FACTORS AFFECTING OXYGEN CONSUMPTION IN WILD-CAUGHT YELLOW-BELLIED MARMOTS (MARMOTA FLAVIVENTRIS)

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Abstract—1. All age groups gained mass during the active season, but mass-gain of adult females was delayed during lactation.

2. The relationship of body mass to metabolic rate varied widely; when the relationship was significant, $R^2$ varied from 10.3 to 72.6%. Body mass affects $V_{O_2}$ more during lactation than at any other period.

3. Mean $V_{O_2}$ of adult males was higher in June than that of adult, non-lactating females.

4. $V_{O_2}$ of reproductive females was significantly higher during lactation than during gestation or postlactation because specific $V_{O_2}$ varied. Specific $V_{O_2}$ of non-reproductive females declined over the active season.

5. Specific $V_{O_2}$ of all age groups declined between the premolt and postmolt periods. The reduced maintenance costs can contribute 20–46% to daily growth.

6. Observed $V_{O_2}$ was lower than the value predicted from intraspecific or interspecific $B:\text{M}$ regressions.

7. $V_{O_2}$ of wild-caught marmots was lower than that of marmots maintained in the laboratory, probably because of dietary differences.

8. Because basal metabolism is a stage on a food-deprivation curve, we suggest that basal metabolic rate is not an appropriate measure of the metabolic activity of free-ranging animals.

INTRODUCTION

The yellow-bellied marmot (Marmota flaviventris) is a diurnal ground-dwelling squirrel that is widely distributed in the western United States, especially in forest clearings and in the alpine of the Cascade, Rocky and Sierra Nevada Mountains (Frase and Hoffmann, 1980). Marmots are active for about 4.5 months and hibernate for the rest of the year. The annual cycle of activity and dormancy is expressed as a circannual rhythm (Davis, 1976; Ward and Armitage, 1981).

Laboratory-held marmots express an annual rhythm of oxygen consumption in which the maximal value of oxygen consumption preceded the maximal value of food consumption by 1 month and that of body mass by 2 months (Ward and Armitage, 1981). The rhythm was expressed in the absence of reproductive activity. Therefore, one purpose of this study was to determine to what extent the rhythm in oxygen consumption is expressed in a population of wild marmots.

The physiology and behavior of marmots suggest that they are energy conservers. Energy is conserved by reducing thermoregulatory costs by avoiding activity when standard operating temperature is stressful and by reduced conductance (Melcher et al., 1989; Armitage et al., 1990), and by reduced metabolic rate in late summer (Kilgore and Armitage, 1978). However, the metabolic rates of laboratory-held marmots measured early in the summer were higher than those predicted from the Kleiber equation or the equation for all Eutheria (McNab, 1988; Armitage et al., 1990). This result is inconsistent with the overall interpretation that marmots are energy conservers. Thus, the second purpose of this study was to compare oxygen consumption of free-ranging marmots with that of laboratory-held animals.

MATERIALS AND METHODS

Oxygen consumption was measured during the active seasons of 1988, 1989 and 1990. All marmots were live-trapped in the morning. Single-door wire mesh traps were set near burrow entrances or in runways and baited with whole oats. Traps were checked between 8 and 10 a.m. MDT. Captured marmots were returned to the laboratory where they were weighed and identified from their individually numbered ear tags. The reproductive state of all adult marmots was determined by nipple condition and scrotal development. Because marmots have been studied since 1962, virtually all animals 1-year-old or older were previously caught, sexed and tagged. All animals when first-caught, such as the young used in this study, received an individually numbered monel metal tag in each ear. Most animals used in this study were caught after emergence from the burrow and had not foraged since the previous afternoon.

In the laboratory, each animal was placed in a wire mesh holding cage that was placed in a plexiglass metabolism chamber provided with six ports for air flow; three ports at one end for air inflow and three ports at the opposite end for air outflow. A port in the top received a thermistor probe connected to a Yellow Springs single channel telemeter for measuring the air temperature within the metabolism chamber. Temperature was maintained at 18°–20°C, which lies in the thermoneutral zone of yellow-bellied marmots (Armitage et al., 1990). The metabolism chamber was placed in an environmental growth chamber. Room air
was drawn through a tube containing drierite before passing into the growth chamber where air circulated through copper tubing to equilibrate to the exposure temperature and then passed through the metabolism chamber, out of the growth chamber, through a tube containing drierite, and through a flow meter. Flow rate was maintained at 4.25 l/min. A small sample of the air flow was diverted after it exited the flowmeter through another tube containing drierite and into an electrochemical oxygen analyser for measuring the amount of oxygen in the air stream.

Output from the oxygen analyser was passed through a transducer that converted the electrical signal into hertz. The hertz output was fed into a Zenith 248 microcomputer equipped with the Data Quest III data analysis system. The hertz value was linearly related to the percentage of oxygen in the air stream. The oxygen analyser was calibrated against room air with the level of oxygen set at 20.93%. Subsequently, the hertz values were converted to ml O₂ for calculations of oxygen consumption. All values were converted to standard temperature and pressure and are expressed as ml O₂/hr or converted to specific V̇O₂ and expressed as ml O₂/kg/hr.

