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 to 0°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 a well-regulated strategy to counter food shortage and increased energy demands during winter.

animal physiology; body temperature; energy demands; hibernation; 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 (T_a) 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 (T_b) is close to T_a (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 T_b values near or below the freezing point (5), Alpine marmots always control their T_b at values above 3–5°C (3, 4).

Marmots rely exclusively on 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 T_b 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 T_b and energy requirements during hibernation as well as in the normothermic state. We therefore continuously measured T_b and MR of marmots during the entire hibernation season. One group of adult Alpine marmots hibernated under seasonally decreasing T_a conditions, and MR and T_b were recorded continuously to obtain the entire spectrum of T_b and MR changes. A second group of marmots was exposed to different T_a values during midwinter, when hibernation bouts are longest (1, 13), to analyze their potential for T_b 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 Hellabrunn Zoo Munich. The latter were bought as juveniles and were raised under normal 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 T_b 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 despite the further drop of Ta, and hibernation bouts lasted longer (e.g., up to 141 h at Ta 7°C). Nevertheless, below a certain Ta threshold of ~5°C, a minimum Tb was maintained constant despite the further drop of Ta, and bout length was shortened (up to 41 h at Ta 2.5°C). Mean minimum Tb of this particular marmot was ~9.5°C at 5°C Ta.

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

Figure 2 shows the time course of MR and Tb of a hibernating Alpine marmot over a time period of 13 days. Tb 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.

Figure 1. Time course of body temperature (Tb) over an entire hibernation season. Ambient temperature (Ta) decreased stepwise from 15°C in autumn to 0°C in spring.
after ~10 h. This initial metabolic suppression (MRinit) was followed by a slightly elevated level of MR when hibernation progressed until the next arousal occurred. Tb 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 (MRmin) 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 Ta 2.5°C, whereas burst frequency remained constant with 13.02 ± 0.48 bursts/day at any Ta. For estimating the true energy costs of a hibernating marmot at a given Ta, we therefore calculated an average hibernation MR (MRhib) that includes MRmin and the metabolic bursts.

Minimum Tb (Fig. 4A) during hibernation was adjusted to Ta within certain limits and decreased in parallel with the decline in Tb. When Tb was lowered below 7°C, Tb was regulated at a level of ~10–11°C. Consequently, the Tb-Ta gradient rose with the drop in Ta, and marmots increased their mean MRhib to defend their preferred hibernation Tb (Fig. 4B). This metabolic response occurred proportionally to the additional cold load. 

Fig. 2. Time course of weight-specific metabolic rate (MR; top) and Tb and Ta (bottom) over a time period of 13 days. Ta was decreased from ~7°C at the end of December through the beginning of January to ~2.5°C in mid-February.

Fig. 3. Twenty-four-hour recordings of weight-specific MR during deep hibernation at different Ta values (11.2, 6.8, 5.1, and 2.5°C). MR fluctuation increased in amplitude with decreasing Ta and reached or even exceeded normothermic resting metabolic rate (RMR, dashed line) at Ta 2.5°C.

Fig. 4. Minimal Tb (A), total MR (B), and weight-specific MR (C) of deep hibernating marmots as a function of Ta. MRinit, minimal observed MR during entrance into hibernation; MRmin, minimal MR during continued hibernation; MRhib, mean MR during continued hibernation. Filled symbols, mean values of individual marmots (values of all bouts at a given Ta were averaged); open symbols, mean of all individuals. Solid line represents Tb = Ta.
load and reached highest values of \( \approx 400 \text{ ml O}_2/\text{h} \) at \( T_a = 0°C \). At \( T_a \), values above \( 11°C \) MR\(_{\text{hib}} \) remained constant at \( \approx 100 \text{ ml O}_2/\text{h} \), 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\(_{\text{init}} \) on \( T_a \), but on a lower level and with a gentler slope (Table 1). However, we observed no significant increase in MR\(_{\text{init}} \) 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\(_{\text{init}} \) with decreasing \( T_a \), whereas the third marmot showed no dependency of MR\(_{\text{init}} \) on \( T_a \) (Table 1).

