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Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar

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Abstract Thermoregulation, energetics and patterns of torpor in the pygmy mouse lemur, *Microcebus myoxinus*, were investigated under natural conditions of photoperiod and temperature in the Kirindy/CFPF Forest in western Madagascar. *M. myoxinus* entered torpor spontaneously during the cool dry season. Torpor only occurred on a daily basis and torpor bout duration was on average 9.6 h, and ranged from 4.6 h to 19.2 h. Metabolic rates during torpor were reduced to about 86% of the normothermic value. Minimum body temperature during daily torpor was 6.8 °C at an ambient temperature of 6.3 °C. Entry into torpor occurred randomly between 2000 and 0620 hours, whereas arousals from torpor were clustered around 1300 hours within a narrow time window of less than 4 h. Arousal from torpor was a two-step process with a first passive climb of body temperature to a mean of 27 °C, carried by the daily increase of ambient temperature when oxygen consumption remained more or less constant, followed by a second active increase of oxygen consumption to further raise the body temperature to normothermic values. In conclusion, daily body temperature rhythms in *M. myoxinus* further reduce the energetic costs of daily torpor seen in other species: they extend to unusually low body temperatures and consequently low metabolic rates in torpor, and they employ passive warming to reduce the energetic costs of arousal. Thus, these energy-conserving adaptations may represent an important energetic aid to the pygmy mouse lemur and help to promote their individual fitness.

Key words Body temperature · Metabolic rate · Torpor · Pygmy mouse lemur, *Microcebus myoxinus* · Environmental conditions · Madagascar

Abbreviations *ANOVA* analysis of variance · *AMR* metabolic rate during active arousal · *MR* metabolic rate · *RMR* resting metabolic rate · *SD* standard deviation · T_a ambient temperature · T_b body temperature · *TMR* torpid metabolic rate · VO_2 rate of oxygen consumption

Introduction

The energetic costs of endothermy are high and this may be problematic especially for small endotherms in habitats that are seasonally cold and unproductive. Torpor as a solution to a temporal energy and water crisis has been utilised by diverse groups of birds and mammals inhabiting the arctic and temperate regions, but is also being exhibited by species which inhabit the subtropical and tropical climates, where seasonal cold and low food and water availability is predictable (Geiser and Ruf 1995; Hudson 1973; Lyman 1982; Wang 1989 for reviews and references).

The genus *Microcebus* is one of the two primate genera known for their ability to enter daily or seasonal torpor in response to low ambient temperatures (T_as) and poor food availability during the cool dry season in

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Madagascar (Bourlière and Petter-Rousseaux 1966; Martin 1972, 1973; Petter-Rousseaux 1975, 1980). *Microcebus* spp. are small, omnivorous, nocturnal primates endemic to Madagascar. Four species of *Microcebus* are currently recognised, ranging in mean body mass from 59 g in the grey mouse lemur (*M. murinus*) to 31 g in the pygmy mouse lemur (*M. myoxinus*), which is the smallest of the living primates (Mittermeier et al. 1994; Schmid and Kappeler 1994; Zimmermann et al. 1998). Both *M. murinus* and *M. myoxinus* are found in the Forêt de Kirindy, a dry deciduous forest in western Madagascar. This region shows marked differences between rainy and dry seasons and a wide diurnal temperature range, associated with food and water sources that are seasonally variable (Hladik 1980; Sorg and Rohner 1996). Thus, unfavourable environmental conditions combined with heat loss from the mouse lemurs' relatively large body surface, suggest considerable advantages of daily or prolonged torpor for energy conservation. Daily torpor is well documented in *M. murinus* and studies on the reduction of metabolic rate (MR) and body temperature (T_{b}) have been performed in the laboratory (Chevillard 1976; Russel 1975), as well as in the field under semi-natural conditions (Ortmann et al. 1996; Schmid 1996, 1997). However, little is known about metabolism and thermoregulation of *M. myoxinus* (Ortmann et al. 1996, 1997; Schmid 1996, 1997). Both *Microcebus* species occur sympatrically in the same region and consequently are exposed to the same environmental constraints. During the day, *M. myoxinus* remains inactive in the dense foliage, occasionally in leaf-nests and hardly ever in tree holes (J. Schmid, unpublished observations). Specific physiological as well as ecological adaptations of *M. myoxinus* still need to be examined and clarified and are therefore of great interest. As an alternative to the experimental setups of studies in the laboratory under constant conditions, we set up outdoor enclosures in a dry forest in western Madagascar, allowing recordings of T_{b} and rate of oxygen consumption (VO_2) of *M. myoxinus* under natural conditions of photoperiod, temperature and humidity.

The aim of the present study was (1) to describe the torpor pattern of *M. myoxinus* during the dry season in Madagascar, and (2) to investigate its thermal and metabolic physiology.

Materials and methods

Study site

The study took place in a deciduous dry forest in western Madagascar (Forêt de Kirindy/CFPF), some 60 km north of Morondava (44°39′E, 20°03′S) during the dry season between April and August in the years of 1994 and 1995. This site is located in the 12,500-ha forestry concession of the Centre de Formation Professionnelle Forestière de Morondava (CFPF). The area around Morondava is characterised by a pronounced seasonality with a rainy season between December and March, followed by a very marked dry season of 7–8 months. Temperature and humidity during the dry season are subject to regular extreme diurnal and nocturnal variations, with cold nights (down to 4 °C) and hot days (up to 32 °C) (Sorg and Rohner 1996). Further information on the Forêt de Kirindy/CFPF is found in Ganzhorn and Sorg (1996).

