TIME AND WARINESS IN YELLOW-BELLIED MARMOTS

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Abstract - The time budget of *Marmota flaviventris* was measured during the summer of 1990 to determine the proportion of time allocated to wariness, a set of behaviors in which a marmot scans the environment presumably to detect potential predators or conspecifics. Wariness occurred in three major forms: (1) sitting or lying on the ground or on an elevated object; (2) alert, when an animal raised its head while walking or foraging; (3) vigilance, when an animal sat upright on its haunches with its forelegs held in front of its chest. Wariness occurred more frequently near the burrow area than far from the burrow area. Most time was allocated to inactivity such as sitting; only about 1.7% to 6.5% of above-ground time was spent feeding. Non-reproductive adult females that were socially subordinate to the reproductive female allocated more time to wariness and yearling females allocated more time to feeding than did the other animal groups. The reproductive female increased her wariness after her litter emerged. Various interactions among season, time of day, location, and animal group indicate adjustment of the time budget to prevailing conditions. The overall wariness strategy of marmots is to spend time near the burrow to assess potential risk before initiating foraging.

IBEX J.M.E. 2:1-8

1. Introduction

The way in which individuals allocate time to various activities affects fitness. Time can be a limiting resource, especially for diurnal animals (Herbers, 1981; Hatch, 1990). Time allocated to one activity is unavailable for other activities. Because reproductive success ultimately is determined by an individual's ability to obtain energy and nutrients from the environment, time diverted from foraging may affect reproductive success. Thus, there is a time budget trade-off between foraging and other activities (Stephens & Krebs, 1986:114).

Individuals must invest time in vigilance, *i.e.*, scanning the environment for the presence of predators (e.g. Holmes, 1984) and many species give alarm calls when a predator is present (e.g. Sherman, 1977; Owings & Leger; 1980, Schwagmeyer & Brown, 1981; Ivins & Smith, 1983). Because numerous studies indicate that animals sacrifice food intake in order to avoid possible predators (Krebs & Kacelnik, 1991), vigilance and other behaviors associated with predator avoidance are considered to be costly.

The pervasive view that vigilance is costly is in marked contrast to the observation that many animals spend a large proportion of their active time resting (Herbers, 1981; Dasilva, 1992). Presumably, animals would reduce time spent resting and increase time spent foraging to compensate for time allocated to vigilance. The cost may not be a loss of daily energy intake, but increased exposure to predators necessitated by allocating time to vigilance and thus spending more total time foraging away from the relative safety of refuges. Foraging is considered to be more risky than resting on the assumption that animals rest in relatively safe places. Most studies do not evaluate the possible costs of vigilance during foraging in the context of the overall behavioral strategy of the species. The purpose of this study was to determine the time budget and vigilance strategy of a colony of yellow-bellied marmots (*Marmota flaviventris*) in order to assess the potential costs of vigilance behavior. We also determined whether time of day, time of season, and age and reproductive status affected the time budget.

2. Study area and methods

Yellow-bellied marmots are large, diurnal, ground-dwelling sciurids that occupy rocky meadows, talus slopes, or cliffs with nearby grassy meadows. The study site was River Colony, locality 1 (Armitage, 1974), in the East River Valley, Gunnison County, Colorado, at an elevation of 2900 m. In the summer of 1990 the population consisted of an adult male, a reproductive female that weaned two young, five non-reproductive adult females (related to the reproductive female, kinship uncertain, but "r", the coefficient of relatedness, most likely 0.25), and four yearling females, daughters of the reproductive female. All animals were individually marked with ear tags

and fur dye. Home or nest burrows (Armitage, 1962) were located in a steep shale bank on the east side of the East River. Meadows occurred on a flat at the top of the bank, to the north of the shale bank along the river and to the east of the flat. The flat was separated from the meadows to the east by a deep gully. The locality was divided into two areas: (1) the area where the nest or home burrows and flat at the top of the bank were located (0.9 ha, designated Near the Burrow Area, NBA) and (2) the meadow areas east of the gully and north of the shale bank (1.8 ha, designated Far from the Burrow Area, FBA). A fence at the edge of the northern meadow area and a second fence at the top of the shale bank in the southern part of the burrow area provided posts where marmots sat or lay.

