Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*)

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**Abstract**

Yellow-bellied marmots (Rodentia: Sciuridae) typically hibernate for eight months. This study explored energetic costs of hibernation in young and adults at 10 and 6°C. Age significantly affected the percent time torpid, total and mass-specific VO₂ use of energy during torpor, and daily mass loss at 6°C. Thus young had a higher mass-specific VO₂ during a torpor bout, which was attributed to higher metabolism during deep torpor. Total VO₂ during a bout was higher in young and there were significant temperature/age interactions; young had a higher VO₂ during torpor and deep torpor at 6°C than at 10°C. VO₂ increased at Tₐs below 6°C. Young had a higher daily mass loss than adults at 6°C. Euthermy increased energetic costs 19.3 times over those of torpor and 23.5 times over those of deep torpor. Energy costs are minimized by spending 88.6% of the hibernation period in torpor, by the rapid decline of VO₂ from euthermy to torpor and by allowing Tₐ to decline at low Tₑ. Torpidity results in average energy savings during winter of 83.3% of the costs of maintaining euthermy. Energy savings are greater than those reported for *Marmota marmota* and *M. monax*.

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**Keywords:** Age; Body temperature; Daily mass loss; Energetics; Hibernation; *Marmota flaviventris*; Metabolic rate; Torpor

1. **Introduction**

All 14 species of marmots hibernate (Bibikow, 1996). No marmot species stores food; all accumulate fat that is the sole source of energy during hibernation. The length of hibernation varies from 4.5 to 8.5 months (Armitage, 1999); thus, different species have markedly different requirements for the amount of fat needed during hibernation. However, among species, neither body mass nor mass loss during hibernation is correlated with the length of the hibernation period, which is the time from immersgence in the autumn to emergence from the burrow the following spring (Armitage and Blumstein, 2002). The lack of a relationship between body mass and the length of hibernation indicates that factors other than maintenance metabolism during hibernation affect the use of fat. Known factors include the initiation of reproduction before emergence and use of fat after emergence until food becomes available (Armitage, 1999; Armitage and Blumstein, 2002).

A major factor that can influence fat use is low burrow temperature. In the alpine marmot (*Marmota marmota*), metabolism increased linearly at
ambient temperatures below 5 °C (Arnold et al., 1991; Ortmann and Heldmaier, 1992). Thus, prolonged exposure to low ambient temperature increases the use of fat and may result in mortality (Arnold, 1990). Long winters decrease survival (Armitage and Downhower, 1974; Arnold, 1993a; Schwartz and Armitage, 2002), probably because animals exhaust their fat resources. Although factors such as the annual rhythm of metabolism (Ward and Armitage, 1981), the annual molt (Armitage and Salsbury, 1993), and a resting metabolic rate lower than that predicted from body size (Armitage, 1998), reduce energy expenditures, they are insufficient to cope with prolonged cold stress.

Three possible major mechanisms may be used by marmots to cope with cold stress. First, marmot species may differ in their energetic efficiency while hibernating. This possibility is supported by three lines of evidence: (1) variation among marmot species in metabolic rates (Benedict and Lee, 1938; Hock, 1969; Vasiliev, 1992), (2) the variation in the rate of mass loss during hibernation (Armitage and Blumstein, 2002); and (3) the variation in fur properties (Bibikow, 1996).

Second, social thermoregulation may occur in many species (Arnold, 1993a). Social thermoregulation reduces metabolic costs as measured by oxygen consumption (Vasiliev, 1992; Vasiliev and Solomonov, 1996) or passive warming through body contact while torpid (Arnold, 1988).

Third, some species of marmots evolved large body size, which enables them to add fat at a rate greater than it is used (French, 1986). Moreover, some species of large marmots add relatively more fat than expected based on their body size (Armitage, 1999). These species may rely on their relatively large fat stores rather than energetic efficiency or social thermoregulation to cope with long winters and/or cold stress.

The present study investigates energy expenditures in the yellow-bellied marmot, Marmota flaviventris. In Colorado, where the social biology and population dynamics of this species have been studied for 40 years (Armitage, 1991), most adults and some young hibernate singly. Most young hibernate with littermates in the same burrow and have the opportunity for social thermoregulation. Thus, we explore the effects of ambient temperature, age, body mass, and single vs. group hibernation (young only) on oxygen consumption and body temperature during complete hibernation bouts.

2. Materials and methods

2.1. Animals and housing

Seven adult (5 females, 2 males) and 13 young (6 females, 7 males) yellow-bellied marmots were captured in the Upper East River Valley, Gunnison County, Colorado in August of 1995 and 1996 (10 each year). Each set of 10 was studied for one winter and returned to Colorado. The marmots were transported to the University of Kansas, Lawrence, where a calibrated temperature-sensitive radio-transmitter (Mini-Mitter VM-FH-LT-DISC) was surgically implanted in the abdominal cavity of each animal. Transmitters were calibrated by Mini-Mitter, Inc. and a calibration table with values from 0 to 43 °C was provided for each animal. The surgery followed animal care guidelines and was performed by the Animal Care Unit veterinarian. Animals were housed singly, except for two groups of three littermate young each, in standard rabbit cages placed in temperature-controlled, walk-in environmental rooms. During a two-week period of recovery from surgery, the animals were maintained at 15 °C at a 12L:12D photoperiod with Purina lab chow and water provided ad libitum. Each cage was provided with a wire mesh nest box and paper towels for nest material.

