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F. Geiser · R. L. Drury · B. M. McAllan · D.-H. Wang

Effects of temperature acclimation on maximum heat production, thermal tolerance, and torpor in a marsupial

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Abstract Marsupials, unlike placental mammals, are believed to be unable to increase heat production and thermal performance after cold-acclimation. It has been suggested that this may be because marsupials lack functional brown fat, a thermogenic tissue, which proliferates during cold-acclimation in many placentals. However, arid zone marsupials have to cope with unpredictable, short-term and occasionally extreme changes in environmental conditions, and thus they would benefit from an appropriate physiological response. We therefore investigated whether a sequential two to four week acclimation in *Sminthopsis macroura* (body mass approx. 25 g) to both cold (16°C) and warm (26°C) ambient temperatures affects the thermal physiology of the species. Cold-acclimated *S. macroura* were able to significantly increase maximum heat production (by 27%) and could maintain a constant body temperature at significantly lower effective ambient temperatures (about 9°C lower) than when warm-acclimated. Moreover, metabolic rates during torpor were increased following cold-acclimation in comparison to warm-acclimation. Our study shows that, despite the lack of functional brown fat, short-term acclimation can have significant effects on thermoenergetics of marsupials. It is likely that the rapid response in *S. macroura* reflects an adaptation to the unpredictability of the climate in their habitat.

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F. Geiser (✉) · R. L. Drury · D.-H. Wang
Zoology, BBMS, University of New England,
2351 Armidale, NSW, Australia
E-mail: fgeiser@metz.une.edu.au

B. M. McAllan
Human Biology, BBMS, University of New England,
2351 Armidale, NSW, Australia

D.-H. Wang
Institute of Zoology, Chinese Academy of Sciences,
19 Zhongguancun Road, Haidian,
100080 Beijing, China

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Abbreviations *ADMR* average daily metabolic rate · *BMR* basal metabolic rate · *C* apparent thermal conductance · *CA* cold-acclimation · HP_{max} maximum cold-induced heat production · *MR* metabolic rate · *RMR* resting metabolic rate · T_a ambient temperature · T_b body temperature · *TMR* torpor metabolic rate · *WA* warm-acclimation

Introduction

Small marsupials appear to differ from placental mammals in their generation of endogenous body heat. Shivering thermogenesis is generally recognised as a major source of heat in marsupials, however, the mechanisms responsible for non-shivering thermogenesis still have not been resolved. Brown adipose tissue (BAT), which appears to be the major source of non-shivering thermogenesis in small placental mammals (Feist and White 1989; Wunder and Gettinger 1996), is either absent in marsupials or appears to be non-functional (Nicol et al. 1997). This difference in the source of heat could be a possible reason as to why temperature acclimation in marsupials, unlike in placentals (Feist and White 1989; Wunder and Gettinger 1996; Wang et al. 1999), does not appear to substantially alter maximum heat production (HP_{max}) or tolerance of low ambient temperature (T_a) (Smith and Dawson 1985; Dawson and Olson 1988; Opazo et al. 1999; Nespolo et al. 2002).

As Australian marsupials appear to be functionally adapted to respond to unpredictable and abrupt changes of environmental conditions (Lovegrove 1996), this apparent physiological inability to react to thermal challenges may seem surprising. If thermal biology is largely unaltered by short-term acclimation, as suggested by some studies, how could Australian

marsupials possibly cope with environmental challenges in the wild? This is of special interest in dasyurid marsupials, which are among the most successful groups of mammals in the Australian arid zone (Hume 1999; Menkhurst and Knight 2001; Geiser 2003), and would seem to require the functional capability to cope with short-term changes in climate.

To resolve whether or not marsupials are capable of changing their thermal biology in response to unpredictable changes in climate, we investigated how short-term acclimation affects the thermal biology, HP_{max}, and the tolerance of low T_a in the dasyurid marsupial *Sminthopsis macroura* (25 g). As torpor is an important part of the thermal strategy of the species (Geiser et al. 1998) we also investigated whether and how torpor use and patterns are affected by temperature acclimation. We selected this nocturnal insectivorous species for our study because it is found in arid-zone Australia and shows several seasonal changes in its thermal biology (Geiser and Baudinette 1987).

