REPRODUCTIVE STRATEGIES OF YELLOW-BELLIED MARMOTS: ENERGY CONSERVATION AND DIFFERENCES BETWEEN THE SEXES

KENNETH B. ARMITAGE

Department of Systematics and Ecology, The University of Kansas, Lawrence, KS 66045-2106

Yellow-bellied marmots (*Marmota flaviventris*) conserve maintenance energy by reducing resting metabolic rate, decreasing conductance, avoiding thermal stress, by an annual cycle of metabolism, and by reducing metabolic rate and conductance following the mid summer molt. Male reproductive strategies include successful dispersal and locating females, establishing a territory and shifting energy use to summer defense, becoming polygynous and including as many females as possible within the territory, spending more time aboveground, and hibernating in the area where females are present. The major female reproductive strategy is the formation of matrilines, which facilitates the acquisition of resources, increases reproductive output, and provides a reproductive competitive advantage. Females also share space and are amicable with close kin, are agonistic toward all other females, may suppress the reproduction of other females, including their daughters, and produce daughter-biased sex ratios when recruitment of daughters is highly probable. Conflict occurs between males and females because female competition limits the number of females that reproduce whereas male reproductive success increases directly with the number of females weaning litters.

Key words: *Marmota flaviventris,* reproductive strategies, matrilines, energy conservation

The yellow-bellied marmot (*Marmota flaviventris*) is one of 14 generally recognized species of marmots (Barash, 1989). All marmot species have a common body plan and any marmot is easily recognized as such (Bibikow, 1996). Many behaviors appear to be common to all species, e.g., vigilance (Armitage et al., 1996) and greeting (Armitage, 1962; Bibikow, 1996). There are at least three social systems: solitary, monogamous, and polygynous; most species apparently are monogamous (Armitage, 1996*a*). In the monogamous species, as represented by *M. marmota,* the family group typically consists of a reproductive territorial pair, non-reproductive adults or subadults, yearlings, and young (Arnold, 1990; Perrin et al., 1993). All species hibernate.

Social grouping of the yellow-bellied marmot differs from that of all other marmot species. The basic social structure consists of one or more female kin-groups with which an adult male associates (Armitage, 1991). Because marmots live in burrows, they are easily located and can be trapped and individually marked. Thus, the sex, age, and relatedness of all individuals is known. Because marmots are diurnal, their behavior is readily observed. Since 1962, we studied yellow-bellied marmots in the Upper East River Valley, Gunnison County, Colorado, at an elevation of 2,900 m. The habitat is patchy and marmots are clumped on the patches consisting of talus or rocky outcrops located in meadows (Svendsen, 1974).

Yellow-bellied marmots must allocate resources to hibernation and reproduction. Unless an individual survives hibernation, there is no opportunity for reproduction. On the other hand, surviving hibernation without sufficient resources for reproduction leads to zero fitness. This paper combines

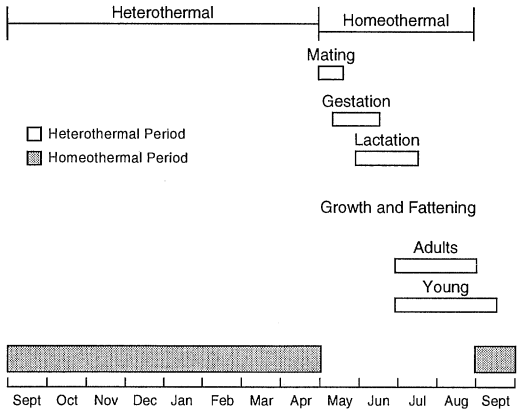

FIG. 1.—The annual cycle of the yellow-bellied marmot in the Upper East River Valley, Gunnison County, Colorado.

studies of energetics and reproduction to ask, how do marmots attempt to maximize their evolutionary fitness; i.e., pass their genes to reproductive descendents. Evolutionary fitness is measured as reproductive success, the production of offspring. The way in which males and females attempt to maximize reproductive success may differ and conflict between the sexes will be addressed.

