

## THE EFFECT OF MOLT ON OXYGEN CONSUMPTION OF YELLOW-BELLIED MARMOTS (*MARMOTA FLAVIVENTRIS*)

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**Abstract**—1. Mean specific  $\dot{V}O_2$  of five adult female yellow-bellied marmots was significantly lower in postmolt individuals than in premolt animals.

2. Mean body temperature did not differ significantly between premolt and postmolt marmots.

3. Conductance was significantly lower in postmolt than in premolt marmots.

4. Because body mass was significantly larger and total  $\dot{V}O_2$  significantly lower in postmolt than in premolt, the decrease in specific  $\dot{V}O_2$  is attributed to decreased conductance and not to the accumulation of metabolically inactive tissues.

### INTRODUCTION

The yellow-bellied marmot (*Marmota flaviventris*) is a hibernating, ground-dwelling squirrel that is widely distributed in the Cascade, Rocky, and Sierra Nevada Mountains of western United States (Frase and Hoffmann, 1980). This species conserves energy by reducing thermoregulatory costs by reduced conductance and by avoiding activity when standard operating temperature is stressful (Melcher *et al.*, 1989; Armitage *et al.*, 1990). Recently we demonstrated that the metabolic rate of wild-caught marmots was much lower than that predicted from body-mass:metabolism relationships (Armitage and Salsbury, 1992).

Furthermore, our results indicated that a considerable savings in maintenance energy occurred when the animals molted. Although we attributed the lower metabolic rate in postmolt than in premolt animals to increased insulation, we could not eliminate the possibility that marmots conserved energy by regulating body temperature at a lower level (Armitage and Salsbury, 1992). Therefore, the purpose of this study was to measure oxygen consumption and body temperature on the same individuals in the premolt and postmolt condition.

### MATERIALS AND METHODS

Five adult females, four of whom had weaned litters, and three female young were each implanted with a Mini-Mitter VM-FH calibrated temperature transmitter late in the premolt period. The reproductive females were all postlactation. All animals were free-ranging and were trapped and brought into the laboratory for measurements and returned to their home areas when measurements were completed. Thus, measurements were made at various times in the molting process, but at least one measurement for each animal occurred in the premolt phase and one in the postmolt phase. The series of measurements began on 3 July 1992 and concluded on 6 September 1992.

$\dot{V}O_2$  and body temperature ( $T_b$ ) were measured simultaneously at 18°C for adults and 20°C for young. Temperature signals were detected with a Mini-Mitter RA-1010 receiver. Oxygen consumption was measured with an electro-chemical oxygen analyser. Output from the temperature receiver and oxygen analyser was stored and analysed with the Data Quest III system installed on a Zenith 248 micro-computer. Details of the trapping, tagging, oxygen measurement system, and measurement procedures are described in detail in Armitage and Salsbury (1992). Conductance

Table 1. Body temperature ( $T_b$ ),  $\dot{V}O_2$  (ml  $O_2$ /hr), body mass (kg), specific  $\dot{V}O_2$  (ml  $O_2$ /g · hr), and conductance ( $C$ ) of five adult female yellow-bellied marmots as related to molting.  $N$  = number of measurements. All values are means  $\pm$  one standard deviation.

	Premolt	Molting	Postmolt	Anova	
				$F$	$p$
$T_b$	37.44 $\pm$ 1.9	38.50 $\pm$ 0.2	37.86 $\pm$ 0.4	1.1	0.37
$\dot{V}O_2$	795.9 $\pm$ 100.5	817.1 $\pm$ 97.0	619.6 $\pm$ 105.9	8.3	0.003
Body mass	2.88 $\pm$ 0.35	3.09 $\pm$ 0.58	3.59 $\pm$ 0.41	5.9	0.012
Specific $\dot{V}O_2$	0.272 $\pm$ 0.051	0.268 $\pm$ 0.033	0.172 $\pm$ 0.021	17.8	<0.001
$C$	0.014 $\pm$ 0.0022	0.0131 $\pm$ 0.0016	0.0087 $\pm$ 0.0011	23.3	<0.001
$N$	7	4	9		

