1995

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

Carmen M. Salsbury and Kenneth B. Armitage

**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.

**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...
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 as 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 immersing 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 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 Salisbury 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 (kJ·d⁻¹) and as specific RMR (kJ·kg⁻¹·d⁻¹), assuming conversion factors of 4.8 kcal·L⁻¹·O₂ and 4.184 kJ·kcal⁻¹ (1 cal = 4.184 J) (Schmidt-Nielsen 1990).

A doubly labeled water technique (¹⁸O²H) was used to estimate field metabolic rate (FMR), or the energetic expenditure of free-ranging males (see Nagy 1983 for details of the technique; Salisbury 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 ¹⁸O and deuterium in the body fluids. A water solution enriched with ¹⁸O (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 ¹⁸O 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 CO₂ 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 kcal/L CO₂ 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; Salisbury and Armitage 1994a).

All metabolic rates were expressed as total (kJ·d⁻¹) or specific (kJ·kg⁻¹·d⁻¹), assuming 4.184 kJ·kcal⁻¹ (Schmidt-Nielsen 1990).

The number, sex, age, and location of all animals within each male’s home range were determined via trapping, radio-telemetry, and observation. The maximum intermale 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 (Salisbury 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 (Salisbury 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 (Salisbury 1993) was subtracted from FMR to yield an estimate of male energy expenditure above maintenance (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 EE* value for males. For males in this study, total RMR was significantly related to body mass (log transformed, n = 34, b = 0.62, R² = 0.16, p = 0.003; Salisbury 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 EE*: those with the lowest EE* estimates composed the "low" group and those with the highest 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 χ² 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 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.

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

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Total EE* (kJ·d⁻¹)</th>
<th>Specific EE* (kJ·kg⁻¹·d⁻¹)</th>
<th>Body mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>9</td>
<td>2134 ± 488.9</td>
<td>620.8 ± 221.2</td>
<td>3.50 ± 0.22</td>
</tr>
<tr>
<td>1990</td>
<td>9</td>
<td>1696 ± 274.9</td>
<td>544.6 ± 249.3</td>
<td>3.18 ± 0.35</td>
</tr>
<tr>
<td>1991</td>
<td>6</td>
<td>2098 ± 1246.0</td>
<td>745.8 ± 522.5</td>
<td>2.97 ± 0.47</td>
</tr>
<tr>
<td>Combined</td>
<td>24</td>
<td>1936 ± 919.5</td>
<td>618.7 ± 335.8</td>
<td>3.21 ± 0.40</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th>Date</th>
<th>Total EE* residuals</th>
<th>Specific EE* residuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>13.06</td>
<td>4.12</td>
</tr>
<tr>
<td>P</td>
<td>0.001</td>
<td>0.05</td>
</tr>
<tr>
<td>R²</td>
<td>0.280</td>
<td>0.091</td>
</tr>
<tr>
<td>df</td>
<td>1.29</td>
<td>1.29</td>
</tr>
<tr>
<td>Body mass (kg)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>2.54</td>
<td>0.74</td>
</tr>
<tr>
<td>R²</td>
<td>0.122</td>
<td>0.397</td>
</tr>
<tr>
<td>df</td>
<td>0.047</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>1.29</td>
<td>1.29</td>
</tr>
</tbody>
</table>

Note: Residuals represent those for total (kJ·d⁻¹) and specific (kJ·kg⁻¹·d⁻¹) energy expenditure above maintenance (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, F₂,20 = 0.51, p = 0.61 and F₂,20 = 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-
The significant relationship between EE* for males and the MID further supports this hypothesis. The trend toward an increase in EE* with the progression of the active season. The data suggest that high-EE* males experience (Salsbury and Armitage 1994a), an important component of the active season (Table 2, Fig. 1) for male marmots is associated with a large rock. Detailed time budgets of adult male 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 free-ranging male marmots. 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. 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 significantly 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 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).

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

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variables</th>
<th>Parameter estimate</th>
<th>F</th>
<th>p</th>
<th>R²</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total EE*</td>
<td>Intercept 582.0, 1.21</td>
<td>0.158</td>
<td>20.06</td>
<td>&lt;0.001</td>
<td>0.690</td>
<td>2,18</td>
</tr>
<tr>
<td>(kJ·kg⁻¹·d⁻¹)</td>
<td>DI 0.90, 39.85</td>
<td>&lt;0.001</td>
<td>18.57</td>
<td>&lt;0.001</td>
<td>0.494</td>
<td>1,19</td>
</tr>
<tr>
<td>Date</td>
<td>21.3, 6.80</td>
<td>0.018</td>
<td>12.63</td>
<td>&lt;0.001</td>
<td>0.583</td>
<td>2,18</td>
</tr>
<tr>
<td>Specific EE*</td>
<td>Intercept 487.6, 67.78</td>
<td>&lt;0.001</td>
<td>8.72</td>
<td>0.002</td>
<td>0.492</td>
<td>2,18</td>
</tr>
<tr>
<td>(kJ·kg⁻¹·d⁻¹)</td>
<td>MID 0.09, 4.10</td>
<td>0.058</td>
<td>8.72</td>
<td>0.002</td>
<td>0.492</td>
<td>2,18</td>
</tr>
<tr>
<td>Total RMR</td>
<td>Intercept 340.6, 640.6</td>
<td>&lt;0.001</td>
<td>12.63</td>
<td>&lt;0.001</td>
<td>0.583</td>
<td>2,18</td>
</tr>
<tr>
<td>(kJ·d⁻¹)</td>
<td>HR 5.5, 25.19</td>
<td>&lt;0.001</td>
<td>12.63</td>
<td>&lt;0.001</td>
<td>0.583</td>
<td>2,18</td>
</tr>
<tr>
<td></td>
<td>MID 0.09, 4.10</td>
<td>0.058</td>
<td>8.72</td>
<td>0.002</td>
<td>0.492</td>
<td>2,18</td>
</tr>
<tr>
<td>Specific RMR</td>
<td>Intercept 108.0, 871.93</td>
<td>&lt;0.001</td>
<td>8.72</td>
<td>0.002</td>
<td>0.492</td>
<td>2,18</td>
</tr>
<tr>
<td>(kJ·kg⁻¹·d⁻¹)</td>
<td>HR 1.2, 17.10</td>
<td>&lt;0.001</td>
<td>8.72</td>
<td>0.002</td>
<td>0.492</td>
<td>2,18</td>
</tr>
<tr>
<td></td>
<td>MID 0.02, 4.04</td>
<td>0.060</td>
<td>8.72</td>
<td>0.002</td>
<td>0.492</td>
<td>2,18</td>
</tr>
</tbody>
</table>

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⁻¹), 20% survived to the next active season. Seven of the 10 males with the highest EE* estimates (range 1971.3–3825.1 kJ·d⁻¹) 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 (χ²adj. = 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 (X̄ = 3.2, SD = 2.54) was significantly greater than the mean for males that did not survive (X̄ = 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 a male's energy expenditure, it is surprising that EE* was not significantly 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 the 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 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 Bovee 1993). This may not be the case 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.

Acknowledgements
We are grateful to D. Van Vuren, D.W. Johos, K.C. Armitage, G. Grey, S. Min, and C. Lenihan for assistance in trapping, radio-location, and implanting radio transmitters. We also thank N. Slade, D. Alexander, and several anonymous reviewers for helpful criticism on an earlier draft of the manuscript. The research was supported by grants from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History, Sigma Xi, the Graduate School at the University of Kansas, and the National Science Foundation (Grants BSR 8614690, 9006772, and 9107543 to K.B.A.).

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