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Reduction of metabolic rate and thermoregulation during daily torpor

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Abstract Physiological mechanisms causing reduction of metabolic rate during torpor in heterothermic endotherms are controversial. The original view that metabolic rate is reduced below the basal metabolic rate because the lowered body temperature reduces tissue metabolism has been challenged by a recent hypothesis which claims that metabolic rate during torpor is actively downregulated and is a function of the differential between body temperature and ambient temperature, rather than body temperature per se. In the present study, both the steady-state metabolic rate and body temperature of torpid stripe-faced dunnarts, *Sminthopsis macroura* (Dasyuridae: Marsupialia), showed two clearly different phases in response to change of air temperature. At air temperatures between 14 and 30 °C, metabolic rate and body temperature decreased with air temperature, and metabolic rate showed an exponential relationship with body temperature ($r^2 = 0.74$). The Q_{10} for metabolic rate was between 2 and 3 over the body temperature range of 16 to 32 °C. The difference between body temperature and air temperature over this temperature range did not change significantly, and the metabolic rate was not related to the difference between body temperature and air temperature ($P = 0.35$). However, the apparent conductance decreased with air temperature. At air temperatures below 14 °C, metabolic rate increased linearly with the decrease of air temperature ($r^2 = 0.58$) and body temperature was maintained above 16 °C, largely independent of air temperature. Over this air temperature range, metabolic rate was positively correlated with the difference between body temperature and air temperature ($r^2 = 0.61$). Nevertheless, the Q_{10} for metabolic rate between normothermic and torpid thermoregulating animals at the same air temperature was also in the range of 2–3. These results suggest that over the air temperature range in which body temperature of *S. macroura* was not metabolically defended, metabolic rate during daily torpor was largely a function of body temperature. At air temperatures below 14 °C, at which the torpid animals showed an increase of metabolic rate to regulate body temperature, the negative relationship between metabolic rate and air temperature was a function of the differential between body temperature and air temperature as during normothermia. However, even in thermoregulating animals, the reduction of metabolic rate from normothermia to torpor at a given air temperature can also be explained by temperature effects.

Key words Daily torpor · Metabolic rate reduction · Temperature · Thermoregulation · Marsupial, *Sminthopsis macroura*

Abbreviations *BM* body mass · *BMR* basal metabolic rate · *C* apparent conductance · *MR* metabolic rate · *RMR* resting metabolic rate · *RQ* respiratory quotient · T_a air temperature · T_b body temperature · T_{lc} lower critical temperature · T_{tc} critical air temperature during torpor · *TMR* metabolic rate during torpor · *TNZ* thermoneutral zone · ΔT difference between body temperature and air temperature · $\dot{V}O_2$ rate of oxygen consumption

Introduction

Heterothermic endotherms are able to substantially reduce their MR and T_b during periods of torpor (Lyman et al. 1982; Wang 1989). Although low MRs and T_bs have been observed in many species, the physiological mechanisms causing the reduction of MR and the interrelations between the drop of MR and T_b during torpor remain controversial (Malan 1986, 1993; Geiser 1988, 1993; Heldmaier and Ruf 1992).

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Because in many species the Q_{10} of MR reduction is between 2 and 3, which characterises the temperature dependence of many biological reactions, it was originally claimed that MR is reduced by the lowered T_b (Tucker 1965; Snapp and Heller 1981). However, Q_{10} values well above 2–3 have been observed in small hibernators and also during entry into torpor (Kayser 1964; Morrison and Ryser 1962; Henshaw 1968; Geiser 1988), and it was concluded that metabolic inhibition, in addition to temperature effects, may cause the low MR during torpor (Malan 1986; Geiser 1988; Storey and Storey 1990).

Recently, this view has been challenged by a new hypothesis, which claims that MR during hibernation and daily torpor is actively downregulated and is entirely independent of T_b. According to this hypothesis MR during both normothermia and torpor is proportional to ΔT, and the drop of T_b is merely a consequence of an actively suppressed MR (Heldmaier and Ruf 1992).