Animals

Microcebus myoxinus were caught in Sherman traps (7.7 cm × 7.7 cm × 30.5 cm) and kept in individual 1-m^3 outdoor cages under conditions of natural photoperiod and temperature. Each enclosure was equipped with fine branches and a wooden nestbox, which was used as sleeping quarter (see below). Animals were fed daily a diet of bananas ad libitum, supplemented with live insects (crickets, cockroaches) and pieces of apples. Water was supplied ad libitum. Mouse lemurs were weighed using a 100-g spring balance (accuracy 0.5 g) before surgery. Afterwards, body mass was measured only once every 2 weeks to keep disturbances and stress as low as possible. T_{b} and MR of *M. myoxinus* was measured for six adult animals, three females and three males (Table 1).

Measurements of MR, T_{a} and T_{b}

Rate of metabolism was measured as VO_2 using a specially designed portable oxygen-analyser assembly built by the authors. The VO_2 of individual lemurs was measured by using their nest-box as a metabolic chamber. The nestbox (17 cm × 10 cm × 9 cm, volume 1.5 l) was made out of plywood (5 mm) and sealed with varnish. Gas was sampled from the side opposite the entrance. The entrance itself was a plastic tube 8 cm long and 1.6 cm in diameter, to reduce gas exchange through the entrance by diffusion. When lemurs were resting in their nestbox the entrance was closed by an adhesive tape leaving only a small slit open for gas inlet.

The air outlet of the nestbox was connected to a custom made O_2-analyser unit which was powered by a solar panel (Siemens M55; 55 W) and batteries (Panasonic LCL 12 V, 24 Ah). The sample air was filtered and dried with silica gel and a continuous flow was adjusted by a membrane pump (KnF Neuberger, Freiburg) at flow rates of 40–280 l h^{-1}. Flow rate of dry air was measured by a custom-made mass flow meter based on the heat-transfer property of air, through measuring the temperature difference before and after passing a heated tube. The heated tube was a 2-cm brass tube with 2 mm internal diameter which was embedded in two layers of polypropylene tubing. Countercurrent air flow through this tubing improved the efficiency of convective heat transport by air. Air temperature was measured by copper-constantan thermocouples prior to entrance into the flow meter and at the outlet of the heated brass tube. With this arrangement measurement of flow rate was not affected by T_{a} (−10 °C to 40 °C). The flow meter was designed to give a proportional change in *ÆT* with changes in flow rate from 40 l h^{-1} to 350 l h^{-1}, and was calibrated by the use of pre-calibrated, commercially available mass-flow meters (Tylan FM 360 and FM 361).

A small sample of air (3 l h^{-1}) was pumped (KnF Neuberger, Freiburg, Micro-Pump Type NMPO2L/W) from the outlet of the mass-flow meter to an oxygen sensor (DrägerSensor O_2, Kiel;

Table 1 *Microcebus myoxinus* kept in captivity for the metabolic investigation in 1994 and 1995 (*f* female, *m* male). Body mass values were taken before, during and after the entire time period of the experiments. The first and last day of data sampling is given for each individual

Microcebus myoxinus	Sex	Body mass (g)	Time period of experiments
No. 7	m	29-30-29-29	04.05.–05.07.1994
No. 8	m	30-30-31-29	11.05.–04.07.1994
No. 10	f	29-29-31	02.07.–03.08.1995
No. 11	m	32-30-33	27.04.–18.05.1995
No. 12	f	36-36-35-35	07.05.–01.07.1995
No. 13	f	37-35-37	30.06.–03.08.1995

28 mm outer diameter, volume of measuring chamber 5 ml). This oxygen sensor is basically an electrochemical fuel cell which is temperature compensated and has a current output proportional to the oxygen content of the air flowing through its measuring chamber (2.6 mA/vol% O_2). By the addition of an adjustable voltage supply and a precision resistor in the output circuit we obtained a zero-point suppression and a voltage signal which changed linearly with the percentage oxygen in air (Fig. 1). In this range, the output changes linearly with the O_2 content of the air (nonlinearity <0.2 vol% O_2 in the range 0–25 vol% O_2), and the inaccuracy of measurements was $< +0.02$ vol% O_2.

The oxygen sensor cells had a life span of up to 9 months depending upon the total duration of their usage. Each sensor had a slightly different output and had to be calibrated separately before they were used in the field. We made calibration gases by using a gas mixing pump (Wösthoff, Bochum, Type G27 3a) as described previously (Heldmaier and Steinlechner 1981; Heldmaier and Ruf 1992). The sensitivity of the sensors slowly decreased with age. Therefore, calibration was repeated in the lab with sensors after using them in Madagascar for 2–3 months, and the results obtained in between two calibrations were corrected by using linear interpolation. The changes we observed were in the order of 0.5% per month (e.g. 0.013 mA/vol% O_2), and in new electrodes this decrease appeared linear. VO_2 was calculated as described previously (Heldmaier and Ruf 1992). CO_2 production of lemurs was not measured, but we assumed a respiratory quotient (RQ) of 0.9 to correct the flow rate of dry air for calculations of metabolic rate (Hill 1972).

During the experiments air flow through the chamber was controlled at about 40 l h^{-1}. In addition, T_a was measured to the nearest 0.1 °C by a copper-constantan thermocouple located near the animals' sleeping corner at middle height in the nestbox. T_a in the chamber, the output of the flow meter, the oxygen sensor cell, and voltages of the power supply were stored on a datalogger (AMR Therm 2281-8) at 1-min intervals. In addition, a separate counter/timer controlled solenoid valve (Bürkert, Ingelfingen, Type 0305-C-03) switched the air flow every hour from sample air to reference air outside the nestbox for 5 min and then returned to sample air. This allowed a zero reading of O_2 in reference air at hourly intervals. The entire set-up including batteries and pumps was housed in a weather proof aluminium box (Zarges, 55 cm × 35 cm × 24 cm). The box was thermally insulated from the inside to improve temperature stability and was opened only once every 1 or 2 days to retrieve the data from the datalogger to a laptop computer via its serial interface. Retrieving the data, resetting of the datalogger as well as calibration routines were performed by custom made computer programs.

