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Comparison of hibernation, estivation and daily torpor in the edible dormouse, *Glis glis*

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Abstract Three major forms of dormancy in mammals have been classified: hibernation in endotherms is characterised by reduced metabolic rate (MR) and body temperature (T_b) near ambient temperature (T_a) over prolonged times in the winter. Estivation is a similar form of dormancy in a dry and hot environment during summertime. Daily torpor is defined as reduced MR and T_b lower than 32 °C, limited to a duration of less than 24 h. The edible dormouse (*Glis glis*) is capable for all three distinct forms of dormancy. During periods of food restriction and/or low T_a, daily torpor is displayed throughout the year, alternating with hibernation and estivation in winter and summer respectively. We recorded T_b, O_2-consumption and CO_2-production in unrestrained dormice at different T_a's for periods of up to several months. Cooling rate and rate of metabolic depression during entrance into the torpid state was identical in all three forms of dormancy. The same was true for thermal conductance, maximum heat production, duration of arousal and cost of an arousal. The only difference between hibernation and daily torpor was found in the bout duration. A daily torpor bout lasted 3–21 h, a hibernation bout 39–768 h. As a consequence of prolonged duration, MR, T_b and also the $T_b - T_a$ gradient decreased to lower values during hibernation bouts when compared to daily torpor bouts. Our findings suggest that all three forms of dormancy are based on the same physiological mechanism of thermal and metabolic regulation.

Key words Circadian clock · Conductance · Energy saving · Metabolic rate · Metabolic depression

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Abbreviations *ADMR* average matabolic rate · *BM* body mass · *C* conductance · *MR* metabolic rate · *RMR* resting metabolic rate · T_a ambient temperature · T_b body temperature · VO_2 rate of oxygen consumption

Introduction

In response to seasonal changes of the environment, many endotherms have evolved the ability to escape unfavourable seasons by dormancy. Three major forms of dormancy have been classified, hibernation, estivation and daily torpor. Hibernation in endotherms is a well-known strategy to escape the winter season temporarily. The entire hibernation season is characterised by a sequence of prolonged hibernation bouts. Their duration may vary with ambient temperature (T_a), season as well as the species, but average duration bouts of deep hibernation are in the order of 2 weeks (Twente and Twente 1965; Twente et al. 1977; Kenagy 1981; French 1982).

Physiological characteristics of hibernation are a reduction of body temperature (T_b) near to T_a, a markedly reduced metabolic rate (MR) and spontaneous arousals by activation of the major heat-producing mechanisms (Bartholomew and Hudson 1960; Kayser 1961; Lyman et al. 1982). The edible dormouse (*Glis glis*) studied here is known as a true hibernator. In autumn the dormouse retreats into a hibernaculum and stays there until the next spring. During this time the dormouse lives from body fat stores, accumulated during the summer season (Vietinghoff-Riesch 1960; Jallageas and Assenmacher 1986).

A similar behaviour with a sequence of prolonged bouts of dormancy may also be observed in summer and is called estivation. Such behaviour is displayed by some species of rodents (*Spermophilus*, *Peromyscus*) living in arid areas of North America and Asia (Shaw 1925; Wade 1930; Kalabukhov 1960; MacMillen 1965; Wang 1978). It is further characterised by a reduction of T_b and MR at only moderate T_as (~20 °C; Hoover et al. 1977; Hudson 1978; Hinds and MacMillen 1985).

The third form of dormancy is shallow or daily torpor. It is characterised by a dormancy bout duration of less than 24 h. Further characteristics are reduced MR and minimum T_b between approximately 10 °C and 25 °C (Hudson 1973); this strategy is used, for example, by the Djungarian hamster (*Phodopus sungorus*). During winter they lower MR and T_b during the diurnal resting period and maintain normothermic T_b during their nocturnal activity period. The hamsters have no extended body fat storage and need to take up food during the wintertime (Heldmaier and Steinlechner 1981a, b; Heldmaier et al. 1999). A similar behaviour is also observed in other rodents (Bartholomew and Cade 1957; Hill 1975; Hudson 1978; Deavers and Hudson 1981; Ruf 1991), in bats (Bartholomew et al. 1970) as well as in lemurs (Ortmann et al. 1997).

Several authors have compared the ecological and physiological differences of hibernation, estivation and daily torpor and considered them as physiologically or ecologically distinct strategies of dormancy (Lyman and Chatfield 1955; Geiser 1988; Geiser and Ruf 1995). Others point out the similarities of hibernation, estivation and daily torpor and see only slight differences (Bartholomew and MacMillen 1961; Hudson 1967; Wang 1978). They argue that most of the differences result from comparisons of different species in different eco-systems (Hudson and Bartholomew 1964). With respect to the more quantitative than qualitative differences, they suggested the terms seasonal and daily torpor (Hudson and Bartholomew 1964) or deep and shallow torpor (Hudson 1967).

Besides these distinct cases of dormancy, there are a few species which use hibernation or estivation as well as daily torpor; e.g. some bats (Hock 1951), some squirrels (Shaw 1921, 1925; Bartholomew and Hudson 1960) and mice (Bartholomew and Cade 1957; Bartholomew and MacMillen 1961). The edible dormouse (*G. glis*) has the ability to display all three forms of dormancy (Wilz 1997). The comparison of physiological responses between all three forms of dormancy in one species can answer the question as to whether there are qualitative or quantitative physiological differences between them. Therefore, we compared metabolic depression, development of hypothermia and the arousal to normothermia in dormice under all three different forms of dormancy.

Materials and methods

Animals

The edible or Fat dormouse (*G. glis*) is a nocturnal rodent and belongs to the family of Gliridae. It is found in central, southern and eastern Europe. It inhabits woodlands and shrub zones except areas above 800 m altitude. Preferred foods are fruits, and to a lesser extent seeds, also insects and leaf-buds (Storch 1978). The dormice used in this experiment were bred and raised in outside aviaries under natural conditions at Marburg University. They had access to water and food ad libitum. The food consisted of apples and a seed mixture (sunflower seed, peanuts, hemp seed). We used five male and two female dormice in this study, all aged between 2 years and 4 years. Their body weight varied between 90 g and 190 g.