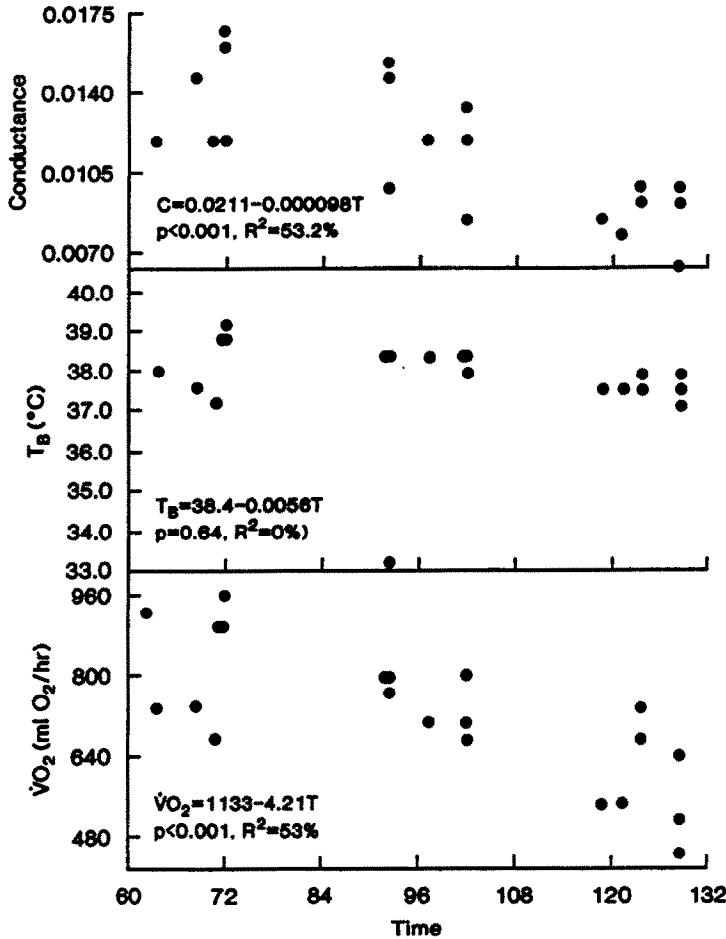


Fig. 1. The relationship of conductance ( $C$ ), body temperature ( $T_B$ ) and oxygen consumption ( $\dot{V}O_2$ ) to time ( $T$ ) for five adult female yellow-bellied marmots. Time is recorded as the number of days past the 30th of April.

was calculated from the  $T_B$  and  $\dot{V}O_2$  data as follows:  $C = \dot{V}O_2/T_B - T_A$  with  $C$  expressed as  $O_2/M/hr^\circ C$ , where  $M$  is body mass in grams.

All statistical analyses were performed with MINITAB. Data were grouped into premolt, molting (any stage of the molt process), and postmolt groups and differences among groups tested by ANOVA. Differences between group means were considered to be statistically significant when the 95% confidence limits of a group did not overlap the mean of another group. Data were regressed against time and the regression tested for significance by ANOVA.

## RESULTS

### Adults

All animals gained mass during the test period (Table 1). Postmolt females were significantly larger than premolt or molting individuals. On average, females gained 710 g between the premolt and postmolt states, a gain of 24.7%.

$\dot{V}O_2$  declined significantly during the molting

period (Fig. 1). Over half of the variation in  $\dot{V}O_2$  was explained by this relationship.  $\dot{V}O_2$  of postmolt females was significantly lower than that of either the premolt or molting animals (Table 1). Specific  $\dot{V}O_2$  also declined significantly during the molting period (specific  $\dot{V}O_2 = 0.413 - 1.90T$ , where  $T =$  time,  $P < 0.001$ ,  $R^2 = 52.3\%$ ). Specific  $\dot{V}O_2$  of postmolt animals was significantly lower than that of either premolt or molting animals (Table 1). From premolt to postmolt, total  $\dot{V}O_2$  declined 23% and specific  $\dot{V}O_2$  declined 37%. Neither  $\dot{V}O_2$  nor specific  $\dot{V}O_2$  differed significantly between the premolt and molting groups.

Body temperature ( $T_B$ ) varied from 33.4 to 39.0°C during the molt period. However,  $T_B$  did not vary significantly over time (Fig. 1) nor did mean  $T_B$  vary significantly among the molt groups (Table 1).

Conductance decreased significantly over time during the molt period (Fig. 1). As with  $\dot{V}O_2$  and specific  $\dot{V}O_2$  this regression explained about half of the variation in conductance over the molt period. Conductance was significantly lower for the postmolt

animals than for the premolt or molting groups but did not differ significantly between the premolt and molting groups. Conductance declined by 36.5% from the premolt to the postmolt group.

