



Resting and field metabolic rates of adult male yellow-bellied marmots, *Marmota flaviventris*

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Resting metabolic rate (RMR) and field metabolic rate (FMR) of wild-caught males were estimated from oxygen consumption and the doubly-labeled water method, respectively. The average FMR:RMR ratio of 6.9 was much greater than ratios reported for other mammals. Total FMR (kJ/day) increased and specific RMR (kJ/kg/day) decreased with time. Neither total RMR nor specific FMR were significantly related to time. The decrease in specific RMR may result from a circannual decrease in maintenance expenditure and a seasonal increase in body mass. Total FMR may increase through the season as conditions for male activity become more favorable.

Key words: Metabolic rates; *Marmota flaviventris*.

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Introduction

An understanding of animal energetics provides valuable insight into the physiology and ecology of organisms. The energetics of mammals has been frequently investigated (Loudon and Racey, 1987; Tomasi and Horton, 1992). Changes in body mass (Fedak and Anderson, 1987; Deutsch *et al.*, 1990), changes in caloric intake (Farrell and Christian, 1987; Gittleman, 1988), and the ratio of litter mass to maternal mass (Millar, 1977) are often used as indirect measures of energetic expenditure. More direct measures of energy expenditure are obtained by monitoring the oxygen consumption of organisms held in the laboratory (Randolph *et al.*, 1977; Farr

and Andrews, 1978; Thompson and Nicoll, 1986). Neither the indirect nor direct measures accurately represent the total energy costs of free-ranging animals, however. The time-energy budget method (Schartz and Zimmerman, 1971) involves monitoring the time free-ranging animals spend performing various behaviors and estimating total energy expenditure based on laboratory measures of the energy costs associated with each behavior. Time-energy budgets, however, do not include energy used for maintenance, thermoregulation, digestion and assimilation of food, growth, and reproduction.

Total energy expenditure including costs of maintenance, thermoregulation, activity, and stress can be measured for free-ranging animals by means of a doubly-labeled water (DLW) method (Nagy, 1975). The DLW method involves injecting hydrogen and oxygen isotopes into the animal and

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measuring the washout rates of the isotopes in order to estimate CO_2 production. Based on laboratory validation studies, estimates of energy expenditure produced by the DLW method are likely to err approximately 8% for mammals in field situations (Nagy, 1989). The time energy-budget method yielded estimates of energy expenditure as much as 44% below or 57% above simultaneous DLW estimates for some bird species (Nagy, 1989a). Although the DLW method cannot be used to estimate the energetic costs of particular behaviors, it is a valuable technique to estimate the comprehensive energy costs or "field metabolic rates" (FMR) of animals living freely in natural environments.

The energetics of adult male yellow-bellied marmots (*Marmota flaviventris*) was the focus of this study. Marmots conserve energy by minimizing resting metabolic rates (RMR) or maintenance costs (Kilgore and Armitage, 1978; Armitage and Salsbury, 1992). Captive, non-reproductive marmots express RMR as a circannual rhythm; rates are high early in the season and gradually decrease as the season progresses (Ward and Armitage, 1981). Behaviorally, marmots minimize thermoregulatory costs by reducing activity when thermal conditions are stressful (Melcher *et al.*, 1990). Marmots also experience reduced maintenance costs due to reduced conductance after the molt (Armitage and Salsbury, 1992; unpub. data). Marmots gain mass throughout the season (Armitage *et al.*, 1976; Salsbury, 1993) while gradually reducing total or absolute RMR, which suggests a shift of energy from maintenance to production (Kilgore and Armitage, 1978). In studies of wild-caught marmots, RMR of reproductive females were elevated during lactation and decreased gradually through the remainder of the active season (Armitage and Salsbury, 1992).

Seasonal trends in metabolic rates for adult male marmots have yet to be examined. The purpose of this study was, therefore, to investigate such trends in adult male marmots. Resting metabolic rates and field metabolic rates were compared to trends in energy expenditure expected based on a general body mass:metabolism relationship (Kleiber, 1961) and data for female marmots.