THE ANNUAL CYCLE

A likely constraint on evolutionary fitness is the need to hibernate. Hibernation is part of an annual cycle, which consists of two phases, heterothermal and homeothermal (Fig. 1). The annual cycle is endogenous (Ward and Armitage, 1981); times of immergence and emergence differ little among years. Emergence in early May may occur through the snow; animals must rely on fat reserves until forage is available. When young are weaned in early July, food is abundant. By late August the vegetation senesces and immergence soon follows. In the active season of four months, reproduction, growth, and preparation for hibernation must occur. Because of the short active season, a female marmot can produce at most one litter a year. If she is unable to breed during the spring reproductive period, she must wait until the following year. Failure to reproduce can negatively impact lifetime reproductive success. Thus, we would expect that natural selection would favor physiological processes that would make annual reproduction possible.

An individual must allocate sufficient resources for successful hibernation or reduced survivorship will limit lifetime reproductive success. Reproduction occurs when energy beyond that required for hibernation and maintenance is available. The energetic costs are such that at least 10 species of marmots regularly skip reproduction, often for two or more years (Bibikow, 1996; K. B. Armitage and D. T. Blumstein, in litt.). Thus we predict that marmots should conserve maintenance energy as much as possible in order to have energy available for reproduction.

ENERGY CONSERVATION

Five major physiological mechanisms reduce energy use (Table 1). The reduced

TABLE 1.—*Physiological mechanisms of energy conservation by yellow-bellied marmots.*

Mechanism	Comment
Reduced metabolic rate	70–80% of that predicted on the basis of body size (Armitage and Salsbury, 1992)
Reduced metabolic rate following molt	Post-molt metabolic rate 63% of pre-molt metabolic rate (Armitage and Salsbury, 1993)
Low conductance (C)	Conductance 87.5% of that predicted on the basis of body size (Armitage et al., 1990)
Reduced C following molt	Post-molt C 62% of pre-molt C (Armitage and Salsbury, 1993)
Annual rhythm of metabolic rate	Metabolic rate decreases as hibernation approaches (Armitage and Salsbury, 1993; Ward and Armitage, 1981)

resting metabolic rate results in a high growth efficiency that facilitates somatic growth as well as fat accumulation (Armitage and Salsbury, 1993; Kilgore and Armitage, 1978). After the summer molt increased insulation reduces conductance, which further decreases resting metabolism and enhances fat accumulation. Resting metabolic rate continues to decrease as a function of the annual rhythm of metabolism. This decrease greatly reduces use of energy and extends the time that marmots can hibernate by about 50 days. Sufficient fat reserves upon emergence seem to be critical for reproduction (Andersen et al., 1976). Even small differences in the timing of snow melt can affect reproductive success; within our study area litter size and the frequency of reproduction were inversely related to the time of snow melt (Van Vuren and Armitage, 1991). At a study site at 3,400 m where extensive snow cover may occur in July, no female produced litters in consecutive years (Johns and Armitage, 1979).

Associated with energy conservation and reduced conductance is an inability to mobilize water for evaporative heat loss when subjected to thermal stress (Armitage et al., 1990). Although low evaporative water loss conserves energy, it raises the question of how marmots cope with heat. Marmots reduce above-ground activity and foraging time during mid day when thermal stress is greatest (Armitage et al., 1996; Melcher et al., 1990). During mid-day, the standard operating temperature exceeds the upper critical temperature (Melcher et al., 1990). Foraging time decreases from 23.2% of the above-ground time in the morning and afternoon to 9.4% at mid-day, and above-ground activity decreases from 64–75% of the time in the morning and evening to 43% of the available time at mid-day (Armitage et al., 1996). Heat stress reduces foraging time, which is extended by hyperthermia; foraging adults permit body temperature to rise to 40°C before retiring to their burrows (Melcher et al., 1989). Considerable foraging occurs while the standard operating temperature is below the lower critical temperature. Although foraging at this time imposes an energetic cost, the cost is minimized by avoiding the coldest temperatures. Smaller infants delay emergence in the morning and immerge earlier in the evening, thereby avoiding the energy costs of low temperature. As a consequence, thermoregulatory costs of yellow-bellied marmots are only 1–6% of their daily energy expenditure (Melcher et al., 1989).