Behavioral observations occurred in the morning from 06.30 to 11.00 (Mountain Daylight Time) and in the afternoon from 15.30 to 18.00, when marmots are most active (Armitage, 1962). The periods varied slightly over the summer as daylength decreased and were adjusted to weather conditions; rainy periods were avoided and observations extended later in the morning on cool days. The summer was divided into three periods. During period I (June 19-24), the reproductive female was nursing the young in her burrow. Period II (June 25-July 7) coincided with the weaning of the young and their early activity above ground. Period III (July 22-29) sampled that part of the active season when marmots are growing and-or fattening for hibernation and the young are fully active.

It became apparent that marmots sitting or lying are wary. Therefore, all such behaviors were combined with vigilance, where a marmot stands upright and scans its environment, and with alert, when a quadrupedal marmot lifts its head and scans, in a general category designated wariness. Other behaviors recorded were feeding, when an individual is biting or chewing vegetation; walking, when an individual is moving from one area to another, but is not biting or chewing during the movement; social behavior, when one individual interacts with another, and individual behaviors, when an individual is grooming, digging, or investigating (by sniffing) adjoining rocks or vegetation.

Marmots were observed with a 15-40 power scope from a hillside about 150 m from the colony. When a marmot was seen, it was followed for two to 20 minutes, depending on how long the animal was visible, and its activity was recorded every 10 seconds. When the observation of one animal was completed, another was found and the procedure repeated. No attempt was made to randomize the choice of animals; each animal was observed as it was located. This procedure was necessary because all animals were not above ground at the same time and sometimes animals went into areas (e.g. the gulley) where they could not be seen. For the entire study, the reproductive female was recorded 64 times; non-reproductive females, 152 times; yearling females, 236 times; adult male, 44 times.

All data were analyzed as percent time spent in each of the four behavioral categories for each observation. The data were organized by time of day (AM or PM), location (NBA or FBA) and period (I, II, III) for each of the four classes of marmots (adult male, reproductive female, non-reproductive females, and yearling females). The data were arcsine transformed and analyzed by a general linear model ANOVA that accounts for different sample sizes in the data cells and tests for interactions among animals, time of day, location, and period (Shaw & Mitchell-Olds, 1993). The GT2 test was used for pairwise comparisons.

3. Results

General pattern. All classes of marmots spent more above-ground time in wariness than in any other activity for all three time periods. Wariness was never less than 69% of the total activity (Fig. 1). Alert and vigilance combined never exceeded 28% of activity; overall, sitting or lying averaged 60% of total activity. By contrast, social and individual behaviors made up less than 4% of the activity except for yearling females (6%) in period II. Social and individual behaviors were too infrequent for further analysis. Walking was always 10% or less of total above-ground activity and feeding varied from 1% to 17% (Fig. 1). The reproductive female spent a greater proportion of time feeding during period I, when lactation occurred, and decreased relative time feeding in periods II and III. By contrast, the adult male increased the proportion of time feeding from period I to period III.