Materials and Methods

Yellow-bellied marmot populations living in the upper East River Valley near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, CO, elevation 2900 m, were observed in this study. The yellow-bellied marmot is a diurnal, group-living, ground-dwelling squirrel that inhabits subalpine and alpine meadows throughout much of the western United States (Frase and Hoffman, 1980). Marmots are generally active 4–5 months of the year and hibernate during the remaining months. Mating occurs in May immediately following the emergence of reproductively mature adults from hibernation. The mating system is facultatively polygynous; generally, males exclusively defend one or more females within their territories throughout the active season.

Marmots living in the upper East River Valley have been studied extensively since 1962 (reviewed by Armitage, 1991). Nearly all individuals are live-trapped annually and upon first capture, individuals are sexed and uniquely numbered with ear tags (see Armitage, 1962, 1974, for more detailed description of trapping and handling techniques). Most adult male marmots were routinely live-trapped during the active seasons of 1989, 1990, and 1991. Captured males were weighed, individually identified by ear tag number, and transported to the laboratory.

Oxygen consumption ($\dot{V}\text{O}_2$) of adult males was measured in the laboratory following procedures described by Armitage and Salsbury (1992). In brief, each male was placed in a chamber connected to a negative pressure flow system and $\dot{V}\text{O}_2$ was measured for 0.5 hr with an electro-chemical oxygen analyzer. Output from the oxygen analyzer was collected on a personal computer using Data Quest III software (Data Sciences, Inc.). During the measurements, animals were held at a constant temperature of 18°C, a temperature within the thermal neutral zone of adult yellow-bellied marmots (Armitage *et al.*, 1990). Measurements were taken on the day of capture between 10:00 and 16:00 hr, a time when marmots are less active and generally remain underground and probably quiescent (Melcher *et al.*, 1990). Males were returned

to their locations of capture following $\dot{V}O_2$ measurements unless additional laboratory work was necessary. The lowest $\dot{V}O_2$ measures observed for a male were averaged to estimate the male's RMR. Observed RMR estimates and values predicted based on Kleiber's (1961) relationship between body mass and metabolism were compared with a *t*-test for paired comparisons.

The DLW method was used to monitor FMR of some males trapped during 1989, 1990, and 1991 (see Lifson and McClintock, 1966; Nagy, 1989b for more detailed description of DLW method). Focal males were transported to the laboratory, weighed, and lightly anesthetized with approximately 1 ml of ketamine hydrochloride. Anesthesia was used to insure that the males were calm and relaxed and experienced little pain during the DLW injection. A preinjection blood sample was obtained from the femoral vein to establish the background levels of the two isotopes in the body fluids. The blood was collected in six microcapillary tubes. The ends of each tube were flame sealed and the tubes were labeled with the time, date, and animal number, and refrigerated. An area of the abdomen was cleaned with alcohol and a water solution enriched with deuterium (D) and oxygen-18 (O-18) was injected intraperitoneally. Males were injected with 0.3 g of O-18 and 0.12 g D per kilogram of body mass, then returned to holding traps in the laboratory and held without food for 3–4 hr to insure that the isotopes thoroughly mixed in the body water (Nagy, 1983). A second blood sample was obtained 3 hr after the injection to establish the equilibrium values of the isotopes within the body fluids. The second blood sample was collected in six microcapillary tubes as above and stored with the preinjection sample. Males were returned to their capture locations soon after the second blood sample was obtained.

To assess the turnover rates of isotopes in the blood, injected animals should be recaptured after O-18 reaches half the injection concentration for best results (Nagy, 1983). The biological half-life of O-18 differs based on body size, taxonomic group, and intake of free water (Nagy, 1983). Based on marmot body size and their obtaining all the free water from food (Melcher, 1987), the recapture interval for marmots was between

3 and 7 days (see Nagy, 1983). Because of the expense of the O-18 enriched water, injections were limited to those males with a high probability of recapture. Some males were equipped with radio-transmitters (Salsbury, 1993) that greatly enhanced recapture success. Recaptured males were carefully weighed and final blood samples were taken either immediately in the field or soon after males were transported to the laboratory. Final blood samples were labeled and stored in the same fashion as for previous samples. All blood samples were analyzed at the Boston University Stable Isotope Laboratory.