Each animal was equilibrated in the growth chamber for 30 min before oxygen consumption was measured. A reading was taken every 30 sec for 30 min. If the readings were not stable, measurements continued until stable values were obtained. Most animals were stable throughout the 30 min recording period and were sitting quiescently with their head tucked under at the completion of the measurements. Some animals appeared to sleep. Most animals were measured between 10 a.m and 4 p.m, a period that coincides with the growth chamber, through a tube containing drierite and into an electrochemical oxygen analyser for measuring the amount of oxygen in the air stream.

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Body temperatures were measured on five adult females prior to and subsequent to the annual molt. Each female was implanted with a calibrated Mini-Mitter VM-FH transmitter. The signal was received with a Mini-Mitter RA-1010 and stored and analysed with the Data Quest III system.

All statistical analyses were performed with MINITAB. When specific V̇O₂ of adult males and females was compared, values for lactating females and molting and postmolt adults were excluded from the analysis. A Student’s t-test was used to compare the means when specific V̇O₂ was regressed against time during June separately for adult males and females; a statistically significant difference between the Y intercepts was tested by calculating the 95% confidence interval around each intercept and determining the amount of overlap.

Mean total and specific V̇O₂ was calculated for premolt and postmolt young, yearlings (animals 1-year-old) and adult (2-years-old or older) females. For reproductive females, values measured after lactation was completed or before lactation began were used as premolt V̇O₂. Premolt and postmolt specific V̇O₂ were compared within each age group with Student’s t-test.

Differences in mean specific V̇O₂ calculated for gestating, lactating and postlactating females, were analysed with a single classification ANOVA. Because the variances around the means for the gestation and postmolt females were not homogeneous, Kruskal-Wallis tests were performed. Females whose reproductive condition indicated that they were lactating, but that did not nurse a litter, were included in these analyses. Specific V̇O₂ values for non-reproductive females were grouped into time periods that corresponded to the reproductive periods and analysed with the Kruskal-Wallis test. Molting and postmolt females were excluded from the analysis.

Body mass of reproductive and of non-reproductive adult females was grouped into four time periods: gestation, lactation, post-lactation and postmolt. Because the variances were homogeneous, values were compared by ANOVA.

Simple linear regressions related body mass to V̇O₂ and specific V̇O₂. Regressions were calculated for all reproductive and all non-reproductive females and for each group of females for each reproductive period. Regressions were calculated separately for 1989 and 1990. Premolt specific V̇O₂ was regressed against body mass for young, yearlings and non-reproductive adult females for 1990. Separate regressions were calculated for each sex for young and yearlings. V̇O₂ and body mass differences between sexes were compared by the t-test.

Mean specific V̇O₂ was calculated for adult females (gestation and post-lactation values combined), non-reproductive females and for each group of females for each reproductive period. Regressions were calculated separately for 1989 and 1990. Premolt specific V̇O₂ was regressed against body mass for young, yearlings and non-reproductive adult females for 1990. Separate regressions were calculated for each sex for young and yearlings. V̇O₂ and body mass differences between sexes were compared by the t-test.

RESULTS

Body mass

All age groups gained mass during the active season (Table 1). Although the gain in mass was statistically significant for all females (P < 0.001), the patterns of gain differed between reproductive and non-reproductive females (Table 1, Fig. 1). The average non-reproductive female gained about 500 g during the gestation and lactation periods whereas the reproductive females gained about 230 g during gestation and maintained a relatively constant mass during lactation. Although both groups of females gained significant mass from the premolt to the postmolt period, the rate of gain was much higher in

<table>
<thead>
<tr>
<th>Table 1. Body mass (kg) of yellow-bellied marmots used in oxygen consumption measurements.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body mass mean ± SD (N)</strong></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>------------------</td>
</tr>
<tr>
<td>Non-reproductive females</td>
</tr>
<tr>
<td>Reproductive females</td>
</tr>
<tr>
<td>Young</td>
</tr>
<tr>
<td>Yearlings</td>
</tr>
<tr>
<td>Adult males</td>
</tr>
</tbody>
</table>

Female reproductive categories correspond to the following time periods (days past 30 April): gestation, 1-56; lactation, 57-86; post-lactation, 87-110. Non-reproductive females molt by the end of the lactation period. N = sample size.
and in yearling males. Among reproductive females, each year body mass affected $V_O_2$ more during lactation than during gestation or postlactation.

The regression coefficient, $b$, varied from $-0.1$ to 1.29 (Table 2). There is no obvious relationship between $b$ and sample size, e.g. $b$ was 0.67 for 15 female yearlings and 0.68 for 94 young, yearlings and adult, non-lactating females. A Spearman rank correlation emphasizes the lack of a relationship between sample size and $b$ ($r_s = 0.06, P > 0.5$).