Finally, hibernation can be successful not only if energy requirements are met, but also, if water needs are satisfied. One can imagine an energetically expensive scenario whereby marmots dig through frozen ground to reach snow as their source of water. But, in reality, resting metabolism probably provides all the necessary water without any additional costs. Metabolic water production exceeds evaporative water loss at all environmental temperatures below 20°C (Armitage et al., 1990).

Reproductive Strategies

Obviously, the reproductive strategies of males and females must converge at some point. The strategies of the two sexes may differ and even conflict (Downhower and Armitage, 1971). A strategy that may increase the reproductive success of males may reduce the reproductive success of females. The converse may also occur. In the following we examine the reproductive strategies of male and female yellow-bellied marmots and describe their differences and conflicts.

Male Strategies

The patchy habitat provides an opportunity for polygyny. Because females are clumped on the patchy habitat, a polygynous male on average produces twice as many young as a monogamous male (Armitage, 1986). Typically juvenile males disperse from their natal colony as yearlings. If a male is to achieve reproductive success, he must solve two problems. First, he must

find a satisfactory hibernaculum and survive the winter. Second, he must find and become resident with one or more adult females. Once resident, the male must exclude other males if he is to maximize his reproductive success. As a consequence adult males are territorial (Armitage, 1974).

The annual reproductive success of an adult male is directly related to the number of females in his harem. Both the number of young and the number of yearlings produced increase linearly with the number of females (Armitage, 1986). However, females pay a cost. As the number of females in a harem increases, the per capita production of young or yearlings decreases linearly. This difference between male and female reproductive success represents one conflict between the sexes. The male should attempt to have as large a harem as possible whereas each female should attempt to limit harem size in order not to lose per capita reproductive output. However, as described below, monogamy is not the best choice for a female.

Male behavior.—Because male reproductive success is directly related to the number of adult females in his territory, we predict that behavior with adult females should be amicable or cohesive. As predicted, amicable behavior between adult males and females is more frequent than expected based upon their frequency in the population (Armitage and Johns, 1982). If males are to maintain exclusive access to females and reduce possible competition with their sons, adult males should be agonistic toward all adult and yearling males. As predicted, agonistic behavior predominates between adult males and between adult and yearling males (Armitage and Johns, 1982). In fact, amicable behavior between adult males is rare, but does occur infrequently between adult and yearling males (Armitage, 1974).

Activity.—Adult males spend more time active than other age-sex groups. An adult male spends 527 minutes per day aboveground whereas adult females average 395 minutes and yearlings, 367 minutes (Armitage et al., 1996). Presumably the additional time allocated to activity by males is part of territorial defense.

Territory size.—Male territories associated with clumped females average about 0.67 ha in size (Armitage, 1974). However, females may be more widely dispersed. One way that a male can increase his reproductive success is by increasing his home-range size to include additional females. From 1989 through 1991, male home-range size was significantly correlated with the maximum distance between females, but not to the number of females, within his home-range (Salsbury and Armitage, 1994*a*).

Energetic costs.—The high level of activity of adult males should increase the expenditure of energy. Consistent with this prediction, male home-range size was the most consistent predictor of resting metabolic rate; larger home ranges were associated with higher metabolic rates. In addition, male energy expenditure above maintenance increased as the defensibility index, a measure of the number and dispersion of females within the home-range of a male, increased (Salsbury and Armitage, 1995).

Another indication that activity is a major source of energy expenditure is the seasonal shift in energy use. Resting metabolic rate did not change through the season, but field metabolic rate increased significantly through the season (Salsbury and Armitage, 1994*b*). This increase was surprising as we expected that field metabolic rate would be higher during the mating season in May. However, early in the summer few intrusions by males into the territorities of resident males are detected. Trapping records revealed that intrusions were common in June and July when field metabolic rate was high. Thus, the major energetic investment of male marmots for reproduction appears to be shifted from the mating season to later in the season when males continue to de-

