Regulation of body temperature and energy requirements of hibernating Alpine marmots (Marmota marmota)

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Ortmann, Sylvia, and Gerhard Heldmaier. Regulation of body temperature and energy requirements of hibernating Alpine marmots (Marmota marmota). Am. J. Physiol. Regulatory Integrative Comp. Physiol. 278: R698–R704, 2000.—Body temperature and metabolic rate were recorded continuously in two groups of marmots either exposed to seasonally decreasing ambient temperature (15 °C) over the entire hibernation season or to short-duration temperature changes during midwinter. Hibernation bouts were characterized by an initial 95% reduction of metabolic rate facilitating the drop in body temperature and by rhythmic fluctuations during continued hibernation. During midwinter, we observed a constant minimal metabolic rate of 13.6 ml O2·kg−1·h−1 between 5 and 15°C ambient temperature, although body temperature increased from 7.8 to 17.6°C, and a proportional increase of metabolic rate below 5°C ambient temperature. This apparent lack of a Q10 effect shows that energy expenditure is actively downregulated and controlled at a minimum level despite changes in body temperature. However, thermal conductance stayed minimal (7.65 ± 1.95 ml O2·kg−1·h−1·°C−1) at all temperatures, thus slowing down cooling velocity when entering hibernation. Basal metabolic rate of summer-active marmots was double that of winter-fasting marmots (370 vs. 190 ml O2·kg−1·h−1). In summary, we provide strong evidence that hibernation is not only a voluntary but also a well-regulated strategy to counter food shortage and increased energy demands during winter.

thermal conductance; metabolic rate; body temperature-ambient temperature gradient; thermoregulation; hibernation physiology

ALPINE MARMOTS (Marmota marmota) overcome the problems of poor food availability and severe environmental conditions during winter by the means of deep hibernation. Toward the end of September, they cease all above-ground activity and retreat into their protected hibernacula where they experience a continuous decrease of ambient temperature (Ta) from 12 to 15°C in autumn to ~0°C in spring (4). They end the hibernation season early in April and thus spend >6 mo in their hibernacula. During prolonged bouts of hibernation, metabolic rate (MR) is reduced to a fraction of the euthermic level, and body temperature (Tb) is close to Ta (13, 28). Thermoregulation continues in deep hibernation like in several species of hibernators or torpor-exhibiting species (7, 11, 16, 17), but unlike various ground squirrels, which exhibit Tb values near or below the freezing point (5), Alpine marmots always control their Tb at values above 3–5°C (3, 4).

Marmots rely exclusively on body fat reserves to fuel all energy demands during hibernation. Therefore, the reduction of MR in deep hibernation is of vital energetic significance during the long winter season. Although low MR and Tb values are described in many species, the mechanisms and physiological control of metabolic reduction are only poorly understood and remain controversial (8, 9, 13–15, 25, 26, 32, 33). Alpine marmots are well known as hibernators and were one of the first species in which physiological changes in hibernation were measured (6). However, there is only poor knowledge concerning the regulation of Tb and energy requirements during hibernation as well as in the normothermic state. We therefore continuously measured Tb and MR of marmots during the entire hibernation season. One group of adult Alpine marmots hibernated under seasonally decreasing Ta conditions, and MR and Tb were recorded continuously to obtain the entire spectrum of Tb and MR changes. A second group of marmots was exposed to different Ta values during midwinter, when hibernation bouts are longest (1, 13), to analyze their potential for Tb and MR regulation in deep hibernation.

MATERIALS AND METHODS

Animal Maintenance

Alpine marmots were either bred in our breeding colony in Philipps University Marburg or in Helabrunn Zoo Munich. The latter were bought as juveniles and were raised under natural climatic conditions and the photoperiod of Marburg (50°49 N, 09 E). During the summer, marmots were kept in family groups in outdoor enclosures provided with artificial burrows and were fed one time per day with green grass and herbs and with a mixture of corn, seed, and rabbit chow (Altromin). A few weeks before the start of the experiments, marmots were provided with precalibrated temperature transmitters (Kronwitter TWS; Oberpfammern or Minimitter, Sunriver, OR). These transmitters allow long-term records of Tb and were surgically implanted in the abdominal cavity under deep Ketanest/Rompun anesthesia. With the onset of the hibernation season (October), marmots were transferred to climate chambers where they stayed in constant darkness until spring.
Experiments and Techniques