**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>
<th>( r )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>MR(_{\text{init}} )</td>
<td>17</td>
<td>MR(_{\text{init}} ) = 74.05 ( \times T_a + 2.02 )</td>
<td>-0.449</td>
<td>NS</td>
<td>MR(_{\text{min}} ) = 28.7 ( \times T_a + 1.58 )</td>
<td>-0.555</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>5</td>
<td>MR(_{\text{init}} ) = 206.5 ( \times T_a + 4.93 )</td>
<td>-0.846</td>
<td>&lt;0.01</td>
<td>MR(_{\text{min}} ) = 78.8 ( \times T_a + 6.23 )</td>
<td>-0.857</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>24</td>
<td>MR(_{\text{init}} ) = 397.2 ( \times T_a + 26.91 )</td>
<td>-0.910</td>
<td>&lt;0.01</td>
<td>MR(_{\text{min}} ) = 150.6 ( \times T_a + 11.2 )</td>
<td>-0.928</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>17</td>
<td>MR(_{\text{init}} ) = 72.5 ( \times T_a + 2.78 )</td>
<td>-0.236</td>
<td>NS</td>
<td>MR(_{\text{min}} ) = 22.8 ( \times T_a + 1.38 )</td>
<td>-0.324</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>7</td>
<td>MR(_{\text{init}} ) = 208.0 ( \times T_a + 15.38 )</td>
<td>-0.781</td>
<td>&lt;0.01</td>
<td>MR(_{\text{min}} ) = 64.9 ( \times T_a + 5.31 )</td>
<td>-0.797</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>21</td>
<td>MR(_{\text{init}} ) = 459.8 ( \times T_a + 31.07 )</td>
<td>-0.905</td>
<td>&lt;0.01</td>
<td>MR(_{\text{min}} ) = 141.5 ( \times T_a + 10.6 )</td>
<td>-0.931</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>7</td>
<td>MR(_{\text{init}} ) = 132.5 ( \times T_a + 7.76 )</td>
<td>-0.539</td>
<td>NS</td>
<td>MR(_{\text{min}} ) = 49.9 ( \times T_a + 2.74 )</td>
<td>-0.577</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>18</td>
<td>MR(_{\text{init}} ) = 189.6 ( \times T_a + 11.81 )</td>
<td>-0.826</td>
<td>&lt;0.01</td>
<td>MR(_{\text{min}} ) = 76.6 ( \times T_a + 5.25 )</td>
<td>-0.870</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>MR(_{\text{init}} )</td>
<td>18</td>
<td>MR(_{\text{init}} ) = 475.7 ( \times T_a + 33.07 )</td>
<td>-0.949</td>
<td>&lt;0.01</td>
<td>MR(_{\text{min}} ) = 190.2 ( \times T_a + 14.1 )</td>
<td>-0.966</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

