

# Reproductive energetics of adult male yellow-bellied marmots (*Marmota flaviventris*)

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**Abstract:** We examined the energy expenditure of adult male yellow-bellied marmots (*Marmota flaviventris*) and its relationship to various female-defense characteristics critical to male reproductive success. Resting metabolic rates of males were estimated in the laboratory via oxygen-consumption analysis, and field metabolic rates were estimated using a doubly labeled water technique. Male home-range size, number of females defended by males, dispersion of females in the habitat, and date into the active season were considered to be predictors of male energy expenditure in excess of maintenance costs (field metabolic rate minus resting metabolic rate). Energy expenditure was best explained by a defensibility index based on the number and dispersion of females defended; expenditure increased with number and dispersion of females. Energy expenditure increased with date into the active season. Environmental constraints on male activity during the mating season may have led to a shift in male reproductive investment to later in the season, when intruder pressure by conspecifics increased. No short-term survival costs were associated with high energy expenditure; males appeared to engage in reproductive behaviors congruent with their physiological capabilities.

**Résumé :** Nous avons mesuré la dépense énergétique chez des mâles adultes de la Marmotte à ventre jaune (*Marmota flaviventris*) et examiné sa relation avec différentes caractéristiques associées à la défense des femelles, caractéristiques très importantes pour le succès reproducteur des mâles. Les taux de métabolisme de base des mâles ont été mesurés en laboratoire par analyse de la consommation d'oxygène et les taux de métabolisme en nature ont été estimés au moyen d'une technique utilisant de l'eau doublement marquée. La taille du domaine vital des mâles, le nombre de femelles défendues par les mâles, la dispersion des femelles dans l'habitat et la date du début de la saison d'activité ont servi d'indicateurs des coûts énergétiques excédant ceux reliés au maintien chez les mâles (taux de métabolisme en nature moins taux de métabolisme au repos). C'est un indice relié à la défense des femelles, indice basé sur le nombre et la dispersion des femelles défendues, qui illustre le mieux la dépense énergétique : la dépense augmente lorsque le nombre et la dispersion des femelles augmentent. La dépense d'énergie augmente aussi à mesure qu'avance la saison d'activité. Les contraintes écologiques exercées sur l'activité des mâles par l'intrusion d'autres individus de la même espèce durant la saison de reproduction peut avoir entraîné le renvoi de l'investissement reproducteur des mâles vers une date ultérieure. Aucune dépense d'énergie élevée ne semble être associée à des coûts de survie à court terme; les mâles semblent s'engager dans des comportements reproducteurs correspondant à leurs capacités physiologiques.

[Traduit par la Rédaction]

## Introduction

The costs of reproduction are critically important in shaping the life-history strategies of organisms. Number of offspring produced and optimal timing of reproductive events in an individual's lifetime are important components of lifetime reproductive success, a measure of individual fitness (Bell 1980; Clutton-Brock 1988). The development of life-history

strategies that maximize lifetime reproductive success is dependent on the trade-off between the costs and benefits of reproduction (Williams 1966; Pianka 1976). The importance of this trade-off led many ecologists to study investment in current reproductive events and its effects on future reproductive success.

The cost of reproduction in mammals has received much attention (Pond 1977; Harvey 1986; Loudon and Racey 1987; Gittleman and Thompson 1988), focused primarily on the costs of gestation and lactation for a variety of ecologically and evolutionarily diverse taxa (white-footed mice, Millar 1978; grey seals, Fedak and Anderson 1982; black-tailed deer, Sadleir 1982; fishers, Powell and Leonard 1983; cotton rats, Mattingly and McClure 1985; bats, Racey and Speakman 1987; red pandas, Gittleman 1988; red deer, Clutton-Brock et al. 1989). Conversely, the costs of reproduction to males

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received little attention. The lower investment per gamete by males, the absence of parental care among most male mammals, and the uncertainty of paternity versus maternity probably account for the bias toward females in investigating costs of reproduction.