Experiment I: hibernation pattern and energy requirements of Alpine marmots under seasonally decreasing temperature conditions. One male and two female adult marmots were housed individually in closed Perspex boxes of 2.6 l volume each. The Perspex boxes were provided with a thin layer of hay and served as metabolic cages. The marmots had no additional nesting material and remained without food or water from October 15th until the end of the hibernation season, i.e., March 5th. Ta within the climate chamber was maintained constant at 7°C Tā until midwinter. They were housed in two groups in wooden nest boxes containing hay as nesting material. During January and February, individual animals were transferred to closed Perspex boxes (as in experiment I). After they reentered deep hibernation, Tā was either increased stepwise from 7 to 15°C or decreased to −0.5°C. Each step lasted at least 24 h, and Tā (5 marmots) and MR (up to 8 marmots) were recorded continuously.

MR of normothermic Alpine marmots was investigated during January 12 and February 22 (n = 6) and between June 26 and August 17 (n = 9) over a Tā range of 35°C. Tā was lowered in steps of 5°C from 30°C to −5°C. Each Tā step lasted until MR established a constant resting level, but each lasted at least 1 h. Techniques. Tā was recorded in 6-min intervals using a computerized recording system. For metabolic measurements, air flow through the metabolic boxes was monitored by mass flow meters (Tylan) and was controlled at 40–50 l/h when marmots were hibernating and 400 l/h during normothermia. The air was dried with silica gel and was analyzed for its O2 and CO2 content with an O2 analyzer (Oxytest S; Hartmann & Braun) and a CO2 analyzer (URAS 2T; Hartmann & Braun). Both are two-channel analyzers comparing sample air from the animal boxes with reference air from the climate chamber. They have a measuring range of 20–21 vol/100 vol O2, 0–1 vol/100 vol CO2, and 0.001 vol/100 vol resolution. The climate chamber was continuously supplied with outside air. A magnetic valve system allowed the measurement of six channels in sequence. The setup admitted continuous records of Tb, Tā, and MR in 6-min intervals for each individual. To prevent marmots from dehydration during hibernation, the surrounding air was humidified.

For measurements of normothermic marmots, individual animals were transferred to Perspex boxes and placed in a climate chamber (500 SD; Weiss). MR was determined as described above but was recorded in 1-min intervals.

MR was calculated according to the equation

\[ MR \text{ (ml O}_2 \text{·h}^{-1}) = dvol/100 \text{ vol O}_2 \times \text{flow (l/h)} \times 10 \]

where dvol/100 vol O2 is reference (surrounding) air minus sample air (animal box).

Resting MR of hibernating and normothermic marmots was calculated by averaging the three lowest values. Thermal conductance (C) was calculated under steady-state conditions, i.e., after Tb had stabilized at a certain value, either from the linear increase of MR with decreasing Tā below the thermoneutral zone or from Tb, Tā, and MR according to the equation

\[ C \text{ (ml O}_2 \text{·kg}^{-1} \cdot \text{h}^{-1} \cdot \text{°C}^{-1}) = MR/(T_b - T_a) \]

Statistical Analysis

Results are given as means ± SE. Data obtained from the same individual at the same Ta were averaged for statistical analysis. “N” is the number of animals, and “n” is the total number of measurements. Differences between means were examined using a Student’s t-test. Regressions were determined by the methods of least squares.

RESULTS

Experiment I: Hibernation Pattern and Energy Requirements of Alpine Marmots Under Seasonally Decreasing Temperature Conditions

Body weight. Body weight decreased during winter from 3,870 ± 138 g (n = 3) in autumn to 2,750 ± 144 g in spring, i.e., marmots lost 1,253 ± 111 g body mass or 32.5 ± 2.5% of the prehibernation mass (PHM). The absolute daily mass loss was 12.8 ± 0.05 g/day, and the weight-specific daily mass loss was 0.33 ± 0.02% PHM/day.