Estimates of RMR from laboratory measurements were converted to units of heat production (in joules) using a conversion factor of 4.8 kcal per liter O_2 and assuming 4.184 kJ/kcal (Schmidt-Nielsen, 1990). Resting metabolic rate was expressed as total RMR (kJ/day) and as specific RMR (kJ/kg/day).

The conversion factor for expressing CO_2 production in units of heat production is highly dependent on the diet of the study animal. Different nutrients result in very different amounts of energy for each liter of CO_2 produced (Schmidt-Nielsen, 1990). Marmots are generalist herbivores (Frase and Armitage, 1989) and diet analyses of marmots and another sciurid species (*Spermophilus beldingi*, Eshelman and Jenkins, 1989) with a diet similar to that of marmots, suggest that the marmot diet is approximately 80% carbohydrate, 15% protein, and 5% fat. A conversion factor for $\dot{V}CO_2$ measures can be calculated based strictly on diet composition using energy equivalents for the different nutrients (Nagy, 1983). This approach, however, assumes that the animal catabolizes nutrients in the diet in the same proportions as in ingested food. If this assumption does not hold, energy equivalents for $\dot{V}CO_2$ may err by 23% (Gessaman and Nagy, 1988). Thus, a more conservative approach was used as suggested by Gessaman and Nagy (1988); a respiratory quotient (RQ) of 0.83 was assumed for marmots, and the corresponding conversion factor of 5.829 kcal per liter CO_2 was selected from Brody (1945). A RQ of 0.83 results in the least amount of error in energy metabolism estimates for herbivores when actual nutrient catabolism is unknown

(Gessaman and Nagy, 1988). FMR estimates were expressed as total FMR (kJ/day) and specific FMR (kJ/kg/day). There are no FMR data for other herbivores similar to marmots in body size and habitat to compare with FMR observed in this study. Thus, observed total FMR was compared to predicted FMR [Nagy, 1987; $\log \text{FMR (kJ/day)} = 0.774 + 0.727 \log \text{body mass (g)}$] for eutherian herbivores. Observed and predicted FMR values were compared using a *t*-test for paired comparisons.

Mean values of total RMR, total FMR, specific RMR, and specific FMR were calculated for each year of the study and for all years combined. Total and specific estimates of RMR and FMR were compared among years in separate analyses of variance. Total and specific estimates of RMR were combined for all years and regressed against the date (expressed as days past April 30) of the measurement. Similarly, estimates of total and specific FMR were combined for all years and regressed against the mid-date of the recapture interval. The relationships of total RMR and specific RMR with body mass were determined by log-log regressions. Log-log regressions were also used to determine the relationships of total FMR and specific FMR with mean body mass of the animal during the measurement period. Additionally, body mass measurements obtained from trap captures of males in this study were combined for all years and regressed against date to determine patterns of body mass change through the season. The percent change in body mass was determined by comparing the mean of measures obtained in May with the mean of measures obtained in August.

The correspondence between RMR and FMR was examined for males for whom a RMR estimate was obtained within 10 days of the mid-date of the FMR recapture interval. Given that the recapture interval varied between 3 and 7 days and that RMR and FMR were not measured simultaneously, RMR measures taken on the day of injection or recapture would be roughly 2–4 days from the mid-date of the FMR recapture interval. Examining only those pairs of RMR and FMR 4 days or less apart would seriously restrict sample size; thus, 10 days were arbitrarily chosen as the acceptable time interval. Pairs of total RMR and FMR and pairs of specific RMR and FMR were combined for all years and the relationships between RMR and FMR were determined with correlation analyses.

