2), animals that remained normothermic (n = 5) moved under the lamp immediately after it was switched on. MR showed a steep decrease at the start of basking and a steep increase once the lamp was turned off (Fig. 1A). The RMR during basking (RMR_{bask}) was reduced by 58% to 2.19 ± 0.34 ml $O_2\,g^{-1}\,h^{-1}$ ($t_9 = 8.7$; $P < 0.001$). During basking planigales sat upright and alternated between basking periods of 10–30 min and periods spent in the shaded side of the chamber of 3–5 min, until the light was turned off (14:00). Two individuals entered torpor, which decreased their MR to 0.37 ± 0.01 ml $O_2\,g^{-1}\,h^{-1}$, presenting a significant reduction of 93% compared to $RMR_{non\text{-}bask}$ ($t_5 = 16.7$, $P < 0.001$; Fig. 1B). Torpor bout duration was 4 h 18 min (05:45 to 10:03) and 10 h 54 min (00:27 to 11:21). Animals moved under the basking lamp while torpid (at 09:31 and 10:48, respectively) and aroused within the next 30 min (Fig. 1B). During the scotophase planigales were highly active and MR increased to 8.22 ± 0.81 ml $O_2\,g^{-1}\,h^{-1}$ (Fig. 1A).

During the 24 h-exposure to the T_a cycle (3), planigales moved under the lamp immediately after it turned on, which caused a steep decrease in MR (Fig. 2) from $RMR_{non\text{-}bask} = 5.67 \pm 0.98$ ml $O_2\,g^{-1}\,h^{-1}$ to $RMR_{bask} = 2.17 \pm 1.0$ ml $O_2\,g^{-1}\,h^{-1}$ (at $T_a = 17.1 \pm 0.3$ °C; n = 3). Without access to the basking lamp, RMR showed a significant increase with decreasing T_a; however, during basking this relationship was not significant (Fig. 3; $RMR_{non\text{-}bask} = -0.258 \times T_a + 9.44$, $F_{1,34} = 138.3$, $P < 0.001$, $R^2 = 0.80$; $RMR_{bask} = -0.022 \times T_a + 2.39$, $F_{1,13} = 0.9$, $P = 0.37$, $R^2 = 0.06$). The basal MR (BMR) was 1.55 ± 0.27 ml $O_2\,g^{-1}\,h^{-1}$ (n = 6), which was measured within their thermal neutral zone (29–34 °C; see [30]) at the end of the cycle ($T_a = 31.3 \pm 0.21$ °C).

The mean T_b at the respirometry measurements (1) was 31.8 ± 1.8 °C at $T_a = 15$ °C and 31.6 ± 0.6 °C at $T_a = 20$ °C. At the 24 h-exposure to 15 °C (2) the mean T_b was 31.4 ± 1.3 °C and at the T_a cycle (3) the mean T_b was 34.3 ± 1.3 °C (measured at $T_a = \sim 31$ °C). T_b was significantly affected by T_a ($F_{3,20} = 6.60$, $P < 0.01$); however, the pairwise comparison revealed that while T_a cycle differed from all other treatments ($P < 0.05$ for all three), the other measurements were indistinguishable ($P > 0.7$ for all three).

3.2. Behavioural observations

All but one animal basked in their home cages even though they had never experienced a basking lamp before. Basking planigales

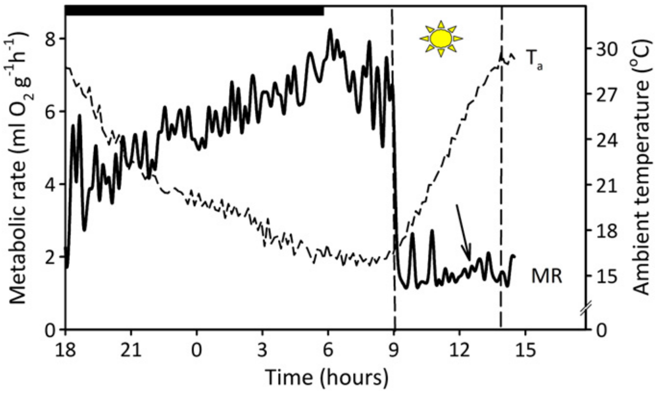

Fig. 2. Metabolic rate (MR, solid line) of a *Planigale gilesi* exposed to an ambient temperature (T_a) cycle (dashed line) with access to radiant heat (vertical dashed lines with sun symbol). The planigale moved under the lamp immediately after it was switched on and stopped basking at 12:52 (arrow). The black bar indicates the scotophase.