Material and methods

Eight adult male *S. macroura*, captive-bred at the University of New England in Armidale, were used in the study. Animals were maintained individually in cages (40 cm×26 cm×16 cm; containing a cardboard tube open at both ends, length 10 cm, diameter 4 cm) under a 12L:12D photoperiod (lights on 0600–1800 hours), which was close to the natural photoperiod at the beginning of the experiment in March. Cages were cleaned and bedding material changed weekly, at which time animals were weighed and, as the species stores fat in its tail, the maximum tail width was measured using vernier callipers. Food, consisting of canned dog food (Pal) and macerated cat food pellets (Friskies Go-Cat), was supplied daily, water was available ad libitum, and meal worms and a calcium/multi-vitamin supplement (PetVite) were provided once per week.

Before measurements began, we implanted temperature-sensitive transmitters (Mini-mitter, Sunriver, ±0.1°C, mass 1.6 g) that had been sterilised in 70% ethanol under aseptic conditions into the body cavity of the animals under Oxygen/Forthane anaesthesia. Animals were allowed to recover from the surgery for 14 days before measurements began. Prior to surgery, transmitters had been calibrated (to the nearest 0.1°C) in a water bath against a precision mercury thermometer traceable to a national standard.

Animals had been exposed to a T_a of 20°C for months prior to the experiments, and were acclimated sequentially to two T_as. Warm-acclimation (WA) to T_a 26±1°C (about 5°C below the thermoneutral zone (TNZ); where resting metabolic rate (RMR) of *S. macroura* is 1.9-times basal metabolic rate (BMR) (Song et al. 1995) for 16 days, was followed by a 12-day period for measurements during which time animals that were not measured remained at 26°C. When measurements of the WA individuals had been completed, animals were exposed to a stepwise reduction in T_a from 26°C to 16°C over a 4-day period, after which they were cold-acclimated (CA) to 16±1°C (about 15°C below the TNZ; where RMR is 4-times BMR; Song et al. 1995) for 16 days, which was again followed by a 12-day period for measurements during which animals not measured were held at 16°C.

Two types of measurements were performed on both WA and CA individuals. Initially, we performed cooling experiments, which began at about 0800 hours. While MR and body temperature (T_b) were being measured, animals were exposed to a T_a that was reduced in steps from about 30°C to 20°C to 15°C. Each T_a was maintained for 2–3 h to determine RMR at each T_a both in air and in helium-oxygen atmospheres (HeO_2, 21% oxygen in helium). Thus, after adjusting T_a, MR and T_b were measured for about 1 h in each atmosphere at each T_a, which usually resulted in good RMRs because animals were not handled when T_a was changed; values of unsettled individuals were excluded. HeO_2 has been used widely in the past to induce HP_{max} and hypothermia in animals without the risk of cold injury and seems to have no other effects apart from increasing heat loss in comparison to air (Rosenmann and Morrison 1974; Geiser et al. 1996; Holloway and Geiser 2001a). When animals were able to maintain a high T_b during exposure to HeO_2 at T_a 15°C for 30 min, we further decreased T_a by about 2°C every 30 min until animals became hypothermic (T_b fell below 32°C) and MR began to decline, after which animals were removed from the metabolic chambers. The effective T_a at which animals became hypothermic in HeO_2 atmosphere was derived by extrapolating the regression line for RMR in air to the intercept with the average HP_{max} in HeO_2 and subtracting the T_a differential from the measured T_a (Fig. 1). Cooling experiments usually lasted for about 9 h, were always completed within the daytime rest phase of *S. macroura* and were conducted 16–20 days after acclimation began.

When cooling experiments were completed, the T_b and MR of each animal was measured from about 1600 hours for 1 day at two T_as of 26°C and 16°C to determine torpor use and patterns and