The primary reproductive investment of males is assumed to be made during the mating season, when males compete for access to females (Trivers 1985, p. 209; Krebs and Davies 1987, p. 163; Horton and Rowsemit 1992). However, a comprehensive estimate of male reproductive investment should also include costs of morphological and (or) behavioral characteristics critical to reproductive success that are maintained or exhibited outside the mating season. For example, territory or female defense outside the mating season may be energetically costly, yet essential, for males attempting to maximize their direct fitness. However, the costs of such behaviors in males have rarely been quantified. Comprehensive estimates of male reproductive investment are necessary for understanding the energetic constraints of reproduction and the ultimate influence of these constraints on the life-history strategies of male mammals.

The purpose of the current study was to examine the energetics of male yellow-bellied marmots (*Marmota flaviventris*). Males are generally polygynous (Armitage 1991) and exclusively defend females in territories throughout the active season, the period of the year during which marmots are not hibernating (Armitage 1974). A male that successfully defends the females in his territory throughout the active season is likely to be the only male to hibernate near the females and, in turn, to mate with the females during the short mating season immediately following emergence from hibernation (Andersen et al. 1976). Males may defend from one to several (six or seven) females by routinely patrolling their territories; the number of females defended is positively related to male reproductive success (Armitage 1986, 1991). Thus, examination of the energetic expenditures of males that defend various numbers of females may cast light on male reproductive investment. If female defense is costly, male energy expenditure should increase with the number and dispersion of females defended and possibly exact a cost in decreased survivorship.

## Materials and methods

### Study animal

Yellow-bellied marmots are large-bodied ground-dwelling squirrels that inhabit subalpine and alpine meadows which contain talus or rock outcrops for burrow sites (Svendsen 1974). The number of yellow-bellied marmots residing in a habitat is determined, in part, by the number and size of burrow systems (Svendsen 1974; Armitage 1991). Large habitats often support colonies consisting of one or more adult males, several adult females, yearlings (animals in their second active season), and young (animals in their first active season) (Armitage and Downhower 1974; Armitage 1991). Conversely, small habitats support lower densities of individuals ranging from single individuals to small groups generally composed of one adult male, one adult female, and young (Armitage and Downhower 1974; Armitage 1991). Adult females (animals 2 or more years of age) show strong site fidelity between years, especially in habitats with extensive burrow

systems (Schwartz and Armitage 1980; Armitage 1984). All yearling males and slightly less than one-half of yearling females disperse from their natal colonies from late May to early July (Armitage and Downhower 1974; Armitage 1991).

Yellow-bellied marmots emerge from hibernation in early to mid-May and adult males are the first to emerge. Adult females, followed by yearlings, emerge several days to 2 weeks after the adult males. Animals enter into hibernation beginning in late August in similar order of emergence, with reproductive females immersing last in early September. Mating occurs during the first 2 weeks following emergence of adults from hibernation and young appear above ground in early July. The onset and duration of the mating season as determined by backdating from litter emergence were consistent among all years of the current study. Mating occurred approximately 1 week to 10 days earlier at the low-altitude sites than at the high-altitude sites, however.

Males are polygynous in habitats that support more than one reproductive female. Males that defend a number of solitary females living in small habitats are also polygynous. When habitat patches are small and isolated, males are often monogamous. Mean length of residency of males is 2.24 years (Armitage 1986), although some males may remain resident up to 6 years (Armitage 1991).