Following the recovery period, conditions for hibernation were established by decreasing the room temperature to either 10 or 6°C, removing food and water, and maintaining constant darkness. The two temperatures were chosen to coincide with the range of burrow temperatures measured in the field (Kilgore and Armitage, 1978). One group of young (two females and one male), two female and three male young, 1 male and 3 female adults hibernated at 10 °C and the other group of young (2 males and 1 female), 1 female and 1 male young, and 2 female adults hibernated at 6 °C. One adult male died in the first week of hibernation.

Torpor bouts were monitored in the environmental rooms and during metabolic measurements. Because we did not have the equipment to measure body temperature in the environmental rooms, the marmots were monitored daily with the aid of a red light to determine hibernation status. No animal aroused from hibernation as a result of daily
monitoring. We determined that yellow-bellied marmots sat up, opened their eyes, and frequently moved around their cages during euthermy. Thus, an animal was recorded as torpid when lying curled with head tucked under or as alert when sitting, eyes open, or moving in the cage. We further verified the accuracy of the visual determination of torpidity by comparing the time spent torpid in the metabolism chamber with the time spent torpid in the environmental rooms. There was little difference (see results). The daily recordings were used to calculate monthly mean values for percent time torpid and alert for each marmot and these values were used to calculate a species-level energy budget for the hibernation period. Hibernating marmots typically have shorter bouts early and late in the hibernation season and longer bouts in mid hibernation (Heldmaier et al., 1993). Thus, monthly mean values of percent time torpid could be influenced by the variation in the date that animals immerged, therefore, we standardized the hibernation periods by establishing 30-day successive periods from 1 to 180 days. Day 1 for each animal was the first day the animal was recorded as torpid. We compared the results from the standardized periods with those from the monthly periods to test whether any effects of time periods or age on percent time torpid was a consequence of the variation in the date of immergence. We used recorded \( T_b \) to determine time torpid and time alert during complete torpor bouts in the metabolism chamber. Animals were weighed periodically.

2.2. \( V_{O_2} \) and \( T_b \) measurements

To measure body temperature (\( T_b \)) and oxygen consumption (\( V_{O_2} \)), the nest box with the torpid marmot was placed in a plexiglass metabolism chamber (57 cm long by 29 cm wide by 28 cm deep for adults and 56 cm long by 23 cm wide by 22 cm deep for young) that, in turn, was placed in an environmental growth chamber and connected to an air flow system such that air was drawn through the metabolism chamber. Flow rate was maintained at 590 ml/min except when small animals removed little oxygen and flow rates were lowered to 75.5 ml/min. The temperature in the metabolism chamber was maintained at the appropriate hibernation temperature except for a few additional measurements at 4 or 2 \( ^\circ C \). Body temperature signals were detected with a Mini-Mitter RA-1010 receiver and oxygen concentrations were measured with an electrochemical oxygen analyzer (Ametek Model S-3A-1). For further details of the recording system, see (Armitage and Salsbury, 1992, 1993). Output signals from the radio receiver and oxygen analyzer were input every 5 min into a Data Quest III data analysis system. All \( V_{O_2} \) values were converted to standard pressure. Hourly means were calculated from the recorded data. \( T_b \) and \( V_{O_2} \) were measured through one entire torpor bout for each group of three young or individual marmot. Each torpor bout was divided into three phases (Fig. 1): arousal (rapid increase in \( T_b \) and \( V_{O_2} \)), euthemy (\( T_b > 30 \, ^\circ C \)) and torpor (\( T_b < 30 \, ^\circ C \), except during arousal). We also defined a period of deep torpor, the time when \( V_{O_2} \) was at low, stable values (Fig. 1). Only during deep torpor did a stable \( T_b \) occur. Thus, only during deep torpor could \( T_b \) and \( V_{O_2} \) be compared among different environmental temperatures (\( T_{E58} \)) without measuring a complete and time consuming torpor bout at each \( T_{E} \). Because \( V_{O_2} \) decreased to low, stable values much more rapidly than did \( T_b \) (Woods, 2001; Woods et al., 2002), \( V_{O_2} \) was considered to be a more reliable indicator of deep torpor than \( T_b \). The hourly means were used to calculate the total \( V_{O_2} \) for each phase of the torpor bout and the sum of the \( V_{O_2} \) for the three phases provided the total \( V_{O_2} \) for the entire torpor bout. In addition, we calculated the percent of time spent and the percent of bout \( V_{O_2} \) expended in each of the three phases of the bout and in deep torpor. During metabolic measurements, body mass ranged from 1250 to 2420 g for young and from 1825 to 2950 g for adults. Body mass at immergence was significantly smaller in young (\( P = 0.002 \)).

2.3. Data analysis

Sample size varied based on the specific question asked and the data contributing to it. Some analyses focus on the individual as the unit of analysis, whereas others focus on the hibernation bout as the unit of analysis. We could detect no year effect in the data; thus data for the two years were combined.

To analyze torpor bout length and percent time torpid in the hibernation rooms, we fitted a repeated measures ANOVA with month or 30-day time period as the within-subjects factor (because individuals were observed over the different months),
Fig. 1. Body temperature and oxygen consumption during a complete hibernation bout for a group of three young marmots at 10 °C.

and age and temperature as between subjects factors (because individuals were assigned to one of two ‘age treatments’ and one of two ‘temperature treatments’). For the within-subjects factor, we used Huynh-Feldt corrected $P$-values and calculated $\eta^2$ as a standardized measure of effect size (Cohen, 1988).