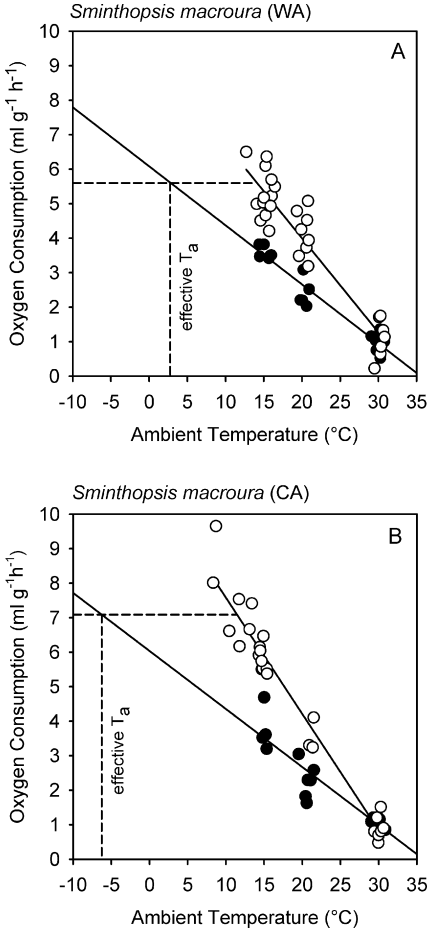

Fig. 1 Oxygen consumption as a function of ambient temperature (T_a) in **A** warm-acclimated (*WA*) and **B** cold-acclimated (*CA*) *Sminthopsis macroura*. *Filled symbols* for measurements in air, *unfilled symbols* in HeO_2. The mean maximum heat production (HP_{max}) is shown by a *broken horizontal line*, the effective T_a where HP_{max} was reached is indicated by a *broken vertical line*. Regression equations in **A** (WA): *air*: $y = 6.08 - 0.171x$ ($r^2 = 0.94$); *HeO_2*: $y = 9.46 - 0.273x$ ($r^2 = 0.88$). Regression equations in **B** (CA): *air*: $y = 6.04 - 0.168x$ ($r^2 = 0.85$); *HeO_2*: $y = 10.96 - 0.337x$ ($r^2 = 0.95$)

average daily metabolic rates (ADMR). These experiments were conducted sequentially after WA and CA during days 21–29 of acclimation. Torpor was defined as a $T_b < 30°C$ and torpor bout duration as the time with a $T_b < 30°C$. As some transmitters in some individuals worked only intermittently in the 24-h measurements of the CA individuals, the time with MR below 75% RMR at the same T_a (Hudson and Scott 1979) was used to calculate torpor occurrence and bout duration.

MR was measured as the rate of oxygen consumption. Animals were placed into 0.75-l glass respirometry chambers (flow rate 500 ml min^{-1}) within a temperature-controlled cabinet (0.5°C) under a 12L:12D photoperiod. Food and water were not available during the measurements. Animals were weighed before and after each measurement and a linear decrease of body mass throughout each measurement was assumed for the calculation of mass-specific MR. Open-flow respirometry was performed with a dual-channel oxygen analyser (Ametek Applied Electrochemistry S-3A/II, Pittsburgh). The millivolt output from two channels (i.e. two individuals were measured simultaneously) was recorded every 3 min. A fresh air sample, taken from outside the building by solenoid valves every 15 min, was used to calculate the O_2 differential in comparison with air from the animal chambers. The flow-rate of dry air passing through the respirometry chamber was controlled with rotameters (7908, Aarlborg, New York) and measured with mass flowmeters (FMA-5606, Omega, Stamford). For both RMR and TMR the lowest three to four consecutive readings (i.e. over 9–12 min) when MR was stable were assumed to represent steady-state values. HP_{max} was determined from the three highest values measured (over 9 min). For calculation of ADMR, measurements were integrated over the entire 23- to 24-h measurements, excluding the 1st hour to exclude the initial high MR due to handling, and converted to Joules assuming 20.083 J ml O_2^{-1}. Calculation of MR was performed according to Eq. 3a from Withers (1977) assuming a RQ of 0.85.

The T_b of individuals was measured every 3 min at the time MR was determined. The transmitter signal from each individual was received with a ferrite rod antenna positioned under the metabolic chamber and connected to a receiver (Geiser et al. 1996). The T_a in the respirometry chamber was read to the nearest 0.1°C by a thermocouple that was inserted 1 cm into the chamber and the T_a readings were amplified by a digital thermometer (Omega DP116). Output from the flowmeter, oxygen analyzer, receiver and digital thermometer were interfaced to a personnel computer using an A/D 14-bit converter card.