Wariness. Animal groups differed in the proportion of time spent wary (Fig. 2). Yearlings spent a smaller proportion and non-reproductive adult females spent a greater proportion of time wary than did the adult male and reproductive female. Only the difference between

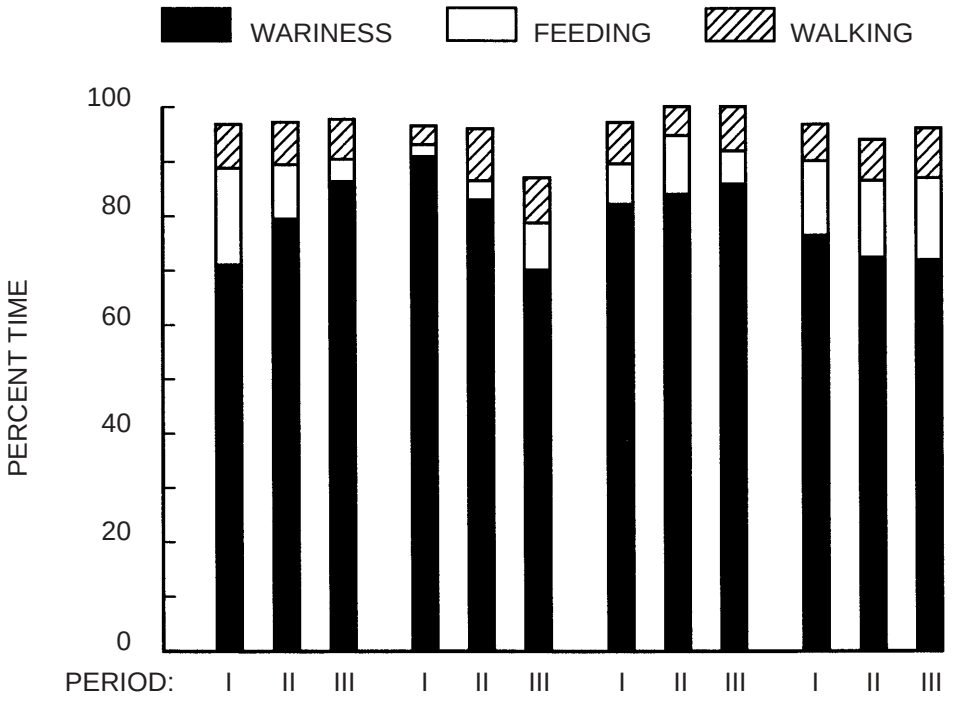

Figure 1 - The percent time allocated to the four major behaviors for the three periods of the summer for each animal group. R = reproductive; A = adult; NR = non-reproductive; YLGS = yearling females. The difference between the top of each bar and 100% is the proportion of time allocated to social and individual behaviours. Wariness includes sitting, lying, head-up alert, and vigilance.

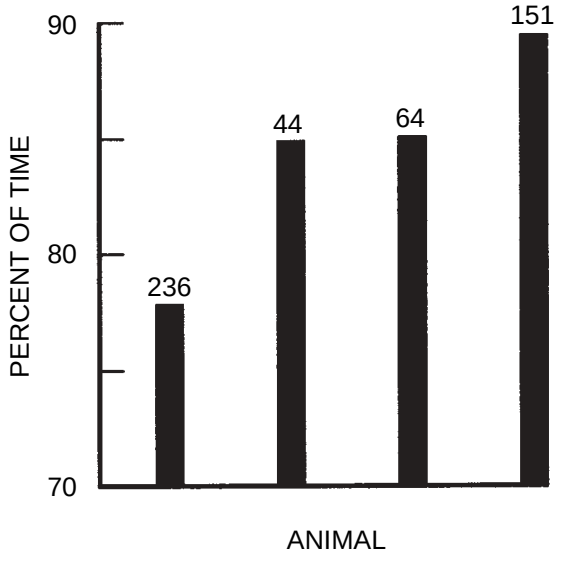

Figure 2 - The percent of time each animal group allocated to wariness. Data are combined across time of day, period of the active season, and location. Numbers at the top of each bar represent sample sizes. Abbreviations as in Fig. 1.