**Adult male vs adult females**

Because sample size for males was inadequate, $V_O_2$ was compared between the sexes only in June. $V_O_2$ of males ($103.50 \pm 345.9, N = 22$) was significantly ($t = 4.8, P = 0.001$) higher than that of females ($726.7 \pm 123.3, N = 35$, lactating females excluded). However, males are significantly larger than females (Table 1); therefore, specific $V_O_2$ was compared between the sexes. Mean specific $V_O_2$ of males ($306.4 \pm 88.0, N = 19$) was higher than that of females ($281.5 \pm 50.1, N = 35$). Although this difference is not statistically significant ($t = 1.33, df = 52, P = 0.20$), the following evidence suggests that the difference is biologically significant. Male values were higher in early June and lower in late June. When specific $V_O_2$ was regressed against time, the regression was nearly statistically significant for males ($P = 0.1$), but not for females; ($P = 0.4$). Specific $V_O_2$ predicted from the regression equations for 1 June, (i.e. the $Y$ intercept) was 541.8 for males and 335.4 for females. The 95% CI around the value for females did not overlap the value for males whereas the 95% CI around the value for males slightly overlapped that for females; the difference is considered statistically significant.

**Reproductive status**

$V_O_2$ of reproductive females was about 33% higher in lactation than in gestation (Table 3). Because body

![diagram](image-url)

**Fig. 1. Metabolic rate and body mass of adult female yellow-bellied marmots during the major phases of the homeothermic period. G = gestation, L = lactation, PL = postlactation, PM = postmolt. For non-reproductive females, gestation corresponds to days 32–56 post-emergence, lactation corresponds to days 57–86 post-emergence, post-molt begins with day 87. For reproductive females, postlactation begins with day 87 and molt usually is completed about day 105–110. Number above each bar is the number of individuals measured. R = reproductive females, NR = non-reproductive females.**

<table>
<thead>
<tr>
<th>Animal group</th>
<th>$N$</th>
<th>$b$</th>
<th>$R^2$ (%)</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All adult females</td>
<td>75</td>
<td>0.41</td>
<td>10.3</td>
<td>0.005</td>
</tr>
<tr>
<td>Non-reproductive females</td>
<td>23</td>
<td>-0.10</td>
<td>0.9</td>
<td>0.67</td>
</tr>
<tr>
<td>Reproductive females</td>
<td>43</td>
<td>0.8</td>
<td>23.3</td>
<td>0.001</td>
</tr>
<tr>
<td>Gestation</td>
<td>10</td>
<td>0.48</td>
<td>1.2</td>
<td>0.76</td>
</tr>
<tr>
<td>Lactation</td>
<td>16</td>
<td>1.29</td>
<td>61.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Postlactation</td>
<td>17</td>
<td>0.69</td>
<td>24.6</td>
<td>0.043</td>
</tr>
<tr>
<td>All yearlings</td>
<td>45</td>
<td>0.12</td>
<td>0.4</td>
<td>0.69</td>
</tr>
<tr>
<td>Reproductive females</td>
<td>35</td>
<td>0.92</td>
<td>14.4</td>
<td>0.02</td>
</tr>
<tr>
<td>Lactation</td>
<td>18</td>
<td>0.78</td>
<td>14.6</td>
<td>0.12</td>
</tr>
<tr>
<td>Postlactation</td>
<td>12</td>
<td>0.57</td>
<td>11.0</td>
<td>0.29</td>
</tr>
<tr>
<td>All young</td>
<td>53</td>
<td>0.49</td>
<td>25.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Males</td>
<td>34</td>
<td>0.55</td>
<td>26.5</td>
<td>0.002</td>
</tr>
<tr>
<td>Females</td>
<td>19</td>
<td>0.43</td>
<td>29.5</td>
<td>0.016</td>
</tr>
<tr>
<td>All yearlings</td>
<td>22</td>
<td>0.55</td>
<td>23.8</td>
<td>0.021</td>
</tr>
<tr>
<td>Males</td>
<td>7</td>
<td>-0.01</td>
<td>0.0</td>
<td>0.98</td>
</tr>
<tr>
<td>Females</td>
<td>15</td>
<td>0.67</td>
<td>35.4</td>
<td>0.019</td>
</tr>
<tr>
<td>All non-reproductive</td>
<td>78</td>
<td>0.70</td>
<td>66.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>All marmots</td>
<td>94</td>
<td>0.68</td>
<td>72.6</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

$N =$ the number of oxygen consumption measurements. All adult females includes all measurements of adult females where sample size was adequate, adult females were sub-divided into the various reproductive categories. All non-reproductive includes young, yearlings and non-reproductive adult females. All marmots excludes only lactating females.

