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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 V_{O_2}, use of energy during torpor, and daily mass loss at 6 °C. Thus young had a higher mass-specific V_{O_2} during a torpor bout, which was attributed to higher metabolism during deep torpor. Total V_{O_2} during a bout was higher in young and there were significant temperature/age interactions; young had a higher V_{O_2} during torpor and deep torpor at 6 °C than at 10 °C. V_{O_2} increased at T_Es 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 V_{O_2} from euthermy to torpor and by allowing T_B to decline at low T_E. 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*.

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 immergence 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

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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 °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}), euthermy ($T_B > 30$ °C) and torpor ($T_B < 30$ °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_Es) 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),

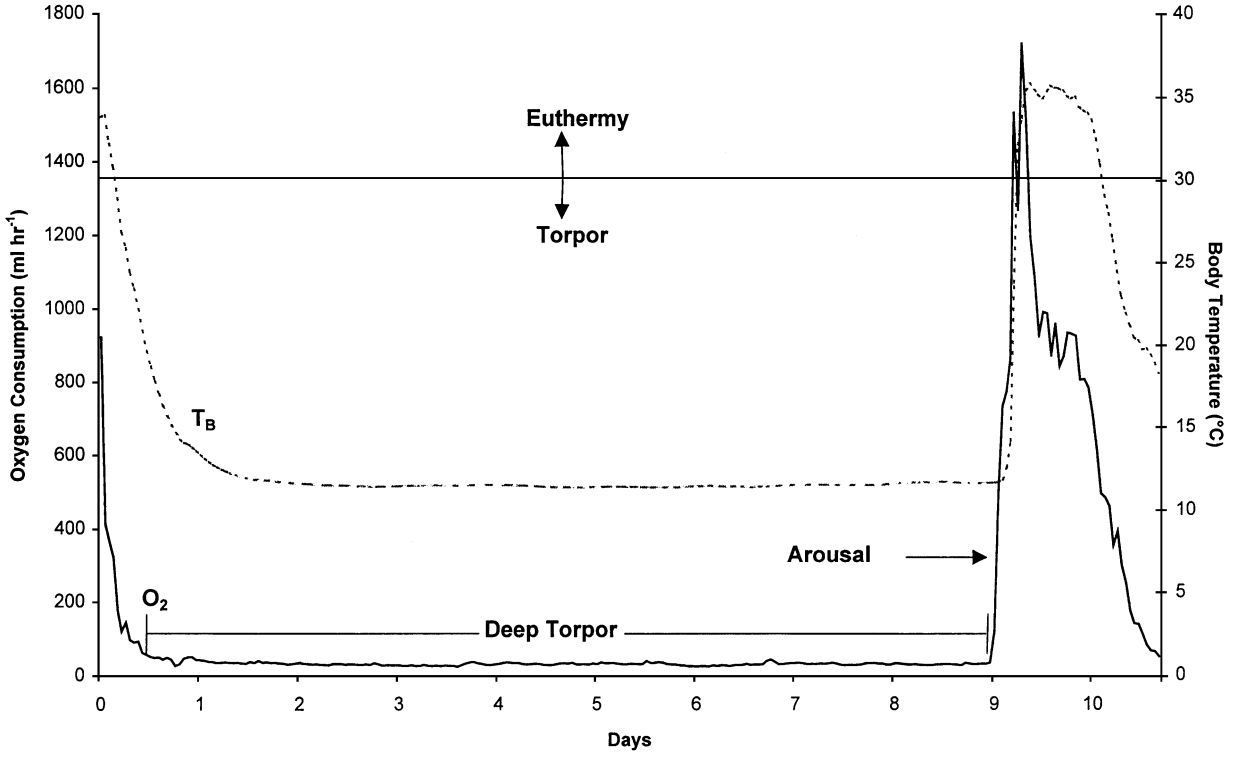

Fig. 1. Body temperature and oxygen consumption during a complete hibernation bout for a group of three young marmots at 10 °C.

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 η^2 as a standardized measure of effect size (Cohen, 1988).