### Young

The  $T_b$  of the young varied from 36.7 to 40.1°C, but did not vary significantly with molt status (pre-molt,  $T_b = 38.8 \pm 0.9$ , postmolt  $T_b = 38.2 \pm 0.96$ ;  $t = 0.94$ ,  $P = 0.38$ ).  $T_b$  was not significantly correlated with oxygen consumption ( $\dot{V}O_2$ ,  $r = 0.24$ ,  $P > 0.05$ ; specific  $\dot{V}O_2$ ,  $r = 0.27$ ,  $P > 0.05$ ).  $\dot{V}O_2$  was highly variable and no pattern in the data emerged. During the laboratory measurements, the young were usually sitting rather than sleeping and sometimes were active. They appeared to be emotionally stressed. For example, one young was sitting; its  $T_b$  averaged 39.37°C and its specific  $\dot{V}O_2$  was 0.312 ml  $O_2/g \cdot hr$ . The animal was retained in the metabolism chamber for an additional 2 hr and the measurements were repeated. The animal was then asleep; its  $T_b$  dropped to 38.16°C and specific  $\dot{V}O_2$  declined to 0.259 ml  $O_2/g \cdot hr$ . A second animal had a similar pattern when it was held in the laboratory overnight and run again the next day. The animal was fed; thus its decline in  $\dot{V}O_2$  was unlikely caused by food deprivation. If the best runs of two young are considered, specific  $\dot{V}O_2$  declined about 20% between premolt and postmolt, much less than the percentage decline of adults and less than that reported previously for a much larger sample size (Armitage and Salsbury, 1992). In contrast to the adults, young increased total  $\dot{V}O_2$  from premolt to postmolt (see also Armitage and Salsbury, 1992). However, considerable variability in the  $\dot{V}O_2$  in this study precludes drawing any conclusions. Because both adults and young gained mass, but only adults decreased  $\dot{V}O_2$ , the reasons for the differences between young and adults remain to be determined.

### DISCUSSION

The results substantiate our earlier interpretation that the decline in  $\dot{V}O_2$  after animals have molted is a consequence of reduced conductance and not because body temperature is regulated at a lower level. Thus, insulative acclimatization characterizes the preparation of marmots for hibernation (Hart, 1957). Apparently yellow-bellied marmots do not decrease body temperature until entering hibernation; body temperature did not decline in free-ranging marmots during the active season nor was there evidence of test drops in body temperature prior to immersion (Melcher *et al.*, 1989).

Part of the variation in the relationship of  $\dot{V}O_2$  with time occurred because the non-reproductive female initiated molting about 3 weeks earlier than the reproductive females. Thus, her metabolism at a given time was lower than that of the other females. Furthermore, her metabolism continued to decrease

in the postmolt period and was lower at the end of the season than that of the other females. The continued decline in  $\dot{V}O_2$  a month after completing molt suggests that other factors may affect the decline in  $\dot{V}O_2$ . This decline is consistent with the circannual rhythm of  $\dot{V}O_2$  that occurred in laboratory marmots (Ward and Armitage, 1981). However, data from one female are insufficient for forming any conclusions.

Our previous calculations of the energy saved as a consequence of the reduced  $\dot{V}O_2$  indicates that adult females would deposit 0.71 g fat/kg body mass per day (Armitage and Salsbury 1992). We repeated the calculations on this data set. Because there were no statistically significant differences in the  $\dot{V}O_2$  of premolt and molting animals, we used the mean of these values as the premolt value. Postmolt adult females used 184 ml  $O_2/hr$  less than when those same females were in the premolt state. For 24 hr, the decrease in  $O_2$  consumption was 4.416 l. The energy equivalent of a liter of  $O_2$  is 4.8 kcal (Schmidt-Nielsen, 1990: p. 569); therefore, the reduced  $\dot{V}O_2$  provides an additional 21.2 kcal/day that may be shifted from maintenance to production. If all the energy is converted to fat at a conversion efficiency of 0.8 (Blaxter, 1989: p. 273), 16.96 kcal of fat are available. Because the energetic value of a gram of fat is 9.4 kcal (Schmidt-Nielsen 1990: p. 171), 1.8 g fat (0.5 g/kg/body mass) could be accumulated daily by the average adult female. This value is similar to but lower than that value previously calculated for a different set of animals (Armitage and Salsbury, 1992). During the average time of 56 days through the molt period, these females grew at an average of 11.4 g/day. If this rate were maintained during growth in the postmolt period prior to hibernation, 15.8% of growth could be attributed to the savings of energy resulting from reduced  $\dot{V}O_2$ .