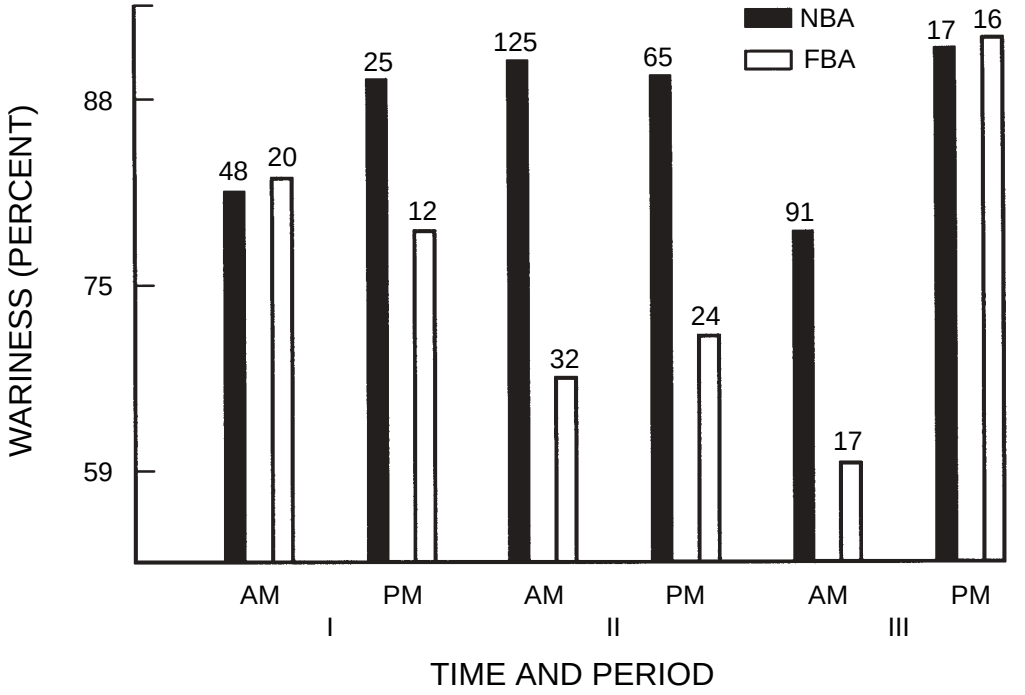

Figure 3 - The relationship of wariness to location, time of day, and period of the summer. Data combined across all animal groups. NBA = near the burrow area; FBA = far from the burrow area, *i.e.* the meadows east of the gulley and north of the steep bank. Numbers at the top of each bar represent sample size. AM = morning period; PM = afternoon period.

the yearling females and the non-reproductive females was statistically significant in pairwise comparisons.

There was a significant period x daytime x location interaction (Fig. 3). Wariness was high FBA in the AM in period I and in the PM in period III whereas wariness was high at all other times when marmots were NBA. Although this interaction requires caution in the interpretation of main effects in the ANOVA because the main affects could be the result of the interaction, the main effects appear to be significant independently of the interaction. Despite the high frequency of wariness when animals were FBA in periods I and III, they usually spent more time wary when near the burrow area ($p = 0.004$, Fig. 3). Also, significantly more time was spent wary in the PM than in the AM ($p = 0.01$). Both location and time of day were statistically significant when tested by pairwise comparisons.

All animal classes spent about the same proportion of their wariness in vigilance; *i.e.* sitting upright, body vertical and with forefeet held in front of the chest. This proportion varied from 25.3% to 27.0%. Animals also used fence posts regularly when these fence posts were present in their home ranges. Only one animal had access to a fence post when NBA. This non-reproductive female used the fence post for 63.8% of her wariness in the burrow area. Three non-reproductive females did not have access to fence posts when FBA. The two non-reproductive females that had access to a fence post, used a fence post for 28.9% of their wariness when FBA. When FBA, yearling females used the fence post for 53.7% of their wariness and the reproductive female and adult male used the fence post for 37% of their wariness.