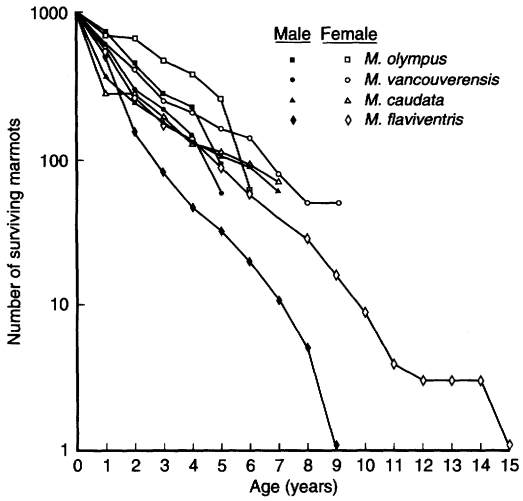

FIG. 2.—Survivorship curves for *M. flaviventris* (O. A. Schwartz, K. B. Armitage, and D. Van Vuren, in litt.), *M. olympus* (Barash, 1973), *M. caudata aurea* (D. T. Blumstein, pers. comm.) and *M. vancouverensis* (Bryant, 1996).

fend females (Salsbury and Armitage, 1994*b*).

Survivorship costs.—For the yellow-bellied marmot, from ages one through nine, male mortality is greater than female mortality (Fig. 2). No known-aged male has lived beyond age nine (O. A. Schwartz, K. B. Armitage, and D. Van Vuren, in litt.). Some of the difference in the survivorship can be attributed to the higher incidence of dispersal in male than in female *M. flaviventris* coupled with higher mortality of dispersers than of residents (Van Vuren and Armitage, 1994). Two-year-old males also move around, presumably while seeking females, and mortality of that age group is high (Armitage, 1991; O. A. Schwartz, K. B. Armitage, and D. Van Vuren, in litt.).

That decreased survivorship of males is in part a consequence of dispersal and searching for females is supported by the survivorship curves for species with delayed dispersal. In *M. olympus, M. caudata aurea,* and *M. vancouverensis,* dispersal is delayed to age two or older (Armitage, 1996) and survivorship is greater at all ages (Fig. 2).

Because males do not move long distances to seek females during the mating season, survivorship is probably enhanced. At this time in the annual cycle, the landscape is often snow-covered and difficult to traverse. It is risky to move large distances because predators, especially coyotes (*Canis latrans*) are active and a male on an excursion has no shelter once he has departed from his burrow and tunnel through the snow. Thus, the male defends his territory from intruders during the summer and hibernates in the same area with the females. Upon emergence the following spring, the male has access to the females with minimal energetic costs and low risk of predation. In some high altitude marmot species where snow-cover may persist for several weeks after the termination of hibernation, mating occurs in the burrow prior to emergence (Bibikow, 1996). This behavior is possible because the entire family group hibernates in the same hibernaculum, which does not occur in our study area.

Female Strategies

Matriline formation.—The basic social unit is a mother with her offspring. This association may lead to the formation of kin groups that persist through time as matrilines (Armitage, 1991). Matrilines are formed by the recruitment of daughters and all matrilines are either mother : daughter or sister : sister groups (Armitage, 1984). Most matrilines become extinct but long-persisting matrilines divide to form new matrilines that may compete with one another (Armitage, 1984, 1987*a*).

Advantages of matrilineal organization.—A numerically dominant matriline may acquire resources, which consist of burrow sites and foraging areas. For example, at Picnic Colony in 1978, the dominant matriline consisting of two littermate sisters occupied the central area of the habitat. An adjacent matriline consisting of a mother and her daughter occupied a less favorable area. By 1981, the formerly dominant matriline was reduced to a single fe-

TABLE 2.—*Mean number of yearlings produced in matrilines of one female. The mean marked with an asterisk differs statistically from the other means.*

Condition	Mean
One matriline present	1.17
Two matrilines present with one female each	1.36
Second matriline present with two or more females	0.56*

male and the competing matriline had increased to three adult females. The single female was displaced to a peripheral area and the mother: daughter matriline now occupied the area with the best burrows and foraging areas (Armitage, 1989).

Matrilines also provide a reproductive competitive advantage. When a matriline consists of one female, she produces an average of 1.17 to 1.36 yearling daughters each year as long as any other matriline present also consists of one female (Table 2). However, if the other matriline consists of two or more females, the annual production of yearlings by the single female is reduced by one-half. This reduction occurs not because of reduced litter size but by the failure to produce a litter about half the time.