To test these hypotheses, we measured MR, T_b and T_a in a small nocturnal marsupial, the stripe-faced dunnart, *Sminthopsis macroura*, both below and above the set-point for T_b during torpor and during normothermia. The species was selected because it displays torpor with no apparent defence of T_b over a wide T_a range above approximately 15 °C and with physiological thermoregulation below this T_a (Geiser and Baudinette 1985). The data were used to determine interrelations between MR, T_b and ΔT in these two temperature ranges during torpor and for comparison with values from normothermic individuals.

Material and methods

Animals

Sminthopsis macroura is a small dasyurid marsupial, which is found in arid and semiarid areas of central Australia (Morton 1983). The seven animals used in the present study were obtained from a breeding colony at La Trobe University, Melbourne, and were transferred to the University of New England in Armidale. All animals were mature males (about 1.5 years old) with a BM ranging between 21 and 35 g. Animals were maintained individually in cages (30 × 22 × 14 cm) containing sawdust, shredded paper and nest-boxes. Cages were cleaned once every week. The photoperiod throughout the experiment was 12L:12D (lights on 0600–1800 hours) and T_a was 20 ± 2 °C. The food, consisting of canned dog food mixed with macerated cat food pellets supplemented with calcium and vitamins, was changed daily. Water was available ad libitum. *Tenebrio* larvae were provided occasionally.

Measurements of MR, T_b and T_a

For determination of MR, measured as rate of oxygen consumption ($\dot{V}O_2$), animals were placed into 0.5-l respiratory chambers within a temperature-controlled cabinet (±0.5 °C). Four channels, three animal channels and one reference channel, were scanned with solenoid valves. Each channel was read for 3 min (i.e. outside air and $\dot{V}O_2$ of each individual was measured every 12 min). The flow rate (about 200 ml·min^{-1}) of dry air through the respiratory chamber was measured with a mass flowmeter (FMA-5606, Omega, Stamford). Oxygen content of air leaving the respiratory chamber and in the reference chamber was consecutively measured with a single channel oxygen analyser (Ametek Applied Electrochemistry S-3A/1, Pittsburgh) fitted with a high resolution output board (80335SE).

Temperature-sensitive transmitters (Minimitter Model X-M, accuracy ± 0.1 °C) were calibrated to the nearest 0.1 °C against a mercury thermometer in a water bath between 5 and 40 °C. The transmitters were implanted intraperitoneally under Halothane anaesthesia. Before the experiments the animals were allowed at least 7 days to recover from the surgery. An antenna consisting of a ferrite rod was placed underneath each respiratory chamber and multiplexed to a receiver (car radio). The transmitter signal was transformed to a square-wave signal after background noise was subtracted.

T_a in the respiratory chamber was measured to the nearest 0.1 °C by a thermocouple inserted about 1 cm into the metabolic chamber. Thermocouple output was amplified by a digital thermometer (Omega DP116). The T_b and T_a of each channel were also determined every 12 min.

Analog outputs from the flowmeter, oxygen analyser, transmitter receiver and digital thermometer were interfaced to a personal computer via a 12 Bit A/D card. Data acquisition and processing were performed with software written by B. Lovegrove, T. Ruf and G. Körtner. $\dot{V}O_2$ values were calculated according to Eq. 3a of Withers (1977) and presented in STPD condition (0 °C, 760 torr, dry). The RQ was assumed to be 0.85, which would result in a maximal error of ±3% in $\dot{V}O_2$ if the RQ was 0.7 or 1.0 (Withers 1977).

Experimental procedures

For determination of TMR and RMR animals were kept in the respiratory chambers at a constant T_a for about 1 day. TMR and RMR were measured at T_as of 7–30 °C. Measurments of BMR were carried out separately between 0930 and 1700 hours after animals had been in the chambers for at least 2 h. BMR was measured at T_as between 25 and 36 °C. T_a was increased progressively in temperature steps of about 1.5 °C with each step lasting for about 2 h, and no more than four T_as were employed on every single day. The light phase inside the cabinet was from 0600 to 1800 hours. BW was recorded before and after each experiment. Food and water were not available during measurements.