Results

Field metabolic rate estimates were collected from early May to mid August (Table 1). Approximately 95% of the data, however, was collected between 16 May and 26 July. Similarly, RMR estimates were collected from mid June to mid August (Table 1), with approximately 95% of the data collected between 12 June and 26 July. Limited access to laboratory equipment prevented early seasonal measurements of RMR. Few FMR and RMR estimates were collected late in the season due to the increased difficulty in trapping males as the season progressed.

Mean RMR values were similar in 1990 and 1991 but the mean for 1989 was significantly higher (Table 1). Mean FMR values were similar for all years of the study. Based on mean values, total FMR

Table 1. Means and standard deviations of metabolic measurements for adult male yellow-bellied marmots

	Year			<i>P</i>	All years
	1989	1990	1991		
T RMR	457.7 ± 89.2* (18)	292.6 ± 72.9 (13)	349.9 ± 72.9 (23)	<0.001	371.0 ± 100.2 (54)
S RMR	129.6 ± 21.8*	87.7 ± 18.1	103.3 ± 25.0	<0.001	108.3 ± 27.5
T FMR	2402.0 ± 935.0 (8)	2144.4 ± 1017.4 (15)	2818.5 ± 1529.1 (12)	0.36	2434.4 ± 1205.0 (35)
S FMR	712.5 ± 196.9	664.3 ± 276.8	919.8 ± 552.3	0.22	762.9 ± 389.6

Metabolic measurements are represented as resting metabolic rate (RMR) and field metabolic rate (FMR).

Total (T) metabolic measurements (kJ/day) and specific (S) metabolic measurements (kJ/kg/day) are presented.

*Indicates means statistically significant from other groups.

was, on average, $6.9 \times$ total RMR and specific FMR was $7.3 \times$ specific RMR.

A coefficient of variation of 49.5% for the combined FMR sample indicates the great amount of variation among measures. The combined RMR sample varied less than FMR with a coefficient of variation of 27.0%. Consecutive measures of specific FMR and RMR for individual males were also extremely variable. Observed total FMR estimates, however, did not differ significantly from predicted values ($t_{34} = 1.63$, $0.10 < P < 0.20$). Observed specific RMR estimates were approximately 48% lower than values predicted by the Kleiber relationship ($t_{53} = 29.80$, $P \ll 0.001$). Body mass increased significantly through the season (body mass = $2.63 + 0.013$ (date), $R^2 = 0.284$, $F_{1,37} = 54.3$, $P \leq 0.001$). The regression explained roughly a third of the variation in the data. Body mass increased approximately 41% from May to August and was significantly greater for males in August than in May (May $\bar{X} = 2.91$ kg, August $\bar{X} = 4.09$ kg, $t_{46} = 3.48$, $P = 0.018$).

Field metabolic rate and body mass were not related (Table 2). Total RMR significantly increased with body mass, although the regression explained little of the variation in RMR. As expected, specific RMR decreased as body mass increased; the decrease was significant for a one-tailed test.

Patterns of change through the season between FMR and RMR differed. Total

FMR significantly increased through the season, although much of the variation in the data was not explained by the regression (Table 2). Specific FMR did not change significantly seasonally. By contrast, specific RMR decreased through the season while total RMR did not change significantly. Again, the regression explained little of the variation in the specific RMR data (Table 2).

Total and specific RMR obtained within 10 days of the mid-date of FMR recapture intervals were not significantly correlated with total and specific FMR ($r_{14} = 0.080$, $P > 0.05$, and $r_{14} = -0.129$, $P \geq 0.05$, respectively).

Discussion

FMR:RMR ratio

The FMR:RMR ratio of 6.9 for males in this study was substantially higher than the ratio of 1.5 reported in a previous study of yellow-bellied marmots (Melcher, 1987) and also much higher than ratios for other mammalian species. The FMR:RMR ratio for *Spermophilus saturatus* ranged between 2.3 and 2.7 for all males combined (Kenagy *et al.*, 1988). Karasov (1992) reported a mean FMR:RMR ratio of 2.65 (range 1.30–5.25) for 17 species of terrestrial mammals. A maximal capacity of expenditure of 4 times basal metabolic rate for mammals and birds living in the field was also reported (Drent and Daan, 1980). However, FMR:RMR ratios of many marsupial species varied from 1.8 to 6.5 (Koteja, 1991).