For all measures of $V_O$, the individual animal or group of three (measured as a group) was the unit of analysis resulting in $N=14$ (one female was omitted because she became euthermic before $V_O$ was measured). Because values for grouped young fell within the range of values for single young, they were included in all analyses as part of the young age group. We fitted linear models (ANCOVA and ANOVA) and estimated the Type III sums of squares to study factors that influenced oxygen consumption. We tested for significant interactions between categorical variables (age and temperature); when there were none, we reran the analysis without the interaction and report these results. Because of small sample sizes, only differences at 6 and 10 °C were tested. Values recorded as percent were arcsine transformed for analysis.

For mass loss, each individual was the unit of analysis resulting in $N=19$.

3. Results

3.1. Torpor bout duration

Marmots immerged between September 30th and November 5th and emerged from April 10th to June 10th. Thirteen animals completed their hibernation periods. Marmots hibernated longer at 6 °C ($\bar{x}=228.4$ days) than at 10 °C ($\bar{x}=190$ days, Mann–Whitney $U=0$, $P=0.001$). The hibernation period of six animals was terminated after 224–254 days in order to return them to the field. Four young emerged after 226–236 days and after three or more days alert, re-entered torpor, a pattern previously reported (French, 1990). Hibernation bouts of grouped young were synchronous.

During measurements of $V_O$ in the metabolism chamber, mean bout length of adults was 12.4 days (range 7.4–15.8) at 10 °C and 15.2 (range 13.6–16.8) days at 6 °C. For juveniles mean bout length was 11.5 (range 9.0–17.1) days at 10 °C
and 9.0 (range 8.8–9.2) days at 6 °C. Neither age nor temperature significantly affected bout length ($N=14$, $P=0.29$).

In the hibernation rooms, mean bout duration for adults varied from 10.8 days in November to 18.8 days in April at 10 °C, and from 9.4 days in October to 23.8 days in January at 6 °C. For juveniles, mean bout duration varied from 9.8 days in November to 13.2 days in December at 10 °C and from 8.7 days in November to 15.7 days in February at 6 °C. ANOVA revealed that both month ($P=0.002$) and age ($P=0.004$) but not temperature ($P=0.44$), significantly affected bout length. Age had a large effect on bout length ($\eta^2=0.552$) and month, a smaller effect ($\eta^2=0.309$). Young had shorter bout lengths and bouts were generally longer in mid-hibernation (Fig. 2, upper). Bout length is greater than the mean of 8.6 days reported for field-hibernating yellow-bellied marmots and more than twice as long as the mean of 4.1 days recorded for laboratory-held marmots (Florang et al., 2000). Longer bouts in mid winter characterize sciurid hibernation (Wang, 1978; Lyman et al., 1982; French, 1988). Shorter bout lengths in young means that young had more frequent bouts over the hibernation period.

### 3.2. Percent time torpid

Because bout duration does not indicate the amount of time in torpor and the amount of time in torpor could vary among treatments, we looked for patterns in the percent of time in torpor in the hibernation rooms and during metabolic measurements. Adults spent more time in torpor ($\bar{x}=87$ and 93.7% at 10 and 6 °C, respectively) than did young ($\bar{x}=83.5$ and 88.8% at 10 and 6 °C, respectively). These values do not differ essentially from those obtained during torpor bouts in the metabolism chamber: adults, 90.0 and 92.7%; young, 84.8 and 86.7%, at 10 and 6 °C, respectively. Percent time torpid in the hibernation rooms was influenced by month ($\eta^2=0.618$) but not by age ($\eta^2=0.073$) nor temperature ($\eta^2=0.166$).

When torpor bouts were standardized for time of immersgence, both time period ($\eta^2=0.381$) and a time-period/temperature interaction ($\eta^2=0.184$) significantly affected percent time torpid. Marmots at 6 °C spent more time torpid in five of the seven time periods (Fig. 2, lower). Thus, standardizing for time of immersions had a minor effect, the time/temperature interaction. Although significant, the eta-squared was only slightly larger than that of temperature in the analysis by months. Thus, time is the major factor in both analyses. The mean values for time in torpor varied from 85 (young at 6 °C) to 90.9% (adults at 6 °C). These values are similar to those summarized by month and during torpor bouts. The differences in the three sets of percent time torpid probably represent random variation due to the ways in which the data were summarized.

### 3.3. Mass loss

DML (daily mass loss in mg/day/g immersgence mass) varied from 0.595 for an adult female at 6 °C to 1.65 for a young male at 10 °C. DML was significantly correlated with percent time active ($r=0.598$, $P=0.022$) and immersgence mass ($r=-0.774$, $P=0.0006$), but not with mass-specific bout $V_{O_2}$ ($r=0.23$, $P=0.44$). The effect of age and temperature was tested with a linear model ($N=19$). Both temperature and age were significant, but there was a significant temperature:age interaction ($P=0.066$). One-way ANOVA revealed a significant effect of age ($P=0.043$) but not of temperature ($P=0.114$). DML did not differ
between young and adults at 10 °C \((P=0.32)\), but was significantly greater in young than in adults at 6 °C \((P=0.031)\). Thus, the temperature:age interaction can be explained by the higher DML of young at 6 °C. In general, DML decreased with increasing immersence mass, increased with percent time active, and was greater in young than adults at 6 °C.

Although the mean loss of mass was less in young that hibernated in groups than in marmots hibernating singly, the difference was not statistically significant whether adults were included (Mann–Whitney \(U=25.5, P=0.24\)) or excluded \((U=22.0, P=0.14)\).