Data analysis

RMR values were determined from the mean of the three lowest consecutive $\dot{V}O_2$ values (i.e. over 36 min) in normothermic individuals whose T_bs were not lower than 33 °C. During 1-day measurements, RMR was determined after the animals had been in the chamber for about 2 h during the afternoon. The means of the corresponding three T_b and T_a readings were also calculated. The T_{lc} was determined by the intercept of two regressions fitted through the split data set, whereby the lowest sum of squares for the two regressions determined the best fit (Yeager and Ultsch 1989). BMR was determined as the mean of all mean values of normothermic individuals within the TNZ. Torpor was defined as MR < 75% of RMR at the same T_a; TMR, T_b and T_a during torpor were obtained by calculating the mean of the consecutive three lowest $\dot{V}O_2$ values (i.e. over 36 min) and corresponding T_b and T_a values. Only steady-state data from torpor bouts longer than 2 h were taken into account. The T_{tc}, which separated thermoregulating and non-thermoregulating animals, was determined as the intercept of two linear regressions fitted to TMR versus T_a (Yeager and Ultsch 1989). A linear decrease of BM throughout each experiment was assumed for calculation of mass-specific MR.

The mass-specific C was calculated from MR, T_b and T_a using the equation:

$$C = \frac{\mathrm{MR}}{T_b - T_a} \quad \text{(Schmidt-Nielsen 1990)}.$$

Q_{10}s for MR at different T_bs were calculated according to the equation:

$$Q_{10} = \left(\frac{\mathrm{MR}_1}{\mathrm{MR}_2}\right)^{\frac{10}{T_{b_1} - T_{b_2}}} \quad \text{(Schmidt-Nielsen 1990)}.$$

Statistics

Data are presented as mean ±1 standard deviation. Differences between means were examined using a Student's t-test. Regressions were determined by the method of least squares. Paired comparisons of regressions were conducted using Student's t-test (Zar 1984). Selection of the appropriate regression models (linear or exponential) was made by comparing the coefficient of determination (r^2) for the linear model with that for the regression of the predicted y-value for the exponential model versus the measured y-value. Direct comparison of r^2 for the linear and the exponential regressions could not be made because the total sum of squares of the logarithmic form of the exponential model does not equal the total sum of squares of the linear regression. Equality of the total sum of squares is essential if r^2 is to be compared (Doran and Guise 1984). Data values obtained from the same individual at the same T_a were averaged for statistical analyses. "N" is for number of animals and "n" for total number of measurements.

Results

The MR and T_b of *S. macroura* showed pronounced daily fluctuations (Fig. 1). During the day the animals were usually resting. After lights off, animals became active and both T_b and MR were generally elevated. Animals entered torpor between 2200 and 0500 hours. When entering torpor, both MR and T_b were reduced and steady-state levels were reached after about 2 h. Torpor was terminated by spontaneous arousal, characterised by a steep increase of MR followed by a rise of T_b (Fig. 1).

Normothermia

S. macroura increased their RMR linearly with decreasing T_a ($r^2 = 0.92, P < 0.01$) when exposed to T_as below the T_{lc} of 31.3 ± 1.0 °C ($N = 7$, $n = 119$, Fig. 2a). The TNZ ranged from T_a 31.3 to 34 °C, and BMR was 0.89 ± 0.08 ml·g^{-1}·h^{-1} (BM = 24.8 ± 2.3 g, $N = 7$, $n = 19$, Fig. 2a).

At the T_{lc} the T_b of resting individuals was 34.3 ± 0.6 °C ($N = 7$, $n = 18$). Below the T_{lc}, T_b was inversely related to T_a ($r^2 = 0.37$, $P < 0.01$). Above the T_{lc}, T_b increased with T_a ($r^2 = 0.65$, $P < 0.01$, Fig. 2b).

ΔT ($T_b - T_a$) increased linearly below the T_{lc} ($r^2 = 0.99, P < 0.01$). Above the T_{lc}, ΔT was also negatively correlated with T_a ($r^2 = 0.75$, $P < 0.01$), but the slope was less steep (Fig. 2c).

C during normothermia was 0.20 ± 0.04 ml·g^{-1}·h^{-1}·°C^{-1} ($N = 7, n = 76$) below the T_{lc}. Above the T_{lc}, C increased markedly with T_a ($r^2 = 0.67, P < 0.01$, Fig. 2d).