Measurements

During experiments, the dormice were kept in wire mesh cages (0.8 × 0.5 × 0.4 m) inside a climate chamber. A revolving door gave them free access to a nesting box (Fig. 1; 2-l respiratory chamber). The temperature in the climate chamber was varied between 2 °C and 15 °C during wintertime, and between 15 °C and 24 °C in summertime. The humidity was maintained at 80–90%. The photoperiod was maintained to be similar to the natural photoperiod, L:D = 8:16 in winter, L:D = 16:8 in summer and L:D = 12:12 in spring and autumn. During the experiments (lasting up to 6 months), the dormice only had access to water ad libitum. Body weight was measured at the start and end of each experiment and in normothermic periods during the experiment, to keep the dormancy bouts undisturbed. Under this arrangement, the dormice could range freely between their nest-box for rest, sleep and dormancy, and the bigger cage for activity. This allowed continuous recording of undisturbed animals over prolonged periods of time.

For determination of MR, the air was pumped out of the respiratory chamber at a rate of 50 l h^{-1} and dried with silica gel (Fluka AG, Ch-Buchs). The flow of dry air was measured by electronic mass flow meters (FM 360, Tylan, D-Eching). As the CO_2 of both the inlet air and the measured air had not been removed, it was necessary to correct the flow rate using the RQ (Hill 1972). The O_2 and CO_2 content was measured with an O_2-analyser (AMETEK S3A/II, USA-Pittsburgh) and a CO_2-analyser (Unor 6 N, Maihak, D-Hamburg). Both were two-channel analysers with two measurement cells which compared air from the respiratory chamber with reference air from the climate chamber. Both analysers had a resolution of 0.001 ΔVol%. A magnetic valve system allowed the measurement of three dormice simultaneously. A fourth channel was used for zero reference checks at regular intervals (Fig. 1). MR was calculated according to the equation by Heldmaier and Steinlechner (1981b):

$$\mathrm{MR}\ [\mathrm{ml\ O_2\ h^{-1}}] = \Delta\mathrm{Vol\%\ O_2\ Flow}\ [\mathrm{l\ h^{-1}}]10$$

T_a was measured with thermocouples placed inside the nest-boxes. T_b was measured with temperature-sensitive radio transmitters (Mini-Mitter, Model V, USA-Sunriver, accuracy 0.1 °C), implanted intraperitoneally. Each transmitter was calibrated in a water bath at a range of between 0 °C and 40 °C before implantation. Transmitter signals were received and processed as described by Ruf and Heldmaier (1987).

All outputs from the gas-analysers, thermocouples, flowmeters and temperature transmitters were interfaced to an IBM-computer via a 16 Bit A/D interface (MDP 8280, Datalog, D-Mönchengladbach) and a PC-Labcard (PCL 718, Datalog, D-Mönchengladbach; see Fig. 1), and processed with software based on a program written by G. Heldmaier and T. Ruf (personal communication).

Data analysis and definitions

As shown in previous studies (Wilz and Heldmaier 1995), edible dormice display daily torpor, hibernation and estivation. To distinguish between these three forms of dormancy, daily torpor was assumed for dormancy bouts lasting less than 1 day, hibernation as dormancy bouts for more than 1 day during the hibernating period from October to May, and estivation as dormancy bouts for more than 1 day during summer from June to September (Wang and Lee 1996). Onset of a bout of dormancy was taken as the last peak of MR before continuous decrease in MR and T_b. Termination of a bout of dormancy was taken as the highest peak of MR after continuous increase of MR and T_b during the arousal.

Resting metabolic rate (RMR) was taken as the average VO_2 over 1 h in normothermic dormice, at a given T_a and constant T_b

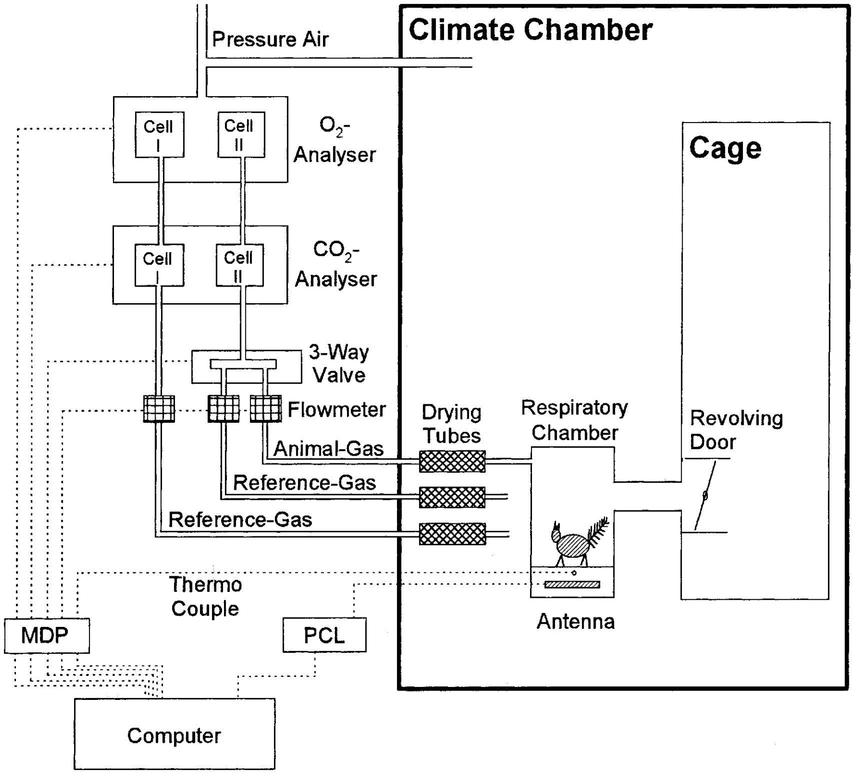

Fig. 1 Experimental set-up for long term recordings of metabolic rate (MR) and body temperature (T_b) in freely moving dormice

