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Population time budget for the yellow-bellied marmot

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Time budgets for 17 behaviors were analyzed for cohort, day-period, season-period and interactions among the main effects for three colonies of yellow-bellied marmots in the Upper East River Valley in western Colorado. These effects explained up to 79% of the variation in the behaviors. Marmots allocated more time (40-60%, 110-265 min daily) above-ground to sitting/lying than to any other activity. Foraging was the other major activity (12-23%, 37 to 94 min daily). Vigilance/alert varied from 1.1 to 14.5% and from 12.0 to 71.7 min daily. Social status affected the time budget, especially time allocated to vigilance/alert. All other behaviors averaged about 5% or less except for out-of-sight and enter-burrow. The adult male cohort spent significantly more time above-ground than all other cohorts and reproductive females allocated significantly more time to foraging than the other cohorts. The amount of time spent above-ground decreased linearly from the down-river site to the up-river site. The proportion of time spent above-ground was significantly less at mid day than in the morning or afternoon. Above-ground activity was lowest during gestation, increased during lactation, remained high during early post-lactation, and declined during the final season-period. The following significant relationships common to the three colonies suggest species characteristics or common environmental influences: more time allocated to foraging and foraging-vigilance in the afternoon and more time allocated to foraging-alert, alert, and locomotion during gestation and lactation than during post-lactation. Marmots adjust their behaviors according to prevailing conditions. The remaining significant relationships can be attributed to specific age-sex cohorts or to habitat differences. Because marmots allocate so much time to sitting/lying, we suggest that energy budgets are not constrained by foraging time but by time required to process ingested food. Similarly, time spent vigilant/alert does not seem to constrain energy intake. Social behavior is not limited by time, but could easily be expanded by spending less time inactive. In general, there do not seem to be tradeoffs among activities. Among other species of ground-dwelling sciurids, social behavior occupies a small proportion of the time budget, but the amount of time allocated to foraging and sitting/lying varies widely.

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INTRODUCTION

Time and energy budgets vary widely among animals. Varying the time budget is a means of coping with a changing environment. Because time is limited, time spent in one activity decreases the time available for some other activity. For example, an aggressive animal could spend so much time chasing other animals that it spends less than average time on mating and reproduction (PIANKA 1988).

Generally time available for foraging is considered to be critical; sufficient time must be allocated to foraging to meet the energy demands of growth, maintenance, and reproduction (S.A. ALTMANN 1974, BEKOFF & WELLS 1981). Time spent in other activities reduces the time available for foraging. However, time must be allocated to activities such as mating and reproduction, predator defense, defense of resources against conspecifics, and self-maintenance.

The allocation of time to various activities is of special importance to hibernating sciurids that have a short active season. The yellow-bellied marmot (*Marmota flaviventris*) has 4-5 months in which to grow, reproduce, and prepare for hibernation (ARMITAGE 1991). Time allocation is influenced by environmental conditions. Yellow-bellied marmots are energy conservers (ARMITAGE et al. 1990); the adaptations for coping with cold environments constrain their activity under heat stress (MELCHER et al. 1990). Thus, for each day during the summer a large part is either unavailable for above-ground activity or above-ground activity is restricted. Furthermore, marmot activity at standard operating temperatures above or below the thermoneutral zone exacts energy costs. The short active season and the daily thermal constraints indicate that allocation of time to various activities is of considerable importance.

This paper describes the time budget of three populations (= colonies) of yellow-bellied marmots. Our objective was to determine how time is allocated among various essential activities, such as foraging and social behavior, which is required to maintain matrilineal structure and defence of matrilineal space (ARMITAGE 1984).

We report both the percentage of time and the number of minutes allocated to 17 behaviors. Both relative and absolute time allocation are presented because animals may keep the proportion of time allocated to an activity constant, but increase or decrease the amount of time depending on the length of time of daily

activity. For example, the proportion of time allocated to foraging may increase throughout the summer, but because days become shorter, the number of minutes spent foraging could decrease. Thus, in order to understand time budgeting, it is important to know how changing the percentage of time allocated to an activity affects the absolute time spent in that activity.

METHODS

This study was conducted in the Upper East River Valley, Gunnison County, Colorado, USA from June 13 through August 14, 1991. Populations of the yellow-bellied marmot, *Marmota flaviventris*, located on the valley slopes and valley floor, range from solitary males or females occupying minihabitat sites to concentrations of up to 11 adult females and one or more adult males with associated yearlings (animals 1-year-old in their second summer) and young (animals in their first summer) that occupy large habitat patches designated colonial sites (SVENDSEN 1974, ARMITAGE 1991).