**Table 2. The relationship between $V_O_2$ and body mass for wild-caught yellow-bellied marmots**

**Body mass and metabolic rate**

The relationship between body mass and $V_O_2$ varied widely among animal groups and between years (Table 2). Of the 18 relationships, 12 were statistically significant and one was nearly so. Among those regressions that were statistically significant, $R^2$ varied from 10.3 to 72.6%. The highest values of $R^2$ occurred when young, yearlings and adults were included in the sample (all non-reproductive and all marmots, Table 2). No relationship of body mass to $V_O_2$ occurred in the non-reproductive females, in females during gestation, in all adult females in 1990...
mass increased only 9% from gestation to lactation, the increase in \( V_O_2 \) occurred primarily because of an increase in specific \( V_O_2 \) (Fig. 1). After lactation, \( V_O_2 \) declined to about the same level as that of gestation (Table 3). Because body mass was essentially unchanged between lactation and postlactation (Table 1), specific \( V_O_2 \) declined about 27% and was slightly lower than that of gestation (Fig. 1). These changes in specific \( V_O_2 \) were statistically significant (ANOVA, 0.01 > P > 0.005).

During the time that \( V_O_2 \) of reproductive females increased (i.e. gestation to lactation), \( V_O_2 \) of non-reproductive females decreased about 4% (Table 3). Because body mass of non-reproductive females increased by 20%, the decrease in \( V_O_2 \) occurred because specific \( V_O_2 \) decreased by 24% (Fig. 1). The change in \( V_O_2 \) of non-reproductive females over the summer was not statistically significant (H = 10.3, 0.01 > P > 0.005); however, the change in specific \( V_O_2 \) was significant (H = 10.3, 0.01 > P > 0.005).

**Premolt vs postmolt**

The \( V_O_2 \) of postmolt reproductive females was only about 9% greater than that of premolt (postlactation). The \( V_O_2 \) of postmolt non-reproductive females was about 15% less than that of premolt (Table 3). \( V_O_2 \) of yearlings was 11% less in the postmolt period than in the premolt; that of young was about 25% higher in the postmolt period (Table 3). All groups gained mass from the premolt to the postmolt period (Table 1). The increase in mass of the young was 97%; therefore, the increase in \( V_O_2 \) was much less than that expected from the gain in mass. Likewise, the changes in \( V_O_2 \) in the other groups cannot be attributed to the changes in body mass. Thus, specific \( V_O_2 \) declined significantly in all groups (Fig. 1, Table 3). The difference between premolt and postmolt specific \( V_O_2 \) was statistically significant for young (t = 3.5, df = 107, P < 0.001), yearlings (t = 6.3, df = 47, P < 0.001) and non-reproductive adult females (t = 2.57, df = 39, 0.05 > P > 0.01), but not for reproductive females (t = 0.22, df = 60, P > 0.5).

One problem with analysing for differences in the premolt/postmolt specific \( V_O_2 \) of adult females is that individuals varied considerably and sample size for postmolt animals was much less than that of premolt animals. If animals with relatively high metabolic rates were disproportionately represented in the postmolt measurements, real differences could be missed. Therefore, we analysed 13 animals, six of whom were reproductive, for whom both premolt and postmolt measurements were available. Postmolt specific \( V_O_2 \) was nearly identical in the two groups (reproductive = 233.6 ± 72.9; non-reproductive = 245.5 ± 36.0). Postmolt specific \( V_O_2 \) was significantly lower than that of premolt (t = 3.6, df = 12, 0.01 > P > 0.001). On average, specific \( V_O_2 \) decreased 24.5% from premolt to postmolt states.

**Observed vs predicted \( V_O_2 \)**

Observed \( V_O_2 \) for each animal group was lower than the value predicted from either intraspecific or interspecific regressions relating specific oxygen consumption to body mass (Table 4). The predicted values ranged from 14 to 54% greater than the observed values. The Eutherian equation provided the estimates closest to the observed values (14–29% higher) whereas the intraspecific regression derived from laboratory measurements of yellow-bellied marmots predicted the highest values (39–54% above measured). Values predicted from the Kleiber equation were 28–42% higher than the observed.

**DISCUSSION**

**Body mass**

The regression coefficient relating \( V_O_2 \) to body mass is generally considered to be 0.75 (Blaxter, 1989; p. 126); however, coefficients determined empirically from large data sets may be as low as 0.71 (calculated from McNab, 1988). Of those regression coefficients that were statistically significant, only three approximated the value determined from interspecific comparisons (e.g. all non-reproductive and all marmots, Table 2). The other significant coefficients were ≥ 0.8 or ≤ 0.55. The lower values are similar to those reported from measurements of laboratory marmots (0.50–0.55, Armitage et al., 1990).