Feeding. The proportion of time spent feeding differed significantly among animal groups ($p = 0.0039$). The mean (calculated from individual values) percent time feeding for each group was: reproductive female, 2.9%; non-reproductive females, 2.9%; adult male, 1.7%; yearling females, 6.5%. Pairwise comparisons revealed that yearling females spent a greater proportion of time feeding than did non-reproductive females. The mean values suggest that the difference between yearling females and other groups is biologically significant for all comparisons.

There was a significant period x daytime x location interaction (0=0.017). Feeding was unusually frequent when animals were NBA relative to FBA in the AM of period I and there was a large decrease in frequency of feeding when FBA in the PM of period III. The marmots spent a greater proportion of time feeding in the AM than in the PM ($p = 0.039$). Generally, marmots spent a greater proportion of time feeding when FBA ($p = 0.0001$). The "p" value indicates that this main effect is statistically significant independently of the interaction. Both main effects relationships were statistically significant in pairwise comparisons. There was a significant animal x location interaction (Fig. 4, $p = 0.05$). The adult male fed equally when NBA or FBA whereas all other animal groups spent a greater proportion of time feeding when FBA.

Walking. There were no significant main effects in the ANOVA analysis, but there were significant interactions and significant pairwise comparisons. Non-reproductive females walked significantly less than yearling females (3.3% vs 5.5%); however, the adult male walked 5.6% of the time and the reproductive female, 4.9% of the time. Overall, marmots spent more time walking in the burrow area (5.1%) than when far from the burrow area (3.5%) except the adult male for which the proportion was reversed (statistically significant animal x location interaction, $p=0.006$). Marmots also spent a significantly greater proportion of their time walking during period III (6.7%) than during period I (4.4%) or period II (4.8%). In addition, there was a statistically significant period x daytime interaction ($p=0.009$), with a shift in period II from more walking in the AM to more walking in the PM, but considerably greater allocation of time to walking in the AM relative to the PM in period III. Finally, there was a statistically significant animal x period x daytime interaction ($p=0.056$). The reproductive female markedly decreased the proportion of time walking in the PM in period III, the adult male spent a small proportion of time walking in the PM and a large proportion, in the AM in period I, and the nonreproductive females and the yearlings spent a greater proportion of their time walking in the PM in period II, but in the AM in periods I and III. Also, the differences between AM and PM were much less for the yearlings than for the other groups.

4. Discussion

The major conclusion from this study is that marmots spend the greatest proportion of their above-ground time in wariness. Much of the wariness is evident in vigilance behavior, but most of the wariness is associated with marmots sitting or lying on fence posts, rocks, or dirt and this behavior occurs more frequently in the burrow area. These results are consistent with other studies that reported that yellow-bellied marmots spend more than 50% of their time sitting (Armitage, 1962; Kilgore & Armitage, 1978) and as much as 90% of their morning activity in various sitting behaviors (Travis & Armitage, 1972). Similarly, Columbian ground squirrels *Spermophilus columbianus* spent 48% (parous females) to 59% (nonparous females) of their total above-ground time vigilant (MacWhirter, 1991). We determined that the adults allocated approximately 87% of their time to wariness before 08.00 and 81% thereafter. The latter value includes late morning when most animals returned from the foraging patches to sit or lie in the burrow area. By contrast, the values for yearling females were 70% and 72%, respectively. Thus, the increased proportion of time that yearling females allocated to foraging seems to result from a greater reduction of wariness overall, but especially early in the morning.

If only those observations in which the time allocated to feeding was greater than 1% are considered, the time allocated to wariness decreases to 70.6% and 54.4% for adults and female yearlings, respectively. This result indicates that yearlings are less wary during feeding and thereby increase the total time allocated to feeding.