Hibernation bout characteristics. Figure 1 shows the Tb course of an Alpine marmot over the entire hibernation season in the laboratory, beginning in early November at −15°C Tb. Bouts of continuous hibernation were periodically interrupted by short phases of normothermia. Tb in deep hibernation was adjusted to the progressively decreasing Tā, and hibernation bouts lasted longer (e.g., up to 141 h at Tā 7°C). Nevertheless, below a certain Tā threshold of −5°C, a minimum Tb was maintained constant despite the further drop of Tā, and bout length was shortened (up to 41 h at Tā 2.5°C). Mean minimum Tb of this particular marmot was −9.5°C at 5°C Tā.

Figure 2 shows the time course of MR and Tb of a hibernating Alpine marmot over a period of 13 days. Tā within the climate chamber was −7°C at the end of December and the beginning of January and was decreased to 2.5°C in mid-February. Each hibernation episode was initiated by a rapid decrease in MR from the normothermic to the torpid level, and minimum values of MR below 20 ml O2·kg−1·h−1 were reached...
after ~10 h. This initial metabolic suppression (MR\textsubscript{init}) was followed by a slightly elevated level of MR when hibernation progressed until the next arousal occurred. \(T_b\) decreased rapidly with the onset of the hibernation bout and continued to decrease through the entire bout. During continued hibernation, marmots maintained a minimum MR (MR\textsubscript{min}) that was periodically interrupted by bursts of heat production. These bursts became more pronounced with increasing cold load (Fig. 3) and reached or even exceeded normothermic resting MR at or below \(T_a\) 2.5°C, whereas burst frequency remained constant with 13.02 ± 0.48 bursts/day at any \(T_a\). For estimating the true energy costs of a hibernating marmot at a given \(T_a\), we therefore calculated an average hibernation MR (MR\textsubscript{hib}) that includes MR\textsubscript{min} and the metabolic bursts.

Minimum \(T_b\) (Fig. 4A) during hibernation was adjusted to \(T_a\) within certain limits and decreased in parallel with the decline in \(T_a\). When \(T_b\) was lowered below 7°C, \(T_b\) was regulated at a level of ~10–11°C. Consequently, the \(T_\text{a}-T_\text{b}\) gradient rose with the drop in \(T_a\), and marmots increased their mean MR\textsubscript{hib} to defend their preferred hibernation \(T_b\) (Fig. 4B). This metabolic response occurred proportionally to the additional cold
load and reached highest values of ~400 ml O$_2$/h at $T_a = 0^\circ$C. At $T_a$, values above 11°C MR$_{hib}$ remained constant at ~100 ml O$_2$/h, irrespective of the increase of $T_b$ from 13.6°C at 11°C $T_a$ to 18.2°C at 15°C $T_a$. We observed a comparable pattern for the dependency of MR$_{min}$ on $T_a$, but on a lower level and with a gentle slope (Table 1). However, we observed no significant increase in MR$_{init}$ with decreasing $T_a$.

The expression of MR in weight-specific units revealed a comparable relationship of MR with $T_a$ (Fig. 4C) with one exception. Two of three marmots exhibited a significant increase of MR$_{init}$ with decreasing $T_a$, whereas the third marmot showed no dependency of MR$_{init}$ on $T_a$ (Table 1).

**Experiment II: Regulation of $T_b$ and Metabolic Heat Production in Hibernating and Normothermic Marmots**

Body weight. Mean body weight of Alpine marmots was 3,090 ± 75 g (n = 8) during hibernation, 3,358 ± 75 g (n = 6) during normothermia in winter, and 3,599 ± 64 g (n = 9) in summer. Body weight was not different between winter hibernation and winter normothermia but differed significantly between both hibernation and summer normothermia (P < 0.01) and winter normothermia and summer normothermia (P < 0.05).

The range of $T_a$ in which Alpine marmots entered deep hibernation ranged from −0.5 to 16°C in the laboratory during midwinter. Any temperatures exceeding these threshold levels induced an immediate arousal from hibernation.