**Table 4. Comparison of specific \( V_O_2 \) (ml O_2/kg/hr) with predicted specific \( V_O_2 \)**

<table>
<thead>
<tr>
<th>Group</th>
<th>Body mass</th>
<th>Observed</th>
<th>Intraspecific</th>
<th>Kleiber</th>
<th>Eutherian</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproductive females</td>
<td>2.783</td>
<td>262.9 ± 73.1 (60)</td>
<td>491.9 ± 34.8</td>
<td>454.7 ± 15.4</td>
<td>372.6 ± 14.7</td>
</tr>
<tr>
<td>Non-reproductive females</td>
<td>2.865</td>
<td>294.1 ± 106.1 (30)</td>
<td>485.0 ± 33.4</td>
<td>451.6 ± 15.1</td>
<td>369.6 ± 14.6</td>
</tr>
<tr>
<td>Yearlings</td>
<td>1.854</td>
<td>362.5 ± 145.6 (56)</td>
<td>608.7 ± 62.3</td>
<td>504.0 ± 25.3</td>
<td>420.0 ± 24.5</td>
</tr>
<tr>
<td>Young</td>
<td>0.790</td>
<td>442.3 ± 190.0 (149)</td>
<td>954.4 ± 148.6</td>
<td>626.0 ± 47.9</td>
<td>540.8 ± 48.1</td>
</tr>
</tbody>
</table>

All postmolt measurements and lactating females are excluded. N = number of measurements.
There are several possible explanations for the wide variation in \( b \) values. First, the animals used in this study were not basal and regression values usually are based on basal metabolism. However, it is unlikely that \( b \) depends on basal metabolism. The similarity between the \( b \) values for young, yearlings, and adult females in 1989 (Table 2) to the values measured at similar temperatures in laboratory-held, basal marmots suggests some other explanation is more likely. Second, the \( b \) values may be affected by the range of body mass. Such an effect is likely; \( b \) values of 0.68–0.70 and the highest \( R^2 \) values occurred when the marmot group included the widest range of body mass (Table 2). However, range of body mass is not the complete answer; high \( R^2 (b = 0.69) \) occurred in a group of adult females. Third, some of the variation likely is random and a function of the animals in that particular sample. Fourth, \( b \) likely is affected by physiological state. Exposure temperature affected \( b \) values of laboratory marmots (Armitage et al., 1990). Interestingly, lactating females expressed one of the strongest relationships between body mass and \( V_O \), \( (R^2 \text{ varied from } 14.6 \text{ to } 61.7\%, \text{ Table } 2; \text{ in } 1991, \text{ } R^2 = 58.8\%, \text{ unpublished data}) \). Lactation is energetically stressful and all females likely function near maximal resting metabolism; thus, body size is more likely to be the remaining major variable affecting \( V_O \) and the \( Bm:\dot{V}_O \) relationship explains much of the variation among females. When conditions are less stressful, other factors may reduce the importance of the relationship between \( V_O \) and body mass. For example, weather conditions affect marmot reproduction (Armitage and Downhower, 1974; Van Vuren and Armitage, 1991); probably these effects influence metabolic rates, and these effects likely depend on habitat exposure as well as physiological condition. In other words, individual variation affects the \( V_O \)-body mass relationship, but the way the relationship is affected is unpredictable and depends on which individuals are sampled at any time.

**Adult males vs adult females**

The higher metabolic rate of males in June and the decrease in \( V_O \) during June in males but not in females is consistent with the mating cycle. Adult male *Spermophilus saturatus* have a high daily energy expenditure (DEE) during mating (Kenagy et al., 1989a). The basal metabolism component of DEE was estimated from the Kleiber equation; changes in DEE were attributed to changes in activity or body mass (Kenagy, 1987). However, changes in resting metabolism probably occur. Both *M. flaviventris* and *S. tridecemlineatus* express annual cycles of \( V_O \) (Armitage and Shulenberg, 1972; Ward and Armitage, 1981). Furthermore, specific \( V_O \) of the Arctic ground squirrel (*S. parryi*) was markedly higher in the spring than in summer and that of mantled ground squirrels (*S. lateralis*) declined in late summer with high values in mid summer (Hock, 1969). There were too few measurements on these species to describe seasonal patterns precisely, but an annual cycle is suggested. Most likely specific \( V_O \) is labile and varies as the ecological/behavioral environment changes over the annual cycle. Because yellow-bellied marmots mate in mid to late May, \( V_O \) of males probably peaks during the mating season and declines thereafter to a low at the time of hibernation. The regression of male \( V_O \) on a day past 1 June suggests that \( V_O \) was higher during the peak mating season. This suggestion needs verification by measuring \( V_O \) of males during May.