Matrilines increase the reproductive output of a kin group. The number of yearlings produced per female does not decrease as matriline size increases but the number of yearlings per matriline is directly related to the number of females in the matriline (Armitage, 1986). Given that adult members of a matriline are related by 0.5, many genes are shared in common. Frequently some of the yearlings are granddaughters of the matriarch who initiated the matriline. Thus, it is likely that inclusive fitness of individual females has both direct and indirect components and is greater than that of females living singly. The advantage of reproduction in a matriline is further supported by demographic analysis. Net reproductive rate (R_0) was calculated for 15 habitat sites for which 7 to 32 years of demographic data were available. R_0 was not correlated with the number of matrilines ($r = 0.17$) on a habitat site, but was significantly correlated ($r = 0.76$, $P < 0.01$) with the number of females per matriline (O. A. Schwartz and K. B. Armitage, in litt.).

Daughter-biased sex ratios.—Although population sex ratios of young are 1:1, female-biased sex ratios occur under the following conditions. When two or more adult females are present in the only matriline on a habitat patch and the mother is young; i.e., her age is below the mean age of the adult population (4.4 yrs.), the sex ratio of the young is 1.81 females: 1.0 males (Armitage, 1987*b*).

The production of more daughters per litter results in the recruitment of more yearling daughters per litter (1.4 versus expected 0.78). This result is not surprising and indicates that recruitment of daughters is in part a function of the number of daughters produced. But the special conditions under which sex-biased litters occur suggests that there may be an additional adaptive benefit. In brief, the number of yearling recruits per female young weaned (0.47) is greater than the expected rate (0.34) based on the population mean (Armitage, 1987*b*).

Kin-shared space use.—The space marmots use contains the essential resources of food and burrows. Females share space mainly with kin related by 0.5 and do not share space in proportion to the degree of relatedness (Armitage, 1996*b*). For example, in 1981 at Picnic Colony, the average space overlap for the mother and two daughters was 45%, whereas the average space overlap between the two matrilines (average $r = 0.09$) was 1.2%. The pattern of space use suggests that female marmots attempt to maximize the direct fitness component of inclusive fitness.

Kin-directed behavior.—As might be expected from the pattern of space use, social behavior is kin-biased. Amicable behavior occurs among close kin about as or more than as expected and occurs much less fre-

TABLE 3.—*Contingency table analysis of the number of two-year-old female yellow-bellied marmots that reproduced under different social environments. The null hypothesis that there is no effect of social environment on reproduction by two-year-old females is rejected,* $\chi^2 = 13.3$, $P < 0.01$.

Condition	Number of two-year-old females	
	Repro-ductive	Non-repro-ductive
Older adult female present		
Reproductive	2	14
Non-reproductive	4	6
Mother present		
Reproductive	11	29
Non-reproductive	5	14
No older females present	22	28

quently than expected among more distant kin. On the other hand, agonistic behavior among close kin occurs much less frequently than expected and much more frequently than expected among more distant kin (Armitage, 1989; Armitage and Johns, 1982).

Reproductive suppression.—One way an animal can increase its genetic representation in the next generation is by reducing the genetic contribution of competitors. Reproductive suppression apparently is widespread among species of marmots (Armitage, 1996*a*). Yellow-bellied marmot females living in close proximity to other adult females are much less likely to wean a litter than females living solitarily (Armitage, 1986). Reproductive suppression is evident in the pattern of reproduction of two-year-old females. If older adult females are present, two-year-old females are more likely to be non-reproductive even when the older females are their mothers (Table 3). A two-year-old female is more likely to reproduce when older adult females are absent.

SUMMARY AND CONCLUSIONS

Both male and female yellow-bellied marmots employ energy conservation mechanisms that reduce the costs of maintenance and increase the probability of surviving hibernation and subsequently reproducing. The high costs of male activity and female lactation occur when food is abundant (Kilgore and Armitage, 1978). Both of these reproductive activities reduce or prevent fattening for hibernation. The males have much less energetic stress than the females and typically reach hibernation mass by late July (Armitage, 1996*c*). Females lactate for three to four weeks and body mass either remains stable or decreases (Armitage, 1996*c*). Thus, energy conservation becomes especially important for females in late summer when fat is accumulated for hibernation and the initiation of reproduction the following spring. When weaning occurs after mid July or when there is a late summer drought, females may be unable to gain sufficient mass to survive hibernation or if surviving hibernation, to reproduce the following year (Armitage, 1994). Hence, behavioral strategies that lead to resource acquisition are especially important to females.