$T_b$ (Fig. 5) was closely adjusted to $T_a$ between 5 and 15°C $T_a$, and we observed a $T_b$-$T_a$ gradient of 1–3°C. Because $T_b$ followed $T_a$, an increase in $T_b$ from 7.8°C at 5°C $T_a$ to 17.6°C at 15°C $T_a$ could be recorded. Below 5°C $T_a$, $T_b$ was maintained more or less stable, but minimal metabolic heat production increased proportionally with decreasing $T_a$ to a maximum of 50 ml O$_2$·kg$^{-1}$·h$^{-1}$. Between 5 and 15°C $T_a$, MR remained constant at 13.6 ± 0.55 ml O$_2$·kg$^{-1}$·h$^{-1}$. At 16°C $T_a$, $T_b$ and MR were elevated again, marmots regulated their $T_b$ at ~4.7°C above $T_a$, and heat production rose to 23.5 ± 2.43 ml O$_2$·kg$^{-1}$·h$^{-1}$.

Thermal conductance was established at a minimal level of 7.65 ± 1.95 ml O$_2$·kg$^{-1}$·h$^{-1}$·°C$^{-1}$. Conductance did not change with $T_a$ but remained constant below and above 5°C $T_a$.

Nevertheless, despite the pronounced increase of energy demands in the cold, hibernation MR remained a fraction of normothermic resting MR (MR$_{norm}$) at any given $T_a$ (Fig. 6). A drop in $T_a$ from 30 to −5°C during winter caused a 2.5-fold rise in MR$_{norm}$ from 190 ml O$_2$·kg$^{-1}$·h$^{-1}$ between 15 and 25°C $T_a$ to 490 ml O$_2$·kg$^{-1}$·h$^{-1}$ at −5°C $T_a$. The true reduction of energy costs by hibernation increased from ~250 ml O$_2$·kg$^{-1}$·h$^{-1}$ at 15°C $T_a$ to 400 ml O$_2$·kg$^{-1}$·h$^{-1}$ at 0°C $T_a$.

The whole extent of energy reduction by the means of hibernation becomes even more pronounced when MR$_{min}$ is compared with MR$_{norm}$ during summer. Summer-active marmots exhibit a higher weight-specific MR at any given $T_a$, and basal MR is doubled compared with fasting marmots during winter. Moreover, the start of the linear increase of MR with decreasing $T_a$, i.e., the lower critical temperature ($T_{lc}$), is shifted to lower $T_a$ values (15 vs. 20°C). However, the slope of the regression line calculated from values below $T_{lc}$ does not differ between winter and summer normothermic marmots.

**DISCUSSION**

Hibernation is a voluntary and well-regulated adaptive response to conditions of low $T_a$ and food shortage.

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**Table 1. Regression characteristics of metabolic rate and weight-specific metabolic rate vs. $T_a$ of hibernating marmots**

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>n</th>
<th>Regression Equation</th>
<th>r</th>
<th>P</th>
<th>Regression Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>MR$_{init}$</td>
<td>17</td>
<td>74.05–3.20 $T_a$</td>
<td>−0.449</td>
<td>NS</td>
<td>28.7–1.58 $T_a$</td>
</tr>
<tr>
<td>MR$_{init}$</td>
<td>5</td>
<td>206.5–14.9 $T_a$</td>
<td>−0.846</td>
<td>&lt;0.01</td>
<td>78.8–6.23 $T_a$</td>
</tr>
<tr>
<td>MR$_{hib}$</td>
<td>24</td>
<td>397.2–26.9 $T_a$</td>
<td>−0.910</td>
<td>&lt;0.001</td>
<td>150.6–11.2 $T_a$</td>
</tr>
<tr>
<td>MR$_{hib}$</td>
<td>17</td>
<td>72.5–2.78 $T_a$</td>
<td>−0.226</td>
<td>NS</td>
<td>22.8–1.38 $T_a$</td>
</tr>
<tr>
<td>MR$_{hib}$</td>
<td>7</td>
<td>208.0–15.38 $T_a$</td>
<td>−0.781</td>
<td>&lt;0.01</td>
<td>64.9–5.31 $T_a$</td>
</tr>
<tr>
<td>MR$_{hib}$</td>
<td>21</td>
<td>459.8–31.07 $T_a$</td>
<td>−0.905</td>
<td>&lt;0.001</td>
<td>141.5–10.6 $T_a$</td>
</tr>
<tr>
<td>MR$_{init}$</td>
<td>8</td>
<td>132.5–7.76 $T_a$</td>
<td>−0.539</td>
<td>NS</td>
<td>49.9–2.74 $T_a$</td>
</tr>
<tr>
<td>MR$_{init}$</td>
<td>18</td>
<td>189.6–11.81 $T_a$</td>
<td>−0.826</td>
<td>&lt;0.01</td>
<td>76.6–5.25 $T_a$</td>
</tr>
<tr>
<td>MR$_{hib}$</td>
<td>18</td>
<td>475.7–33.07 $T_a$</td>
<td>−0.949</td>
<td>&lt;0.001</td>
<td>190.2–14.1 $T_a$</td>
</tr>
</tbody>
</table>