\( T_a \), ambient temperature; MR, metabolic rate; MR\(_{\text{init}} \), MR\(_{\text{min}} \), and MR\(_{\text{hib}} \), initial, minimum, and hibernation MR, respectively; NS, not significant.
increased in amplitude with increasing cold load. At Ta
metabolic bursts in marmots were rather small but
well below resting MR. At high Ta values (11–15°C Ta),
curred in much shorter intervals with an amplitude
was adjusted just below the actual Tb, which
is consistent with the sliding set point for Tb during
hibernation proposed by Heller et al. (18).
Metabolic reduction always precedes the drop in Tb,
Tb is not metabolically defended. However, this is not
true in Alpine marmots and has been demonstrated
in true hibernators like woodchucks (23), golden ham-
sters (22), and golden-mantled ground squirrels (15) as
well as in torpor-exhibiting species like Dzungarian
hamsters (14) and lemurs (29).
During continued hibernation, MR is slightly ele-
vated 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 hiberna-
tion. Regular fluctuations of MR during hibernation
have previously been recorded (10, 34), but they oc-
curred in much shorter intervals with an amplitude
well below resting MR. At high Ta values (11–15°C Ta),
metabolic bursts in marmots were rather small but
increased in amplitude with increasing cold load. At Ta
values at and below 2.5°C, the amplitude of these
bursts reached or even exceeded normothermic resting
MR at that Ta, as shown in Figs. 2 and 3. This finding is
especially remarkable as this particular marmot hiber-
nated at ~12°C Ta.
It has been shown that species displaying hiberna-
tion or torpor can elevate their heat production at low
Ta values to defend a minimal Tb, but the results of this
study demonstrate that marmots defend their minimal
Tb with patterned pulsatile increases in metabolism.
Additional cold load evokes a proportional increase of
MRmin (Fig. 4 and Table 1) and a major increase in burst
amplitude. The latter results in a proportional but
steeper rise of MRhib with decreasing Ta compared with
MRmin (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 Ta.
It is generally accepted that the ability for thermo-
regulation persists during that part of the hibernation
process when Tb reaches the set point of metabolic
defense (16, 17, 19, 22, 24, 36), and it seems reasonable
that the physiological processes underlying the regu-
lation at low Ta values during hibernation, torpor, and
normothermia are similar (14, 20, 32). At Tb values
above the Tb set point, i.e., above the animal's preferred
Tb, there is no need for counteractive heat production.
Tb passively followed changes in Ta, and minimal MR
stabilized at a plateau of 13.6 ± 0.55 ml O2·kg−1·h−1
ever a wide range of Tb. This stability of heat produc-
tion has previously only been described for hibernating
ground squirrels (15), and it contradicts expected tem-
perature effects on MR. Furthermore, it suggests an
active control of MR at a minimum rate independent
from Tb. Otherwise, we would expect an increase in MR
with increasing Tb, i.e., a Q10 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 Q10
value of 1.2 over a Tb range of 9.8°C (Tb 7.8°C at Ta 5°C
vs. Tb 17.6°C at Ta 15°C).
This observation conflicts with those made by several
investigators (8, 12, 21, 30, 35). They found an exponen-
tial relationship between Tb and MR in the range where
Tb is not metabolically defended. However, this is not
the case in hibernating marmots. Metabolic heat produc-
tion can be better described as a function of the
temperature gradient between Tb and Ta, which is valid
for all data obtained in deep hibernation and for those
recorded at Tb values >5°C, i.e., above the threshold of
metabolic defense. We conclude that MR is actively
shut down and a Q10 effect may become irrelevant. As
long as Tb is close to Ta, minimum MR values can be
reached irrespective of the actual Tb, whereas Q10
effects alone only allow two- to threefold reduction of
MR per 10°C decrease in Tb.
Considering the effects of Q10, one would expect that
hibernators would reduce Tb as fast as possible and
force the drop in Tb by behavioral and physiological
means, i.e., a stretched posture, sweating, and saliva
spread 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

Fig. 6. Effect of Ta on minimal weight-specific MR of hibernating (●),
winter-fasting (■), and summer-active (○) Alpine marmots. For
regression analysis, values below the thermoneutral zone, i.e., Ta ≥20°C
Tb in winter and Ta ≤15°C Tb in summer, were used. When calculated
from the linear increase of MR with decreasing Ta, a thermal
conductance of 11.8 ml O2·kg−1·h−1·°C−1 during winter and 12.3 ml
O2·kg−1·h−1·°C−1 during summer was obtained.
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 $T_a$ (−20 to −40°C) we obtained values of 6–7 ml O$_2$·kg$^{-1}$·h$^{-1}$·°C$^{-1}$. These were directly calculated from $T_b$, $T_a$, 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 $T_b$. The uncoupling of metabolic heat production and absolute $T_b$ during hibernation or torpor allows maintenance of very low MR even at high $T_b$, as long as $T_b$ is close to $T_a$. Alpine marmots experience temperatures that do not allow minimal metabolism over the whole hibernation season because $T_a$ 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, $T_a$ drops below the 5°C threshold, and energy requirements increase due to the active defense of $T_b$. 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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