The lack of agreement between the current and previous estimates of the FMR:RMR ratio for marmots is perplexing. No data from adult males were used to generate the previous ratio of 1.5 (Melcher, 1987), however. Also, the different techniques used in the two studies to estimate FMR probably account for some of the disparity. FMR was estimated with the time energy-budget method by Melcher (1987). The time energy-budget method generally yields low estimates of FMR compared to the DLW method because the time energy-budget method does not include thermoregulatory costs (Nagy, 1989). Marmots, however, have very low thermoregulatory costs due to inactivity when temperatures

Table 2. Relationships of metabolic measurements with date (days past April 30) and body mass (kg) for adult male yellow-bellied marmots

		Metabolic measures			
		T RMR	T FMR	S RMR	S FMR
Date	<i>N</i>	54	35	54	35
	<i>a</i>	466.0	1413.0	157.0	565.0
	<i>b</i>	-1.43	22.60	-0.73	4.38
	<i>R</i> ²	0.053	0.183	0.184	0.066
	<i>P</i>	0.095	0.010	0.001	0.137
Body mass (kg)	<i>N</i>	54	35	54	35
	<i>a</i>	2.22	2.99	2.22	2.99
	<i>b</i>	0.62	0.70	-0.38	-0.30
	<i>R</i> ²	0.155	0.062	0.063	0.012
	<i>P</i>	0.003	0.148	0.066	0.523

Metabolic measurements are represented as resting metabolic rate (RMR) and field metabolic rate (FMR). Total (T) metabolic measurements (kJ/day) and specific (S) metabolic measurements (kJ/kg/day) are presented.

are unfavorable and Melcher (1987) considered the costs of thermoregulation in her calculations of FMR. Perhaps other expenditures not detectable with the time energy-budget method such as the varying costs of social stress and fluctuating RMR, led to estimates of FMR different from those in this study.

Low RMR estimates and/or high FMR estimates for marmots compared to previously studied mammalian species can account for the higher FMR:RMR ratio for marmots. The tissue growth efficiency of marmots is over 5 times that of other mammalian herbivores (Kilgore and Armitage, 1978); thus, marmots may have relatively low maintenance costs compared to other mammalian herbivores. Additionally, observed $\dot{V}O_2$ for female marmots was on average 35% lower than that predicted by the Kleiber (1961) relationship between body mass and metabolism (Armitage and Salsbury, 1992). Observed RMR for males in this study were also lower than predicted values. Thus, the FMR:RMR ratio for marmots is likely to be higher than FMR:RMR ratios based on predicted values of RMR. The discrepancy between the ratio for marmots and *S. saturatus* may be because RMR for *S. saturatus* was estimated using the Kleiber relationship (Kenagy *et al.*, 1988).

Although FMR varied greatly among males in this study, the variation seems reasonable as FMR includes the varying energetic costs of all behavioral and physiological activities an animal performs in the field. Some of the variation in FMR may have resulted from observing adult males of different ages and reproductive states. The mean total FMR value (Table 1) is 15% greater than a predicted value based on mean male body mass ($\bar{X} = 3.24$ kg, $N = 139$). However, FMR estimates generated in this study were not significantly higher overall than predicted FMR values; thus, it appears that the high FMR:RMR ratios of marmots is not due to faulty FMR measurements. The conversion factor used in this study to represent $\dot{V}CO_2$ in energy equivalents was 24.4 J/ml CO_2 , a factor much greater than that based strictly on diet composition (21.5 J/ml CO_2). Use of the conversion factor based on diet composition generates lower FMR estimates

and, in turn, lower FMR:RMR ratios. Previously, many investigators used conversion factors based strictly on diet composition which may partially explain the low FMR:RMR ratios reported for other mammals relative to marmots. Field metabolic rate estimates were calculated using the diet-based conversion factor; total and specific FMR:RMR decreased to 5.8 and 6.1, respectively. The new ratios were still substantially greater than most ratios reported for other mammals. Thus, the conversion factor used in this study may account for some, but not all, of the elevation of the FMR:RMR ratios of marmots.