during this time. Minimum MR in daily torpor was taken as the average of the VO_2 during 30 min before beginning of arousal. Minimum MR in hibernation and estivation was taken as the average of VO_2 over at least 6 h, whereby T_b and T_a should be in steady state during this time. The T_b changed most rapidly on the beginning of entrance into dormancy. Cooling rate on entrance to dormancy was determined as the decrease of T_b below 32 °C T_b for 20 min, and standardised by expressing cooling rate per hour. The duration of arousal was taken from the point of first and continuous increase of the MR to the point of the highest value of MR whereby the T_b should have reached 32 °C or more. The mass-specific thermal conductance (C) in normothermia was calculated using the equation by Scholander et al. (1950):

$$C = MR(T_b - T_a)^{-1}$$

Calculations of C in dormancy using the equation of Scholander et al. produced no reliable results. During daily torpor we rarely obtained steady state conditions of T_b. Furthermore, in hibernation and estivation the differences between T_a and T_b become smaller than 0.4 °C. Based on the accuracy of the thermocouples (± 0.1 °C) and the temperature transmitters (± 0.1 °C) the gradients become inaccurate. Therefore we used the cooling curve at the entrance to hypothermia for calculation of C in dormancy. As shown by Bartholomew and Tucker (1963), thermal conductance can be calculated by the slope of the cooling process, if heat production, T_a, T_b and the specific heat capacity of tissue are known. We determined the slope of the cooling curve (curve fitting by SigmaPlot) and calculated C according to the equation given by Ruf (1991).

Statistics

Differences between means were examined using a Student's *t*-test or a Mann-Whitney-rank-sum-test (Zar 1996). Regressions were determined by the method of least squares. Regressions were compared according to Weber (1986). Circular statistics were made with the Watson-Williams-test and the Rayleigh-test (Batschelet 1981; Zar 1996).

Results

Under laboratory conditions, the dormice ($N = 7$) showed daily torpor throughout the year. This alternated in winter with prolonged bouts of hibernation and in summer with prolonged bouts of estivation (Fig. 2). The daily torpor bouts lasted between 3 h and 21 h ($N = 7$, $n = 78$; where N is the number of animals and n is the number of measurements/data points), the hibernation bouts between 39 h and 768 h ($N = 7$, $n = 56$) and the estivation bouts between 69 h and 106 h ($N = 1$, $n = 5$). A dormancy bout with a duration of 21 h through 39 h was never observed.

In dormancy MR is reduced to a fraction of the MR observed in normothermia. The average minimum MR in hibernation is about 0.017 ml O_2 g^{-1} h^{-1}, in estivation 0.031 ml O_2 g^{-1} h^{-1} and in daily torpor 0.053 ml O_2 g^{-1} h^{-1} (Fig. 3). The MR of all three forms of dormancy is positively correlated with the T_a between 8 °C and 22 °C. Between 8 °C and 4 °C there is no obvious change in the MR with T_a or with T_b. At T_a below 4 °C, the MR rises again to defend the T_b and prevent it from further approaching the freezing point (Fig. 3). The minimum T_b observed in a hibernating dormouse during our studies was 0.7 °C at a T_a of 0 °C. The statistical analysis showed significantly higher MR in daily torpor in comparison to hibernation and estivation (data points of hibernation and estivation together: $n = 147$, mean $= 0.019$, SD $= 0.007$; daily torpor: $n = 47$, mean $= 0.053$, SD $= 0.029$; $P < 0.001$). In order to determine whether this significant difference was

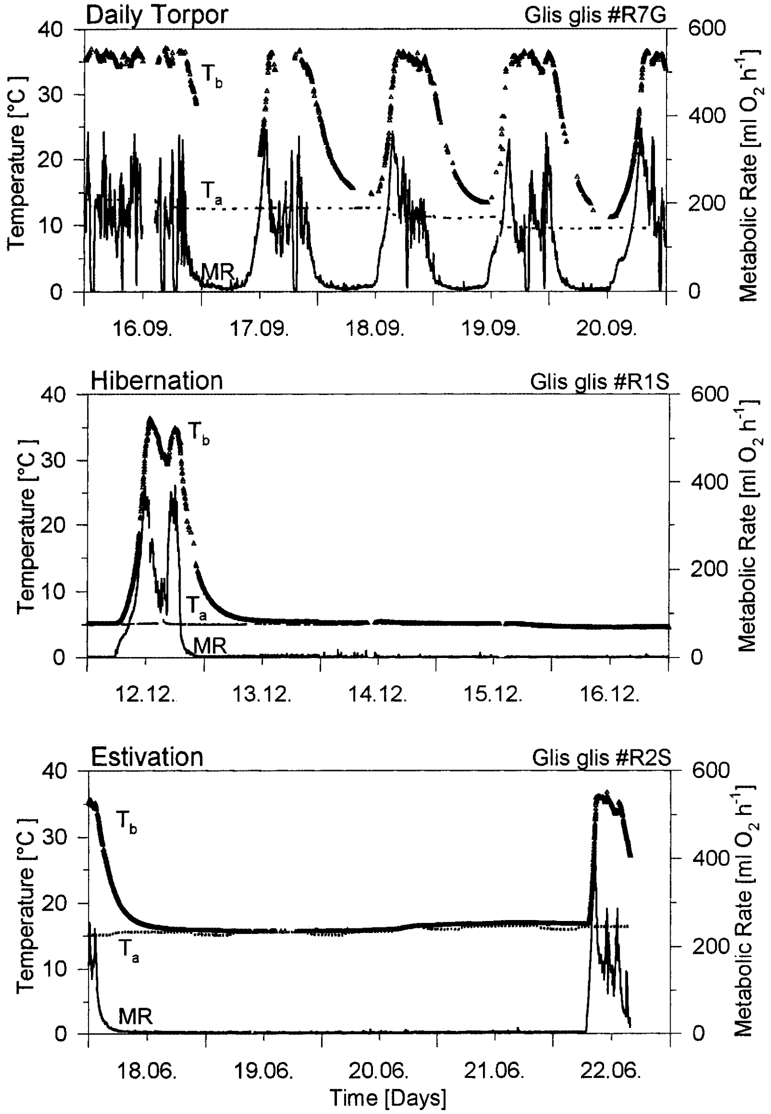

Fig. 2 Examples of daily torpor, hibernation and estivation in dormice. All plots show MR (expressed as $\dot{V}O_2$, *solid line*), ambient temperature (*dotted line*) and body temperature (*triangles*) over 5 days in winter, summer and autumn. The photoperiod was L:D 8:16 h in winter, L:D 16:8 h in summer and L:D 8:16 h in autumn. The zero drops of MR during normothermia mark the time when the dormouse spontaneously leaves the respiratory chamber

affected by the different time spent in dormancy, we compared the MR after 8 h into hibernation, estivation and daily torpor. At this time we found no difference in the MR of hibernation, estivation and daily torpor (Fig. 3, inset diagram).