**Reproductive status**

The most striking effect of reproduction was the increase in \( V_O \) of lactating females. The 33% increase in \( V_O \), results from a 9% increase in body mass; the rest of the increase can be attributed to an increase in specific \( V_O \) of 24%. However, two methods of estimating the increase in specific \( V_O \), produced values of 19% (specific \( V_O \) from Fig. 1) to 22% (mean \( V_O \) from Table 3 divided by mean body mass from Table 1). Thus, a value of 20% appears to be a reasonable estimate and is similar to the percentage increase in specific \( V_O \) from gestation to lactation reported for *S. saturatus* (Kenagy et al., 1989b). However, the value for *S. saturatus* is the peak increase measured in late lactation whereas the increase for *M. flaviventris* is the average for the entire period of lactation. We measured the percentage increase in late lactation compared to gestation for nine females; the mean increase was 59%. The increase in \( V_O \) probably represents, in part, the energetic cost of the synthesis of milk (Kenagy et al., 1989b). Yellow-bellied marmots wean their young at about 25 days and the ground squirrels complete major lactation at about 35 days. The period of lactation of yellow-bellied marmots is much less than that expected for a ground-dwelling sciuroid of that body size (Armitage, 1981). The shorter period of lactation is likely possible because of a higher rate of milk synthesis, as indicated by the higher relative increase in \( V_O \) by marmots than by ground squirrels. Marmots weigh about 34 g at birth (Frase and Hoffmann, 1980) and about 500 g at weaning. Thus, marmots grow at the average rate of 18.6 g/day during lactation; young mantled ground squirrels grow at the rate of 2.13 g/day. The ratio of infant growth to female mass (g/kg) is 6.60 for *M. flaviventris* and 8.40 for *S. saturatus*. Because *M. flaviventris* is much larger than *S. saturatus*, the lower absolute growth is expected because growth rate increases more slowly than body mass (Calder. 1984: p. 278). Therefore, body mass was converted to metabolic body mass (Kleiber, 1975: p. 384f) in order to correct for differences in body size. The ratio of infant growth to female mass (g/kg\(^{1.71}\)) is 6.0 for *S. saturatus* and 8.6 for *M. flaviventris*. Thus, growth during lactation is relatively greater in the yellow-bellied marmot than in the mantled ground squirrel. The relatively higher growth rate of the young marmots requires a relatively greater investment by the mother; this greater investment is consistent with the high specific \( V_O \) during lactation. Energy expenditure for lactation was significantly correlated with the post-natal growth rate of the litter for five species of laboratory-reared *Peromyscus* (Glazier, 1985). Glazier suggested that metabolic rate causally determined the rate of energy expenditure during lactation. The comparison here of *M. flaviventris* and *S. saturatus* is consistent with that interpretation.

Weaned marmots grow at an average rate of 14 g/day (Armitage et al., 1976), a rate that is lower
The conductance was 9% higher in the premolt state. The temperature in free-ranging marmots during the premolt and postmolt, respectively. Conductance was 0.0164 and 0.0123 ml O₂/g/hr during premolt and postmolt, more extensive series of measurements of VO₂, and body temperature on a larger number of animals. Interestingly, the percentage decrease in specific VO₂ is nearly the same as the decrease in conductance. This similarity indicates that the postmolt decrease in specific VO₂ is primarily, if not entirely, a consequence of increased insulation produced by the molt. Although increased insulation is important for coping with the low temperatures of hibernation, the decreased metabolic cost associated with increased insulation may significantly affect the preparation for hibernation.

The deposition of fat as the energy source for hibernation can occur only when assimilated energy exceeds maintenance energy. Any mechanism that decreases maintenance costs provides more energy for production at the same level of ingestion. The lower specific VO₂ of premolt animals reduces daily oxygen consumption considerably below that of postmolt adult females. Postmolt young use 4.4181 O₂/kg/day less than premolt young, postmolt yearlings use 4.8431 O₂/kg/day less than premolt yearlings and postmolt adult females use 1.7571 O₂/kg/day less than premolt adult females. These specific values may be converted to total savings per individual per day by multiplying each specific value by the mean body mass of that group. Thus, young save 6.9141 O₂/individual/day, yearlings, 13.7061 O₂/individual/day, and adult females, 5.9741 O₂/individual/day. The energy equivalent of a liter of O₂ is 18.6 g/day during lactation. The higher energy equivalent of a liter of O₂ is 4.8 kcal (Schmidt-Nielsen, 1990: p. 569). Therefore, the reduced VO₂ provides a daily surplus of 33.19 kcal (21.21/kg) for young, 65.79 kcal (23.25/kg) for yearlings and 28.68 (8.4/kg) for adult females. We assumed that all surplus energy was used for the synthesis of fat. We used a conversion efficiency of 0.8 (Blaxter, 1989: p. 273): this value should be a reasonable estimate as it is the value for the conversion of carbohydrates to fat; however, the vegetation also contains fat, with a higher conversion efficiency, and protein, with a lower conversion efficiency. Thus, young could deposit 2.82 g of fat daily (33.19 kcal × 0.8 × 9.4 kcal/g fat (Schmidt-Nielsen 1990: p. 171) or 1.81 g fat/kg body mass. The equivalent values are 5.60 g or 1.98 g/kg for yearlings and 2.44 g or 0.71 g/kg for adult females. Marmots grow at the average rate of 12-14 g/day; thus, the savings in energy expenditure that result from molting can provide 20-46% of daily growth. Therefore, postmolt marmots can spend less time foraging to maintain a steady rate of growth or increase fat deposition at the same level of foraging. Marmots apparently decrease foraging time in late summer (Armitage, 1991) rather than increase growth rate. The factors that limit growth rate, e.g., rate of digestion and assimilation of herbage, protein content of food, etc., are unknown. Much future work is required to integrate physiological mechanisms with foraging strategies.