$T_a$, ambient temperature; MR, metabolic rate; MR$_{init}$, MR$_{min}$, and MR$_{hib}$, initial, minimum, and hibernation MR, respectively; NS, not significant.
that occur during winter. The results of our study clearly demonstrate that entrance into hibernation is facilitated by an initial maximum suppression of metabolic heat production to values even below 10 \(ml O_2 \cdot kg^{-1} \cdot h^{-1}\). The transition to this level of reduced metabolism requires \(\sim 10\) h, and it is maintained for around 1 day. Due to the shut off of heat production, \(T_b\) starts to decline and continues its decline throughout the entire hibernation bout. Minimum \(T_b\) is generally reached after several days and just before arousal. The decline in \(T_b\) is very regular and smooth, indicating that the threshold of counteractive metabolic heat production is always adjusted just below the actual \(T_{b'}\), which is consistent with the sliding set point for \(T_b\) during entrance into hibernation proposed by Heller et al. (18). Metabolic reduction always precedes the drop in \(T_{b'}\), and it is evident that hypometabolism is the cause of hypothermia and not its result. This finding is not unique in Alpine marmots and has been demonstrated in true hibernators like woodchucks (23), golden hamsters (22), and golden-mantled ground squirrels (15) as well as in torpor-exhibiting species like Djungarian hamsters (14) and lemurs (29).

During continued hibernation, MR is slightly elevated and is frequently interrupted by bursts of heat production. This pattern of MR control was rather unexpected but clearly demonstrates continuation of active regulation of metabolism, even in deep hibernation. Regular fluctuations of MR during hibernation have previously been recorded (10, 34), but they occurred in much shorter intervals with an amplitude well below resting MR. At high \(T_a\) values (11–15°C \(T_a\)), metabolic bursts in marmots were rather small but increased in amplitude with increasing cold load. At \(T_a\) values at and below 2.5°C, the amplitude of these bursts reached or even exceeded normothermic resting MR at that \(T_a\), as shown in Figs. 2 and 3. This finding is especially remarkable as this particular marmot hibernated at \(\sim 12°C\) \(T_a\).

It has been shown that species displaying hibernation or torpor can elevate their heat production at low \(T_a\) values to defend a minimal \(T_b\), but the results of this study demonstrate that marmots defend their minimal \(T_b\) with patterned pulsatile increases in metabolism. Additional cold load evokes a proportional increase of \(MR_{min}\) (Fig. 4 and Table 1) and a major increase in burst amplitude. The latter results in a proportional but steeper rise of \(MR_{hib}\) with decreasing \(T_a\) compared with \(MR_{min}\) (Table 1). An alternative strategy to the rise in amplitude would be to increase burst frequency in the cold, but we found no indication that marmots make use of this mechanism. On the contrary, we counted a constant number of metabolic burst per day (13.02 ± 0.48 bursts/day) irrespective of the change in \(T_a\).