Temperature-sensitive radio transmitters (Minimitter Model X, accuracy ±0.1 °C) enclosed in a plastic capsule and sealed with a paraffin-wax coating were calibrated to the nearest 0.1 °C against a mercury thermometer in a water bath between 5 °C and 40 °C. The transmitters were implanted into the peritoneal cavity under deep anaesthesia [0.05 ml/100 g body mass Ketavet (100 mg/ml), 0.01 ml/100 g body mass Rompun (2% solution)] and were allowed to position themselves freely. A coated transmitter capsule weighed between 1.4 g and 1.5 g, about 4–5% of the mean body mass (Schmid and Kappeler 1994). Mouse lemurs were allowed to recover from the surgery for at least 7 days. Surgery had to be repeated after 5–8 weeks when the experiments were finished and the transmitters needed to be taken out. Transmitter signals were received through commercial radios with an integrated ferrite rod antenna placed on each wooden nestbox. Signals were either sampled manually using a stopwatch (irregular intervals) or automatically every 6 min and stored on a personal computer as described in more detail elsewhere (Ruf and Heldmaier 1987). Due to the low transmission range of the transmitters the signal could only be recorded when the mouse lemur entered its nestbox, but not when it stayed in the enclosure.

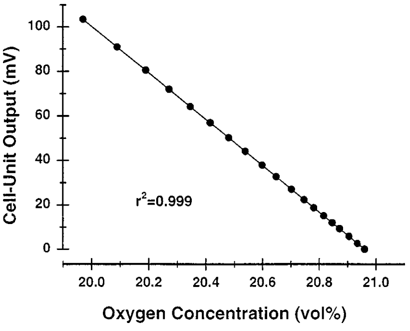

Fig. 1 Example calibration curve for our oxygen analysis setup with the DrägerSensor O_2

Mouse lemurs appeared healthy and maintained stable body masses during the course of the investigation (Table 1), and no problems resulted from the use of intraperitoneal transmitters. However, one individual died of unknown causes after 45 days. There were no signs of infections caused by the surgery or the transmitter. Data collected during the week before it died were not included in the calculations to avoid possible artefacts due to illness.

Experimental procedure

For determination of MR mouse lemurs were measured for complete 24-h cycles on different days. Every day, VO_2 was monitored of one individual because there was only one portable oxygen analyser available. Measurements of T_b were carried out at the same time and up to three individuals were measured simultaneously. In contrast to laboratory studies performed under constant T_a, mouse lemurs in this study were exposed to natural conditions, and accordingly T_a varied between different experimental days.

Data analysis

All subsequent analyses were based on VO_2 and temperature recordings during the dry season. Animals were considered to be torpid when the T_b was at or below 30 °C (Geiser and Baudinette 1987). Arousal was divided into two different phases: (1) passive arousal characterised by an increase of T_b with T_a during which VO_2 remained approximately constant at the torpid level, and (2) active arousal with T_b rising due to a marked increase in VO_2 (rise of 10% per minute). Using VO_2 and T_b, we were able to determine the time an active arousal started to within 10 min. Parameters analysed included: (1) time of day, T_b and Ta at the onset of each torpor bout, given by the last measurement before T_b or MR started to decrease continuously; (2) duration of entry into daily torpor defined as the time between T_b starting to decrease until T_b reached the minimal value; (3) duration of passive arousal from torpor defined as the time between T_b starting to rise and the marked increase in VO_2; (4) duration of active arousal from torpor defined as the time between VO_2 rising noticeably and T_b reaching a stable, normothermic value; (5) time of day and T_b at the end of each torpor bout, given by the last measurement before T_b stopped increasing; (6) duration of torpor bout in hours; and (7) rate of temperature change during entry into and arousal from daily torpor.

For calculations of MRs during the different activity states only data from periods of 20–25 min with minor alterations of VO_2 (±10%) were taken into account. Resting metabolic rate (RMR) was determined from the mean of 20 consecutive VO_2 values in normothermic individuals whose T_bs were not lower than 30 °C. Torpid metabolic rate (TMR) during torpor was obtained by calculating the mean of 20 consecutive VO_2 values when T_b was minimal. Metabolic rate during active arousal (AMR) was determined from the mean of all VO_2 values during the period of active arousal. Mean T_a and T_b values were calculated from the corresponding time frame. Mass-specific metabolism was not determined because the mouse lemurs were not weighed before and after each registration period.

To calculate the energetic benefit of spontaneous daily torpor we compared RMR with TMR and calculated the metabolic reduction for each individual and experimental day separately. For calculations of the energy expenditure, MRs were converted to units of kilojoules per day and a RQ of 0.9 and 20.1 J ml^{-1} O_2 was assumed (Schmid-Nielsen 1997). For each individual and experimental day we calculated the energy expenditure consisting of TMR, RMR and AMR. Daily energy savings due to daily torpor were then given as percentage deviation of the energy expenditure for a 24-h period, which was calculated assuming that mouse lemurs would have remained normothermic for the entire 24-h period.

A maximum $\alpha = 0.05$ was used to accept significance in statistical tests. Data are presented as mean ± standard deviation (SD) unless otherwise stated. Differences between means were examined using Student's *t*-test and analysis of variance (ANOVA), and the effect of T_a on the physiological variables measured was tested using linear regression or partial correlations (Sachs 1992; Sokal and Rohlf 1981). Data obtained from the same individual were averaged for statistical analyses considering variable T_a. *N* refers to the total number of individuals and *n* to the number of measurements.