### 3.4. Body temperature

Because of transmitter failure, we could not measure \(T_b\) during all metabolic measurements. During deep torpor at 10 °C, mean \(T_b\) of individuals ranged from 11.5 to 13.3 °C \((\text{population } \bar{x}=12.5 \pm 0.5, N=7)\). At 6 °C, mean \(T_b\) during deep torpor ranged from 6.7 to 8.5 °C \((\text{population } \bar{x}=7.8 \pm 0.5, N=6)\). At 2 °C, mean \(T_b\) ranged from 4.9 to 6.3 °C \((\text{population } \bar{x}=5.5 \pm 0.5, N=4)\). At 4 °C, the mean \(T_b\) of two marmots was 5.6 °C. Thus, yellow-bellied marmots maintained on average a \(T_b\) approximately 2.5 °C higher than \(T_b\) at 10 °C, but maintained a smaller difference of approximately 1.5 °C at lower \(T_E\)s, and increased the difference to 3.5 °C at the lowest \(T_E\).

### 3.5. Oxygen consumption/mass-specific (ml·g\(^{-1}\)·h\(^{-1}\))

We fitted ANCOVA models to the subsets of the hibernation bout, which included the independent variables of age, mass, and \(T_E\). For the complete hibernation bout (Fig. 1), neither body mass \((P=0.56)\) nor \(T_E\) \((P=0.31)\) significantly affected \(V_{O_2}\); but age \((P=0.014)\) did. Young had a higher \(V_{O_2}\) than adults (Fig. 3). \(V_{O_2}\) of young increased at 2 °C, but the sample size was too small for statistical analysis. Time did not permit measuring complete bouts for adults at 2 °C.

The overall linear model for \(V_{O_2}\) during torpor, \((T_b<30 \pm \text{°C})\), was not statistically significant \((N=14, P=0.46)\); temperature, body mass, and age did not affect \(V_{O_2}\). \(V_{O_2}\) of young increased at 2 °C (Fig. 4). For the portion of the bout that included only deep torpor, the variables explained 35.3% of the variation. \(V_{O_2}\) during deep torpor was higher in young than in adults and higher at 6 °C than at 10 °C (Fig. 4); both temperature \((P=0.078)\) and age \((P=0.072)\) were statistically significant and mass \((P=0.8)\) had no effect. \(V_{O_2}\) increased at 4 and 2 °C for both adults and young.

When marmots were euthermic, temperature \((P=0.015)\) but neither body mass \((P=0.99)\) nor age \((P=0.33)\) significantly affected \(V_{O_2}\). The overall model was significant \((P=0.047)\) and explained 39.4% of the variation. Euthermic \(V_{O_2}\) was higher at 6 °C than at 10 °C (Fig. 5) but that of young did not increase at 2 °C. \(V_{O_2}\) during euthermy was 16–18.6 times \(V_{O_2}\) during torpor at 10 °C and 18–24.6 times, at 6 °C. \(V_{O_2}\) during euthermy was 21–24 times \(V_{O_2}\) during deep torpor at 10 °C and 23–26 times, at 6 °C.

\(V_{O_2}\) was highest during arousal and rapidly declined after reaching a peak (Fig. 1). Although \(V_{O_2}\) was higher at 6 °C than at 10 °C (Fig. 5), none of the measured variables significantly affected arousal \(V_{O_2}\) (age, \(P=0.9\); mass, \(P=0.89\); tem-
3.6. Oxygen consumption/total VO$_2$ (ml O$_2$·h$^{-1}$)

The critical factor in hibernation energetics is the total amount of energy expended, which is expressed as total VO$_2$. We again fitted ANCOVA models to subsets of the hibernation bout data that included the following independent variables: age, hibernation temperature, and body mass. During torpor and deep torpor, total VO$_2$ was significantly affected by both mass (torpor, $P=0.042$; deep torpor, $P=0.008$) and a temperature x age interaction ($N=14$, torpor $P=0.06$, deep torpor $P=0.006$). Temperature did not affect VO$_2$ of adults whereas VO$_2$ of young was higher at 6 °C than at 10 °C (Fig. 6). The model explained 39.3% of the variation in total VO$_2$ during torpor and 68.1%, during deep torpor. During a complete hibernation bout age ($P=0.02$) but neither mass ($P=0.11$) nor temperature ($P=0.30$) significantly affected mean VO$_2$. VO$_2$ of young was greater than that of adults (Fig. 6). The model explained 37.8% of the variation.

During euthermy both mass ($P=0.0007$) and temperature ($P=0.016$) but not age ($P=0.30$)
significantly affected total VO₂. Larger marmots had a higher VO₂ and VO₂ was higher at 6 than at 10 °C. The model explained 80.7% of the variation. Neither mass (P = 0.28), age (P = 0.95), nor temperature (P = 0.17) significantly affected total VO₂ during arousal; the overall linear model was not statistically significant (N = 14, P = 0.14), but explained 23.5% of the variation in VO₂. Active total VO₂, the sum of euthermy and arousal, was significantly affected by mass (P = 0.013) and temperature (P = 0.062), but not by age (P = 0.74). Active total VO₂ was higher at 6 than at 10 °C and larger animals used more O₂ than smaller animals (Fig. 6).

3.7. Energy budget

Clearly, energy expenditures were much greater during active periods than during torpor (Figs. 3 and 6). On average, marmots spent only 8.9% of the time euthermic (7% by adults; 10.9% by young), but expended 52.0% of their energy (48% by adults; 55.6% by young) during euthermy. By contrast, an average of 88.6% of the time was spent torpid, but torpor used only 30.7% of the energy. Age (P = 0.023), but not temperature (P = 0.39) significantly affected the allocation of time to torpor. The model explained 32.0% of the variation. Only age (P = 0.004) and neither temperature (P = 0.74) nor body mass (P = 0.82) significantly affected the relative expenditure of energy during torpor. The model explained 54.0% of the variation. Young spent less time torpid (85.9 vs. 91.4%) and expended relatively less energy (25.5 vs. 36.4%) during torpor than adults.