The considerable variation among animal groups, with time of day, season, and location indicates that yellow-bellied marmots adjust their time budgets to prevailing conditions. The high rate of wariness by the non-reproductive adult females likely can be attributed to

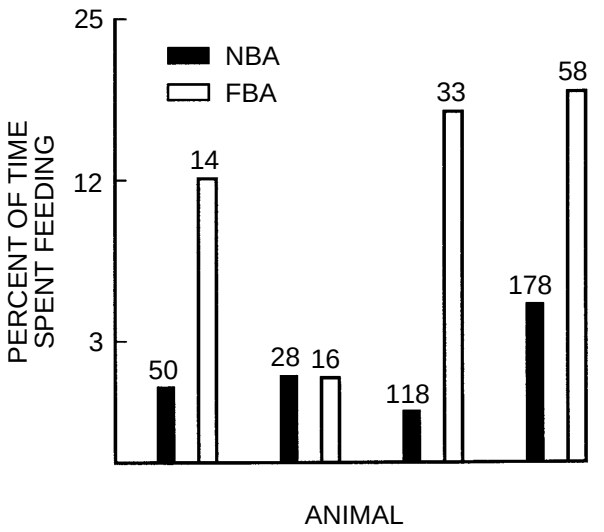

Fig. 4 - The relationship of time spent feeding to location and animal group. Data are combined across time of day and period of the active season. Numbers at the top of the bars represent sample size.

their subordinate status and to their location. These females were harassed by the reproductive female and they lived at the periphery where individuals are more wary than those that live centrally (Armitage, 1962; Hoogland, 1981). The low frequency of wariness by yearlings compared to adults contrasts with the higher frequency of wariness by yearlings than by adults in California yellow-bellied marmots (Carey & Moore, 1986) and in hoary marmots (*M. caligata*, Holmes, 1984). There is no obvious explanation for this difference but it may be due to the social status of the yearlings in the populations. The yearling sisters that spent the smallest proportion of their time alert (Fig. 2) had the highest space-use overlap of any of the animal groups, which indicates that the yearlings tended to forage near one-another and thereby reduce alertness, not only because of a possible group effect (e.g., Barash, 1973), but also because their behaviors were entirely amicable. Kinship, in general, influences the use of foraging areas (Frase & Armitage, 1984). The high rate of feeding by yearling females is consistent with their requirement to both grow and accumulate fat for hibernation.

The increased level of wariness by the reproductive female in periods II and III is associated with activity of her litter above ground. The associated decrease in time allocated to feeding is consistent with her decreased metabolic rate following lactation (Armitage & Salsbury, 1992).

What is surprising is the relatively low proportion of above-ground time allocated to feeding, 1.7% to 6.5% averaged over the study period. This value is lower than the average of approximately 23% reported for four different populations in our study area (Frase, 1983; Melcher *et al.*, 1989). We estimate from published figures that Wyoming yellow-bellied marmots spent about 25% of their time foraging (Armitage, 1962) and Olympic marmots (*M. olympus*) spent about 25-30% (Barash, 1973), and that hoary marmots (*M. caligata*) spent about one-third of their time foraging (Barash, 1980). Columbian ground squirrels spent from 36% (parous females) to 50% (nonparous females) of their aboveground time foraging (MacWhirter, 1991). Two factors probably contribute to the time-budget differences. First, we report time spent feeding whereas the other studies report foraging, which includes time spent walking while feeding. Second, we may have inadequately sampled feeding time. Animals frequently went into the gully where they probably fed but, because they could not be seen, feeding was not recorded.

Regardless of the actual time allocated to feeding, marmots spent more time sitting and/or lying than feeding. This pattern appears to be an example of Herbers' case 2 (Herbers, 1981) in which the time spent feeding by herbivores in seasons of high productivity depends primarily on metabolic rates and nonfeeding activity levels. Yellow-bellied marmots are energy conservers, metabolic rates are lower than predicted from body mass (Armitage & Salsbury, 1992) and overall activity, especially activity when metabolism would be increased by the thermal environment, is reduced (Melcher et al., 1989). The reduction in feeding time following weaning (Fig. 1; Frase, 1983) suggests that the amount of time spent feeding depends on current metabolic needs. It is likely that marmots spend little time searching but much time ingesting and digesting (Stephens & Krebs, 1986:116). Perhaps digestive time is the critical factor and accounts for much of the diurnal inactivity (Weiner, 1992).