Male yellow-bellied marmots must survive dispersal, find females, and establish a territory (Table 4). Reproductive success of a male depends on how many females successfully reproduce in his territory. But female strategies conflict with male strategies. Reproductive suppression by females may increase the dominant female's genetic representation in the next generation, but it decreases the male's representation because the number of offspring that could be produced by that male is reduced. Furthermore, females determine the number of females living on a habitat patch. The number of breeding females increases when daughters are recruited (Armitage, 1996*a*). The territorial male benefits during this period of population growth. Competition both within and between matrilines reduces recruitment and the number of resident females subsequently declines (Armitage 1975, 1996*a*), thus reducing the number of females with whom a male can breed. The

TABLE 4.—*Summary of reproductive strategies of yellow-bellied marmots.*

Males	Females
Survive dispersal	Form matriline: acquire resources
Locate females	Increase reproductive output
Become territorial	Daughter-biased sex ratios
Spend more time aboveground	Share space with close kin
Be polygynous	Amicable behavior with close kin
Shift energy use to summer defense	Agonistic behavior toward other females
Hibernation in area with females	Reproductive suppression

best a male can do is exclude intruders, hibernate with the females, and mate with whatever number of estrus females is present the following spring.

Female reproductive success is closely tied to matriline formation. Matriline formation increases the liklihood that a female's daughters will live and reproduce. The matrilineal group is more successful at acquiring resources and increasing reproductive output (Table 4). All of the female strategies enhance the reproductive success of individual females. These strategies should be considered ways of increasing direct fitness. Females cooperate; e.g., space-sharing with close kin, when that can lead to reproductive dividends. However, females will compete; e.g., reproductive suppression, when that can increase direct fitness. Thus formation of matrilines is best viewed as a mechanism for increasing direct fitness with any indirect fitness gains as a secondary bonus.

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LITERATURE CITED

ANDERSEN, D. C., K. B. ARMITAGE, AND R. S. HOFFMANN. 1976. Socioecology of marmots: female reproductive strategies. Ecology, 57:552–560.

ARMITAGE, K. B. 1962. Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). Animal Behaviour, 10:319–331.

———. 1974. Male behaviour and territoriality in the yellow-bellied marmot. Journal of Zoology (London), 172:233–265.

———. 1975. Social behavior and population dynamics of marmots. Oikos, 26:341–354.

———. 1984. Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability. Pp. 377–403, *in* Biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.

———. 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies. Pp. 303–331, *in* Ecological aspects of social evolution (D. S. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey, 551 pp.

———. 1987*a*. Social dynamics of mammals: reproductive success, kinship, and individual fitness. Trends in Ecology and Evolution, 2:279–284.

———. 1987*b*. Do female yellow-bellied marmots adjust the sex ratios of their offspring? The American Naturalist, 129:501–519.

———. 1989. The function of kin discrimination. Ethology, Ecology and Evolution, 1:111–121.

———. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annual Review of Ecology and Systematics, 22:379–407.

———. 1994. Unusual mortality in a yellow-bellied marmot population. Pp. 5–13, *in* Actual problems of marmots investigation (V. Yu Rumiantsev, ed.). ABF Publishing House, Moscow, Russia, 256 pp.

———. 1996*a*. Social dynamics, kinship, and population dynamics of marmots. Pp. 113–128, *in* Biodiversity in marmots (M. Le Berre, R. Ramousse, and L. Le Guelte, eds.). International Marmot Network, Moscow-Lyon, 276 pp.

———. 1996*b*. Resource sharing and kinship in yellow-bellied marmots. Pp. 129–134, *in* Biodiversity in marmots (M. Le Berre, R. Ramousse, and L. Le Guelte, eds.). International Marmot Network, Moscow-Lyon, 276 pp.