Activity (euthermy plus arousal) required 69.4% of the energy expenditure during hibernation. The smaller European ground squirrel (Spermophilus citellus) and Richardsons ground squirrel (S. richardsonii) used 86 (Strijkstra, 1999) and 75.6% (Wang, 1978), respectively, during arousal episodes. Apparently the larger marmot has a relatively higher cost during torpor, but a relatively lower cost during activity, than the smaller ground squirrels.

At both 6 and 10 °C, active AMMR (average monthly metabolic rate) of adults and young typically was several times greater than torpid AMMR (Tables 1 and 2). Only month significantly affected the variation in active AMMR (N = 32, P = 0.0001); the overall model was highly significant (P = 0.0001) and explained 71.3% of the variation. Torpid AMMR was significantly affected by age (P = 0.036), temperature (P = 0.0004), and month (P = 0.0001); the linear model explained 70.9% of the variation. Torpid AMMR was less in young than in adults and greater at 6 than at 10 °C.

Hibernation resulted in considerable energy savings. For the entire hibernation period, energy savings averaged 69.2 and 69.5% for adults and young, respectively, at 10 °C (Table 1) and 83.3 and 73.7% for adults and young, respectively, at 6 °C (Table 2) of the energy expended by euthermic marmots during winter. Energy savings were greater when compared with summer, euthermic marmots. Energy savings averaged 86.8 and 80.2% for adults and young, respectively, at 10 °C and 88.1 and 78.8% for adults and young, respectively, at 6 °C.

Energy savings also are evident in the comparison of daily mass loss with predicted daily mass loss. If yellow-bellied marmots remained euthermy-
Table 1
Energy budget for hibernating yellow-bellied marmots at 10 °C

<table>
<thead>
<tr>
<th>Time spent</th>
<th>AMMR (1 O₂·mol⁻¹)</th>
<th>Energy saved (%)</th>
<th>Winter</th>
<th>Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ad Yg</td>
<td>Active Torpid</td>
<td>Ad Yg Ad Yg</td>
<td>Ad Yg Ad Yg</td>
</tr>
<tr>
<td>Oct.</td>
<td>22 28</td>
<td>200.7 165.9</td>
<td>3.4 3.5</td>
<td>12.3 26.3 62.3 54.5</td>
</tr>
<tr>
<td>Nov.</td>
<td>80 84</td>
<td>49.8 35.7</td>
<td>11.9 10.2</td>
<td>72.6 79.3 88.2 87.3</td>
</tr>
<tr>
<td>Dec.</td>
<td>84 89</td>
<td>41.2 25.3</td>
<td>12.9 11.2</td>
<td>76.8 84.1 90.0 90.2</td>
</tr>
<tr>
<td>Jan.</td>
<td>87 85</td>
<td>33.4 34.6</td>
<td>13.4 10.7</td>
<td>79.9 80.3 91.4 87.8</td>
</tr>
<tr>
<td>Feb.</td>
<td>94 91</td>
<td>14.4 19.4</td>
<td>13.5 10.7</td>
<td>87.2 86.0 94.5 91.4</td>
</tr>
<tr>
<td>Mar.</td>
<td>88 84</td>
<td>30.9 36.9</td>
<td>13.5 10.6</td>
<td>80.9 79.3 91.8 87.3</td>
</tr>
<tr>
<td>Apr.</td>
<td>90 68</td>
<td>24.9 71.4</td>
<td>13.4 8.3</td>
<td>83.0 64.1 92.7 77.9</td>
</tr>
<tr>
<td>May</td>
<td>69 46</td>
<td>79.8 124.5</td>
<td>10.6 5.8</td>
<td>61.2 56.7 83.3 65.2</td>
</tr>
</tbody>
</table>

Average monthly metabolic rate (AMMR) was calculated from the mean hourly metabolic rates determined during measurements of $V_{O_2}$. A mean value was used for adults and for young. Active combines euthermic plus arousal and torpid includes all values when $T_b<$ 30 °C, except during arousal. Mean body mass for adults was 2076 g for adults and 1817 g for young. Energy saved (ES) for winter is calculated from an AMMR for which animals were considered to be euthermic compared to the total AMMR (AMMR active + AMMR torpid); i.e. 1-total AMMR euthermic AMMR = % ES. Euthermic AMMR was calculated from euthermic $V_{O_2}$ recorded during torpor bouts. For summer euthermia, mean values for post-molt adults and young from (Armitage and Salsbury, 1992) were used for euthermic AMMR.

Table 2
Energy budget for hibernating yellow-bellied marmots at 6 °C. Mean body mass was 2625 g for adults and 1961 g for young. Calculations and symbols as described for Table 2.