It is unclear why the low RMR of marmots compared to other mammals did not also yield low FMR for marmots. Certainly, the great variation in the data and small sample sizes may have precluded the appearance of a correlation between RMR and FMR. Resting metabolic rate was also not correlated with FMR for some other mammal species (Hayes, 1989; Koteja, 1991). Conceivably, FMR may be more affected by fluctuating activity levels over short periods of time than RMR. The lack of correspondence between RMR and FMR indicates that caution is necessary when laboratory measures are extrapolated to field expenditures (Koteja, 1991).

Lower than expected RMR estimates for marmots and high FMR:RMR ratios reported in this study suggest that natural selection may have favored economical energy use during rest coupled with the capacity to achieve high rates of metabolism during activity in marmots. Low maintenance costs increase the proportion of energy available for production, specifically fat production crucial for survival of hibernation. Periodic increases in metabolism during activity may lead to higher rates of net energy gain and, in turn, greater absolute quantities of energy available for storage. More study is necessary, however, to determine if and how marmots are morphologically and physiologically adapted to economize energy at rest while processing energy at a high rate during activity.

RMR vs. body mass and date

The seasonal increase in body mass of males in this study is consistent with the

linear increase in body mass with time observed for male marmots in previous studies (Armitage *et al.*, 1976). Males of different ages and much different overall body sizes were considered in this study; thus, little of the variation in body mass was explained by the relationship with time during the active season.

The slope of the relationship between total RMR and body mass for males (Table 2) was similar to previously reported regression slopes for female marmots, younger marmots, and all marmots combined (Armitage *et al.*, 1990; Armitage and Salsbury, 1992). Much of the variation in RMR, however, was not explained by body mass. Other factors such as random variability among males, varying stress levels among males during handling, or varying physiological states among males may better explain the variation in RMR.

Interestingly, total RMR did not change significantly through the season, although body mass increased as the season progressed. In fact, the trend in total RMR was to decrease with time through the season. The relationship between total RMR and time may be contrary to the relationship between total RMR and body mass because time only weakly explained variation in body mass. Also, total RMR may not increase with increases in body mass because total RMR essentially represents the maintenance cost of lean body mass which may change little through the season. Seasonal or circannual effects on total RMR may negate any increases in total RMR expected as the season progresses and animals gain mass. Laboratory-held marmots exhibited circannual rhythms in RMR; RMR steadily decreased as the active season progressed and animals approached hibernation (Ward and Armitage, 1981). A similar trend was observed for wild-caught female marmots; RMR decreased steadily through the season for non-reproductive females and post-reproductive females (Armitage and Salsbury, 1992). Additionally, molting resulted in decreased thermal conductance and, in turn, reduced maintenance costs for all young, yearling, and adult female marmots (Armitage and Salsbury, 1992; unpubl. data). Perhaps circannual and molt effects explain the tendency for total RMR to decrease with time despite the corre-

sponding increase in body mass. Multiple regression results of total RMR against mass and date, support the idea that total RMR is oppositely influenced by body mass and date [$\log \text{total RMR} = 2.32 + 0.807(\log \text{body mass}) - 0.00298(\text{date})$, $F_{2,51} = 10.87$, $R^2 = 0.299$, $P < 0.001$]. The negative relationships between RMR and time are consistent with the idea that marmots conserve energy by lowering maintenance costs. Marmots, by lowering RMR, may allocate more energy to growth, activity, and preparation for hibernation; an adaptive strategy for species with a short active season.