Torpor

The T_{lc} of *S. macroura* occurred at T_a of about 14 °C. Between T_as of 30–14 °C, torpid individuals showed no evidence of thermoregulation. Both steady-state TMR and T_b in this T_a range decreased with T_a ($r^2 = 0.64$, $P < 0.01$; $r^2 = 0.93$, $P < 0.01$, respectively, Fig. 2a,b), but ΔT remained constant at 2.1 ± 0.9 °C ($N = 7$, $n = 31$, Fig. 2c). Therefore, the C decreased with

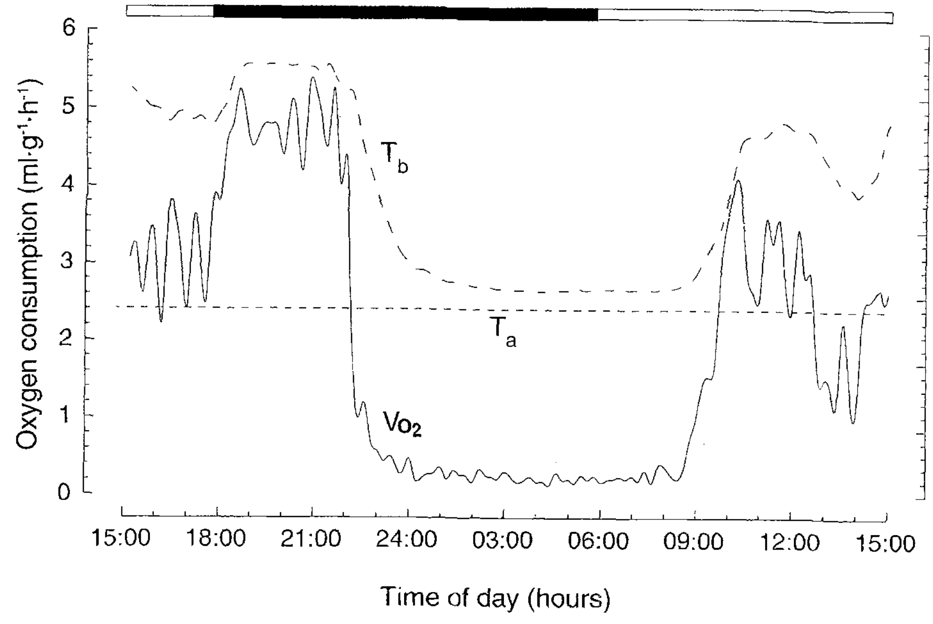

Fig. 1 Fluctuations of oxygen consumption ($\dot{V}O_2$) and body temperature (T_b) of *S. macroura* at an air temperature (T_a) of 19 °C. Food and water were not available. The animal entered torpor just before midnight and aroused at about 0900 hours. The *dark bar* indicates the scotophase

T_a ($r^2 = 0.50$, $P < 0.01$) to the minimum value of 0.09 ± 0.05 ml·g^{-1}·h^{-1}·°C^{-1} ($N = 7$, $n = 13$) at T_a of 14–19 °C, which was significantly lower than the C of normothermic individuals in the same T_a range ($P < 0.01$, Fig. 2d).

Below the T_{tc}, the response of TMR to T_a was reversed and showed an increase with a drop of T_a ($r^2 = 0.58$, $P < 0.01$, Fig. 2a). The T_b in this T_a range did not fall with T_a, but was regulated above 16 °C (Fig. 2b), which resulted in an increase of ΔT ($r^2 = 0.27$, $P < 0.05$, Fig. 2c). With the onset of thermoregulation, C gradually increased with the decreasing T_a ($r^2 = 0.43$, $P < 0.01$) to levels observed during normothermia (Fig. 2d).

In the T_a range in which T_b of torpid *S. macroura* was not metabolically defended, TMR was positively related to T_b (Fig. 3). Both linear ($r^2 = 0.79$) and exponential ($r^2 = 0.74$) fits were appropriate. However, the exponential fit provided the better model, because the r^2 for the regression of the predicted y-value for the exponential model versus the measured y-value ($r^2 = 0.83$) was larger than that for the linear model (Fig. 3). The Q_{10} for TMRs between T_b 16 °C at a T_a of