Physiological variables between treatments were compared using a repeated measures ANOVA or paired *t*-tests. Linear regressions were fitted by the method of least squares and differences between regression were determined using ANCOVA. Numerical values are means ± SD for the number of individuals (n) measured.

Results

Body mass of *S. macroura* (n = 8) at commencement of WA was 24.9 ± 2.2 g and increased significantly ($F_{(1,7)} = 15.13$; $P < 0.01$) to 27.2 ± 3.3 g after 18 days of WA. During CA body mass did not change (26.0 ± 2.6 g at beginning, 26.2 ± 2.3 g at end, $P > 0.5$). Tail width increased somewhat during WA from 6.6 ± 1.5 mm to 7.5 ± 1.2 mm, but the increase was not significant ($P = 0.072$) and CA also did not significantly affect tail width.

Temperature acclimation had several significant effects on the thermal biology and energetics of *S. macroura*. RMR increased linearly with decreasing T_a in both air and HeO_2 atmosphere (Fig. 1). However, following CA animals could maintain a high MR and consequently a high T_b at lower T_a than following WA. The HP_{max} of WA animals in HeO_2 (5.6 ± 0.7 ml g^{-1} h^{-1}; $n = 8$) was significantly lower ($F_{(1,7)} = 19.11$; $P < 0.01$) than in CA animals (7.1 ± 1.3 ml g^{-1} h^{-1}; $n = 8$). These HP_{max} values occurred at T_a 14.1°C (effective T_a 2.8°C) in WA and T_a 11.5°C (effective T_a –6.3°C) in CA animals. The MR in air at the thermoneutral T_a 30°C was 0.98 ± 0.26 ml g^{-1} h^{-1} in WA individuals ($n = 8$), which increased somewhat to 1.08 ± 0.14 ml g^{-1} h^{-1} in CA individuals ($n = 8$), but the difference was not significant ($P > 0.1$).

In contrast to the response in air atmosphere, where the slope of RMR as a function of T_a, and consequently the apparent thermal conductance (C) did not differ between CA and WA (slope and intercept $P > 0.5$, ANCOVA), the slope of the regression line in HeO_2 atmosphere was significantly steeper ($F_{(1,37)} = 8.99$; $P < 0.01$; ANCOVA) and C significantly higher in CA in comparison to WA individuals. This is likely because the CA animals in HeO_2 maintained a higher T_b (Fig. 2; $F_{(1,29)} > 4.3$; $P < 0.05$ slope and intercept ANCOVA) as a

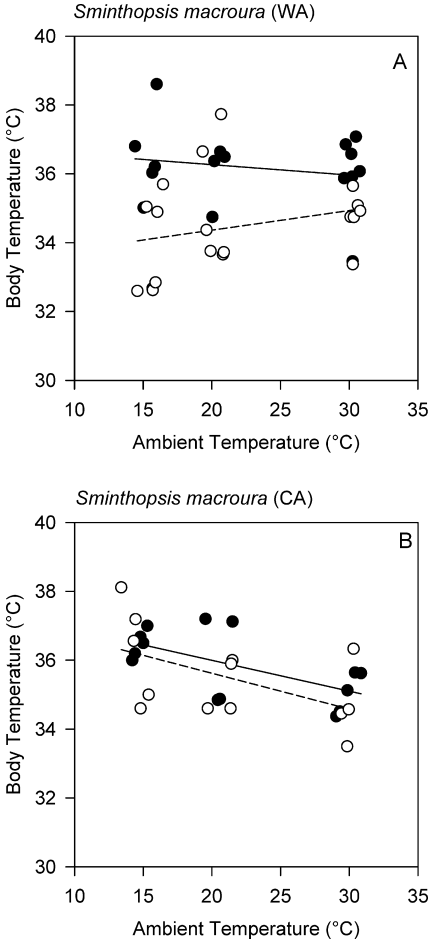

Fig. 2 Body temperatures (T_b) as a function of T_a in **A** WA and **B** CA *S. macroura*. *Filled symbols* for measurements in air, *unfilled symbols* in HeO_2. Regression equations in **A** (WA):*air*: $y = 36.87 - 0.03x$ ($r^2 = 0.03$); *HeO_2*: $y = 33.22 + 0.057x$ ($r^2 = 0.07$). Regression equations in **B** (CA): *air*: $y = 37.78 - 0.089x$ ($r^2 = 0.38$); *HeO_2*: $y = 37.70 - 0.104x$ ($r^2 = 0.28$)