In hibernation, the average difference between the minimum T_b and T_a was 0.2 °C, in estivation 0.4 °C. But in daily torpor, a difference of 2.1 °C between minimum T_b and T_a was recorded (Fig. 4, compare also with Fig. 2). This was significantly larger as compared to the $T_b - T_a$ gradient present during hibernation and estivation. Daily torpor episodes lasted only several hours which could reduce the development of hypothermia. Therefore we compared the $T_b - T_a$ gradient 8 h after the onset of dormancy. At this point in time we found no difference in the $T_b - T_a$ gradient between hibernation, estivation and daily torpor (Fig. 4 inset diagram). The average gradient between T_b and T_a for hibernation and estivation after 8 h of cooling is 2.12 °C ($N = 3$, $n = 29$, SD = 0.4 °C) and for daily torpor 2.49 °C ($N = 3$, $n = 24$, SD = 0.86). This result shows that cooling rates are identical in all three forms of dormancy.

The cooling rate at the time of entry into dormancy is correlated with the T_a. At a T_a of 4 °C the cooling rate is about 8 °C h^{-1}, at 21 °C the cooling rate is about 4 °C h^{-1}. The statistical analysis showed no significant difference between daily torpor and hibernation. The three data points displaying the cooling rate during estivation are within the range of the other forms of dormancy (Fig. 5).

The cooling process for hibernation and daily torpor is uniform at the same T_a. Figure 6 shows the original data for MR, T_a and T_b from the entry into hibernation and daily torpor, plus the calculated cooling function. During entrance into dormancy the conductance does not change with time or temperature and is on average 0.056 ml O_2 g^{-1} h^{-1} °C^{-1} ($N = 6$, $n = 29$, SD = 0.009). The conductance is equal for dormice in all three forms of dormancy. It amounts to 0.056 ml O_2 g^{-1} h^{-1} °C^{-1}

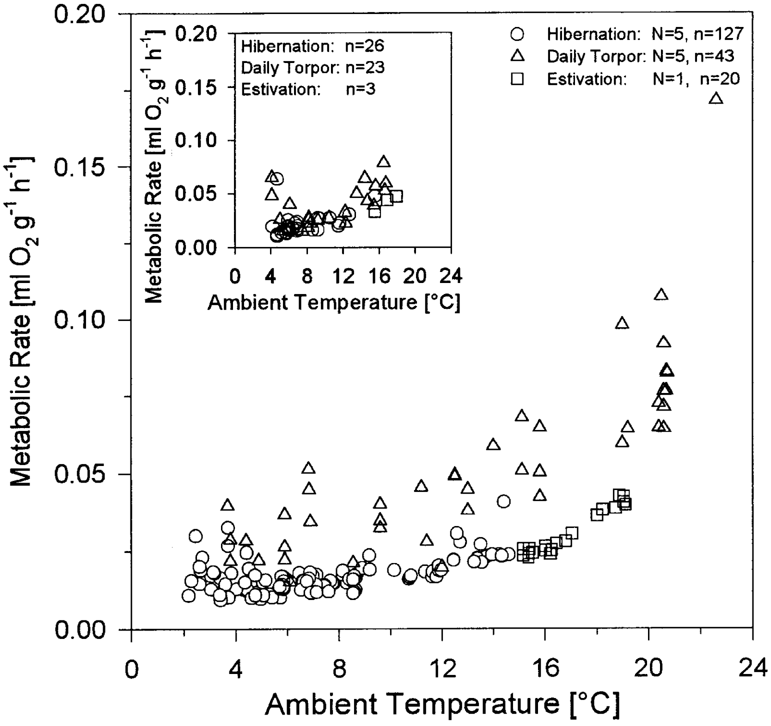

Fig. 3 Minimum MR in dormancy. The average minimum MR in hibernation (*circles*) is 0.017 ml O_2 g^{-1} h^{-1}, in estivation (*squares*) 0.031 ml O_2 g^{-1} h^{-1} and in daily torpor (*triangles*) 0.053 ml O_2 g^{-1} h^{-1}. The *inset diagram* shows the MR 8 h after entrance into dormancy