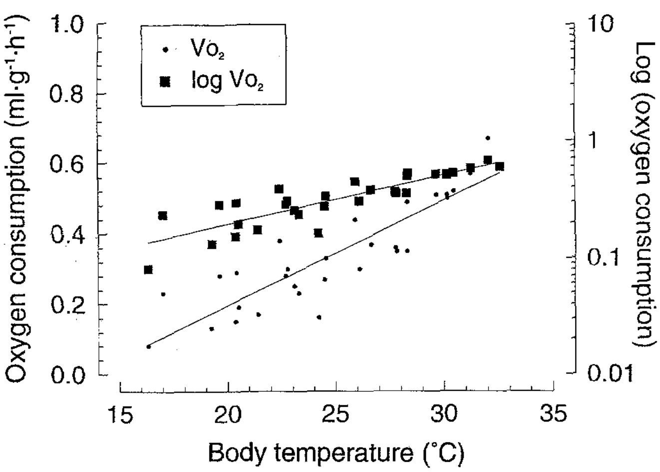

Fig. 3 Metabolic rate during torpor (TMR) as a function of body temperature (T_b) above the critical air temperature during torpor (T_{tc}) in *S. macroura*. Both linear fit (●) (TMR = − 0.41 + 0.03 T_b, $r^2 = 0.79$, $P < 0.01$) and exponential fit (■) (log TMR = − 1.56 + 0.04 T_b, $r^2 = 0.74$, $P < 0.01$) were appropriate. However, the exponential fit provided the better model, because the r^2 for the regression of the predicted y-value for the exponential model versus the measured y-value ($r^2 = 0.83$) was larger than that for the linear model