### Study area and animal capture

Yellow-bellied marmots living in the upper East River Valley near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado (38°56' to 38°59'N, 106°58' to 107°01'W, elevation 2800–3660 m asl), have been the focus of study since 1962 (Armitage 1991). Each year, all animals at four major study sites, as well many other animals at several smaller sites throughout the valley, are livetrapped, weighed, sexed, and ear-tagged and dye-marked for individual identification (for detailed trapping and handling methods see Armitage 1962; for detailed description of study sites see Armitage 1974). Adult males routinely livetrapped throughout the active seasons of 1989, 1990, and 1991 are the focus of this study. Trapping of males began no later than 10 days following emergence from hibernation and continued until 2–3 weeks prior to immergence into hibernation. Captured males were individually identified by ear-tag number and weighed, and their reproductive state was assessed on the basis of scrotal condition. Most males were equipped with implanted radio transmitters (after Van Vuren 1989) and their daily locations were monitored to determine home-range size (Salsbury and Armitage 1994a). Locations visited more than once by a male were plotted on topographic maps and considered part of the male's home range. The long-axis distance, estimated as the distance between the two most distant locations, and the short-axis distance, estimated as the distance between the two most distant locations perpendicular to the long axis, were calculated for each male's home range. Home-range size was estimated by the area (ha) of the ellipse generated by the long and short axes. A single estimate of home-range size was used for each male each season, as males routinely visited the same locations within their home ranges throughout each active season (C.M. Salsbury, unpublished data). Further, home range and territory are used synonymously in this study, as male marmots generally defend their entire home range (Armitage 1974).

### Measuring energy expenditure and female defense characteristics

Beginning approximately 5–6 weeks post emergence and continuing until 2–3 weeks prior to immergence into hibernation, captured males were transported (maximum distance approximately 2 km) to the laboratory, where their oxygen consumption was monitored (following procedures described by Armitage and Salsbury 1992) to obtain estimates of resting metabolic rate (RMR). In brief, each male was placed in a chamber connected to a negative pressure flow system and oxygen consumption was detected for 0.5 h with an electrochemical oxygen analyzer. Output from the analyzer was collected on a personal computer using Data Quest III software (Data Sciences, Inc.), and the lowest values for each male were averaged to estimate RMR. RMR was expressed as total RMR ( $\text{kJ} \cdot \text{d}^{-1}$ ) and as specific RMR ( $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ ), assuming conversion factors of  $4.8 \text{ kcal} \cdot \text{L}^{-1} \text{ O}_2$  and  $4.184 \text{ kJ} \cdot \text{kcal}^{-1}$  ( $1 \text{ cal} = 4.184 \text{ J}$ ) (Schmidt-Nielsen 1990).

A doubly labeled water technique ( $^3\text{HH}^{18}\text{O}$ ) was used to estimate field metabolic rate (FMR), or the energetic expenditure of free-ranging males (see Nagy 1983 for details of the technique; Salsbury 1993). Briefly, males were lightly anesthetized with ketamine hydrochloride (50 mg/kg) and a blood sample was collected from the femoral vein of each male to determine the background levels of  $^{18}\text{O}$  and deuterium in the body fluids. A water solution enriched with  $^{18}\text{O}$  (15 at. % in 1989 and 1990; 97 at. % in 1991) and deuterium (99 at. % in all years) was then injected intraperitoneally. Males were injected with 0.3 g  $^{18}\text{O}$  and 0.12 g deuterium per kilogram of body mass. Males were held for 3 h in the laboratory without food and water following the injection to allow for equilibration of the isotopes in the body fluids. A second blood sample was collected from the femoral vein following the equilibration period and males were promptly released at their capture location. Injected males were recaptured 3–7 days after injection and carefully weighed, and a third blood sample was collected. Most initial captures and recaptures of males were made during the morning activity period (07:00–10:30). Doubly labeled water was administered throughout each active season to males that had a high probability of recapture, and repeated measures on males were made at least 2 weeks apart. All blood samples were sent to the Boston Stable Isotope Laboratory and analyzed using isotope ratio mass spectrometry. Estimates of  $\text{CO}_2$  production were generated from linear equations suggested by Lifson and McClintock (1966) (see also Nagy 1980). A respiratory quotient of 0.83 was assumed for marmots, and the corresponding conversion factor of  $5.829 \text{ kcal/L CO}_2$  was selected from Brody (1945). A respiratory quotient of 0.83 results in the least amount of error in energy metabolism for herbivores when the actual rate of nutrient catabolism is unknown (Gessaman and Nagy 1988; Salsbury and Armitage 1994b). All metabolic rates were expressed as total ( $\text{kJ} \cdot \text{d}^{-1}$ ) or specific ( $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ ), assuming  $4.184 \text{ kJ} \cdot \text{kcal}^{-1}$  (Schmidt-Nielsen 1990).