<table>
<thead>
<tr>
<th>Time spent</th>
<th>AMMR (1 O₂·mol⁻¹)</th>
<th>Energy saved (%)</th>
<th>Winter</th>
<th>Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ad Yg</td>
<td>Active Torpid</td>
<td>Ad Yg Ad Yg</td>
<td>Ad Yg Ad Yg</td>
</tr>
<tr>
<td>Oct.</td>
<td>76 21</td>
<td>94.6 253.4</td>
<td>11.6 3.5</td>
<td>72.4 14.6 80.4 31.1</td>
</tr>
<tr>
<td>Nov.</td>
<td>92 89</td>
<td>30.5 34.2</td>
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ic at the metabolic rates measured in late summer (Armitage and Salsbury, 1992), adults would use 17.46 l O₂·day⁻¹ and young would use 12.02 l O₂·day⁻¹. If we assume that fat is the substrate metabolized and that oxidation of 1 g of fat requires 2 l O₂ (Schmidt-Nielsen, 1990), then adults would lose an estimated 8.73 g·day⁻¹ and young would lose 6.01 g·day⁻¹. Mean daily mass loss during hibernation was 2.91 g for adults and 2.49 g for young at 10 °C and 1.98 and 2.10 g for adults and young, respectively, at 6 °C. Thus, adults would save 66.7% of body mass at 10 °C and 77.3% at 6 °C. Young would save 58.6% of body mass at 10 °C and 65.1% at 6 °C. Thus, young realize smaller energy savings than adults whether measured as oxygen consumption or mass loss.

4. Discussion

4.1. Age

A major finding of this study was the significant effect of age on bout length in the hibernation rooms, the relative allocation of time and energy to torpor, mass-specific and total oxygen consumption, DML, and torpid AMMR. Thus, young had a higher mass-specific oxygen consumption during a torpor bout, which was a consequence of a higher metabolism during deep torpor. Total oxy-
gen consumption during a torpor bout was also higher in the young. Furthermore, young, but not adults, had a higher metabolism during torpor and deep torpor at 6 °C than at 10 °C. Mass-specific metabolism during torpor at 10 °C was higher in three juvenile *M. marmota* than in two adults (Kayser, 1961). These results emphasize the need to include both young and adults in future studies of hibernation energetics. The higher metabolism of young can be attributed to differences in fur properties. Heat loss is greater in young than in adults at low ambient temperatures; young have less fur depth, shorter hair length, and a smaller hair diameter than adults (Melcher, 1987). If this interpretation is correct, then young should have a higher conductance than adults. In our study, all young had a significantly higher conductance (0.0029–0.0065 ml O$_2$·g$^{-1}$·h$^{-1}$·°C) than did the one adult (0.0021 ml O$_2$·g$^{-1}$·h$^{-1}$·°C) for which we had adequate data.

French (1990) reported that adults spent more time euthermic than did young, the opposite of our results. There is no obvious explanation for this difference. Our results are consistent; young spent more time euthermic in the environmental rooms (not statistically significant) and during measurements of oxygen consumption; therefore, the differences between the two studies are not likely the result of errors in our recording of torpor in the environmental rooms. One possible source of the difference between the two studies is the difference in body mass. The young used by French weighed approximately 1.2 kg at the onset of hibernation, approximately 1 kg less than our young weighed. Our adults weighed approximately 2.6 kg at the onset of hibernation, approximately 0.5 kg less than the adults used by French. Perhaps there was a marked effect of small mass on the torpor cycle that we did not find because our young were so much larger and responded more like adults.

The postulated explanation for the difference between our results and those of French (1990) may also explain why there was no significant effect of mass on mass-specific oxygen consumption. A rank analysis of mass-specific oxygen consumption vs. body mass revealed a negative relationship ($r_s = -0.419$, $0.2 > P > 0.1$); marmots of smaller mass tended to have higher rates of mass-specific oxygen consumption. The relationship is in the expected direction, but the range of body mass may have been too narrow to adequate-

ly test for a mass/mass-specific VO$_2$ relationship. In addition, the overlap in body mass between young and adults may confound the effects of mass with the effects of age. This relationship requires further study with a greater range of body mass while controlling for age.

### 4.2. Total VO$_2$

We expected mass to significantly affect total VO$_2$, but mass significantly affected only euthermic (and hence active consumption) and torpor (including deep torpor). We further investigated possible effects of mass by examining Spearman rank correlations between mass and total VO$_2$. Significant values of $r_s$ occurred for torpor ($r_s = 0.65$, $P = 0.01$), euthermic ($r_s = 0.74$, $P < 0.01$), arousal ($r_s = 0.51$, $0.05 > P > 0.025$), and active VO$_2$ ($r_s = 0.71$, $P < 0.01$) and a nearly significant value occurred for deep torpor ($r_s = 0.40$, $0.1 > P > 0.05$). Thus the rank correlations confirm the predicted relationship between mass and total VO$_2$. Larger marmots expended more energy than did smaller marmots. Given that each component of the bout cycle evidenced a positive relationship between mass and VO$_2$, why was total bout VO$_2$ not also significantly affected by mass ($r_s = 0.29$, $P > 0.2$)? The answer apparently is a consequence of individual variation; individuals varied in their total VO$_2$, some individuals ranked high in arousal but low in bout. For example, neither the rankings for bout VO$_2$ and arousal VO$_2$ ($r_s = 0.213$, $P > 0.4$); nor rankings for euthermic and torpid VO$_2$ ($r_s = 0.48$, $0.2 > P > 0.1$) were significantly correlated. Also, mass explained variable amounts of the variation in ranks in total VO$_2$, ranging from 55% for euthermic to 16% for deep torpor. When individual variability is combined with the low correlations, then mass does not significantly affect bout VO$_2$ and the effect of age, which did not significantly affect any of the individual components of the bout, becomes the predominant influence on total bout VO$_2$.

This analysis emphasizes the importance of effects of individual variability. Our use of linear models in the analysis of VO$_2$ allowed us to determine the effects of the variables (e.g. mass, age, temperature) and possible interactions among the variables (e.g. Fig. 2). The linear models also provided an estimate of the amount of variation explained by the measured variables. These estimates (adjusted $R^2$) ranged from 23.5 to 80.7%, which again
emphasizes the high degree of individual variability. Conversely, the $R^2$ values indicate that the measured variables are more important in some phases of the torpor cycle than in others. For example, $V_{O_2}$ during arousal had a large component of individual variability whereas $V_{O_2}$ during euthermia had a small individual variability component.