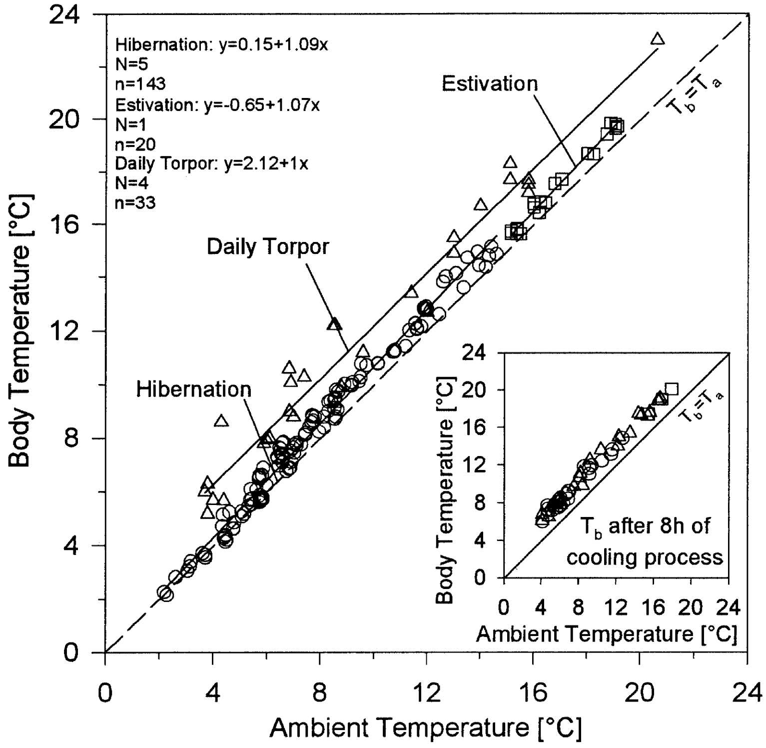

Fig. 4 Gradient between T_b and ambient temperature (T_a) in hibernation (○), estivation (□) and daily torpor (△). The *inset diagram* shows the T_b after 8 h of the cooling process. At this point of time there is no difference between the average $T_b - T_a$ gradient for daily torpor (2.49 °C, $N = 3$, $n = 24$, SD = 0.86) and hibernation and estivation (2.12 °C, $N = 3$, $n = 29$, SD = 0.4)

which is also identical with the conductance in normothermic dormice (C = 0.055 ml O_2 g^{-1} h^{-1} $°C^{-1}$, $N = 6$, $n = 50$, SD = 0.013; Fig. 6, inset diagram).

The duration of arousal from dormancy is temperature dependent. Due to the greater temperature gradient, an arousal from a low T_a lasted longer than from a high T_a. It required 1.2 h at $T_a = 22$ °C and the duration of arousal rose up to 9 h at 2 °C (Fig. 7). There was no significant difference between hibernation and daily torpor; the three data points of estivation also fitted in the regression function of hibernation and daily torpor.

Maximum heat production during arousal was always reached towards the end of the arousal process (see Fig. 2). The total energy required for arousal from a

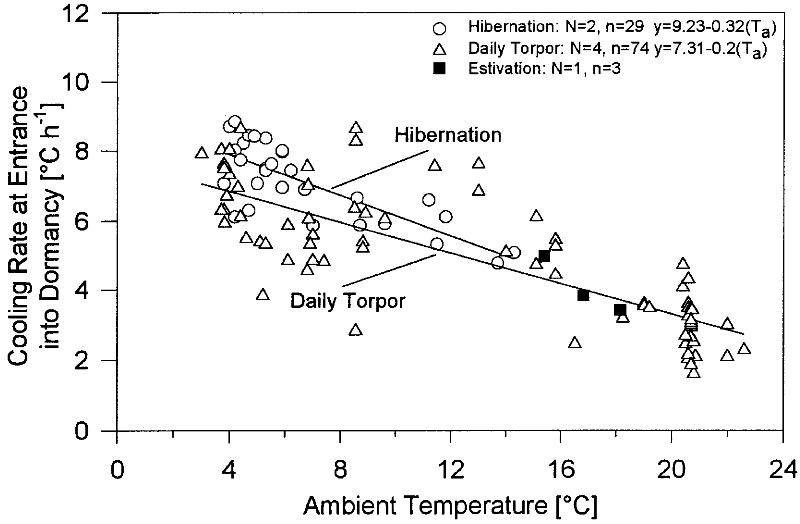

Fig. 5 Cooling rate at the beginning of dormancy. The regressions for hibernation (○) and daily torpor (△) are not significantly different. The three data points of estivation (■) fit the regression line for daily torpor and hibernation

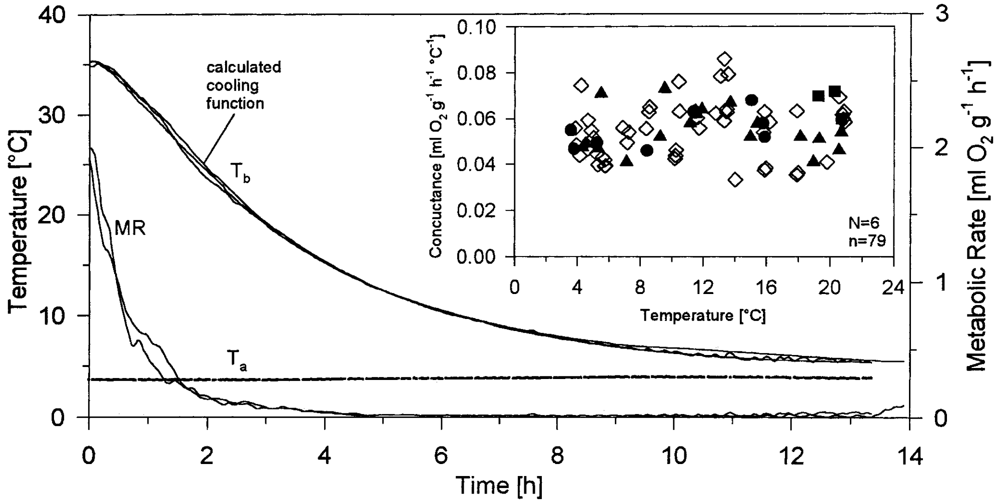

Fig. 6 Registration of T_a, T_bs and MRs on two different days at the same T_a during entrance into hibernation and into a bout of daily torpor. Also shown is the calculated cooling curve. The *inset diagram* shows the data points of the calculated conductance in normothermia (◇), daily torpor (◆), hibernation (●) and estivation (■)

low T_a was greater than from a high T_a. The cost of arousal at 2 °C is approximately 5 ml O_2 g^{-1} and approximately 1 ml O_2 g^{-1} at 22 °C. There was no statistical difference between hibernation and daily torpor. The few data points we obtained from estivating dormice were within the range of hibernation and daily torpor (Fig. 7, inset diagram).

The active periods of dormice, measured as time outside the respiratory chamber, were highly variable. In normothermia the summarised activity time per day was 0.5–7 h, with an average duration of 3 h (SD = 1.7 h, $N = 4$, $n = 41$). On days with daily torpor, the average duration of activity was 2 h (SD = 1.44 h, $N = 4$, $n = 65$). It is obvious that in hibernation and estivation the dormice remained inactive in their nest-boxes.