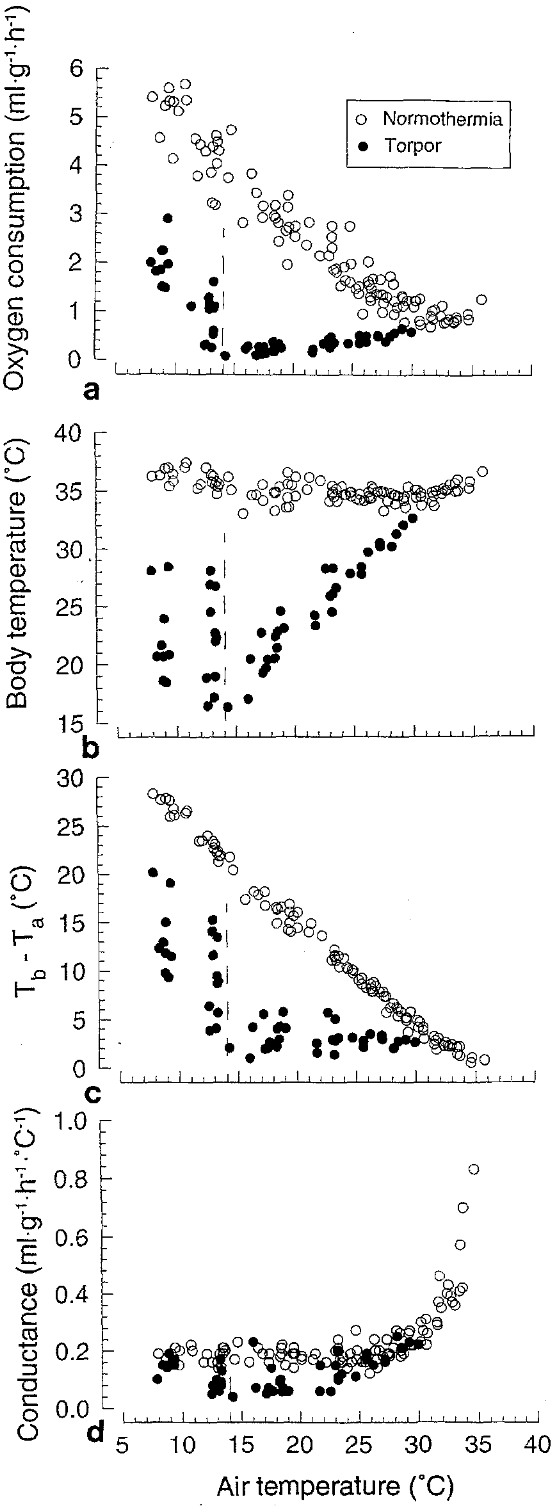

Fig. 2a–d The effect of air temperature (T_a) on **a** metabolic rate measured as rate of oxygen consumption, **b** body temperature, **c** the temperature differential between T_b and T_a, and **d** apparent conductance during daily torpor (●) and normothermia (○) in *S. macroura* ($N = 7$). Regression equations for physiological variables during torpor above 14 °C were: log TMR = − 1.41 + 0.04 T_a, $r^2 = 0.64$, $P < 0.01$; $T_b = 3.69 + 0.97\,T_a$, $r^2 = 0.93$, $P < 0.01$; $\Delta T = 3.69 - 0.03\,T_a$, $r^2 = 0.01$, $P = 0.59$; $C = -0.09 + 0.01\,T_a$, $r^2 = 0.50$, $P < 0.01$. Regression equations for physiological variables during torpor below 14 °C were: TMR = 4.24 − 0.26 T_a, $r^2 = 0.58$, $P < 0.01$; $T_b = 22.8 - 0.04\,T_a$, $r^2 = 0.001$, $P = 0.90$; $\Delta T = 22.8 - 1.04\,T_a$, $r^2 = 0.27$, $P < 0.05$; $C = 0.26 - 0.01\,T_a$, $r^2 = 0.43$, $P < 0.01$. Regression equations for physiological variables during normothermia below the T_{lc} were: RMR = 6.68 − 0.19 T_a, $r^2 = 0.92$, $P < 0.01$; $T_b = 36.8 - 0.08\,T_a$, $r^2 = 0.37$, $P < 0.01$; $\Delta T = 36.7 - 1.08\,T_a$, $r^2 = 0.99$, $P < 0.01$; $C = 0.16 + 0.02\,T_a$, $r^2 = 0.11$, $P > 0.05$. Regression equations for physiological variables during normothermia above the T_{lc} were: RMR = 0.64 + 0.01 T_a, $r^2 = 0.06$, $P > 0.05$. $T_b = 20.5 + 0.44\,T_a$, $r^2 = 0.65$, $P < 0.01$; $\Delta T = 19.4 - 0.53\,T_a$, $r^2 = 0.75$, $P < 0.01$. $C = -3.25 + 0.11\,T_a$, $r^2 = 0.67$, $P < 0.01$

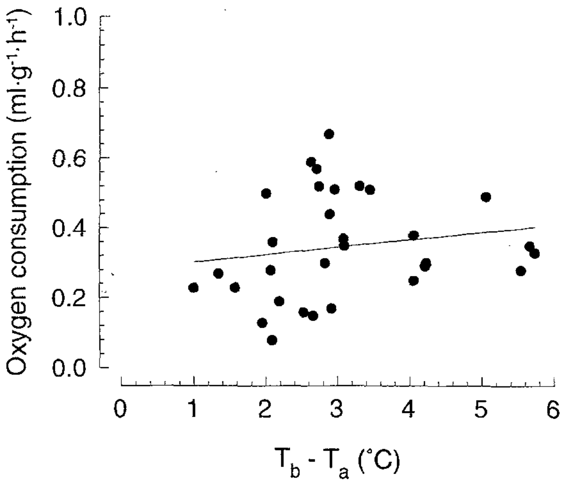

Fig. 4 Metabolic rate during torpor (TMR) as a function of the temperature differential (ΔT) between body temperature (T_b) and air temperature (T_a) above the critical air temperature during torpor (T_{tc}) in *S. macroura*. The equation for the regression was: TMR = 0.28 + 0.02 ΔT, $r^2 = 0.03$, $P = 0.35$

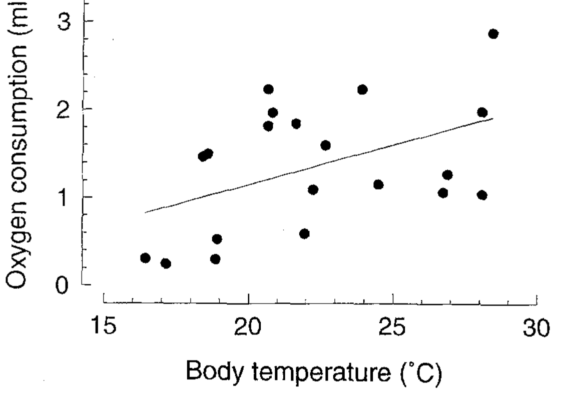

Fig. 5 Metabolic rate during torpor (TMR) as a function of body temperature (T_b) below the critical air temperature during torpor (T_{tc}) in *S. macroura*. The equation for the regression was: TMR = − 0.66 + 0.09 T_b, $r^2 = 0.21$, $P = 0.04$