**Premolt vs postmolt**

The decline in VO₂ in the postmolt period is not associated with a decrease in body temperature. Body temperatures of three females ranged from 36.7 to 37.5°C during premolt and from 36.4 to 37.8°C during postmolt (Armitage, unpublished data). There was no evidence of a decline in body temperature in free-ranging marmots during the active season (Melcher et al., 1989). Conductance (Armitage et al., 1990) was measured for one adult female that completed molt. At 6°C, conductance decreased from 0.0112 ml O₂/g/hr during premolt to 0.0081 ml O₂/g/hr during premolt. At 18°C, conductance was 0.0164 and 0.0123 ml O₂/g/hr during premolt and postmolt, respectively. Conductance decreased about 25%. Conductance was determined for two adult females in partial molt. On average, conductance was 9% higher in the premolt state. The value determined from the partially molted animals along with the conductance of the fully molted adult indicate that insulative acclimatization characterizes the preparation of marmots for winter and hibernation (Hart, 1957). This interpretation should be confirmed by a more extensive series of measurements of VO₂, and body temperature on a larger number of animals.

Observed vs predicted VO₂

The lower than expected observed VO₂ is counterraductive. We expected the observed to be higher than the predicted, especially for values predicted from the intraspecific regression, which was derived from
measurements of yellow-bellied marmots maintained in the laboratory (Armitage et al., 1990). Because the laboratory marmots were collected from the same population used for this study, population differences probably cannot account for the differences in VO₂ between laboratory and field marmots. Because basal metabolism was measured on laboratory marmots, VO₂ would be expected to be lower (rather than 40–50% higher) than that of field marmots that were not basal and that could have elevated values initiated by the emotional stress of capture and handling. We can find no errors in measurement. The most likely source of error is in the measurement of flow rate. Flow rate used in the laboratory study was 28% greater than that used in the field study. However, the same flow meter and calibration curve were used in both studies; thus, flow rate seems an unlikely source of the differences in VO₂. The predicted values were calculated for measurements made in the laboratory at 20°C whereas the field animals were measured at 18°C. Regression coefficients relating VO₂ to body mass differed little for marmots measured at 15°C and 20°C and mean VO₂ values were virtually identical (Armitage et al., 1990); thus, the differences in predicted and observed O₂ cannot be attributed to temperature differences during measurement.

One major difference between the two groups of marmots was diet. Field animals feed on a variety of forbs and grasses (Frase and Armitage, 1989) whereas laboratory animals were fed Purina Lab Chow ad lib. (Armitage et al., 1990). Animals fed lab chow may receive hormones that stimulate metabolism (Wunder, 1979). However, our animals expressed a circannual rhythm in which maximal and minimal VO₂ preceded the maximal and minimal values of food consumption by at least 1 month; thus, it is likely that hormones in the food were not driving metabolic rate.

We suggest that dietary differences likely affect metabolic rate directly. The annual cycle of mass change is regulated; when body mass of hibernators is manipulated, mass returns to a level appropriate for that time of year (Morosovský, 1978). Energy balance, and thus regulation of body mass, could occur by controlling energy expenditure. Intake in excess over that needed to achieve an appropriate mass could be used in diet-induced thermogenesis (DIT) (Rothwell and Stock, 1981). A low-protein diet most effectively induces DIT (Rothwell and Stock, 1983). A high cellulose diet increased the metabolic rate of captive water voles (Woodall, 1989). Animals apparently increase energy intake as a consequence of increasing ingestion to meet protein needs; the excess energy intake is expanded as DIT. Laboratory marmots fed lab chow had a diet higher in protein content than the average protein concentration of 16% for the plants used as food by free-ranging marmots (Frase and Armitage, 1989). Thus, the free-ranging marmots would more likely express DIT than the laboratory animals.

However, highly palatable and high energy diets induce higher VO₂. Energy level of diet affected VO₂ of piglets more than the temperature at which the animals were maintained (Macari et al., 1983) and pigs maintained on a high plane of nutrition produced more heat after 30 hr of fasting than pigs maintained on a low plane of nutrition (Koong et al., 1982). Resting VO₂ of captive dormice was higher on a cafeteria feeding system than on a stock diet (Rothwell and Stock, 1986). VO₂ did not return to normal until 4 days after removal of the cafeteria diet. Resting VO₂ decreased when animals shifted from a cafeteria to a stock diet. The laboratory diet of marmots probably affected their metabolism in a way similar to the high energy or cafeteria diets described above. VO₂ differences between the laboratory and field populations probably reflect the different effects of their diets.