For all measures of V_{O_2}, 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_2} 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_2} 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

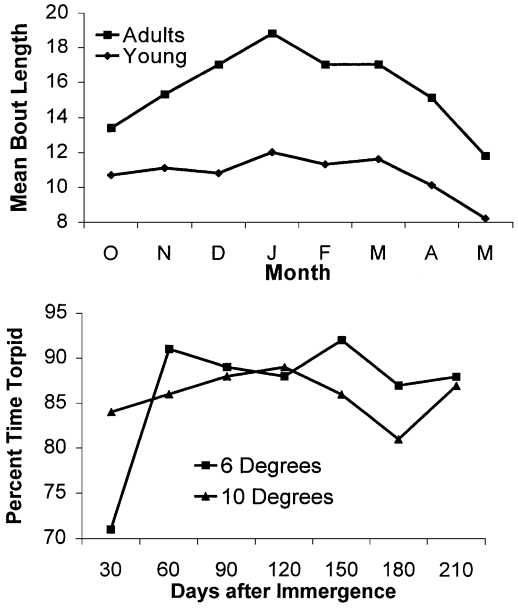

Fig. 2. Length of hibernation bouts (moving average of number of days) for young and adult marmots (upper) and percent time torpid (standardized to the first day of immergence) at 6 and 10 °C (lower).

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 (Florant 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 ($P<0.001$, $\eta^2=0.618$) but not by age ($P=0.374$, $\eta^2=0.073$) nor temperature ($P=0.167$, $\eta^2=0.166$).

When torpor bouts were standardized for time of immergence, both time period ($P=0.001$, $\eta^2=0.381$) and a time-period/temperature interaction ($P=0.043$, $\eta^2=0.184$) 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 immergence 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 immergence 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 immergence 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 immergence 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 (population $\bar{x}=$ 12.5 °C, $N=7$). At 6 °C, mean T_B during deep torpor ranged from 6.7 to 8.5 °C (population $\bar{x}=$ 7.8 °C, $N=6$). At 2 °C, mean T_B ranged from 4.9 to 6.3 °C (population $\bar{x}=5.5$ °C, $N=4$). 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_E at 10 °C, but maintained a smaller difference of approximately 1.5 °C at lower T_Es, and increased the difference to 3.5 °C at the lowest T_E.

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

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, ($T_B<30$ °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

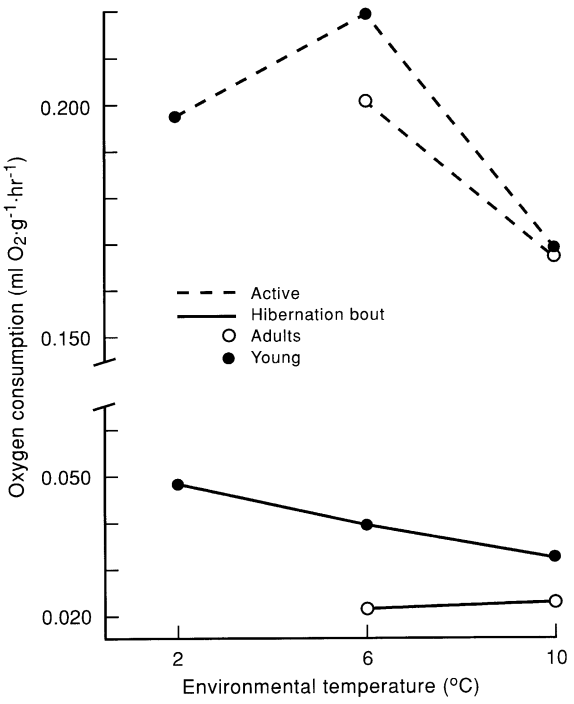

Fig. 3. The relationship between mass-specific oxygen consumption and environmental temperature during the active period (active = euthermy + arousal) and during a complete hibernation bout for young and adult yellow-bellied marmots. For adults, $N=3$ at 10 °C and 2 at 6 °C; for young, $N=6$ at 10 °C, 3 at 6 °C, 1 at 2 °C for bout and 2 for active.