Results

The MR and T_b of *M. myoxinus* showed pronounced daily fluctuations during the dry season in Madagascar. Both males and females frequently entered spontaneous daily torpor, but could also remain normothermic within 24-h measurements. The number of experimental days when torpor was observed increased with the time of year and with decreasing air temperatures. In May, mean minimal T_a was 16.3 °C (±1.7 °C) and torpor occurred on 57.5% (±30.3%) of experimental days ($N = 4$, $n = 80$). In June ($T_a$min = 11.1 ± 2.1 °C), animals were torpid on 97.4% (±3.0) ($N = 4$, $n = 54$), whereas in July ($T_a$min = 11.9 ± 1.8 °C) torpor was observed on 99.2% (±1.7%) ($N = 5$, $n = 61$) of days observed.

Normothermia

In Figure 2 the course of VO_2 and T_b over the diurnal resting phase for a normothermic mouse lemur individual is shown. The animal entered its nestbox just before dawn and after approximately 1 h a reduction in VO_2 accompanied by a decrease of T_b from 36.4 °C to 35.0 °C was observed. During the following hours the mouse lemur maintained a stable normothermic T_b. The mean normothermic VO_2 of 98 ml O_2 h^{-1} was subject to more pronounced fluctuations between 105.7 ml O_2 h^{-1} and 79.6 ml O_2 h^{-1}, which might be due to the lemurs activity in the nestbox. From about 1100 hours to 1300 hours, T_a remained approximately constant and T_b and VO_2 also showed only minor fluctuations.

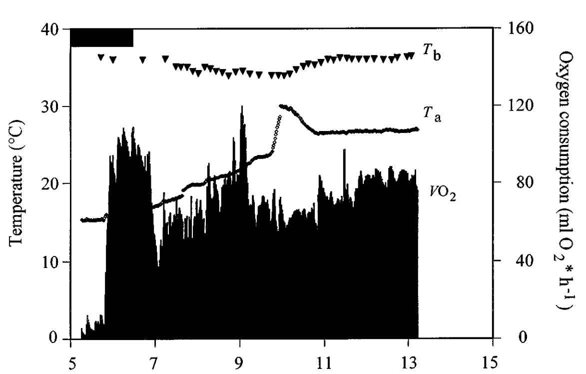

Fig. 2 Registration of oxygen consumption (VO_2), body temperature (T_b) and ambient temperature (T_a) over time from 0500 hours to 1500 hours of a *Microcebus myoxinus* individual (No 8; 07.06.1994) remaining normothermic. VO_2 and T_a are both registered once a minute, and individual data points of T_b are registered at irregular intervals. The *dark bar* indicates period of darkness from 0500 hours until 0630 hours

For the detection of daily rhythms of normothermic T_b only data of entire normothermic 24-h periods were analysed. The typical pattern of T_b of *M. myoxinus* showed considerable diurnal variations (Fig. 3). During the active phase (1800–0600 hours) the mouse lemur controlled its body temperatures within the range 38.5–35.0 °C, whereas during the inactive daytime (0600–1800 hours) T_b was lowered to non-torpid values down to 31.8 °C.

Five out of six mouse lemurs measured showed days of normothermia with a similar pattern of daily fluctuations in T_b as described above. The mean T_b of normothermic individuals during the active phase was 37.0 °C (±0.56; $n = 32$), which was significantly higher than the mean T_b of 35.2 °C (±1.03; $n = 45$) during the inactive resting phase (*t*-test: $t = 8.66$; $P < 0.0001$).

Torpor

On days when torpor occurred, the MR and T_b of *M. myoxinus* showed pronounced fluctuations (Fig. 4). On this particular day, the animal entered torpor at about 0145 hours and both VO_2 and T_b decreased dramatically. MR during torpor decreased and was only about 12% of RMR observed in the early afternoon. T_b reached a minimum of 9.7 °C. Torpor lasted for 10.4 h and was terminated by arousal. Arousal was divided into a passive increase of T_b to 22.6 °C along with T_a

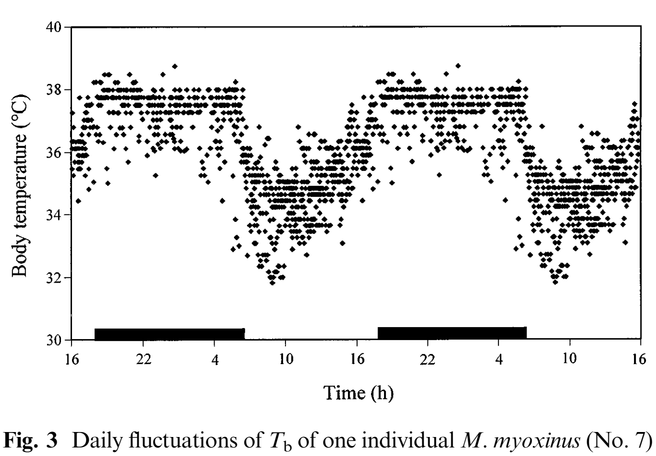

Fig. 3 Daily fluctuations of T_b of one individual *M. myoxinus* (No. 7) over 14 completely normothermic days between 11.05.1994 and 07.06.1994. Data are double plotted and the *dark bars* indicate the periods of darkness