14 °C and T_b 32 °C at a T_a of 30 °C was 2.56, and the Q_{10} for MR between the BMR at T_b 34.3 °C and TMR at T_b 16 °C at a T_a of 14 °C was 2.79. In contrast to T_b, ΔT ($T_b - T_a$) was not related to the TMR in the T_a range in which T_b was not regulated ($P = 0.35$, Fig. 4).

In the T_a range below the T_{tc} where T_b was regulated, T_b was also correlated with TMR ($r^2 = 0.21$, $P = 0.04$, Fig. 5). In contrast to the situation at high T_as, in this T_a range ΔT ($T_b - T_a$) increased with decreasing T_a and TMR showed a significant relationship with ΔT (Fig. 6). Both the slope and the intercept for the regression of TMR versus ΔT were not significantly different from those for the regression of RMR versus ΔT ($P = 0.50$, $P = 0.31$, respectively, Fig. 6). The Q_{10} for

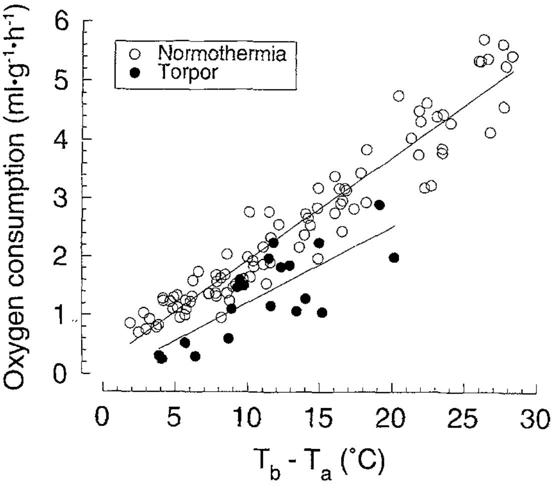

Fig. 6 Metabolic rate during torpor (TMR) (●) below the critical air temperature (T_{tc}) and the resting metabolic rate of normothermic individuals (RMR) (○) below the lower critical temperature (T_{lc}) as a function of the temperature differential (ΔT) between body temperature (T_b) and air temperature (T_a). The equations for the regressions were TMR = − 0.08 + 0.13 ΔT, $r^2 = 0.61$, $P < 0.01$; $RMR = 0.17 + 0.18\,\Delta T$, $r^2 = 0.92$, $P < 0.01$. Both the slope and the intercept of the two regressions were not significantly different ($P = 0.50$, $P = 0.31$, respectively)

MR between RMR at T_b 34.9 °C and TMR at T_b 22.7 °C at a T_a of 10 °C was 2.38.

Discussion

Two responses of TMR to T_a

Torpid *S. macroura* showed two clearly different responses of TMR to a change of T_a. Above a T_{tc}, when T_b of torpid animals was above the set-point for T_b during torpor, T_b was not defended and both TMR and T_b fell with T_a. Below the T_{tc}, when T_b of torpid animals was metabolically defended, TMR was inversely related to T_a. Similar observations have been reported for many mammalian hibernators (Hock 1951; Davis and Reite 1967; Heller and Colliver 1974; Geiser and Kenagy 1988; Song and Zeng 1991) and for daily torpor in mammals and birds (Hainsworth and Wolf 1970; Nagel 1985; Geiser and Baudinette 1987). The differences between these two responses must be kept in mind when interrelations between physiological variables measured during torpor are to be investigated.

Reduction of TMR

In the T_a range in which T_b was not metabolically defended, TMR showed an exponential relationship to T_b. Since the Q_{10} between BMR and TMR in this T_a range was between 2 and 3, it is likely that the reduction of TMR below BMR was mainly caused by temperature effects. The ΔT in this T_a range was constant and was not related to TMR. These findings do not support the interpretations of Heldmaier and Ruf (1992) who suggested that TMR is always a function of ΔT. However, in their study all values of TMR, most of which were determined below the set-point for T_b during torpor, were analysed as a single data set and, therefore, do not explain the thermal response of TMR above the set-point.