The number, sex, age, and location of all animals within each male's home range were determined via trapping, radiotelemetry, and observation. The maximum interfemale distance (MID), estimated as the distance between the burrow systems of the two most distant adult females within each male's home range, was calculated as an estimate of female dispersion

(Salsbury and Armitage 1994a). Males that defended a single female were assigned a MID value of zero. A defensibility index (DI) was also calculated for each male's home range by multiplying the number of adult females defended and MID (Salsbury and Armitage 1994a). DI therefore increased with the number and dispersion of females within a male's home range.

Because we were primarily concerned with the relationships between male activity costs and female defense, RMR measured at approximately the same time as FMR (Salsbury 1993) was subtracted from FMR to yield an estimate of male energy expenditure above maintenance ( $\text{EE}^*$ ). Marmots have low thermoregulatory costs (2–9% of daily energy expenditure; Melcher 1987), owing to inactivity when temperatures are unfavorable. Thus, thermoregulatory costs were considered a minor component of the  $\text{EE}^*$  value for males. For males in this study, total RMR was significantly related to body mass (log transformed,  $n = 54$ ,  $b = 0.62$ ,  $R^2 = 0.16$ ,  $p = 0.003$ ; Salsbury and Armitage 1994b). Total RMR was predicted in 17 of 31 cases when no observed value corresponding to FMR was available; this was generally the case for early-season measures. Also, energy expenditures of two males were sampled in consecutive active seasons and 6 of 18 males were sampled on multiple occasions within a single active season (3 males were sampled twice and 3 males were sampled 3 times). Multiple sampling of individuals resulted in departures from independence within the data; therefore, unless otherwise noted, all estimates for an individual within a season were averaged. Eliminating data for males sampled in two or more active seasons to maintain independence would severely reduce already critically small sample sizes, however. Thus, all statistical analyses must be treated with caution.

### Male survivorship

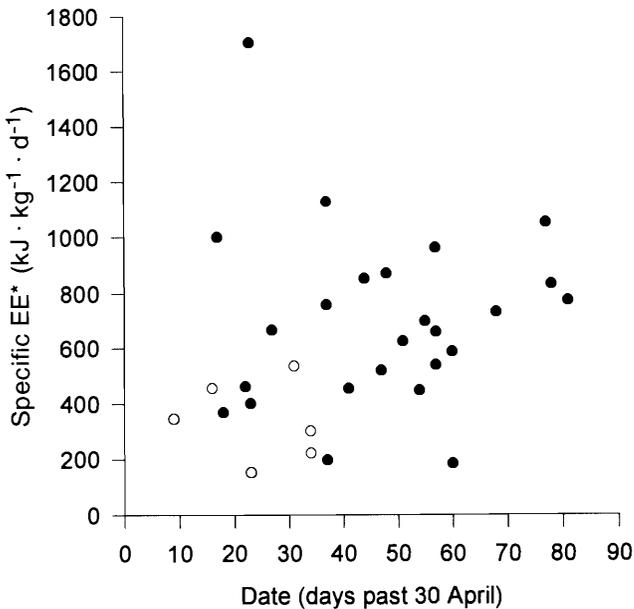
Survivorship of males to the next active season was examined. Males were evenly divided into two groups on the basis of  $\text{EE}^*$ ; those with the lowest  $\text{EE}^*$  estimates composed the "low" group and those with the highest  $\text{EE}^*$  estimates the "high" group. Values for the two males sampled in multiple years were included and treated as independent to improve sample size. The percentage of males in each group surviving to the next active season and still detectable within the study area was calculated. The survival of males in the two groups was compared with Yates' corrected  $\chi^2$  test. Also, the relationship of male survival to number of females defended was examined. The mean number of females defended by males that survived to the next active season was compared with the mean number of females defended by males that did not survive, using a one-tailed Student's  $t$  test.