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-

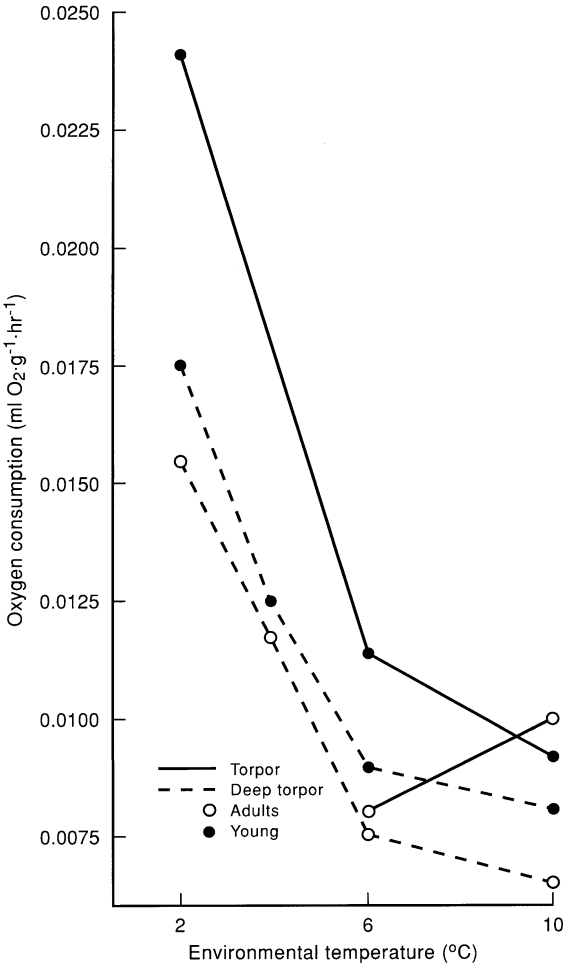

Fig. 4. The relationship between mass-specific oxygen consumption and environmental temperature during torpor and deep torpor for young and adult yellow-bellied marmots. For adults, N for 10 and 6 °C as in Fig. 2, $N=1$ at 4 and 2 °C; for young, N for 10 and 6 °C as in Fig. 2, $N=1$ at 4 °C and 3 at 2 °C.

perature, $P=0.14$). The overall linear model was not statistically significant ($N=14$, $P=0.43$).

In order to calculate the energy costs of hibernation where animals were recorded as alert or torpid, we combined V_{O_2} of euthermy and arousal to obtain an active (=alert) V_{O_2}. As expected, the pattern of active V_{O_2} was the same as that of euthermy (Figs. 3 and 5). Again, temperature ($P=0.005$) but not age ($P=0.78$) or mass ($P=0.91$) explained significant variation in active V_{O_2}. Mean active V_{O_2} was higher at 6 °C than at 10 °C (Fig. 3).

3.6. Oxygen consumption/total V_{O_2} ($ml\ O_2 \cdot h^{-1}$)

The critical factor in hibernation energetics is the total amount of energy expended, which is expressed as total V_{O_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 V_{O_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 V_{O_2} of adults whereas V_{O_2} of young was higher at 6 °C than at 10 °C (Fig. 6). The model explained 39.3% of the variation in total V_{O_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 V_{O_2}. V_{O_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 ($P=0.30$)

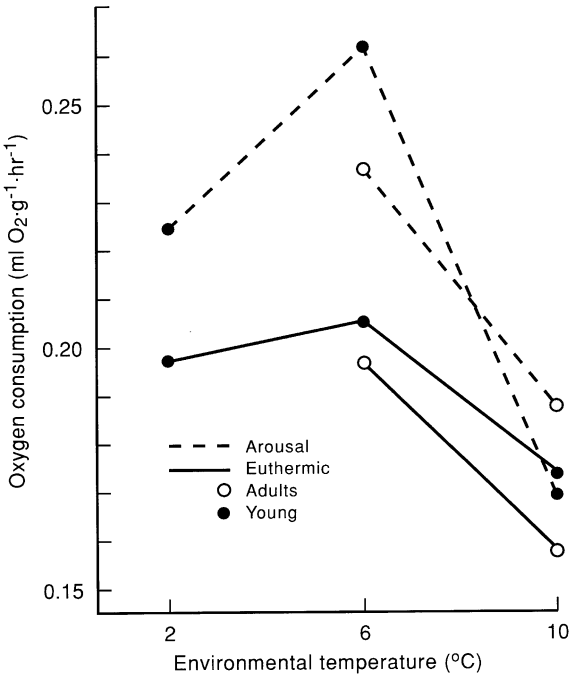

Fig. 5. The relationship between mass-specific oxygen consumption and environmental temperature during euthermy and arousal for young and adult yellow-bellied marmots. For adults, N as in Fig. 2; for young N at 10 and 6 °C as in Fig. 2, $N=3$ at 2 °C for arousal and 2 for euthermic.