Marmots emerge from hibernation in early May and immerge from late August to early September. All animals at all study sites were trapped, weighed, and sexed. Each individual was marked with a non-toxic fur dye for visual identification and first-caught animals received a uniquely numbered Monel metal tag in each ear for permanent identification (ARMITAGE 1962, 1974).

Study populations

Three colonial populations were chosen for time budget studies. River Colony (elevation 2852 m) occupies meadows adjoining the East River. This site receives direct sun from shortly after sunrise until late afternoon when Gothic Mountain shades the site. Most home burrows (ARMITAGE 1962) are located in a steep, shale bank between the meadow area and the river (see ARMITAGE 1974 for photograph of the site). A fence that runs along the top of the bank provides sites for sitting. Marmots at this site were observed for 194 hr. In the following description of the sex-age composition of the population, the number of observations for each animal in each cohort is given in parentheses. The population consisted of three matrilines (ARMITAGE 1984); one with an 8-year-old (212) and four 2-year-old females (291, 230, 216, 189) and two with two 4-year-old females each (60, 57, 34, 19). No adult female was reproductive. No adult male was present but one yearling male (123) and one yearling female (176), offspring of the 8-year-old female, were present.

Picnic Colony (elevation 3048 m) occupies a steep slope with a large talus area in the center of the slope. The slope faces east-northeast so that it receives direct sun from sunrise until mid afternoon when the mountain slope blocks the sun from the southwest and west. Some sun reaches the slope through low areas in the valley ridge. Most of the home burrows are located in the talus slope and animals forage in the adjoining meadows (ARMITAGE 1974). Large boulders are used as sites for sitting and lying. The population, observed for 279 hr, consisted of closely-related females organized into three matrilineal groups: a 6-year-old female (292) and her non-littermate 4-year-old sister (44), a pair of 5-year-old littermate sisters (421, 342) and the 2-year-old daughter (261) of one of them; and a 4-year-old female (218) with her 3-year-old non-littermate sister (7). All females, except the 2-year-old, weaned litters. An adult male (222), a yearling female (123), and six yearling males (77, 73, 73, 65, 62, 13) were present. The number of yearling males varied from time to time; usually three were present at any one observation period.

Marmot Meadow (elevation 2938 m) occupies a gently sloping meadow on the east side of the valley (ARMITAGE 1974). A rock outcrop at the north side of the meadow provides a site for home burrows and boulders for sitting and lying. Direct sun reaches this site much later in the morning than at the other sites and persists much later in the afternoon because the

western sun shines through a mountain pass onto the meadow until sunset. Both the 7-year-old female (437) and her 3-year-old daughter (839) weaned litters. An adult male was present at the start of the study, but was not seen after June 21 and was excluded from the analysis. This population was observed for 183.2 hr.

Behaviors and sampling procedures

Seventeen behaviors were recorded: foraging, foraging-alert, foraging-vigilance, alert, vigilance, sitting, lying, locomotion, out-of-sight, enter-burrow, investigation, social interaction, grooming, gathering-grass, chirping, digging, and play. These behaviors are described in Table 1.

Table 1.

Description of the behaviors recorded during observation bouts.

Foraging:	animal with head down eating. Movement between eating bouts was recorded as locomotion.
Foraging-alert:	head up, looking around while chewing food.
Foraging-vigilance:	sitting up on haunches and looking around while chewing food.
Alert:	head up and looking around while sitting, lying, or foraging and not chewing food.
Vigilance:	sitting upright on the haunches, forelegs held in front of the chest, and surveying the surroundings.
Sitting:	stationary, supporting weight over the haunches and front legs.
Lying:	reclined on the substrate, may be partially propped up by front legs, but the legs do not fully support the body mass.
Locomotion:	running or walking from one location to another.
Out-of-sight:	above-ground animal not visible.
Enter-burrow:	animal enters a burrow and is not visible.
Investigation:	exploration of immediate environment by apparent sniffing of rocks, vegetation, ground, etc.; may include cheek-rubbing (ARMITAGE 1976) and includes slow walking while sniffing.
Social interaction:	greeting, flight, or chase (ARMITAGE 1962, 1973).
Grooming:	scratching an anterior part of the body with a hind-foot or chewing at the fur, usually while sitting on haunches and chewing at some part of the body that can be reached by the mouth; includes allogrooming where one individual chews at the fur of another individual.
Gathering-grass:	pulling at grass, usually dried, with the mouth and pushing the grass toward the back of the jaw with the fore feet, the grass is not eaten but is carried into a burrow.
Chirping:	high-pitched vocalizations (WARING 1966).
Digging:	scratching the substrate with the fore feet or excavating dirt from a burrow.
Play:	a variety of motor patterns, including chase/flee, hide/seek, grapple, and mouth-spar (JAMIESON & ARMITAGE 1987).