We further compared the energy-saving potential of hibernation, estivation and daily torpor, by measuring the MR while the dormice stayed in their nest-boxes. To calculate the total energy requirement per day in active dormice, it was necessary to consider the time the dormouse spent active outside the respiratory chamber (activity time). We measured MR of normothermic dormice in their nest box and assumed that they had this MR also outside their nest box. This calculated value of MR for outside activity was added to the measured MR while they were in their box and gave the estimated total energy requirement per day, average daily metabolic rate (ADMR).

$$\begin{aligned}\text{ADMR} = {} & (\text{activity time [h] average MR [ml O}_2\ \text{h}^{-1}]) \\ & + \text{measured } \dot{V}\text{O}_2 \text{ per day [ml O}_2]\end{aligned}$$

The energy requirement per day in normothermia changed with the T_a. At a T_a of 4 °C, the oxygen consumption per day was about 7 l and decreased with increasing T_a to 3 l at a T_a of 21 °C (Fig. 8). To calculate the energy saving potential of dormancy, we compared the energy required per day in normothermia with the energy required per day in dormancy. If the energy requirement per day in normothermia is taken as 100%, the possible energy saving is 99.6% at 4 °C by hibernation and 96.5% at 19 °C with estivation. The energy

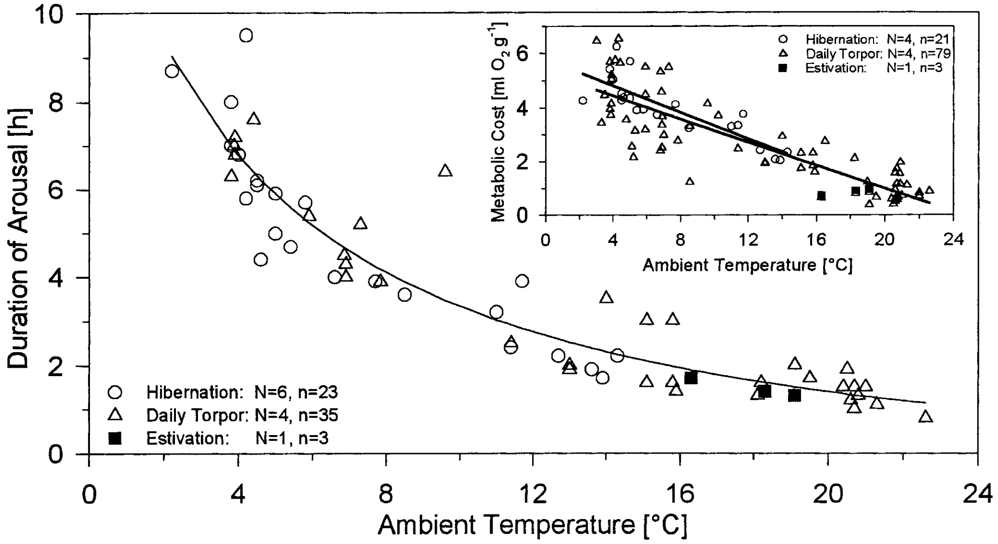

Fig. 7 Duration of arousal from dormancy. Data points are shown from hibernation (○), estivation (■) and daily torpor (△). The energy cost for arousal from different ambient temperatures is shown in the *inset diagram*. Also shown are three data points of estivation (■) and the regression lines from hibernation (○) and daily torpor (△)

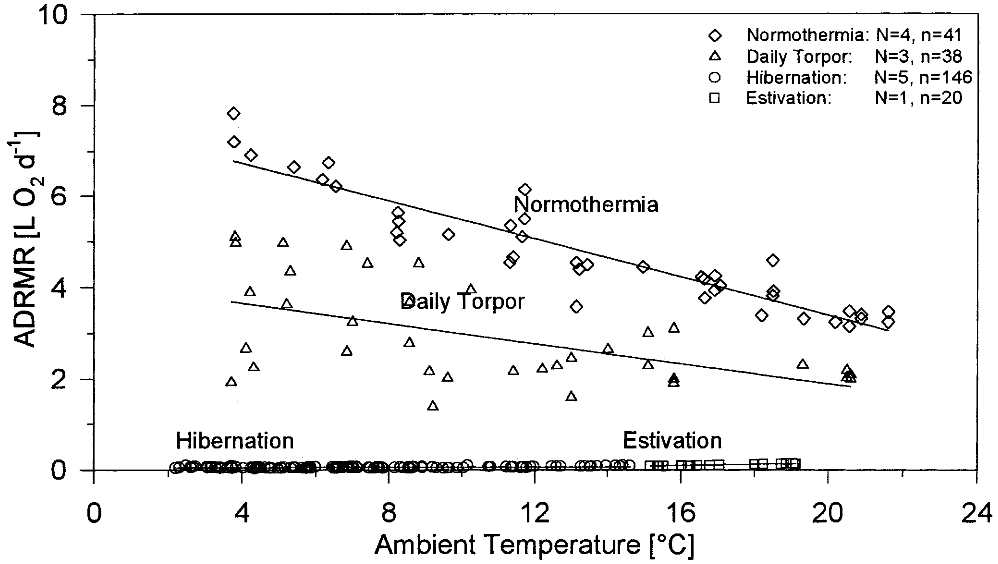

Fig. 8 Energy requirements per day in normothermia and dormancy. The data for hibernation and estivation were obtained on days without arousals. The data for daily torpor were taken from days with a bout duration of more than 12 h and includes the energy requirements during torpor, arousal as well as the active period of the day

saving by daily torpor amounts to 43% at 4 °C and 21% at 19 °C. Besides the effect of ambient temperature, the duration of the bout is also important for energy saving in daily torpor. If the bout is longer than 16 h, the daily energy saving by daily torpor can increase up to 80% (Fig. 8).