4.3. Environmental temperature ($T_E$)

Adults were much less affected by environmental temperature than were young. Interestingly, active $V_{O_2}$ but not torpor $V_{O_2}$ was significantly higher at 6 °C than at 10 °C in both age groups. As a consequence, mass-specific $V_{O_2}$ for the entire bout was not significantly affected by temperature. Although we had only a few measurements below 6 °C, $V_{O_2}$ clearly increased. Similar increases at temperatures below 5 °C were reported for *M. marmota* (Ortmann and Heldmaier, 1992), *M. monax* (Benedict and Lee, 1938), *M. camtschatica* (Vasiliev, 1992), and *M. flaviventris* (Luecke and South, 1972). At $T_E$ ranging from 5 °C to as high as 15 °C, bout $V_{O_2}$ is relatively constant in *M. flaviventris* (Figs. 3 and 6), *M. marmota* (Ortmann and Heldmaier, 1992), and *M. monax* (Benedict and Lee, 1938). Active and euthermic $V_{O_2}$ of young decreased at 2 °C (Figs. 3–6). These values were strongly influenced by grouped young whose values generally were lower than those of single young. Although there was no statistical significance for group effects on $V_{O_2}$, the decline in $V_{O_2}$ at 2°C probably was a result of a sampling bias favoring groups.

Hibernating marmots typically maintain their $T_b$ above $T_E$ during torpor: *M. marmota*, 2–8 °C (Heldmaier et al., 1993); *M. monax*, 1–3 °C (Benedict and Lee, 1938), 2–5.5 °C (Lyman, 1958); *M. flaviventris*, 4.5–9.0 °C (Hock, 1969), 3 °C (Florant and Heller, 1977), 2.5–3.5 °C (Luecke and South, 1972). At least three factors influence the temperature difference between $T_E$ and $T_b$. First, individual marmots maintained at the same $T_E$ maintain different $T_b$s; second, marmots may maintain higher $T_b$s early and late in the hibernation period than they do during mid hibernation (Heldmaier et al., 1993); third, $T_E$ influences the difference between $T_b$ and $T_E$. In this study, during deep torpor, a mean difference of 2.45 °C (range 1.5–3.3 °C) was maintained at 10 °C; a mean of 1.8 °C (range 0.7–2.7 °C) at 6 °C; a mean of 1.6 °C (range 1.0–2.2 °C) at 4 °C; a mean of 3.4 °C (range 2.9–4.2 °C) at 2 °C. As $T_E$ became more stressful at 6 and 4 °C, marmots permitted their $T_b$s to decrease and maintained a smaller $T_b$–$T_E$ difference. However, at 2 °C, the $T_b$–$T_E$ difference increased such that the mean $T_b$ at 4 °C (5.63 °C) differed little from that at 2 °C (5.46 °C). The similarity in these two values suggests that yellow-bellied marmots attempt to maintain an average $T_b$ not lower than approximately 5.5 °C.

Clearly $T_E$s below 6 °C impose a high energetic cost. Bout $V_{O_2}$ of juveniles at 2 °C was approximately 17% higher than bout $V_{O_2}$ at 6 °C and approximately 41% higher than at 10 °C. Most of the increase occurred during deep torpor; $V_{O_2}$ was approximately 97% higher at 2 °C than at 6 °C. The high cost during deep torpor (Figs. 4 and 6) was compensated in part by a reduction in costs of active (euthermia + arousal) $V_{O_2}$ (Figs. 3 and 6). However, active $V_{O_2}$ was obtained for only one individual and this result needs to be viewed with caution. Because the sample size during deep torpor at 2 °C was much larger ($N=4$), we believe that the increase of $V_{O_2}$ during deep torpor is more indicative of the energetic costs of hibernation at low $T_E$.

The high energetic cost at low $T_E$ was partially compensated by the concomitant decrease in $T_b$. We calculated the theoretical metabolic rate at 2 °C by using the following equation, MR = C ($T_b$–$T_E$), in which we substituted the mean $T_b$ maintained at 6 °C for the mean $T_b$ maintained at 2 °C, and used the value for minimal conductance. For four animals, the theoretical MR averaged 1.97 times (range 1.44–2.7) the measured MR during deep torpor. In addition, $T_b$ fluctuated more widely at 2 °C than it did at higher $T_E$ (difference between maximal and minimal $T_b$: 0.46° ($N=2$) at 10 °C; 0.50° ($N=4$) at 6 °C; 1.04° ($N=2$) at 4 °C; 2.02° ($N=4$) at 2 °C. Similar $V_{O_2}$ fluctuations were observed in *M. marmota*; when $T_b$–$T_{E}$ gradients were small, the amplitude of the fluctuation was small and became larger when $T_b$–$T_{E}$ gradients were large, especially when $T_b$ was below 3 °C (Heldmaier et al., 1993). We calculated a theoretical MR for each animal at 2 °C by assuming that $T_b$ was maintained at the highest value measured during deep torpor and compared the theoretical MR with the actual MR. The theoretical MR at 2 °C averaged 1.45 times (range 1.26–1.65) the actual value.
We suggest that allowing $T_E$ to fluctuate is an energy-conserving strategy that reduces the cost of maintaining an average minimal $T_E$ at low $T_B$. If a fluctuating $T_E$ is part of an energy-conserving strategy, then the fluctuations should become greater as temperature stress increases. Although our sample size is small, the data are consistent with this prediction. Cycling of $T_E$ and MR probably varies considerably among individuals. We had data for three cycles each for a juvenile and an adult. Peaks of MR (followed by a peak in $T_B$) averaged 10.8 h in the 1175 g juvenile and 23 h in a 1910 g adult.