The effect of diet on metabolism raises the question of which metabolic measurement represents the metabolic activity of free-ranging animals. The postulated effect of diet on VO₂ is often rejected on the basis that basal metabolism was not measured (i.e. animals were not postabsorptive) and when animals become basal, the effect of diet disappears (discussion and references in Blaxter, 1989: p 135f). VO₂ decreases when animals are food-deprived (Kleiber, 1975: p 246; Nagy and Pistole, 1988). We measured body mass and VO₂ of an adult, non-reproductive female marmot for 6 days. VO₂ on day 1 was measured a few hours after the animal was trapped. She was maintained in the laboratory with water but no food and VO₂ and body mass were measured daily. After day 5, she was fed, but food was withdrawn at dusk to mimic natural conditions where animals do not feed from sunset until after sunrise. VO₂ declined about 29% between days 1 and 2, then declined about 7% per day during the next 3 days (Fig. 2). VO₂ increased about 57% per day during the next 3 days (Fig. 2). VO₂ of northern elephant seal pups declined linearly after feeding. Similarly, VO₂ of northern elephant seal pups declined linearly during the postweaning fast and increased significantly when fed, even though they were fasted 12–18 hr before VO₂ was measured (Rea and Costa, 1992). Loss of body mass by the female marmot varied from 20 to 40 g/day except between days 2 and 3 when mass decreased 115 g (Fig. 2). This loss was associated with a large defecation and possibly represents when the animal became post-absorptive.

If the interpretation of mass loss as an indication of when the animal became postabsorptive is correct, many of the animals measured in the laboratory study may not have been postabsorptive as they were food deprived for a minimum of 24 hr (Armitage et al., 1990).
comparisons, but even this comparison is susceptible measured because food deprivation initiates a de-
will not become basal. If an animal encounters ever basal in its natural environment. Its resting 
effects of diet will not be apparent if BMR is 
defined as basal. But it is unlikely that an animal is 
starvation, its 
will decline, but not stop at basal.

The results of this preliminary food-deprivation 
study indicate that basal metabolism (BMR) is not an 
appropriate measure of the metabolic activity of 
free-ranging animals. BMR is an arbitrary point on 
the metabolic curve of a food-deprived animal. The 
effects of diet will not be apparent if BMR is 
measured because food deprivation initiates a de-
crease in \( V_{\text{O}} \), and the curve will pass through the point 
defined as basal. But it is unlikely that an animal is 
ever basal in its natural environment. Its resting 
metabolism will be affected by its diet; because most 
individuals feed several times throughout the day, \( V_{\text{O}} \) 
will not become basal. If an animal encounters starvation, its \( V_{\text{O}} \), will decline, but not stop at basal.

Furthermore, the use of BMR as an index of main-
tenance metabolism for studies of energy budgets or 
as the basis for estimating the costs of activities such 
as foraging, lactation, etc. will overestimate the cost 
of the activity and underestimate the cost of mainten-
ance because BMR underestimates the real cost of 
resting or quiescent metabolism. The only use of 
BMR is as a standard measure for interspecific 
comparisons, but even this comparison is susceptible 
to error depending on where along the food-deprived 
metabolic curve any particular set of measurements is 
designated as basal.

It seems likely that any study relating \( V_{\text{O}} \) to some 
ecological parameter or life history trait must estab-
lish standard conditions appropriate to the study. For 
example, thermogenic capacity of shrews was not 
related to basal metabolism (animals fasted for 2 hr) 
(Sparti, 1992).

Marmots as energy conservers

The earlier analysis of energy-use by yellow-bellied marmots suggested that marmots have a two-energy 
strategy, a high-energy strategy during reproduction and a low-energy strategy during preparation for 
hibernation (Armitage et al., 1990). However, that 
interpretation was based on marmots maintained on 
lab chow in the laboratory and is incorrect. This 
study clearly determined that minimal metabolism at 
times during the homeothermal phase (Morrison and 
Galster, 1975) is less than that predicted from 
body mass regressions for basal metabolism. Even the 
mean specific \( V_{\text{O}} \) of lactating females is about 7% 
less than that predicted from the equation for euther-
rian mammals (McNabb, 1988). Thus, throughout 
the active season yellow-bellied marmots maintain 
relatively low metabolic rates. However, the earlier 
suggestion that the higher rates early in the 
active season may be associated with growth and reproduction (Armitage et al., 1990) may be correct. 
For example, non-reproductive females grow more 
rapidly early in the summer when \( V_{\text{O}} \) is high than late 
in the summer when \( V_{\text{O}} \) is lower. A possible 
relationship between growth and/or reproduction (e.g. activity of males) requires further investigation 
and this relationship could form the basis for the 
circannual rhythm of metabolism.

What is critical to an animal is its total energy 
expenditure, not its specific metabolism. Marmots 
compensate for an increase in body-size, which would 
increase total metabolism, by decreasing mass-
specific metabolism. Metabolism declines following 
the molt. Metabolic costs are further reduced by 
decreasing above-ground activity and by minimizing 
the costs of thermoregulation by reducing activity at 
those times of the day when ambient temperature 
would increase \( V_{\text{O}} \) (Melcher et al., 1989). By 
minimizing maintenance metabolism, marmots can 
grow, reproduce, and prepare for hibernation in the 
short active season of 4–5 months. Because the 
anual cycle of marmots is similar to that of other 
hibernating, ground-dwelling squirrels, we predict 
that similar patterns of metabolic adaptation occur in 
these other species as well.

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