———. 1996*c*. Seasonal mass gain in yellow-bellied marmots. Pp. 223–226, *in* Biodiversity in marmots (M. Le Berre, R. Ramousse, and L. Le Guelte, eds.). International Marmot Network, Moscow-Lyon, 276 pp.

ARMITAGE, K. B., AND D. W. JOHNS. 1982. Kinship,

reproductive strategies and social dynamics of yellow-bellied marmots. Behavioral Ecology and Sociobiology, 11:55–63.

ARMITAGE, K. B., J. C. MELCHER, AND J. M. WARD, JR. 1990. Oxygen consumption and body temperature in yellow-bellied marmot populations from montane-mesic and lowland-xeric environments. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology, 160:491–502.

ARMITAGE, K. B., AND C. M. SALSBURY. 1992. Factors affecting oxygen consumption in wild-caught yellow-bellied marmots (*Marmota flaviventris*). Comparative Biochemistry and Physiology, A. Comparative Physiology, 103:729–737.

———. 1993. The effect of molt on oxygen consumption of yellow-bellied marmots (*Marmota flaviventris*). Comparative Biochemistry and Physiology, A. Comparative Physiology, 106:667–670.

ARMITAGE, K. B., C. M. SALSBURY, E. BARTHELMESS, R. GRAY, AND A. KOVACH. 1996. Population time budget of the yellow-bellied marmot. Ethology, Ecology and Evolution, 8:69–95.

ARNOLD, W. 1990. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behavioral Ecology and Sociobiology, 27:239–246.

BARASH, D. P. 1973. The social biology of the Olympic marmot. Animal Behaviour Monographs, 6:171–245.

———. 1989. Marmots. Social behavior and ecology. Stanford University Press, Stanford, California, 360 pp.

BIBIKOW, D. I. 1996. Die Murmeltiere der Welt. Westarp Wissenschaften, Magdeburg, Germany, 228 pp.

BRYANT, A. 1996. Reproduction and persistence of Vancouver Island marmots (*Marmota vaucouverensis*) in natural and logged habitats. Canadian Journal of Zoology, 74:678–687.

DOWNHOWER, J. F., AND K. B. ARMITAGE. 1971. The yellow-bellied marmot and the evolution of polygamy. The American Naturalist, 105:355–370.

JOHNS, D. W., AND K. B. ARMITAGE. 1979. Behavioral ecology of alpine yellow-bellied marmots. Behavioral Ecology and Sociobiology, 5:133–157.

KILGORE, D. L., JR., AND K. B. ARMITAGE. 1978. Energetics of yellow-bellied marmot populations. Ecology, 59:78–88.

MELCHER, J. C., K. B. ARMITAGE, AND W. P. PORTER. 1989. Energy allocation by yellow-bellied marmots. Physiological Zoology, 62:429–448.

———. 1990. Thermal influences on the activity and energetics of yellow-bellied marmots (*Marmota flaviventris*). Physiological Zoology, 63:803–820.

PERRIN, C., J. COULON, AND M. LE BERRE. 1993. Social behavior of alpine marmots (*Marmota marmota*): seasonal, group and individual variability. Canadian Journal of Zoology, 71:1945–1953.

SALSBURY, C. M., AND K. B. ARMITAGE. 1994*a*. Home-range size and exploratory excursions of adult, male yellow-bellied marmots. Journal of Mammalogy, 75: 648–656.

———. 1994*b*. Resting and field metabolic rates of adult male yellow-bellied marmots, *Marmota flaviventris*. Comparative Biochemistry and Physiology, A. Comparative Physiology, 108:579–588.

———. 1995. Reproductive energetics of adult male yellow-bellied marmots (*Marmota flaviventris*). Canadian Journal of Zoology, 73:1791–1797.

SVENDSEN, G. E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. Ecology, 55:760–771.

VAN VUREN, D., AND K. B. ARMITAGE. 1991. Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. Canadian Journal of Zoology, 69:1755–1758.

———. 1994. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? Oikos, 69:179–181.

WARD, J. M., JR., AND K. B. ARMITAGE. 1981. Circannual rhythms of food consumption, body mass, and metabolism in yellow-bellied marmots. Comparative Biochemistry and Physiology, A. Comparative Physiology, 69:621–626.

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