4.4. Costs of euthermy vs. torpor

Overall, euthermy increased costs an average of 19.3 times over those of torpor and 23.5 times over those of deep torpor. These values are higher than the 14.8 times increase of euthermy over deep hibernation reported previously for M. flaviventris (Thorpe et al., 1994) and are comparable to those reported for other species. Active $V_O_2$ was 23.5 times hibernation $V_O_2$ in M. camtschatica (Vasiliev and Solomonov, 1996); euthermy $V_O_2$ was approximately 26 times deep torpid $V_O_2$ (Heldmaier et al., 1993) and 19 times whole bout $V_O_2$ (Ortmann and Heldmaier, 1992) in M. marmota; and euthermy $V_O_2$ was 26 times deep torpor $V_O_2$ in M. monax (Lyman, 1958). The high costs of euthermy are expressed in mass loss as DML was significantly correlated with the percent time active; i.e. the more time a marmot spends euthermic the greater is its mass loss. This result also is consistent with the report that woodchucks lost their mass during arousal and that mass loss during torpor could not be measured (Bailey and Davis, 1965).

Arousals incurred the most expensive use of energy; $V_O_2$ increased an average of 21.3 times over that of torpor. This value is similar to the 23.7 reported elsewhere (Thorpe et al., 1994). The rapid decline in $V_O_2$ once euthermy is reached again suggests that metabolic performance is geared to minimize energy costs.

4.5. Energy budget

Energy saved during hibernation is greater in M. flaviventris at 6 °C than in M. monax at 6 °C and M. marmota at 5 °C. For the entire hibernation period, the winter energy savings averaged 83.3% for the yellow-bellied marmot, 43.2% for M. monax (Armitage et al., 2000), and 43.8% for the alpine marmot (calculated from Table 1 in (Heldmaier et al., 1993). Part of the reason for a greater energy savings by M. flaviventris compared to M. monax is that M. monax required much more time to reach deep torpor following an arousal (Armitage et al., 2000). Energy savings by M. flaviventris is similar to but less than the 87.8% reported for S. richardsonii, a much smaller species (Wang, 1978, 1979). For summer energy savings, the mean values are 88.1% for the yellow-bellied marmot, 51.9% for the woodchuck, and 71.9% for the alpine marmot. The major reason for these differences lies in the amount of time spent torpid. For a nine month hibernation, S. richardsonii was torpid on average 93.9% of the time; M. flaviventris, 87.4%, for an eight month hibernation; M. marmota, 62.8%, for a seven month hibernation and M. monax, 52.5%, for a five month hibernation. Possibly sciurids with a longer hibernation period spend more time torpid and thus have a higher winter energy savings.

The differences in energy savings and time spent torpid indicate that M. flaviventris is energetically more efficient during hibernation than M. marmota and M. monax. This interpretation is supported by mass loss during hibernation. M. flaviventris lost on average 2.09 g/day whereas M. marmota lost 8.56 g/day (calculated from Table 1 in Heldmaier et al., 1993) and M. monax, 5.27 g/day (Armitage et al., 2000). DML was also lower in M. flaviventris, 0.94 vs. 1.95 for M. marmota and 1.94 for M. monax. If all values from both 10 and 6 °C are included for M. flaviventris, DML becomes 1.19, still much lower than the DML of M. marmota and M. monax.

Social thermoregulation reduces mass loss in M. marmota; the rate of loss depends on group size and whether juveniles are present (Arnold, 1993b). Social thermoregulation may compensate for the lower energetic efficiency of M. marmota compared to M. flaviventris. M. flaviventris generally hibernates singly in our study area, although young may hibernate in the same burrow (Lenihan and Van Vuren, 1996). We did not find a significant energy savings in young hibernating in groups in comparison with young hibernating singly, but the trend was for less mass loss in group hibernators. Daily mass loss (2.4 g) of young in our study was significantly greater ($t=2.6$, d.f. = 27, $P=0.02$) than the 1.8 g of naturally hibernating young in
1991, but did not differ \((t = 0.9, d.f. = 30, P > 0.2)\) from the 2.6 g of naturally hibernating young in 1992 (Lenihan and Van Vuren, 1996). Climatically, 1991 and 1992 differed, but the way in which climate impacted the marmots is unknown. Also, litter sizes varied from 1–8 and the way in which group size might have affected mass loss is unknown. The low mean daily mass loss of 1991 in comparison with the higher rate of our laboratory animals suggests that group hibernation may be important for young yellow-bellied marmots. The effect of group hibernation on the energetics of young marmots requires further study under controlled conditions.

*M. flaviventris* and *M. marmota* and *M. monax* occur on different phylogenetic branches in the evolution of the genus *Marmota* (Kruckenhauser et al., 1998; Steppan et al., 1999). *M. flaviventris* developed a series of energy efficient strategies, e.g. more time torpid, to minimize the costs of hibernation. By contrast, *M. marmota* developed social thermoregulation, which involves alloparental care, to minimize hibernation costs. The solitary *M. monax* uses a combination of large size and a short hibernating season as its major strategy (Armitage et al., 2000). It would be of considerable interest to examine other species of marmots in the two subgenera to determine the degree to which the three strategies described here are utilized and how the strategies are related to marmot phylogeny.

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**References**