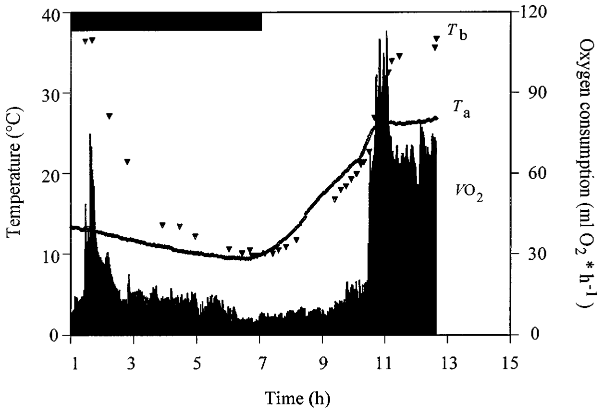

Fig. 4 Time-course of VO_2 and T_b over time for one *M. myoxinus* (No. 8; 03.06.1994) entering torpor. The animal entered torpor at about 0130 hours and actively aroused between 1000 hours and 1100 hours. Minimal T_b of 9.7 °C was reached at 0700 hours when T_a was 9.8 °C. The *dark bar* indicates period of darkness

when VO_2 remained approximately constant, followed by a steep increase of VO_2 which further raised the T_b to normothermic values of around 34 °C. Afterwards VO_2 decreased again, and was maintained at an RMR sufficient for maintaining normothermia. All six pygmy mouse lemurs examined in this study entered torpor, showing a similar torpor pattern as described above for the single animal. However, in few torpor episodes only moderate or no overshoot of the MR over RMR was observed.

Body temperatures during daily torpor in *M. myoxinus* showed pronounced variations between days. For the period of investigations, individual means of minimal T_b and torpor length in torpid animals were calculated (Table 2). The lowest individual T_b recorded for a torpid mouse lemur was 6.8 °C (No. 7) which occurred in June 1994 at a minimal T_a of 6.3 °C and a torpor bout length of 10.2 h. The mean duration of daily torpor bouts was 9.6 h (±1.4) and ranged from 4.6 h (minimum) to 19.2 h (maximum) for all *M. myoxinus* investigated. Prolonged torpor, i.e. more than 1 day, was never observed.

Figure 5 shows a 24 h temperature profile of torpor episodes recorded for all six individuals. The data were double-plotted for easy visual examination. After dawn, mouse lemurs became active and T_b was generally elevated. Entry into daily torpor occurred between 2000 and 0620 hours with a mean time of day of 0536 hours for all six animals. Mean time of day of arousal from daily torpor was clustered around 1254 hours and varied between torpor episodes by less then 4 h (1042–1448 hours).

When pooling all torpor events, a significant negative correlation between minimal T_b and duration of torpor was found (Fig. 6). The lower the T_b during torpor the longer the torpor lasted. Torpor bout length increased with decreasing temperature difference between T_b and T_a (ΔT). The longer a torpor episode lasted the more T_b approached T_a (Fig. 7). The lowest ΔT of 0.2 °C occurred during a torpor bout lasted for 11.4 h ($T_b = 9.7$ °C), whereas the highest ΔT of 13.3 °C was observed during a torpor episode of 6.1 h ($T_b = 19.5$ °C).

Changes of T_b during torpor

The mean rate of cooling during entry into daily torpor was 4.2 ± 0.8 °C h^{-1} and did not differ between individuals (Table 3). The mean duration of entry into torpor (5.2 ± 1.3 h) did also not vary significantly between individuals. Normothermic T_b (35.4 ± 0.4 °C) before the onset of torpor did not differ between individuals. Entry durations correlated with minimal T_b and were longer the lower the T_b dropped (Pearson correlation: $r = -0.61$, $n = 29$, $P < 0.001$). The two steps of arousal from daily torpor were basically different. The mean duration of the passive arousal was significantly longer, the mean rewarming rate significantly lower, and the mean T_b increase significantly more pronounced than the means of active arousal (Table 3). On average, *M. myoxinus* actively aroused from daily torpor when T_b and T_a reached 27.4 ± 1.9 °C and 27.5 ± 1.3 °C, respectively. Duration of passive arousal was negatively correlated with T_b at the onset of the passive arousal ($r = -0.50$, $n = 21$, $P = 0.02$). No significant correlation was found between the duration of active arousal and T_b at the onset of the active arousal.

Metabolic rate

When interrelations between physiological variables such as TMR, RMR and T_b are investigated, it must be

Table 2 Individual mean duration of torpor and minimal body temperature ($T_b$min) in torpid *M. myoxinus*, and the associated mean minimal ambient temperature ($T_a$min). Values are mean ± SD; number of measurements are given in parentheses. The lowest $T_b$min registered for each individual is also given

ID	Sex	Duration of torpor (h)	$T_b$min (°C)	$T_a$min (°C)	Lowest $T_b$min (°C)
No. 7	m	8.6 ± 2.1 (19)	15.8 ± 6.0 (25)	13.4 ± 4.4 (25)	6.8
No. 8	m	8.4 ± 2.5 (10)	14.6 ± 5.4 (15)	12.3 ± 3.9 (15)	7.9
No. 10	f	11.9 ± 3.9 (11)	11.3 ± 2.8 (31)	11.0 ± 2.0 (31)	8.0
No. 11	m	8.3 ± 1.7 (9)	20.9 ± 3.5 (23)	17.3 ± 2.0 (23)	14.7
No. 12	f	9.9 ± 2.0 (24)	16.8 ± 4.8 (30)	13.5 ± 4.0 (30)	9.8
No. 13	f	10.7 ± 3.7 (13)	14.0 ± 5.0 (24)	10.8 ± 2.0 (24)	9.3