Dormice show a clear timing of entrance into dormancy. On average, the mean hour for entrance to hibernation is 0.20 a.m. ($n = 40$, $P < 0.0001$); entrance to daily torpor starts on average about 2.5 h later at 2.56 a.m. ($n = 126$, $P < 0.0001$). Both mean hours differ significantly ($P < 0.01$; Fig. 9).

Discussion

The aim of our work was to compare several physiological parameters in different forms of dormancy. The results showed that there exist only quantitative but no qualitative differences in all measured physiological parameters between hibernation, estivation and daily torpor. This suggests that hibernation, estivation and daily torpor are based on the same physiological mechanisms for downregulation of MR and T_b. The gradual difference between them can be considered as a result of the different bout durations for hibernation, estivation and daily torpor.

The slight differences observed between hibernation and estivation are a result of the different T_as. This fact influences all temperature-dependent parameters like cooling rate, duration of the arousal, cost of the arousal, minimum MR, $T_b - T_a$ gradient and energy saving potential. If the responses are compared at the same level of T_a, there are no differences between the different forms of dormancy. In temperature-independent parameters like bout-duration and conductance,

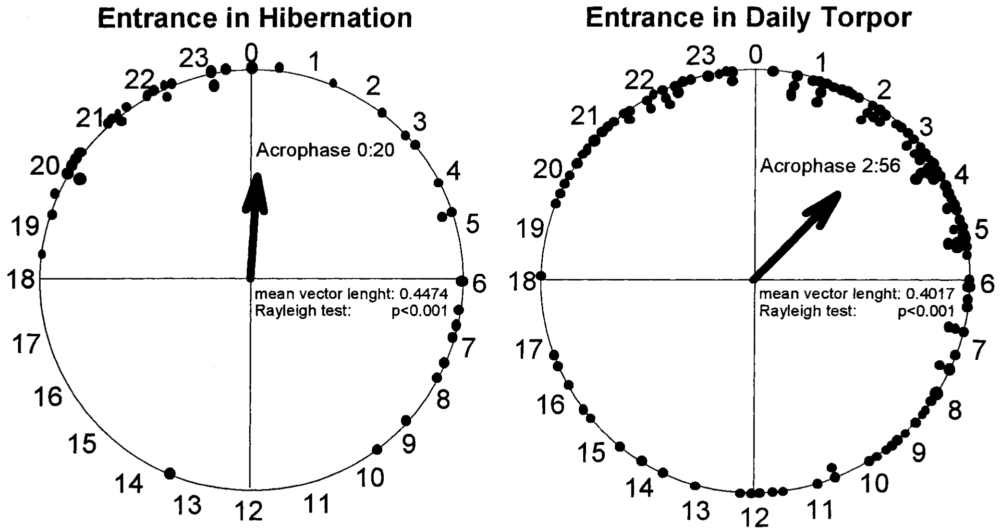

Fig. 9 Timing of entrance in dormancy. The *left 24 h clock* shows 40 samples of entrance in hibernation and the mean vector. The *mean vector direction* shows the acrophase (peak hour; 0.20 a.m.); the *mean vector length* gives the variance. The *right 24 h clock* shows 126 samples of entrance in daily torpor and the mean vector. Both mean vectors differs significantly ($P < 0.01$)

there is absolute conformity between hibernation and estivation. The coincidence of hibernation and estivation is best demonstrated with original records at different T_a (Fig. 10). The course of T_b and MR are quite similar in hibernation and estivation, except during variations in T_a which cause gradual differences as demonstrated in Figs. 4–8. This study only contains data from one dormouse in estivation; similar results were obtained during ongoing experiments with estivating dormice ($N = 3$, Ralf Elvert, personal communication).

The comparison of daily torpor with hibernation and estivation shows only one important difference: hibernation and estivation bouts are always longer than bouts of daily torpor. A bout of daily torpor lasts 21 h in maximum, whereas a hibernation bout lasts 39 h minimum. The maximum recorded length of a hibernation bout was 768 h. There is a clear gap of 18 h between the longest daily torpor bout and the shortest hibernation bout.

The duration of a daily torpor bout is never long enough to let the dormice reach a steady state in their $T_b - T_a$ gradient. As the exponential equation for cooling shows (Fig. 6), the dormice need 30–40 h to cool down to reach their minimum $T_b - T_a$ gradient. This could never be archived during a bout of daily torpor since the cooling process was interrupted by arousal during late afternoon. All daily torpor bouts are terminated by an arousal before T_b reaches the possible minimum $T_b - T_a$ gradient. This necessarily causes a higher $T_b - T_a$ gradient as compared to hibernation or estivation (Fig. 4).

The minimum MR in daily torpor is a little higher than in hibernation or estivation. The average MR of dormice in hibernation and estivation is about 0.017 ml O_2 g^{-1} h^{-1} and 0.031 ml O_2 g^{-1} h^{-1}, respectively, and correlates with the estimated minimum MR for all species in hibernation (0.037 ml O_2 g^{-1} h^{-1}, Geiser and Ruf 1995). The minimum MR for daily torpor in dormice amounts to 0.053 ml O_2 g^{-1} h^{-1} and differs