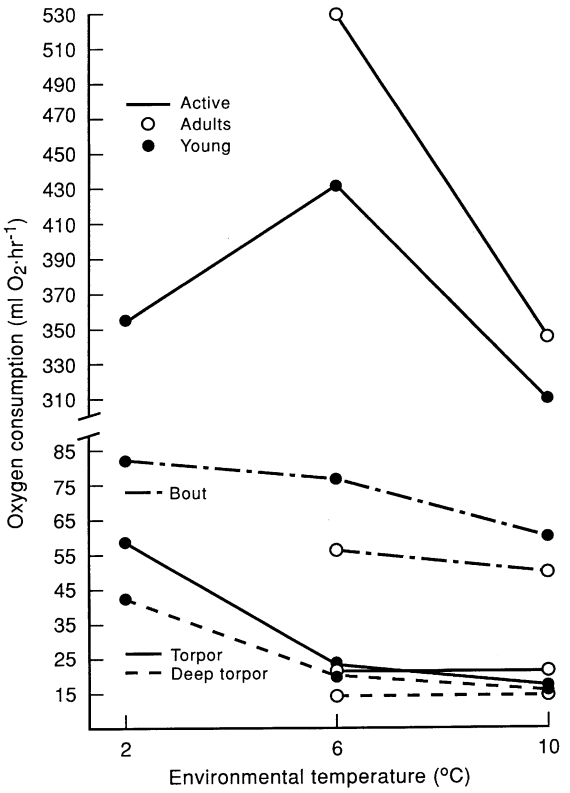

Fig. 6. The relationship between total oxygen consumption and environmental temperature during a hibernation bout for young and adult yellow-bellied marmots. For adults, *N* as in Fig. 2; for young, *N* as in Fig. 2 for active and bout and as in Fig. 3 for torpor and deep torpor.

significantly affected total V_{O_2}. Larger marmots had a higher V_{O_2} and V_{O_2} 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 V_{O_2} during arousal; the overall linear model was not statistically significant ($N=14$, $P=0.14$), but explained 23.5% of the variation in V_{O_2}. Active total V_{O_2}, 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 V_{O_2} was higher at 6 than at 10 °C and larger animals used more O_2 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 Richardson's 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 eutherm-

Table 1
Energy budget for hibernating yellow-bellied marmots at 10 °C

	Time spent		AMMR (l O_2·mo^{-1})				Energy saved (%)			
	Torpid (%)		Active		Torpid		Winter		Summer	
	Ad	Yg	Ad	Yg	Ad	Yg	Ad	Yg	Ad	Yg
Oct.	22	28	200.7	165.9	3.4	3.5	12.3	26.3	62.3	54.5
Nov.	80	84	49.8	35.7	11.9	10.2	72.6	79.3	88.2	87.3
Dec.	84	89	41.2	25.3	12.9	11.2	76.8	84.1	90.0	90.2
Jan.	87	85	33.4	34.6	13.4	10.7	79.9	80.3	91.4	87.8
Feb.	94	91	14.4	19.4	13.5	10.7	87.2	86.0	94.5	91.4
Mar.	88	84	30.9	36.9	13.5	10.6	80.9	79.3	91.8	87.3
Apr.	90	68	24.9	71.4	13.4	8.3	83.0	64.1	92.7	77.9
May	69	46	79.8	124.5	10.6	5.8	61.2	56.7	83.3	65.2

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 euthermy 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 × 100 = % ES. Euthermic AMMR was calculated from euthermic V_{O_2} recorded during torpor bouts. For summer euthermy, mean values for post-molt adults and young from (Armitage and Salsbury, 1992) were used for euthermic AMMR.

ic at the metabolic rates measured in late summer (Armitage and Salsbury, 1992), adults would use 17.46 l O_2·day^{-1} and young would use 12.02 l O_2·day^{-1}. If we assume that fat is the substrate metabolized and that oxidation of 1 g of fat requires 2 l O_2 (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-

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.