Sites were usually observed for entire days. Observers arrived at the site before sunrise prior to marmot emergence and remained until after sunset after marmots immerged. Each day was divided into three "day-periods": morning (from first emergence until 10:00 hr), mid day (10:00-16:00 hr), and afternoon (16:00 until 0.5 hr past the last observed activity). The length of the morning and afternoon periods varied with changing photoperiod over the summer. Activity in all day-periods varied with weather conditions; steady rain of more than 0.5 hr disrupted observations; marmots generally retired to their burrows.

Both scan sampling and focal animal sampling were used (J. ALTMANN 1974). At the start of each day-period, and once every 30 min thereafter, we scanned the population and recorded each animal seen or known to be active (e.g., a foraging animal might move behind a bush and be temporarily out of sight). Between censuses, we observed individual animals. Each observation bout consisted of recording a focal animal's behavior (Table 1) every 30 sec for 5 min. In deciding which animal to observe, we chose the first one that we could find, when the bout was finished, another animal was located and the bout repeated. When another animal could not be found (e.g., only one animal active), the same animal was observed as in the previous bout. To facilitate observations, two observers were stationed at the same site for the morning and evening periods when marmots are most active (ARMITAGE 1962). Two observers could keep track of where individual marmots were active and reduced potential bias in the data that could occur if sampling were restricted to a few individuals that were easily found.

Data analysis

The total number of observations and the number of observations per behavior were tallied for each animal for each day-period for each day at each site. Average values for each behavior for each individual animal were calculated for each day-period; thus each animal contributed no more than one data point for each day-period in the statistical analyses. For example, the 2109 total observations at Picnic were condensed to 255 statistical samples. Behavioral frequencies (per cent time allocated to each behavior) were calculated and sorted into groups based on cohort, day-period, day, and site. Cohorts consisted of the following: reproductive females, non-reproductive females, adult male, yearling females, and yearling males. The average frequency for each behavior was calculated for each group. The average time (minutes) spent per individual per behavior was calculated by multiplying the average frequency by the day-period length (minutes). The average time per individual statistic is largely dependent on the length of the day-period; thus, it is not a standard measure across day-periods and days.

From the census data, we determined the average number of animals in each cohort active in each day-period. The total time (minutes) animals in a cohort spent per behavior was calculated as the product of the average time spent per individual and the average number of individuals active in the cohort. Finally, a population-based estimate of the total time spent per individual per behavior was generated by dividing total time by the total number of marmots in the cohort, including those animals known to be resident at a site but not observed. Thus, the population-based estimates of total time resulted from extrapolating data collected for those animals observed in each cohort to all animals present in the cohort.

The time available for above-ground activity was calculated for each day of observation. Time available for the morning period was the number of minutes between the time the first animal appeared and 10:00 hr. For mid day, the time available was 360 min. For the afternoon period, time available was the number of minutes from 16:00 hr until the last animal immerged. Values calculated for each day were averaged to produce a mean value for the entire study period for each colony.

We used a general linear model (GLM) ANOVA (SAS Institute, Inc.) to compare behavior among cohorts among day-periods throughout the season for each population. We used the type III method as it provides the most readily interpretable tests when the number of observations per cell varies. A potential error in the use of this method is that significant differences may be missed; i.e., a true effect may be rejected when, in fact, it really exists (SHAW

& MITCHELL-OLDS 1993). Thus, the finding of significant effects is likely to be conservative. However, because we did so many statistical comparisons, the probability of obtaining a significant result by chance increases. Thus, the conservative nature of the model III analysis likely compensated for the likelihood of obtaining significance by chance.

Because the season at up-valley populations may lag the season of down-valley populations by as much as 21 days (VAN VUREN & ARMITAGE 1991), seasonal events were adjusted to the reproductive cycle rather than to absolute time. The season was divided into five season-periods: gestation, lactation, and three 10-day post-lactation periods. Each behavior was analyzed separately for each colony because the data files were too large to consider all behaviors in a single analysis. Selected behaviors were compared among colonies. Three main effects, cohort, day-period, and season-period, and all possible interactions were considered in GLM ANOVA. Multiple comparisons of means (GT2 method) were performed to distinguish which levels within the main effects differed significantly. Each GLM ANOVA was repeated with the non-significant interaction terms removed to increase the power of the test. For the main effects, the cohorts were compared over all day-periods and season-periods; day-periods were compared over all cohorts and season-periods, and season-periods were compared over all cohorts and day-periods.

Two analyses were performed for each behavior. One compared the arcsin transformed average frequencies for each cohort and another compared the population-based estimates of total time (min) spent per individual for each cohort. Because so many analyses were run, only those significant at $P \leq 0.01$ were considered in order to avoid Type II errors (SOKAL & ROHLF 1981). However, all significant results are displayed in Table 4. In the following discussion, many statistically significant results are not described because no plausible biological interpretation was available.