### Statistical analysis

Analyses were performed using the Minitab (version 6.1; Minitab, Inc.) and SAS (SAS Institute Inc.) statistical software packages.

An analysis of variance was used to compare total and specific  $\text{EE}^*$  values for males between years. Male home-range size, number of females defended, total number of residents within a male's home range, MID, DI, and date into the season (represented as the number of days past 30 April for all 3 years) were considered predictor variables for

**Fig. 1.** Specific energy expenditure (EE\*), according to date (represented as days past 30 April), of adult male yellow-bellied marmots. Multiple measures for males sampled more than once in an active season are included. ○, measurement taken during the mating season.



total and specific EE\* and total and specific RMR in four separate stepwise multiple regressions (SAS Institute Inc.). No models that contained correlated predictor variables or departed from normality were considered. Residuals of all significant models were examined for deviations from normality using the NSCORES procedure in Minitab.

The influence of date was most likely underestimated in the stepwise procedure, as the data were averaged for males multiply sampled within an active season. Thus, a stagewise regression procedure (Draper and Smith 1981, p. 337) was used to better determine the influence of date on EE\*. Predicted and residual values of both total and specific EE\* were produced for the complete unaveraged data set using prediction equations (single-variable DI model) generated in the stepwise multiple regression procedure. Residuals of both total and specific EE\* were then separately regressed against date. The residuals were also regressed against male body mass to test for a possible effect of body mass on male EE\*.

## Results

A total of 31 measures of EE\* were collected from early May to late July (range 9–81 days past 30 April; Fig. 1). Six of the 31 measures were collected during the mating season as determined by backdating from litter emergence. Three of the 6 males sampled during the mating season were also sampled later in the active season. Mean total and specific EE\* (Table 1) did not differ significantly among years (ANOVA,  $F_{[2,18]} = 0.51$ ,  $p = 0.61$  and  $F_{[2,18]} = 0.63$ ,  $p = 0.53$ , respectively). Thus, data from all years of the study were combined in the statistical analyses.

Both total and specific EE\* residuals were positively related to date, but neither group of residuals was related to male body mass (Table 2). Thus, although date was not a signifi-

**Table 1.** Total and specific energy expenditure (EE\*) and body mass of adult male yellow-bellied marmots.

Year	<i>n</i>	Total EE* (kJ · d <sup>-1</sup> )	Specific EE* (kJ · kg <sup>-1</sup> · d <sup>-1</sup> )	Body mass (kg)
1989	6	2134.4 ± 898.0	602.8 ± 221.2	3.50 ± 0.22
1990	9	1696.8 ± 724.9	544.6 ± 249.3	3.18 ± 0.35
1991	6	2098.8 ± 1246.0	745.8 ± 522.5	2.97 ± 0.47
Combined	21	1936.6 ± 919.5	618.7 ± 335.8	3.21 ± 0.40

**Note:** Values are presented as means ± 1 SD. EE\*, energy expenditure above maintenance; *n*, number of males.

**Table 2.** Stagewise regression of metabolic measurements of adult male yellow-bellied marmots.

	Total EE* residuals	Specific EE* residuals
Date		
<i>F</i>	13.06	4.12
<i>P</i>	0.001	0.05
<i>R</i> <sup>2</sup>	0.280	0.091
<i>df</i>	1,29	1,29
Body mass (kg)		
<i>F</i>	2.54	0.74
<i>P</i>	0.122	0.397
<i>R</i> <sup>2</sup>	0.047	0.000
<i>df</i>	1,29	1,29

**Note:** Residuals represent those for total (kJ · d<sup>-1</sup>) and specific (kJ · kg<sup>-1</sup> · d<sup>-1</sup>) energy expenditure above maintenance (EE\*).

cant predictor variable in the stepwise procedure for specific EE\*, specific EE\* did appear to increase as the season progressed when the unaveraged data sample was considered in the stagewise regression procedure. However, the relationship between EE\* and date was weak, in part because of high EE\* values for 3 males (Fig. 1). The seasonal increase in EE\* may confound the results of the stepwise analyses because EE\* measures for males multiply sampled within a season were averaged. However, in an effort to preserve the independence of the data and because the relationship between EE\* and season was weak, we felt justified in using averaged EE\* measures in our analyses.