It is generally accepted that the ability for thermoregulation persists during that part of the hibernation process when \(T_b\) reaches the set point of metabolic defense (16, 17, 19, 22, 24, 36), and it seems reasonable that the physiological processes underlying the thermoregulation at low \(T_a\) values during hibernation, torpor, and normothermia are similar (14, 20, 32). At \(T_a\) values above the \(T_b\) set point, i.e., above the animal’s preferred \(T_{b'}\), there is no need for counteractive heat production. \(T_b\) passively followed changes in \(T_a\), and minimal MR stabilized at a plateau of 13.6 ± 0.55 \(ml O_2 \cdot kg^{-1} \cdot h^{-1}\) over a wide range of \(T_{b'}\). This stability of heat production has previously only been described for hibernating ground squirrels (15), and it contradicts expected temperature effects on MR. Furthermore, it suggests an active control of MR at a minimum rate independent from \(T_{b'}\). Otherwise, we would expect an increase in MR with increasing \(T_{b'}\), i.e., a \(Q_{10}\) within the range of two to three, which is “normal” for in vitro systems (27) and is supposed to be valid during natural hypothermia. In hibernating marmots, for instance, we calculated a \(Q_{10}\) value of 1.2 over a \(T_{b'}\) range of 9.8°C (\(T_b\) 7.8°C at \(T_a\) 5°C vs. \(T_b\) 17.6°C at \(T_a\) 15°C).

This observation conflicts with those made by several investigators (8, 12, 21, 30, 35). They found an exponential relationship between \(T_{b'}\) and MR in the range where \(T_b\) is not metabolically defended. However, this is not the case in hibernating marmots. Metabolic heat production can be better described as a function of the temperature gradient between \(T_{b'}\) and \(T_b\), which is valid for all data obtained in deep hibernation and for those recorded at \(T_b\) values ≤ 5°C, i.e., above the threshold of metabolic defense. We conclude that MR is actively shut down and a \(Q_{10}\) effect may become irrelevant. As long as \(T_b\) is close to \(T_{b'}\), minimum MR values can be reached irrespective of the actual \(T_{b'}\), whereas \(Q_{10}\) effects alone only allow two- to threefold reduction of MR per 10°C decrease in \(T_{b'}\).

Considering the effects of \(Q_{10}\), one would expect that hibernators would reduce \(T_{b'}\) as fast as possible and force the drop in \(T_{b'}\) by behavioral and physiological means, i.e., a stretched posture, sweating, and saliva spreading or increased thermal conductance. Such a response has never been reported for Alpine marmots or other species displaying hibernation or torpor. On the contrary, marmots in the field huddle together in extended family groups with close body contact in a well-insulated hibernaculum. They show a curled body.
position and synchronize their arousal events as well as the reentry into hibernation (1, 3). Moreover, marmots additionally minimize their thermal conductance to slow down cooling velocity and maintain this level of reduced thermal conductance over the entire temperature range where hibernation occurs. Our results indicate that thermal conductance is nearly cut in half during hibernation compared with normothermia. Such a significant reduction of thermal conductance attending the entrance into torpor has previously only been found one time (31). The ability of an active reduction of thermal conductance during hibernation is supposed to be of considerable energetic significance but is not typical for hibernators (14) and should therefore be interpreted with caution. In our study, thermal conductance has been calculated in two different ways, and from single measurements of normothermic marmots at very low Ta (−20 to −40°C) we obtained values of 6–7 ml O2·kg⁻¹·h⁻¹·°C⁻¹. These were directly calculated from T₀, T₀ and MR (data not shown) and are within the range of thermal conductance of hibernating marmots. It seems feasible that even normothermic marmots may reduce thermal conductance down to the hibernation level, and thermal conductance calculated from the regression slope possibly overestimates minimal conductance in normothermia.

Nevertheless, marmots display a variety of adaptations, behavioral and physiological, which all together apparently prevent a rapid decrease of T₀. The uncoupling of metabolic heat production and absolute T₀ during hibernation or torpor allows maintenance of very low MR even at high T₀, as long as T₀ is close to T₀. Alpine marmots experience temperatures that do not allow minimal metabolism over the whole hibernation season because T₀ in natural hibernacula decreases exponentially from −12–15°C in October to 0°C in spring (4). However, an active metabolic suppression would allow hibernation under optimal energetic conditions at least until mid-December. During December, T₀ drops below the 5°C threshold, and energy requirements increase due to the active defense of T₀. Marmots are herbivorous and do not cache food but rely exclusively on their body fat reserves. Body fat is the only source to fuel both the 6-mo hibernation season and reproduction that occurs immediately after emergence from hibernation (3). However, winter is a major time of mortality in marmots (2), and unfavorable harsh winter conditions presumably have created selection for adaptations that reduce energy costs during hibernation. Reduced energy costs and lower body weight loss over winter enhance fertility and improve reproductive success in the following spring.

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