The decline in specific  $\dot{V}O_2$  from premolt to postmolt of 37% was almost identical to the 36.5% decline in conductance. This similarity in the percentage decline of specific  $\dot{V}O_2$  and conductance indicates that decreased specific  $\dot{V}O_2$  occurred because of decreased conductance. Specific  $\dot{V}O_2$  would be expected to decline if  $\dot{V}O_2$  remained constant and body mass increased as it did by 21.6%. However,  $\dot{V}O_2$  decreased by 23%, less than that of specific  $\dot{V}O_2$ . There are two implications of this difference between the percentage decline of  $\dot{V}O_2$  and of specific  $\dot{V}O_2$ . Because  $\dot{V}O_2$  declined, the decrease in specific  $\dot{V}O_2$  cannot be attributed to the increase in mass, but because they declined at different rates (we would expect that the percent decline in  $\dot{V}O_2$  and specific  $\dot{V}O_2$  would be identical), some of the increase in mass must have included tissues of low metabolic rate. Probably some, if not all, of the gain in mass over the molt period was the addition of fat. If fat deposits have lower metabolic rates than lean tissues, then metabolic rate would change more slowly than mass and the decrease in  $\dot{V}O_2$  caused by the increase in insulation; i.e. decreased conductance, would be less

than the decrease in specific  $\dot{V}O_2$ , which incorporates the decrease due to increased mass and the decrease derived from the decrease in  $\dot{V}O_2$ .

What is critical to the animal is its total metabolic expenditures. The decrease in  $\dot{V}O_2$  may be important in preparing for hibernation, but is likely critical to survival through the hibernation period. Adult yellow-bellied marmots spontaneously arouse from hibernation in the spring (French, 1990) and spend more time at high  $T_b$  during dormancy and arouse with proportionately more fat unused that is available for euthermia prior to the availability of forage than do smaller hibernators (French, 1986). If we assume that the 23% reduction in  $\dot{V}O_2$  prevails during hibernation, we can estimate the impact of this saving on the pattern of hibernation. In our area marmots hibernate for about 230 days. Without the energy saving made possible by molt, marmots could hibernate only for about 177 days [230 - (0.23 × 230)]. Thus, they would arouse in early March instead of early May and in most cases would be unable to forage for as much as 75 days. The other alternative would be to emerge at the usual time with no fat; however, the animals would have to rely on the metabolism of lean tissues until new plant growth was available, which could be as long as 30 days in years of extensive snow cover. Interestingly, in one of our study sites at 3400 m where extensive snow cover may occur in July, no female produced litters in consecutive years (Johns and Armitage, 1979). Fat stores were critical for reproduction; the alternative strategies of moving to an area where forage appeared early or delaying pregnancy until food became available were not successful (Andersen *et al.*, 1976). Within our study area, litter size and the frequency of reproduction were inversely related to the time of snow melt; the later the snow melts the longer females must rely on fat for maintenance and reproduction and the less time that is available for accumulation of new fat reserves (Van Vuren and Armitage, 1991).

Marmots lose hair and increase conductance after emergence from hibernation. Increased conductance by reducing insulation seems to be essential for coping with the thermal load of summer as marmots cannot mobilize sufficient water for the evaporative dissipation of heat (Melcher *et al.*, 1989, 1990; Armitage *et al.*, 1990). Interestingly, seasonal changes in conductance of the Cape porcupine, *Hystrix africaeustralis*, increase heat loss during the summer and decrease heat loss in the winter. Although this pattern parallels that of yellow-bellied marmots, winter-acclimated Cape porcupines increase  $\dot{V}O_2$  and food ingestion (Haim *et al.*, 1990). The alternative of increasing  $\dot{V}O_2$  and food ingestion is unavailable to marmots; thus, their physiology and behavior emphasize energy conservation. Energy conservation in-

cludes reduced thermoregulatory costs,  $\dot{V}O_2$  and conductance less than predicted on the basis of body size, reduced above-ground activity, seasonal decline in  $\dot{V}O_2$ , and postmolt decline in conductance.

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