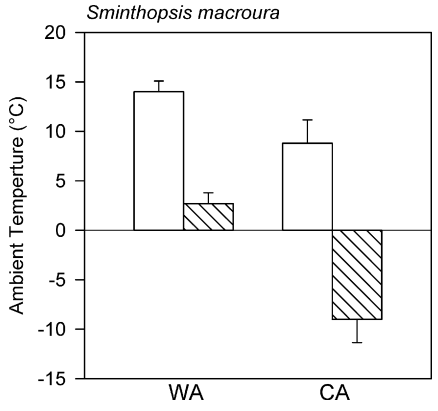

Fig. 3 T_a (*clear*) and effective T_a (*hatched*) at which WA ($n=8$) and CA ($n=8$) *S. macroura* became hypothermic in a HeO_2 atmosphere

function of T_a in comparison to WA animals. Whereas slope and intercept of T_b versus T_a did not differ between air and HeO_2 atmospheres in CA animals ($P>0.5$), the intercept in WA animals in HeO_2 was significantly lower than in air ($F_{(1,32)}=14.54$; $P<0.001$).

Because CA animals were able to increase MR more during cold exposure than WA animals, the T_a at which they became hypothermic (T_b fell below 32°C) differed between treatments (Fig. 3). The T_a where hypothermia was induced in HeO_2 atmosphere was significantly higher ($F_{(1,7)}=28.18$; $P<0.001$, ANOVA) in WA (T_a 14.0 ± 1.1°C, effective T_a 2.7 ± 1.1°C; $n=8$) than in CA animals (T_a 8.8 ± 2.4°C, effective T_a –9.0 ± 2.4°C; $n=8$).

Temperature acclimation affected torpor patterns only marginally. Torpor occurrence was similar among acclimation groups and T_a measured (WA 7/8 individuals at both T_a 26°C and 16°C, but one individual became hypothermic and was unable to arouse at 16°C; CA 6/8 individuals at T_a 26°C and 8/8 individuals at T_a 16°C). Torpor duration was also unaffected by acclimation and T_a (WA: 309 ± 119 min, T_a 26°C; 367 ± 201 min, T_a 16°C; CA: 387 ± 326 min, T_a 26°C; 341 ± 256 min, T_a 16°C). Nevertheless, the TMR at T_a 16°C was significantly lower ($t=2.47$; $P<0.05$) in the WA animals (0.150 ± 0.066 ml g^{-1} h^{-1}; $n=7$) than in the CA animals (0.313 ± 0.263 ml g^{-1} h^{-1}; $n=7$), despite the high SD in the latter. The ADMR at T_a 16°C was about 1.5-times (WA) and 1.7-times (CA) greater than at T_a 26°C; however, temperature acclimation did not significantly affect ADMR (WA: 26.6 ± 4.9 kJ day^{-1}, T_a 26°C; 39.6 ± 7.5 kJ day^{-1}, T_a 16°C; CA: 22.1 ± 7.5 kJ day^{-1}, T_a 26°C; 37.8 ± 9.1 kJ day^{-1}, T_a 16°C).

Discussion

Our study shows that short-term temperature acclimation can substantially alter heat production and cold tolerance in a marsupial. Acclimation to cold increased the HP_{max} of the arid zone *S. macroura* by 27% and the effective T_a they were able to withstand during short-term cold exposure was lowered by about 9°C.

Our findings are in agreement with long-term studies on seasonal acclimatisation in marsupials. In winter both thermal tolerance and HP_{max} in sugar gliders (*Petaurus breviceps*) held in outdoors enclosures were improved in comparison to summer (Holloway and Geiser 2001b). However, our results differ from other studies on temperature acclimation in small marsupials in the laboratory. Acclimation of *Dasyuroides byrnei* for 4–6 weeks to either cold (T_a 10°C) or warm (T_a 25°C) did not affect peak metabolic rates, although CA individuals were able to maintain a stable T_b longer at low T_a (Smith and Dawson 1985). Moreover, in comparison to WA, CA *D. byrnei* showed increased metabolic rates over the entire range of T_a tested (Smith and Dawson 1985). This is in contrast to winter-acclimatised *D. byrnei*, which show reduced RMR in comparison to summer (Geiser and Baudinette 1987) and unlike the *S. macroura* in the present study, which, when measured in air showed similar RMR as a function of T_a, and consequently C, after WA and CA. In short-tailed opossums, *Monodelphis domestica*, MR increased at most T_a investigated following CA, but HP_{max} and thermoregulation at low T_a did not change significantly in comparison to WA individuals (Dawson and Olsen 1988). In mouse-opossums, *Thylamys (Marmosa) elegans,* the major effect of cold-acclimation was a reduction of the cost of rewarming from torpor (Opazo et al. 1999) and a rise of BMR (Nespolo et al. 2002).