Because there is so much inactivity, it seems likely that wariness does not impart a fitness

cost. Obviously, more time could be allocated to foraging, if that time were needed. All above-ground time is risky and marmots probably increase wariness when the perceived risk is greater. The real cost is the failure to detect predators. Observed predation on yellow-bellied marmots occurred when marmots were close to their burrows but failed to detect a coyote hiding nearby (Armitage, 1982). However, survivorship of philopatric marmots is high (Van Vuren, 1990:57) and those that were killed by predators were primarily those classified as living peripherally (Van Vuren, 1990:65). Thus risk may be more a function of where an individual lives, which is related to its social status, than to foraging time *per se*. Resolving these issues will be difficult because predation is rarely observed (Armitage, 1982).
The higher level of wariness in the burrow area rather than far from the burrow area is directly related to the overall wariness strategy of yellow-bellied marmots. When emerging from its burrow, a marmot sits near the burrow entrance or on some nearby elevated object and scans the surrounding environment. Only after some period of scanning does the marmot begin foraging. This behavior pattern was described for alpine marmots 100 years ago (Figuier, 1892). Apparently, the marmot scrutinizes the environment for predators and/or agonistic conspecifics and does not venture forth until there is little or no perceived risk. All subsequent alert and vigilance behaviors can be considered as sampling to determine if risk has changed and the sampling-time increases with the perceived potential risk. When a marmot returns to the burrow area, it again sits or lies near the entrance. Marmots enter the burrow primarily when heat stressed (Melcher *et al.*, 1990). Why marmots remain above ground is unknown, but a likely hypothesis is that it is more risky to allow conspecifics to encroach on one's space or for potential predators to approach undetected than to be exposed while sitting or lying. Because marmots are vulnerable when they come above ground and do not know where a predator may be hiding and because they are vulnerable to badgers when badgers approach undetected and enter the burrows (Armitage unpublished data; see also MacWhirter, 1992), it may be advantageous to spend as much time above ground as possible. During this time marmots remain wary. In effect, marmot above-ground activity is characterized by wariness, the single most frequent behavior in the time budget.

5. Acknowledgements

The research was conducted at the Rocky Mountain Biological Laboratory, Colorado and supported by Grants BSR-8614690 and BSR-9006772 to KBA from the National Science Foundation. We thank Dennis Johns and Kevin Armitage for assistance in trapping and marking animals and Carmen Salsbury for performing the statistical analyses. Participation in this study by MCC was supported by a grant from the Ing. Aldo Gini Foundation of Padova. The figures were prepared by Sharon Hagan, Jan Elder and Judy Wiglesworth typed the manuscript.

References

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

ARMITAGE, K., B. (1974) - Male behaviour and territoriality in the yellow-bellied marmot. *J. Zool., Lond.*, 172: 233-265.

ARMITAGE, K., B. (1982) - Marmots and coyotes: behavior of prey and predator. *J. Mamm.*, 63: 503-505.

ARMITAGE, K., B. & C., M., SALSBURY (1992) - Factors affecting oxygen consumption in wild-caught yellow-bellied marmots (*Marmota flaviventris*). *Comp. Biochem. Physiol.*, 103A: 729-737.

BARASH, D., P. (1973) - The social biology of the Olympic marmot. *Anim. Behav. Monogr.*, 6: 173-245.

BARASH, D., P. (1980) - The influence of reproductive status on foraging by hoary marmots (*Marmota caligata*). *Behav. Ecol. Sociobiol.*, 7: 201-205.

CAREY, H., V. & P., MOORE (1986) - Foraging and predation risk in yellow-bellied marmots. *Amer. Midl. Nat.*, 116: 267-275.