FMR vs. body mass and date

The lack of a relationship between FMR and body mass for marmots is perplexing as FMR significantly scales to body mass in interspecific comparisons (Nagy, 1987). Although total RMR, a component of total FMR, increased with body mass of males in this study, many other factors such as activity levels, thermal stress, and social stress, may have more dramatically influenced FMR. Further, the range in the body mass of males in the current study was probably too small to detect a significant change in FMR with body mass.

The seasonal increase in total FMR could not be explained by an increase in total RMR with time. The increase in total FMR may have resulted from increased activity levels of males as the season progressed. Detailed activity budgets were not conducted for males observed in this study. However, time spent above ground and movement away from the burrow entrance are minimal early in the season when the ground is snow covered (Armitage and Downhower, 1974; K. B. Armitage, pers. obs.; C. M. Salsbury, pers. obs.). Also, following emergence from hibernation, little or no forage is available and marmots must live on energy reserves remaining from hibernation (Van Vuren and Armitage, 1991); thus, marmots may conserve energy by minimizing activity. As the season progresses and snow cover diminishes, food becomes more abundant (Van Vuren and Armitage, 1991), and escape burrows critical for avoiding predators become exposed and available for use (Armitage, 1986). Previous time-budgets of colonial animals indicate

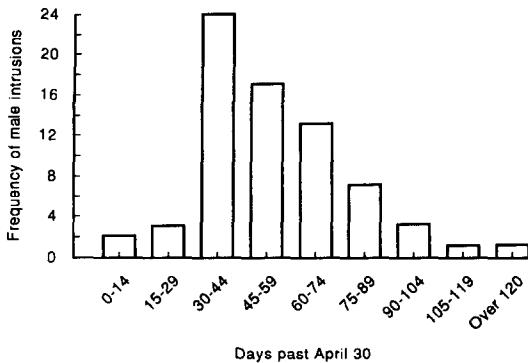


Fig. 1. Frequency of intrusions by adult male yellow-bellied marmots into male occupied habitat. Date of intrusions is represented as days past April 30.

that above ground activity increases seasonally and decreases just prior to hibernation (Kilgore and Armitage, 1978). Although detailed accounts of the daily movement patterns of males through the season are not available, males did make short excursions from their home ranges (Salsbury and Armitage, 1993) and the majority of the short excursions were made in June following snow melt. Additionally, trapping data from 17 consecutive active seasons indicates that intrusions by adult males into male occupied habitats are rare in May and common in June and July (Fig. 1). Therefore, conditions appear more favorable for activity as the season progresses. Interestingly, thermal conditions are less favorable for activity late in the season (Melcher *et al.*, 1990). Also, male marmots appear to greatly reduce activity just prior to hibernation (Melcher, 1987; unpub. data). The increase in FMR with time of males in this study may not, however, be contrary to reduced activity and unfavorable thermal conditions late in the active season. None of the FMR estimates were collected late in the active season due to the extreme difficulty of trapping adult males at that time. Based on activity patterns, we predict that FMR decreases as hibernation approaches.

The hypothesis that FMR increased with time as a result of increased energy expenditure for activity is consistent with the changing social dynamics experienced by males. Yearling marmots emerge from hibernation soon after adults (Armitage, 1965; Johns and Armitage, 1979). Upon emergence of yearlings, there is a greater number of individuals with whom an adult

male must interact socially. All male yearlings and nearly one-half of female yearlings eventually disperse from their natal area from late May to July (Armitage, 1991) and adult males interact with yearlings throughout the dispersal period. Although social interactions with adults may not directly induce dispersal of yearlings, the majority of adult male interactions with yearlings are agonistic (Downhower and Armitage, 1981). Increased social interactions, especially agonistic interactions, could conceivably result in higher energetic expenditure due to increased activity, stress, and thermal exposure. Males may need to increase time spent patrolling during early and mid summer to exclude any males that attempt to immigrate into their home ranges (Fig. 1); males that settle in a resident male's home range are potential threats to the male's reproductive success the following mating season. Thus, the greater energy expenditures following the mating season coincides with the time that males more actively defend territories to exclude competing males and to assure access to adult females during the next spring mating season.

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