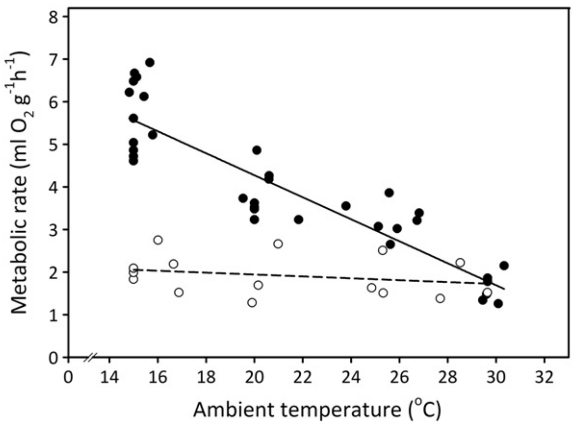

Fig. 3. The effect of ambient temperature on resting metabolic rate during basking (RMR_{bask}; open circles and dashed line) and non-basking ($RMR_{non\text{-}bask}$; closed circles and solid line) in *Planigale gilesi*. See text for regression equations and F-statistics.

were observed stretching out and flattening their bodies in a fashion identical to that of animals in the wild (see Fig. 2 in [29]), which was different to the basking posture in the metabolic chamber. Overall, planigales spent 44 h in Side E during times of video observation, 92% of which was spent basking, while most of the remaining 8% was spent grooming. Basking began at 09:45 h ± 74 min, but basking duration varied greatly among individuals (Table 1). Therefore, animals were divided into three groups according to their basking patterns: basking on more than 86% of days (Group A, $n=3$); basking only after food withdrawal (Group B, $n=3$); and no basking at all (Group C, $n=1$).

Group A showed a significant increase in basking duration on days of food withdrawal ($F_{5,15}=7.3$, $P<0.01$). Most animals employed short basking periods of 2–10 min before retreating into the sheltered side for 20–40 min, before positioning themselves under the basking lamp again. Given that RMR at $T_a=20$ °C was 3.48 ± 0.13 ml O_2 g^{-1} h^{-1} and that MR during basking was unaffected between T_as of 15 °C and 30 °C (Fig. 3), it can be assumed that basking planigales in their home cages achieved reductions in RMR of around 37%.

Activity levels differed significantly ($F_{13,35}=13.0$, $P<0.001$), and were affected by individual ($P<0.001$), but not by food regime ($P=0.71$). All planigales showed clear nocturnal activity patterns, with 88 ± 8% of activity recorded at night; this percentage of nocturnal activity differed significantly among individuals, ranging from 75 to 97% ($F_{6,42}=16.7$, $P<0.001$).

4. Discussion

Our study demonstrates the importance of basking for behavioural thermoregulation in Giles' planigale, the smallest mammal known to bask. Planigales actively left their shelter to position themselves under a radiant heat source, which resulted in significant reductions in energy expenditure. Observations in home cages showed that basking duration increased in response to food withdrawal, while activity levels remained stable. These findings support previous reports of basking in free-ranging planigales indicating that basking positively affects their energy budget. It appears that these benefits outweigh the increased risk of predation during basking.

The potential energetic benefits of basking in mammals have long been discussed [2,3], but only a few studies have focussed on the actual energetic implications of this behaviour. Stripe-faced dunnarts *S. macroura* were able to maintain RMR values at their BMR level at T_as ranging from 12 °C to 22 °C when exposed to radiant heat [18]. When fat-tailed dunnarts *S. crassicaudata* were given the choice of either staying in a shelter or moving into an open space to gain radiant heat [20], all dunnarts actively moved under the heat source and achieved reductions in RMR of up to 74%. We made similar findings for the sympatric Giles' planigale, which reduced RMR due to basking by more than 50% when exposed to either a constant T_a of 15 °C or a T_a cycle. Importantly, during basking the usual relationship between T_a and MR, where decreasing T_a causes an increase in MR, was no longer valid, and MR was not affected by a difference in T_a of 13 °C (15 °C versus 28 °C). These results demonstrate that during basking the costs of thermoregulation were reduced by radiant heat absorption, resulting in a RMR that is largely independent of T_a. This is remarkable for very small endotherms like planigales and dunnarts that normally have relatively high costs of living.