DASILVA, G., L. (1992) - The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. An. Ecol.*, 61: 79-91.

FIGUIER, L. (1892) - Mammalia: their various forms and habits. Adapted by E. P. Wright. *London: Cassell & Co. Ltd.*

FRASE B. A. (1983) - Spatial and behavioral foraging patterns and diet selectivity in the social yellow-bellied marmot. *The University of Kansas, Lawrence, Kansas: Unpublished Ph.D. Dissertation.*

FRASE, B., A. & K., B., ARMITAGE (1984) - Foraging patterns of yellow-bellied marmots: role of kinship and individual variability. *Behav. Ecol. Sociobiol.*, 16: 1-10.

HATCH, S., A. (1990) - Time allocation of Northern Fulmars *Fulmaris glacialis* during the breeding season. *Ornis Scand.*, 21: 89-98.

HERBERS, J., M. (1981) - Time resources and laziness in animals. *Oecologia*, 49: 252-262.

HOLMES, W., G. (1984) - Predation risk and foraging behavior of the hoary marmot in Alaska. *Behav. Ecol. Sociobiol.*, 15: 293-301.

HOOGLAND, J., L. (1981) - The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62: 252-272.

IVINS, B., L. & A., T., SMITH (1983) - Responses of pikas (*Ochotona princeps*, Lagomorpha) to naturally occurring terrestrial predators. *Behav. Ecol. Sociobiol.*, 13: 277-285.

KILGORE, D., L., JR. & K., B., ARMITAGE (1978) - Energetics of yellow-bellied marmot populations. *Ecology*, 59: 78-88.

KREBS, J., R., & A., KACELNIK (1991) - Decision-making, pp. 105-136. In: Krebs J. R. & Davies N. B., Edits. Behavioural ecology: an evolutionary approach, 3rd ed. *Oxford, England: Blackwell Scientific Publications*.

MACWHIRTER, R., B. (1991) - Effects of reproduction on activity and foraging behaviour of adult female Columbian ground squirrels. *Can. J. Zool.*, 69: 2209-2216.

MACWHIRTER, R., B. (1992) - Vocal and escape responses of Columbian ground squirrels to simulated terrestrial and aerial predator attacks. *Ethology*, 91: 311-325.

MELCHER, J., C., ARMITAGE, K., B. & W., P., PORTER (1989) - Energy allocation by yellow-bellied marmots. *Physiol. Zool.*, 62: 429-448.

MELCHER, J., C., ARMITAGE, K., B. & W., P., PORTER, (1990) - Thermal influences on the activity and energetics of yellow-bellied marmots (*Marmota flaviventris*). *Physiol. Zool.*, 68: 803-820.

OWINGS, D., H. & D., W., LEGER (1980) - Chatter vocalizations of California ground squirrels: predator- and social-role specificity. *J. Comp. Ethol.*, 54: 163-184.

SCHWAGMEYER, P. & C., BROWN (1981) - Conspecific reaction to playback of thirteen-lined ground squirrel vocalizations. *J. Comp. Ethol.*, 56: 25-32.

SHAW, R. G. & MITCHELL-OLDS, T. (1993) - Anova for unbalanced data: a review. *Ecology*, 74: 1638-1645.

SHERMAN, P., W. (1977) - Nepotism and the evolution of alarm calls. *Science*, 197: 1246-1253.

STEPHENS, D. W. & J. R. KREBS (1986) - Foraging theory. *Princeton, New Jersey, USA: Princeton University Press*.

TRAVIS S. E. & K. B. ARMITAGE (1972) - Some quantitative aspects of the behavior of marmots. *Trans. Kan. Acad. Sci.*, 75: 308-321.

VAN VUREN, D. (1990) - Dispersal of yellow-bellied marmots. *The University of Kansas, Lawrence, Kansas: Unpublished Ph. D. Dissertation*.

WEINER, J. (1992) - Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *TREE*, 7: 384-388.