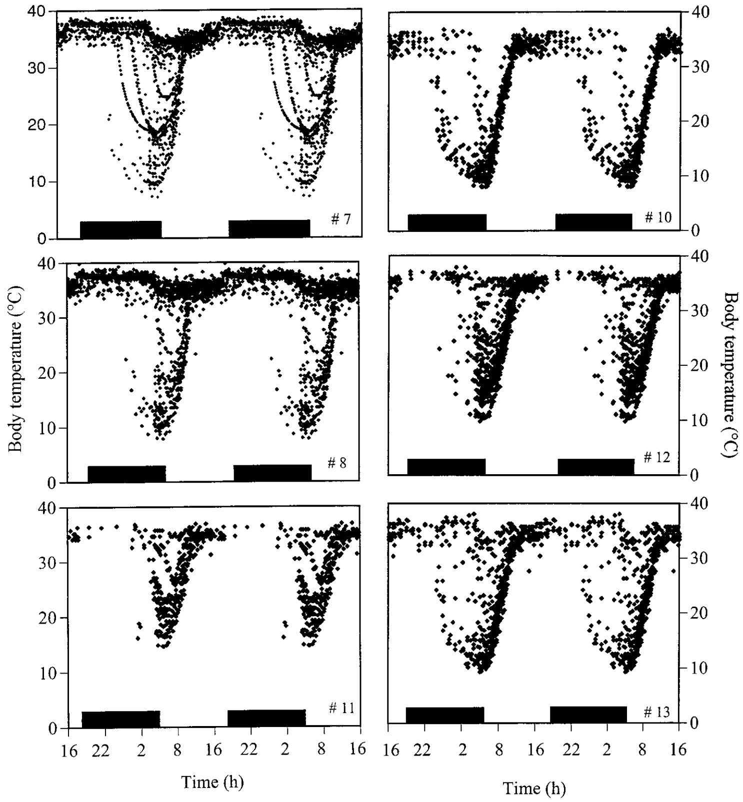

Fig. 5 Two-day double-plots of T_b in six *M. myoxinus* individuals measured between 15 and 33 experimental days when torpor was observed. *Left columns* show three males, *right columns* show three females. *Dark bars* indicate periods of darkness

kept in mind that environmental conditions varied between different experimental days as well as within the same experimental day.

The $\dot{V}O_2$ varied and indicated a clear torpid and normothermic level (for illustration see Fig. 4). With torpor onset $\dot{V}O_2$ decreased form normothermic to torpid level where it then remained more-or-less constant for a certain period of time. Mean RMR of pygmy mouse lemurs was 66.5 ± 15.7 ml O_2 h^{-1} ($N = 6$; mean body mass: 33 ± 3 g; mean T_a: 28.1 ± 1.9 °C) and during torpor decreased to a mean TMR of 9.5 ± 4.3 ml O_2 h^{-1} ($N = 6$; mean body mass: 32.6 ± 3.4 g; mean T_a: 14.3 ± 4.4 °C), i.e. a reduction by 85.6 ± 6.1% ($N = 6$; mean body mass: 32.6 ± 3.4 g). Percentage reduction of $\dot{V}O_2$ during torpor was related to T_a (partial Spearman rank correlation: $r_s = -0.46$, $n = 25$, $P = 0.02$) and consequently T_b ($r_s = -0.45$, $n = 24$, $P = 0.03$). Mean AMR (81.4 ± 16.7 ml O_2 h^{-1}; $N = 6$; mean body mass: 32.5 ± 3.1 g; mean T_a: 28.6 ± 2.1 °C) was 26.0 ± 27.3% higher than mean RMR.

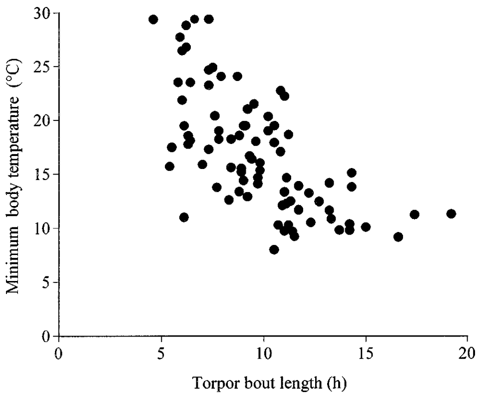

Fig. 6 Torpid minimal T_b plotted against duration of torpor during the investigation periods of 1994 and 1995, when pooling all individual torpor events ($N = 6$; $n = 83$). Note the significant relationship between both parameters as indicated by the exponential fit [T_b min = 38.01 − 3.06(torpor length) + 0.08(torpor length^2), $r^2 = 0.48$, $P < 0.0001$]

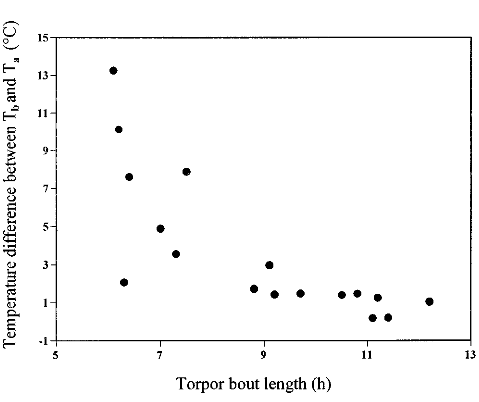

Fig. 7 Temperature difference between T_b and T_a (ΔT) in one *M. myoxinus* (No. 7, n = 17) as a function of duration of torpor bouts. ΔT decreases with increasing length of torpor bouts [exponential fit: ΔT = 40.37 − 7.16(torpor length) + 0.32(torpor *length*^{2}), $r^2 = 0.67$, $P = 0.0004$)

Table 3 Changes of T_b during entry into and arousal (passive and active) from daily torpor in *M. myoxinus* ($N = 6$) and associated physiological and environmental data (mean ± SD). Differences between individuals were tested using *ANOVA*. Student's *t*-test was used for comparisons between passive and active arousal for each parameter