Differences in the response to temperature acclimation in marsupials and differences between temperature acclimation and seasonal acclimatization in endotherms in general could be due to a number of reasons. It is not unexpected that seasonal acclimatization results in different thermoenergetic responses within the same species, because during acclimatization more than one environmental variable is altered and a long time period is available for physiological and morphological changes. In contrast, during thermal acclimation only one environmental variable is altered, usually for a short time period, and the physiological response is likely to be different or less pronounced (Holloway and Geiser 2001b).

When differences among related species to temperature acclimation are considered it is possible that marsupials from different habitats or climates (i.e. South American versus Australian) differ in their response. However, the observed differences in the response of arid zone dasyurid marsupials obviously cannot be explained by climate or habitat, but rather are likely to be due to effects of size and also experimental protocol. *Dasyuroides byrnei* at a body mass of about 120 g shows less pronounced seasonal changes in thermal biology than the smaller *S. macroura* (25 g) and *S. crassicaudata* (17 g) (Geiser and Baudinette 1987) and consequently *Dasyuroides* is likely to show a less pronounced response to temperature acclimation than *Sminthopsis* spp. Moreover, unlike in the present study, where T_b readings were available throughout the metabolic measurements and permitted a continuous monitoring of

normothermic T_b, previous studies on dasyurids relied on MR only to determine maximum heat production, perhaps at sub-optimal T_b. These previous experiments were also conducted over longer measurement periods (2.5 h; Smith and Dawson 1985) than in the present study (9 min). Thus, it is possible that the animals were unable to reach their true HP_{max} because they were exhausted, or fuel became limiting. The physiological response to temperature acclimation observed here in *S. macroura* seems to be appropriate for a species living in a highly unpredictable environment, and it is likely that other, especially small, marsupials from changeable habitats use similar approaches.

In agreement with previous studies on carnivorous marsupials, *S. macroura* was able to substantially increase metabolic rates during acute cold exposure despite their relatively low BMR (MacMillen and Nelson 1969; Dawson 1989). The metabolic scope (i.e. the ratio of maximum cold-induced metabolism/BMR) was 8.0 for CA and 6.3 for WA individuals, similar to that of other marsupials (Hinds and MacMillen 1984; Dawson 1989; Hinds et al. 1993). While this thermal performance seems impressive and begs for a functional explanation, mechanisms of heat production in carnivorous marsupials, as for marsupials in general, remain controversial. Whereas BAT is responsible for much of the improved thermogenic response in winter or CA small placental mammals (Feist and White 1989; Wunder and Gettinger 1996; Merritt et al. 2001), BAT in marsupials appears to be either absent or non-functional (Nicol et al. 1997; Rose et al. 1999). However, marsupials are able to use vasoconstrictor-induced non-shivering thermogenesis in skeletal muscle (Eldershaw et al. 1996), which may improve during cold acclimation. Moreover, CA increases thyroid secretion by 3.1-fold in comparison to warm acclimation in *Antechinus stuartii* (Withers and Hulbert 1988) and increases liver, kidney and caecum size in *Thylamys elegans* (Nespolo et al. 2002), which also may contribute to a rise in heat production. Marsupials also are known to possess uncoupling proteins that may be thermogenic, but are associated with tissues other than BAT (Clements et al. 1998), and shivering tremor is reduced after CA in *D. byrnei* (May 2003), suggesting involvement of non-shivering thermogenesis. Thus, it is likely that together with improved shivering thermogenesis, non-shivering thermogenesis plays a role in the adjustment of the physiological thermoregulatory response to cold exposure in marsupials.

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