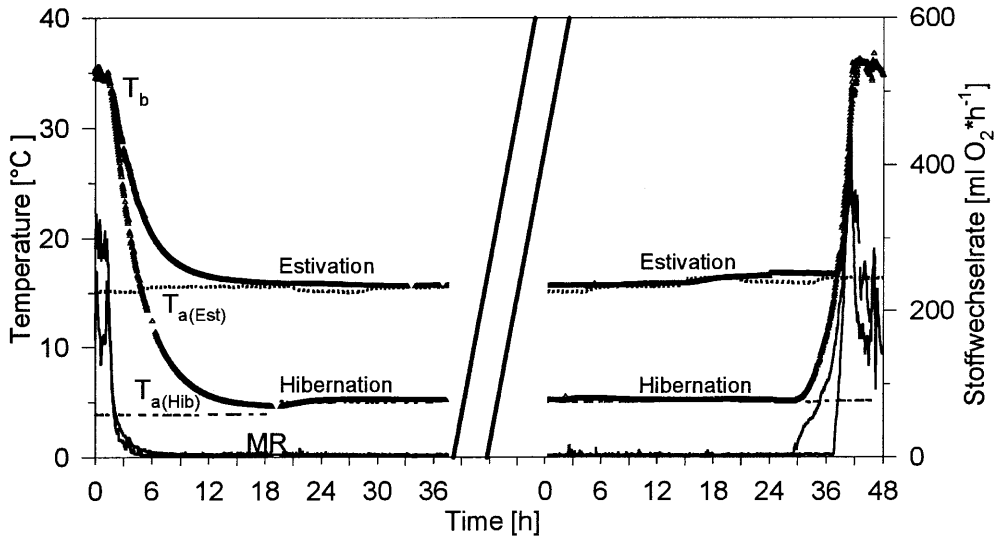

Fig. 10 Hibernation and estivation. Shown is T_a, T_b and MR of an estivation bout in summer at T_a ~17 °C and a hibernation bout in winter at T_a ~5 °C. Entrance and arousal of the bouts are time corrected for start and end at the same time. The middle parts of the bouts are omitted

significantly from minimum MR in hibernation and estivation (Fig. 3). This value is much less than the estimated minimum MR for all species in daily torpor, which is 0.535 ml O_2 g^{-1} h^{-1} (Geiser and Ruf 1995), i.e. minimum MR during daily torpor in dormice is close to the level of hibernation and estivation. This raises the question as to whether the MR during daily torpor really differs from metabolic downregulation in hibernation or whether this difference results from the shorter duration of torpor bouts which does not allow minimum MR. Metabolic downregulation occurs much faster than development of hypothermia, but 8 h after entrance into dormancy a slightly elevated MR is still maintained in hibernation as well as in daily torpor. This correlates with the slightly elevated $T_b - T_a$ gradient at this point of time, and explains the slightly elevated MR and $T_b - T_a$ gradient in daily torpor as a consequence of the interrupted cooling process and metabolic depression in daily torpor. This demonstrates that there are no qualitative differences between daily torpor, hibernation and estivation.

At T_as between 8 °C and 22 °C there was an increase in MR with temperature, which shows an apparent Q_{10} of 2.5. This Q_{10} is in the range of reasonable Q_{10} for physiochemical temperature effects of temperature on metabolic rates. It coincides with a slightly elevated $T_b - T_a$ gradient in dormice hibernating at higher T_a's (Fig. 4). However, one has to be careful since the mere existence of such a correlation does not allow us to decide whether metabolic rate is the consequence of a temperature effect or whether it is due to regulated control of metabolic rate to maintain a $T_b - T_a$ gradient (Heldmaier and Ruf 1992). If we extrapolate the MR of dormant dormice to the normothermic level of 36 °C by this apparent $Q_{10,}$ we obtain an MR which is only 23% of the normothermic RMR at thermoneutrality. This suggests that 77% of metabolic reduction in dormancy is caused by metabolic downregulation from the normothermic to the dormant state, whereas additional metabolic reduction is achieved by temperature dependent downregulation during dormancy. If we consider that entrance into dormancy usually occurs at T_as below thermoneutrality with elevated MR, the percentage of metabolic downregulation is even higher than 77%.

In the literature there is little information to be obtained about MR in dormant dormice. The data for daily torpor, found by Wyss (1932), amounts to 0.26 ml O_2 g^{-1} h^{-1} at 5 °C and is ten times higher than we found in our work. This may be the result of different methods; Wyss calculated the MR from heat-loss, which may overestimate results if the cooling process is not completed to steady state – as is the case in dormice during daily torpor. The MR of dormice in hibernation reported by Wyss (1932) amounts to 0.01 ml O_2 g^{-1} h^{-1} at 3 °C and by Kayser (1940) to 0.025 ml O_2 g^{-1} h^{-1} at 11 °C. Both data for MR in hibernation are in agreement with our results, if the T_a is taken into account.

The minimum thermal conductance of dormice in normothermia reaches 0.055 ml O_2 g^{-1} h^{-1} °C^{-1} at T_as below $T_a = 21$ °C. It is not raised or reduced in daily torpor, hibernation or estivation. This result is contradictory to the hypothesis of Snyder and Nestler (1990); their results show a decrease of the C in dormancy in relation to normothermia. Unfortunately, their data of C in dormancy were calculated by the formula of Scholander et al. (1950), using averages of MR and T_b at given T_a, which may be affected by non-steady state conditions. Our results are in agreement with a detailed analysis of conductance in Djungarian hamsters by simultaneous direct and indirect calorimetry, which also showed a constant thermal conductance during torpor bout cycles (Heldmaier and Ruf 1992). In accordance with the constant minimum conductance, there is no difference in the cooling rate at entrance into dormancy between daily torpor, hibernation and estivation.

Our results demonstrate that except for the differences in the bout length, all other measured parameters of hibernation, estivation and daily torpor do not allow qualitative differentiation between the three forms of dormancy. If we assume the same physiological mechanisms as a basis for all three forms of dormancy, the question remains how the dormouse can choose between a short bout of daily torpor and a prolonged bout of hibernation or estivation. At entrance into dormancy, there is no observable difference in metabolic downregulation or the cooling rate of T_b in hibernation and daily torpor (Fig. 6). A possible mechanism to control the bout length is indicated by the timing of entrance in dormancy. The peak hour of entrance to hibernation occurs shortly after midnight but daily torpor bouts start 2.5 h later. A similar difference for the onset of long or short dormancy bouts was also observed in the garden dormouse (Daan 1973) and the pocket mouse (French 1977). These results show that entry into dormancy is controlled by the circadian clock, and this control may even persist during prolonged hibernation in constant conditions (Wollnik and Schmidt 1995). The different circadian timing for entry into hibernation or daily torpor could suggest that the dormice decide at the entry into a dormancy bout whether this will be prolonged hibernation or a short daily torpor bout. Alternatively, it could suggest that an early entry into a bout of dormancy shortly after midnight may allow the dormice to reach a state where they become insensitive to an internal arousal signal for the termination of a daily torpor bout during late afternoon, whereas those dormice entering dormancy 2.5 h later are still susceptible to this internal signal for arousal.

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