	Time spent		AMMR (l O_2·mo^{-1})				Energy saved (%)			
	Torpid (%)		Active		Torpid		Winter		Summer	
	Ad	Yg	Ad	Yg	Ad	Yg	Ad	Yg	Ad	Yg
Oct.	76	21	94.6	253.4	11.6	3.5	72.4	14.6	80.4	31.1
Nov.	92	89	30.5	34.2	13.6	14.3	88.2	83.3	91.6	86.6
Dec.	92	89	30.5	34.2	13.6	14.3	88.6	83.9	91.8	87.0
Jan.	94	82	23.6	57.7	14.4	13.6	90.1	76.3	93.0	80.9
Feb.	95	92	17.8	23.2	13.5	13.8	91.0	86.4	93.6	89.0
Mar.	92	90	31.5	32.1	14.1	15.0	88.2	84.3	91.6	87.4
Apr.	97	91	11.4	27.9	14.4	14.7	93.1	85.4	95.1	88.2
May	58	81	165.5	61.0	8.9	13.5	54.7	75.2	67.8	80.0

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 $O_2 \cdot g^{-1} \cdot h^{-1}$ °C) than did the one adult (0.0021 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ °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 adequately test for a mass/mass-specific V_{O_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 V_{O_2}

We expected mass to significantly affect total V_{O_2}, but mass significantly affected only euthermy (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 V_{O_2}. Significant values of r_s occurred for torpor ($r_s = 0.65$, $P = 0.01$), euthermy ($r_s = 0.74$, $P < 0.01$), arousal ($r_s = 0.51$, $0.05 > P$ 0.025), and active V_{O_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 V_{O_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 V_{O_2}, why was total bout V_{O_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 V_{O_2}, some individuals ranked high in arousal but low in bout. For example, neither the rankings for bout V_{O_2} and arousal V_{O_2} ($r_s = 0.213$, $P > 0.4$); nor rankings for euthermic and torpid V_{O_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 V_{O_2}, ranging from 55% for euthermy to 16% for deep torpor. When individual variability is combined with the low correlations, then mass does not significantly affect bout V_{O_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 V_{O_2}.

This analysis emphasizes the important effects of individual variability. Our use of linear models in the analysis of V_{O_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 euthermy 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_Es 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° 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_Bs; second, marmots may maintain higher T_Bs 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°) was maintained at 10 °C; a mean of 1.8 °C (range 0.7–2.7°) at 6 °C; a mean of 1.6 °C (range 1.0–2.2°) at 4 °C; a mean of 3.4 °C (range 2.9–4.2°) at 2 °C. As T_E became more stressful at 6 and 4 °C, marmots permitted their T_Bs 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_Es 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 (euthermy + 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_E 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_B to fluctuate is an energy-conserving strategy that reduces the cost of maintaining an average minimal T_B at low T_E. If a fluctuating T_B 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_B 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* (Thorp 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); euthermic 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 euthermic 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).

Arousal 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 (Thorp 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

Armitage, K.B., 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu. Rev. Ecol. Syst. 22, 379–407.

Armitage, K.B., 1998. Reproductive strategies of yellow-bellied marmots: energy conservation and differences between the sexes. J. Mamm. 79, 385–393.

Armitage, K.B., 1999. Evolution of sociality in marmots. J. Mamm. 80, 1–10.

Armitage, K.B., Blumstein, D.L., 2002. Body-mass diversity in marmots. In: Armitage, K.B., Rumiantsev, V.Yu. (Eds.), Holarctic Marmots as a Factor of Biodiversity. ABF PH, Moscow, pp. 22–40.

Armitage, K.B., Downhower, J.F., 1974. Demography of yellow-bellied marmot populations. Ecology 55, 1233–1245.