	Entry	Arousal	
		Passive	Active
Duration of torpor (h)	5.2 ± 1.3	3.6 ± 0.2 $t = 10.69$; $P < 0.0001$	1.0 ± 0.3
T_b change (°C)	19.7 ± 3.9*	13.3 ± 3.6* $t = 4.29$; $P = 0.0016$	6.4 ± 1.6
Rate of T_b change (°C h^{-1})	4.2 ± 0.8	3.6 ± 0.9 $t = -3.52$; $P = 0.0065$	7.0 ± 1.9
T_b at the onset (°C)	35.4 ± 0.4	14.6 ± 5.0** $t = 5.84$; $P = 0.0002$	27.4 ± 1.9
T_a at the onset (°C)	15.7 ± 3.5***	11.2 ± 5.1** $t = 7.02$; $P < 0.0001$	27.5 ± 1.3

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Torpor clearly decreased metabolic expenditure considerably. On average for all *M. myoxinus* individuals measured, hypometabolism during spontaneous daily torpor reduced daily energy costs by 39.0% (±7.9%). To estimate the energy saving due to passive heating during arousal, a mean value of MR was calculated assuming that only active heat production is required to raise T_b from torpid to normothermic levels. In torpid mouse lemurs the mean rewarming rate of active arousal was 7.0 °C h^{-1} (Table 3). Assuming a linear heat production during arousal (not taking changes in $T_b - T_a$ gradient or thermal conductance into account), the mean duration of arousal would be 2.8 h to cover the mean temperature difference of 19.7 °C between the mean minimum torpid T_b and normothermia. The calculated mean energy expenditure during active arousal would be 4.6 kJ day^{-1}, in contrast to 1.6 kJ day^{-1} when passive heating is included (mean duration of active arousal measured was 1.0 h; see Table 3). Thus, rewarming from daily torpor without passive heating would increase energetic costs of arousal by an extra 181%.

Discussion

M. myoxinus exposed to semi-natural environmental conditions in western Madagascar is capable of entering into and spontaneously arousing from daily torpor, but can also remain normothermic during the dry season when T_a is low. These results expand the current knowledge of energetics of primates capable of exhibiting torpor.

Normothermia

There is a clear pattern of thermoregulation for normothermic *M. myoxinus*. Its daily rhythm of T_b varied between 31.8 °C and 37.9 °C. This significant variation in normothermic T_b between the active nocturnal and the inactive diurnal phase of *M. myoxinus* is similar to that reported for other prosimian species of which T_b investigations exist (*Galago senegalensis*, *G. demidovii*: Dobler 1978; *Nycticebus coucang*: Müller 1979; *Galago crassicaudatus*: Müller and Jaschke 1980; *Microcebus murinus*: Ortmann et al. 1997; Schmid 1996, 1997). It has also been suggested that in birds and mammals the amplitude of these daily rhythms in T_b is dependent upon body mass with the greatest amplitudes found in smaller species (Aschoff 1982, 1983; Refinetti and Menaker 1992).

Torpor

Torpid mouse lemurs showed the typical curled up body posture which reduced their surface area (Wünnenberg 1990). VO_2 and T_b showed pronounced diurnal changes and were reduced to the lowest values during torpor. Torpor in *M. myoxinus* occurred on a strictly daily basis and never lasted for more than about 19.2 h. This is in agreement with observations on grey mouse lemurs, *M. murinus*, which also show only daily torpor when held under appropriate experimental conditions (Ortmann et al. 1997; Schmid 1996, 1997). However, based on 3 years of mark-recapture data, there is strong evidence that grey mouse lemurs in addition may show prolonged torpor and remain inactive for several months (Schmid 1997; Schmid and Kappeler 1998; Schmid 1999). Before prolonged periods of inactivity, *M. murinus* accumulate large fat stores in body and tail. We therefore, cannot preclude the possibility that free-ranging *M. myoxinus* may also enter into hibernation under natural circumstances. However, we never observed prehibernational fattening in *M. myoxinus* which is characteristic for *M. murinus* (Martin 1973; Schmid and Kappeler 1998) as well as for many endotherms undergoing prolonged torpor (Mrosovsky 1983; Wang 1989).

The recorded increase in torpor frequency over the season may be due to a variety of parameters such as circannual rhythm, photoperiodism and other environmental signals. At the beginning of the dry season, when T_a was relatively high and daylength was comparatively long, *M. myoxinus* mainly remained normothermic. With subsequent decreases in T_a and daylength, the frequency of entering into daily torpor increased dramatically. However, during warm overnight temperatures (approximately 18 °C) in June and July, i.e. in the middle of the dry season, mouse lemurs did not lower their T_bs below 30 °C, suggesting a response to changes in T_a. Remaining alert and active probably reflects a survival advantage although it may not be as metabolically economical as exhibiting daily torpor.

The pattern of daily torpor obtained in the present study is comparable to that of the grey mouse lemur (Ortmann et al. 1997; Schmid 1996, 1997). The lowest torpid T_b of 6.8 °C was observed in June 1994 when air temperature was almost down to 6 °C, and in four of the other animals minimal T_b was also below 10 °C. Similar minimal values have been reported for grey mouse lemurs (7.7–13.3 °C; $N = 10$; Schmid 1997) determined under equivalent experimental conditions. The level of critical T_b is species dependent and it seems problematic to compare results obtained under different environmental conditions. However, T_bs of pygmy mouse lemurs in this study were extremely low compared to other daily heterotherms for which minimum T_bs range between 10 °C and 30 °C (Geiser and Ruf 1995). Minimum T_bs falling as low as 5 °C during daily torpor are only known from the honey possum *Tarsipes rostratus* (Withers et al. 1990). The body temperature during torpor is typically within 2 °C of the ambient until a "critical" level is reached below which the animal either increases metabolism or initiates arousal (Hudson 1973; Lyman 1948; Ortmann 1989). The level of critical T_b varies among species that are capable of exhibiting daily torpor and hibernation. It is not clear from the present study that T_b is regulated below a critical temperature in *M. myoxinus*. In most torpor events registered, *M. myoxinus* lowered its T_b almost down to T_a regardless of its value and the decline of T_b was not stopped until daily sun radiation warmed up the surrounding environment. The fact that in Kirindy forest nightly air temperatures usually never fall below 4 °C (Hladik 1980), combined with the fact that daily rewarming occurs reliably around midday makes an active defence of its T_b during torpor not really necessary. However, in *M. myoxinus* minimal T_b torpor during torpor is a function of torpor length and T_a. The longer a torpor bout lasted the lower T_b dropped towards T_a and the difference between T_b and T_a decreased. These results were generally consistent with those of physiological studies on other heterothermic animals under laboratory conditions (Bartels et al. 1998; Geiser 1986; Vogt and Lynch 1982; Webb and Skinner 1996), with a strong correlation between torpor duration and surrounding T_a.