Basking presents a trade-off between an increased risk of predation and energetic advantages [17]. In the planigales' habitat, individuals are exposed to aerial predators (birds of prey), terrestrial predators (cats and foxes), and underground predators (snakes). Given this high predation pressure, it is surprising that planigales in the wild were observed to leave their shelter to bask in the open [29]. We simulated conditions in the wild by giving planigales the choice between either gaining heat in the open or remaining under protective cover without heat access. Usually captive planigales are very anxious, show minimal diurnal activity, hide in their nest boxes throughout the day and avoid open spaces. However, when an opportunity for basking was provided, we observed animals entering the cage side without shelter for the direct purpose of gaining radiant heat, as basking accounted for >90% of the time spent here. The energetic benefits of gaining radiant heat therefore seemed to outweigh the risk of predation. Similarly, during the respirometry measurements, all individuals left the protected side of the metabolic chamber and moved under the heat source when T_a was around 15 °C. However, in the home cages their willingness to leave the nest box and move into the open space was lower than in the metabolic chamber, most likely due to reduced energetic constraints in their home cages (i.e. higher T_a and presence of nesting material). The energy shortage induced through food deprivation either triggered the use of basking or caused an increase in basking duration. This supports previous studies for free-ranging animals, where a correlation between increased basking and reduced food availability was found [5,15,17]. Activity levels were unaffected by food restriction, which contradicts findings for spiny mice [35], but supports data for dunnarts [36]. It appears that planigales regulate basking rather than activity levels to compensate for a decreasing energy supply.

The patterns of basking behaviour observed in our study were highly variable among individuals as well as between experimental set-ups. The intra-specific variability in basking occurrence and duration in home cages was possibly a consequence of animals' personality, which can affect individual responses to a given situation [37], and can cause intra-specific differences in response to certain experimental conditions [35]. Individual basking periods were frequent but short, which was similar to findings during

Table 1
Time spent basking (min day^{-1}) on seven consecutive days of recording. Basking times of <5 min day^{-1} were omitted. Days when food was withdrawn on the previous night are marked as *. Group A basked on >86% of days with increased basking duration after food withdrawal ($n=3$), Group B basked only after food withdrawal ($n=3$), and Group C did not bask at all ($n=1$).

Animal	Group	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
1	A	0	9	113*	68	30	94*	32
3	A	13	13	6	59*	24	36*	22
6	A	28	190	54	136	369*	407	365*
4	B	0	0	0	0*	0	36*	0
5	B	0	0	10*	0	41*	0	0
7	B	0	0	0	0	210*	0	55*
2	C	0	0	0	0	0	0	0

respirometry measurements. This pattern resembles the shuttling regulatory system of lizards [38], where a T_a near the lower T_b setpoint triggers behavioural thermoregulation used to increase T_b, and vice versa. In the metabolic chamber planigales at 15 °C remained under the light until it was turned off while individuals exposed to the T_a cycle stopped basking once T_a reached ~28 °C. Thus it appears that at that point the benefits from the radiant heat source are met by T_a, enabling planigales to retreat back to shelter without having to increase endogenous heat production. The different basking postures observed between the two experimental set-ups were unexpected; because the flattened posture used in the home cages was identical to observations of basking planigales in the wild (see Fig. 2 in [29]), we assume this to be the normal basking posture. The upright position of animals in the respirometry chamber is most likely due to the restricted room in the chamber and a state of alertness in the unfamiliar environment. Generally, it appears that planigales maximise the uptake of radiant heat by adjusting their basking posture to increase the surface area of their dark fur exposed (Plate 1), while minimising the risk of predation by keeping basking periods as short as possible.

The interaction of torpor and basking in marsupials has recently been reviewed showing an increasing number of heterothermic species observed basking during arousal from torpor [25]. Planigales are among the species that are able to achieve the highest savings during torpor, with substantial energy reductions of up to 95% measured at T_as between 13 and 15 °C [30]. Similarly, we measured reductions in energy expenditure of 92% when compared to normothermic values. Although the low number of torpor bouts observed in our study does not allow for further interpretation, the two torpid individuals that were seen moving under the heat lamp to employ heat-assisted arousal strongly suggest that planigales achieve reduced torpor arousal costs. This has been demonstrated for two sympatric dunnart species [18,20]; for the fat-tailed dunnart it was estimated that the combination of torpor and basking can reduce their daily energy expenditure by 64% [19], and similar reductions are probable for Giles' planigale.

Our data show that Giles' planigale, as the smallest mammal known to bask, is able to maintain stable normothermic RMRs over a wide range of T_as when provided with a radiant heat source. For animals in the wild during winter this would reduce daily energy needs enormously, which in return would decrease foraging pressure and therefore the risk of predation. Overall, our study emphasises the importance of basking behaviour in a very small heterothermic mammal, thus providing further evidence of the effectiveness of this energy saving tool that has been largely overlooked in the past. Our results demonstrate that an animal's ecology must always be considered to be a combination of physiological and ethological parameters, which cannot be understood on their own.

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