The most influential predictor variable of both total and specific EE\* was DI (Table 3), which was a more powerful predictor of EE\* than its components, MID and number of females, considered independently. Specific EE\* was best described by DI alone, whereas date, in addition to DI, was an important predictor of total EE\* (Table 3). Male body mass explained little of the variation in total or specific EE\*.

Stepwise multiple regression for total and specific RMR revealed that male home-range size was the most influential predictor variable in both cases (Table 3). Maximum inter-female distance also contributed significantly to the prediction models for total and specific RMR. Residuals from the two-variable model for total RMR did deviate from normality ( $r_{20} = 0.915$ ,  $p < 0.005$ ); thus, statistical inferences must be viewed with caution.

**Table 3.** Stepwise multiple regression of metabolic measurements of male yellow-bellied marmots.

Dependent variable	Independent variables			Model				
	Parameter estimate	F	P	F	p	R <sup>2</sup>	df	
Total EE* (kJ · d <sup>-1</sup> )	Intercept	582.0	2.17	0.158	20.06	<0.001	0.690	2,18
	DI	0.90	39.85	<0.001				
	Date	21.3	6.80	0.018				
Specific EE* (kJ · kg <sup>-1</sup> · d <sup>-1</sup> )	Intercept	487.6	67.78	<0.001	18.57	<0.001	0.494	1,19
	DI	0.24	18.57	<0.001				
Total RMR (kJ · d <sup>-1</sup> )	Intercept	340.6	640.06	<0.001	12.63	<0.001	0.583	2,18
	HR	5.5	25.19	<0.001				
	MID	0.09	4.10	0.058				
Specific RMR (kJ · kg <sup>-1</sup> · d <sup>-1</sup> )	Intercept	108.0	871.93	<0.001	8.72	0.002	0.492	2,18
	HR	1.2	17.10	<0.001				
	MID	0.02	4.04	0.060				

Note: DI, defensibility index; EE\*, energy expenditure above maintenance; HR, male home-range size; MID, maximum interfemale distance; RMR, resting metabolic rate.

Of the 10 males with the lowest EE\* estimates (range 615.4–1815.7 kJ · d<sup>-1</sup>), 20% survived to the next active season. Seven of the 10 males with the highest EE\* estimates (range 1971.3–3825.1 kJ · d<sup>-1</sup>) survived to the next active season. The data suggest that high-EE\* males experience higher survival compared with low-EE\* males; however, the difference was not statistically significant ( $\chi^2_{\text{adj.}} = 3.23$ ,  $df = 1$ ,  $p = 0.072$ ). The result was the same when either total or specific EE\* was used. The mean number of adult females defended by males that survived to the next active season ( $\bar{x} = 3.2$ ,  $SD = 2.54$ ) was significantly greater than the mean for males that did not survive ( $\bar{x} = 1.6$ ,  $SD = 0.924$ ,  $t = 2.37$ ,  $df = 18$ ,  $0.025 > p > 0.01$ ).