The effect of temperature on enzyme and tissue metabolism is well documented for both ectothermic and endothermic organisms (Roberts and Smith 1967; Geiser and McMurchie 1984; Aloia and Raison 1989). In agreement with the values determined in vitro, the Q_{10} of mammalian TMR is generally within the range 2–3 (Tucker 1965; Tähti 1978; Snapp and Heller 1981). However, Q_{10}s above this range have been observed for MRs of small hibernators and during entry into torpor and it appears that in these cases metabolic inhibition, in addition to temperature effects, may cause a further reduction of TMR (Malan 1986, 1988; Geiser 1988). Nevertheless, as pointed out by Snapp and Heller (1981), some of the Q_{10} values above the "normal" range can also be due to experimental artefacts such as "BMRs" measured below the TNZ or determination of TMR during apnoea. Moreover, illogical or inconsistent calculations comparing thermoregulating and non-thermoregulating individuals for calculating Q_{10}s for TMR (Snyder and Nestler 1990) may lead to values that are not within the predicted range (Malan 1993). The logic behind applying Q_{10} to endotherms is unsound (Snyder and Nestler 1990) only when basic rules for calculation of Q_{10} as an expression of the direct effect of temperature on rates (Schmidt-Nielsen 1990) are violated.

The minimum C of both normothermic and torpid *S. macroura* were close to those calculated for similar-sized rodents (Snyder and Nestler 1990). The C of torpid animals was similar to that of normothermic inactive animals at high T_as below the T_{lc}, but it decreased with T_a in non-thermoregulating torpid animals. This lowered C may prevent T_b from reaching the set-point during torpor, which would induce an increase of TMR. Our findings appear to be in contrast to those by Heldmaier and Ruf (1992), who reported similar conductance in torpid and normothermic hamsters, *Phodopus sungorus*. However, their measurements concentrated on T_as below the set-point for T_b. At very low T_as, C of torpid *S. macroura* was also similar to that of normothermic individuals.

Although the C of torpid thermoregulating *S. macroura* at very low T_as was indistinguishable from that of normothermic individuals, their TMR was only about 25–40% of RMR, demonstrating that a reduction of C is not a prerequisite for a low TMR as has been suggested by Snyder and Nestler (1990). Moreover, a C lower than that of normothermic individual is obviously not required for thermoregulation during torpor.

T_b regulation during torpor and temperature effects

Below the critical T_a torpid *S. macroura* showed the ability of T_b regulation. The metabolic heat production in this T_a range was proportional to ΔT, demonstrating that animals compensated for the increased heat loss at low T_as. Metabolic defence of T_b during torpor has been demonstrated during hibernation and daily torpor (Hainsworth and Wolf 1970; Wolf and Hainsworth 1972; Heller and Hammel 1972; Heldmaier and Ruf 1992). Since both the slope and the intercept of TMR as a function of ΔT in torpid and normothermic *S. macroura* were similar, it appears that the physiological processes underlying thermoregulation at low T_as during torpor are the same as those during normothermia. Although T_b of both normothermic and torpid thermoregulating *S. macroura* was independent of T_a, it increased slightly at very low T_as. Heller and Colliver (1974) have observed the same phenomenon in hibernating ground squirrels, *Spermophilus lateralis*. Nevertheless thermoregulation of *S. macroura* during daily torpor was less precise than during normothermia, since T_b during torpor was maintained in the range between 16 and 28 °C. This response suggested a relatively variable set-point for T_b during daily torpor.

Our results suggest that thermoregulation during torpor and effects of T_b on TMR are not mutually exclusive. As during normothermia, the ability of thermoregulation does exist during the entire processes of torpor. Torpid animals show this ability whenever their T_bs reach a set-point for T_b during torpor, at which T_b is metabolically defended. When T_bs do not reach a set-point for T_b, TMR appears to be well explained by the effect of low T_b on metabolic reactions. Furthermore, even in thermoregulating animals, the drop of MR from normothermia to torpor appears to be a function of T_b. These observations strongly suggest that the steady-state MR during daily torpor is largely a function of T_b.

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