Armitage, K.B., Salsbury, C.M., 1992. Factors affecting oxygen consumption in wild-caught yellow-bellied marmots (*Marmota flaviventris*). Comp. Biochem. Physiol. 103A, 729–737.

Armitage, K.B., Salsbury, C.M., 1993. The effect of molt on oxygen consumption of yellow-bellied marmots (*Marmota flaviventris*). Comp. Biochem. Physiol. 106A, 667–670.

Armitage, K.B., Woods, B.C., Salsbury, C.M., 2000. Energetics of hibernation in woodchucks. In: Heldmaier, G., Klingenspor, M. (Eds.), Life in the Cold. Springer, Berlin, pp. 73–80.

Arnold, W., 1988. Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). J. Comp. Physiol. B 158, 151–156.

Arnold, W., 1990. The evolution of marmot sociality: I. Why disperse late? Behav. Ecol. Sociobiol. 27, 229–237.

Arnold, W., 1993a. Energetics of social hibernation. In: Carey, C., Florant, G.L., Wunder, B.A., Horwitz, B. (Eds.), Life in the Cold. Westview Press, Boulder, pp. 65–80.

Arnold, W., 1993b. Social evolution in marmots and the adaptive value of joint hibernation. Verh Dtsch. Zool. Ges. 86, 79–93.

Arnold, W., Heldmaier, G., Ortmann, S., Pohl, H., Ruf, T., Steinlechner, S., 1991. Ambient temperatures in hibernacula and their energetic consequences for alpine marmots (*Marmota marmota*). J. Therm. Biol. 16, 223–226.

Bailey, E.D., Davis, D.E., 1965. The utilization of body fat during hibernation in woodchucks. Can. J. Zool. 43, 701–707.

Benedict, F.G., Lee, R.C., 1938. Hibernation and Marmot Physiology. Carnegie Institution of Washington, Washington.

Bibikow, D.I., 1996. Die Murmeltiere der Welt. Westarp Wissenschaften, Magdeburg.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences. 2nd ed. Lawrence Erlbaum Associates, Hillsdale, NJ.

Florant, G.L, Heller, H.C., 1977. CNS regulation of body temperature in euthermic and hibernating marmots (*Marmota flaviventris*). Am. J. Physiol. 232, R203–R208.

Florant, G.L., Hill, V., Ogilvie, M.D., 2000. Circadian rhythms of body temperature in laboratory and field marmots (*Marmota flaviventris*). In: Heldmaier, G., Klingenspor, M. (Eds.), Life in the Cold. Springer, Berlin, pp. 223–231.

French, A.R., 1986. Patterns of thermoregulation during hibernation. In: Heller, H.C., Musacchia, X.J., Wang, L.C.H. (Eds.), Living in the Cold: Physiological and Biochemical Adaptations. Elsevier, New York, pp. 393–402.

French, A.R., 1988. The patterns of mammalian hibernation. Am. Scientist 76, 569–575.

French, A.R., 1990. Age-class differences in the pattern of hibernation in yellow-bellied marmots, *Marmota flaviventris*. Oecologia 82, 93–96.

Heldmaier, G., Ortmann, S., Körtner, G., 1993. Energy requirements of hibernating alpine marmots. In: Carey, C., Florant, G.L., Wunder, B.A., Horwitz, B. (Eds.), Life in the Cold. Westview Press, Boulder, pp. 175–183.

Hock, R.J., 1969. Thermoregulatory variations of high-altitude hibernators in relation to ambient temperature, season, and hibernation. Fed. Proc. 28, 1047–1052.

Kayser, C.H., 1961. The Physiology of Natural Hibernation. Pergamon Press, London.

Kilgore, D.L., Armitage, K.B., 1978. Energetics of yellow-bellied marmot populations. Ecology 59, 78–88.

Kruckenhauser, L., Pinsker, W., Haring, E., Arnold, W., 1998. Marmot phylogeny revisited: molecular evidence for a diphyletic origin of sociality. J. Zool. Syst. Evol. Res. 37, 49–56.

Lenihan, C., Van Vuren, D., 1996. Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*). Can. J. Zool. 74, 297–302.