## Discussion

The significant relationship between EE\* for males and the defensibility of females suggests that male yellow-bellied marmots paid an energetic price for their reproductive opportunities. The increase in total and specific EE\* with female defensibility may reflect the increased locomotory expenditure of males. Locomotory costs may constitute a sizeable portion of the total energy expenditure of free-ranging mammals (Kenagy and Hoyt 1989; Karasov 1992; but see Garland 1983). However, only a small portion of energy was attributed to activity among free-ranging yellow-bellied marmots (Kilgore and Armitage 1978). The low expenditure for activity reflected the small proportion of time animals spent above ground. If the attractiveness of a habitat for males increases with the number of females residing there, then the amount of aboveground activity necessary for a defending male to exclude intruding males may increase with female number. Likewise, more male movement may be necessary if females are not clumped or readily observable from a single lookout such as a large rock. Detailed time budgets of adult male yellow-bellied marmots are needed, however, to estimate the amount of male locomotory activity related to female number and spacing.

If locomotory costs constitute a sizeable portion of a male's energy expenditure, it is surprising that EE\* was not signifi-

cantly related to home-range size. Home-range areas calculated in this study may not accurately represent the areas that males routinely patrol. The long-axis distance of a male's home range was, however, positively correlated with MID (Salsbury and Armitage 1994a), an important component of DI. The significant relationship between EE\* and DI suggests that the distance between the most remote females may be a better indicator of the area males routinely patrol than home-range area.

The importance of male home-range size in explaining the variation in both total and specific RMR is perplexing, especially as home-range size was not correlated with body mass for males in this study (Salsbury and Armitage 1994a). The relationship may indicate that some males are physiologically more capable of meeting the energy demands of maintaining a large home range. The relationship between RMR and MID further supports this hypothesis.

The trend toward an increase in EE\* with the progression of the active season (Table 2, Fig. 1) for male marmots is somewhat contrary to patterns of reproductive investment inferred for other male ground squirrels. In some species, males suffer from a more severe loss of body fat, higher levels of wounding, and higher rates of mortality during the mating season than during the nonmating season (*Spermophilus beecheyi*, Holekamp and Nunes 1989; *Spermophilus richardsonii*, Michener and Locklear 1990). The energy expenditure (FMR) of male *Spermophilus saturatus* was high early in the active season, when mating occurred, and decreased through the remainder of the season despite an increase in body mass (Kenagy 1987; Kenagy et al. 1988). Male yellow-bellied marmots, however, spent little energy during the mating season relative to the postreproductive period. The seasonal increase in energy expenditure of male marmots may be due to increased male activity after snowmelt and continual defense of females throughout the active season. Although detailed time-budget data are necessary to clearly elucidate the activity patterns of males, previous studies indicate that male activity and movement are nominal during the mating season and increase as the season progresses (Kilgore and Armitage 1978; Salsbury and Armitage 1994a).

Additionally, the frequency of intrusions by adult males into habitats occupied by males is minimal in May and increases substantially in June and July (Salsbury and Armitage 1994a). The increased intruder frequency in June and July may enhance defense costs as males defend females in territories exclusive of other males not only during the mating season but throughout the active season. Exclusive defense of females throughout the season may be critical to male reproductive success the following active season because defending males are likely to have sole access to their defended females during the short mating season (Andersen et al. 1976). Thus, in contrast to those sciurid species where males experience intense scramble competition and energy expenditure during mating, male yellow-bellied marmots appear to avoid high levels of activity, male–male competition, and associated energy expenditure during mating.

Investing in future reproduction seems to be a risky strategy considering that energy expenditure to insure future reproduction may reduce the probability of survival to the next breeding season. The short-term survival costs of defending females were negligible for males in this study, however. In fact, males that survived were generally those that defended more females. It is unlikely that high EE\* detrimentally influences subsequent reproduction, as previous studies indicate that males associating with several females, even widely spaced females, experience the highest lifetime reproductive success (Armitage 1986, 1991; K.B. Armitage, unpublished data). The inability to detect costs of current reproduction with respect to future reproduction and survival is common among observational studies of natural populations (Reznick 1985; Clinton and Le Boeuf 1993). This is not to say that reproduction is not costly for male yellow-bellied marmots. Male reproductive investment is most likely subject to the constraints of physiological condition. Thus, males may only engage in reproductive behaviors for which they are physiologically suited.

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