Daily torpor usually is restricted to the animal's inactive resting phase but can also be expanded into their activity phase (Hudson 1973). In the present study entry into daily torpor was widely scattered within an 11-h time frame (2000–0620 hours). Arousal from torpor, on the other hand, did follow a coherent timing pattern and was mostly observed shortly after midday (1254 hours). This is similar in the simultaneous study on the grey mouse lemur (Schmid 1996, 1997), in which arousal from daily torpor also clustered around noon (1354 hours). The timing of arousal in mouse lemurs investigated under natural temperature conditions can easily be explained by the daily cycle in T_a characterised by a regular daily increase to about 30 °C. Because T_a controls the termination of torpor, torpor bouts can only be expanded by shifting the torpor onset towards the night time (Ortmann et al. 1997). Known factors influencing entry into daily torpor are photoperiod, air temperature, food availability and body mass (Geiser and Baudinette 1987; Pohl 1967; Ruf et al. 1993). However, it does not seem clear from this study which environmental cues were used for initiating torpor in *M. myoxinus*. A minor problem was that the mouse lemurs were restricted in movements and social interactions when held individually in enclosures and possibly entered torpor because they were "bored". However, this explanation remains speculative and to describe crucial factors determining entry into torpor would require long-term recordings of torpor patterns and T_b under controlled laboratory conditions.

Arousal from torpor is an energetically expensive event, and often an overshoot of oxygen consumption beyond the resting normothermic level is observed (Hudson 1973; Wang 1978, 1989). In *M. myoxinus* this high energy cost is dramatically reduced due to the initial passive rewarming of T_b along with the rising T_a without a noticeable increase in MR. The second step of arousal characterised by an active heat production caused a steep rise of T_b from 27 °C to normothermia within an hour. Passive rewarming from lethargy was also reported for the grey mouse lemur (*M. murinus*; Ortmann et al. 1997; Schmid 1996, 1997), the edible dormouse (*Glis glis*; Wilz 1994), the echidna (*Tachyglossus aculeatus*; Nicol and Andersen 1996) and some bat species (*Eptesicus fuscus*; Hamilton and Barclay 1994; *Antrozous pallidus*; Vaughan and O'Shea 1976). A still open question is why should *M. myoxinus* initiate an active increase of T_b to normothermic values when they reached the threshold T_b of 27 °C? A possible explanation is based on the fact that torpid animals are much less aware of their environment and more susceptible to predation than are normothermic individuals (French 1986, 1988, 1992). Especially during the dry season the predation pressure of owls and snakes on mouse lemurs are extremely high (Goodman et al. 1991, 1993; Rasoloarison et al. 1995). This might be one of the major threats to *M. myoxinus* because this species merely sleeps without any particular shelter in dense foliage and slack leaf-nests (J. Schmid, unpublished observations). On only one occasion an individual was found in a tree hole in a rotten tree trunk during its daytime rest. It remains questionable if a torpid *M. myoxinus* is generally capable of arousing from torpor at low body temperature without the initial support of external heat. For instance, it was found that individuals of *M. murinus* died as a result of their inability to arouse from torpor when T_a remained below 10 °C (Andriantsiferana and Rahandraha 1974 cited in Müller 1983). While this study was performed under laboratory conditions, my study was conducted at natural T_a. Although mouse lemurs possibly cannot arouse from torpor independently it is not risky since free-ranging mouse lemurs can rely on the daily rewarming.

Torpor in *M. myoxinus* leads to on average a reduction in $\dot{V}O_2$ of 86% of RMR. Energy savings increase primarily due to the longer durations of torpor as well as the greater depth of torpor (i.e. lower T_b) in mouse lemurs. Other studies in daily heterotherms revealed that minimum $\dot{V}O_2$ (percentage of BMR) during daily torpor was between 4.4% and 67% of BMR (Geiser and Ruf 1995). This relatively large variability can be explained by the differences in experimental conditions, i.e. natural and laboratory investigations. The calculated energy savings by daily torpor compared to entire normothermic days was 39% in *M. myoxinus*. This is similar to the 38% saving observed in the grey mouse lemur (Schmid 1997) and the up to 31% in small rodents (*Peromyscus*; Vogt and Lynch 1982) exhibiting daily torpor.

This study clearly shows that the smallest living primate *M. myoxinus* displays daily torpor when kept in artificial nestboxes under natural conditions of temperature and photoperiod. Torpor in *M. myoxinus* is a physiological adaptation that is used to reduce energy expenditure during times of cold exposure and food shortage, which seasonally occurs in the dry deciduous forest of western Madagascar. Daily T_b rhythms reduce the expensive costs of arousal in *M. myoxinus* in two ways. First, low environmental temperature cycle allows for prolonged torpor bouts with rather low T_b to occur in daily torpor allowing for prolonged periods of low MRs. Second, the daily increase in T_as allows an increase in T_b through passive heating which reduces the costs of rewarming from daily torpor.

When interrelations between physiological variables such as TMR, RMR and T_b are investigated, it must be kept in mind that environmental conditions varied between different experimental days as well as within the same experimental day.

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