Luecke, R.H., South, F.E., 1972. A possible model for thermoregulation during deep hibernation. In: South, F.E., Hannon, J.P., Willis, J.R., Pengelley, E.T., Alpert, N.R. (Eds.), Hibernation and Hypothermia, Perspectives and Challenges. Elsevier, New York, pp. 577–604.

Lyman, C.P., 1958. Oxygen consumption, body temperature and heart rate of woodchucks entering hibernation. Am. J. Physiol. 194, 83–91.

Lyman, C.P., Willis, J.S., Malan, A., Wang, L.C.H., 1982. Hibernation and Torpor in Mammals and Birds. Academic Press, New York.

Melcher, J.C., 1987. The Influence of Thermal Energy Exchange on the Activity and Energetics of Yellow-Bellied Marmots. Ph.D. dissertation, University of Kansas, Lawrence.

Ortmann, S., Heldmaier, G., 1992. Energetics of hibernating and normothermic alpine marmots. In: Bassano, B., Durio, P., Gallo Orsi, U., Macchi, E. (Eds.), 1st Int. Symp. on Alpine Marmot (*Marmota marmota*) and gen. Marmota. Torino, pp. 221–226.

Schmidt-Nielsen, K., 1990. Animal Physiology: Adaptation and Environment. Cambridge University Press, Cambridge, New York.

Schwartz, O.A., Armitage, K.B., 2002. Correlations between weather factors and life-history traits of yellow-bellied marmots. In: Armitage, K.B., Rumiantsev, V.Yu. (Eds.), Holarctic Marmots as a Factor of Biodiversity. ABF PH, Moscow, In press.

Steppan, S.J., Akhverdyan, M.R., Lyapunova, E.A., et al., 1999. Molecular phylogeny of the marmots (Rodentia: Sciuridae): tests of evolutionary and biogeographic hypotheses. Syst. Biol. 48, 715–734.

Strijkstra, A.M., 1999. Periodic Euthermy During Hibernation in the European Ground Squirrel: Causes and Consequences. Ph.D. dissertation, Rijksuniversiteit, Groningen.

Thorp, C.R., Ran, P.K., Florant, G.L., 1994. Diet alters metabolic rate in the yellow-bellied marmot (*Marmota flaviventris*) during hibernation. Physiol. Zool. 67, 1213–1229.

Vasiliev, V.N., 1992. Hibernation in black-capped marmot (*Marmota camtschatica* Pallas, 1811). In: Bassano, B., Durio, P., Gallo Orsi, U., Macchi, E. (Eds.), 1st Int. Symp. on Alpine Marmot (*Marmota marmota*) and gen. Marmota. Torino, pp. 67–68.

Vasiliev, V.N., Solomonov, N.G., 1996. Body temperature and metabolism in hibernating marmots (*Marmota camtschatica* Pallas, 1811). In: Le Berre, M., Ramousse, R., Le Guelte, L. (Eds.), Biodiversity in Marmots. Int. Marmot Network, Moscow/Lyon, pp. 265–266.

Wang, L.C.H., 1978. Energetic and field aspects of mammalian torpor: the Richardson's ground squirrel. In: Wang, L.C.H., Hudson, J.W. (Eds.), Strategies in Cold: Natural Torpidity and Thermogenesis. Academic Press, New York, pp. 109–145.

Wang, L.C.H., 1979. Time patterns and metabolic rates of natural torpor in the Richardson's ground squirrel. Can. J. Zool. 57, 149–155.

Ward, J.M., Armitage, K.B., 1981. Circannual rhythms of food consumption, body mass, and metabolism in yellow-bellied marmots. Comp. Biochem. Physiol. 69A, 621–626.

Woods, B.C., 2001. Diet and Hibernation of Yellow-Bellied Marmots: Why Are Marmots So Fat? Ph.D. dissertation, University of Kansas, Lawrence.

Woods, B.C., Armitage, K.B., Blumstein, D.L., 2002. Yellow-bellied marmots depress metabolism to enter torpor. In: Armitage, K.B., Rumiantsev, V.Yu, (Eds.). Holarctic Marmots as a Factor of Biodiversity. ABF PH, Moscow, In press.