RESULTS AND DISCUSSION

Time spent above-ground

The average number of minutes available for daily activity ranged from 657.6 at River to 744.6 at Picnic. However, the number of minutes used (= activity) ranged from 354.2 at Picnic to 414.3 at River (Fig. 1). Both the proportion of the avail-

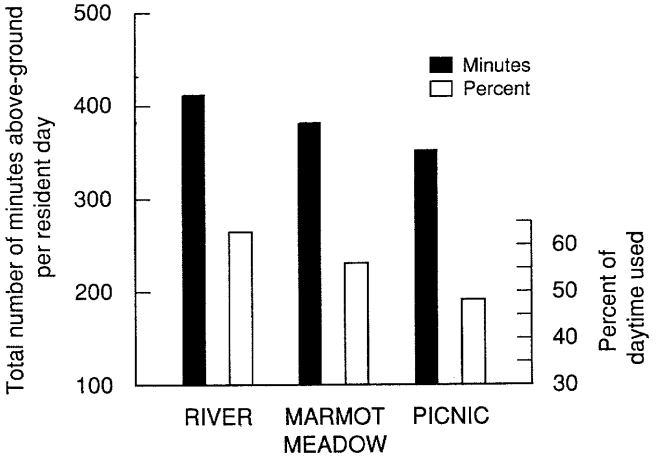

Fig. 1. — The average amount of time spent above-ground per resident per day for three populations of yellow-bellied marmots.

able time and the amount of time used decreased slightly from River located down-valley to Picnic, the colony located farthest up-valley. The difference between River and Picnic was statistically significant ($P = 0.0001$).

The distribution of minutes used varied significantly among all day-periods ($P = 0.0001$; mid day > afternoon > morning, Fig. 2). However, the proportion of time used was generally higher in the morning and afternoon and low at mid day (Fig. 2). The number of minutes active in the morning varied little among colonies, but Picnic used a much lower proportion of the available time. There was a significant

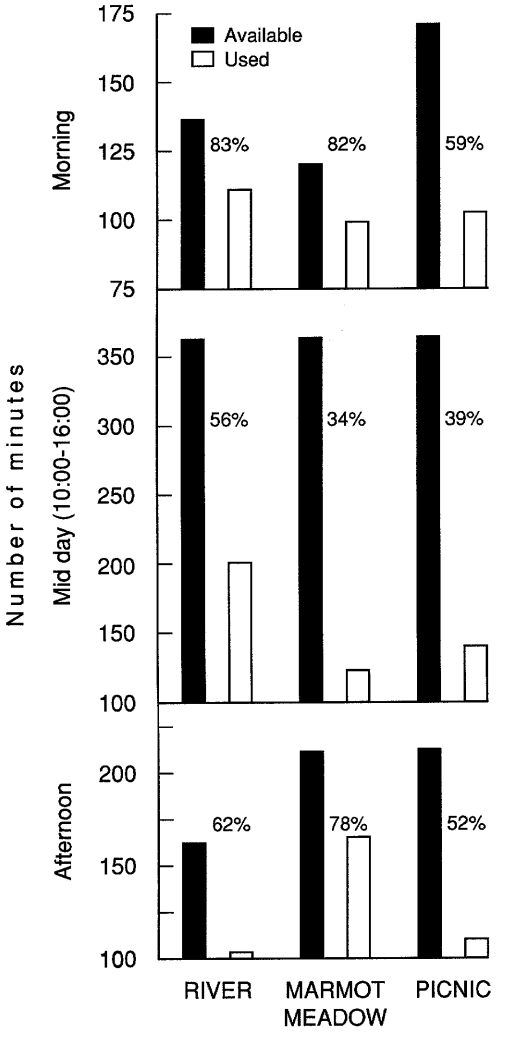

Fig. 2. — The relationship between the time available and the time used for above-ground activity for each day-period for three populations of yellow-bellied marmots.

colony X day-period interaction (P = 0.0001). Animals at Marmot Meadow were more active in the afternoon and marmots at River were more active at mid day (Fig. 2). Across all three colonies, animals were active for 74.9% of the available time in the morning; 43.1%, in mid day; and 64.1%, in the afternoon.

Above-ground activity varied seasonally; it was lowest during gestation, increased during lactation, remained high during the first and second 10-day post-lactation periods, and declined during the final season-period (Fig. 3). A significant season-period X day-period interaction (P = 0.029) revealed that the number of minutes of above-ground activity increased by 36% at mid day during the first 20 days post-lactation. The increase occurred primarily because reproductive females increased time above-ground during the same post-lactation periods when other cohorts changed little or not at all (Table 2). This increase coincides with the development of

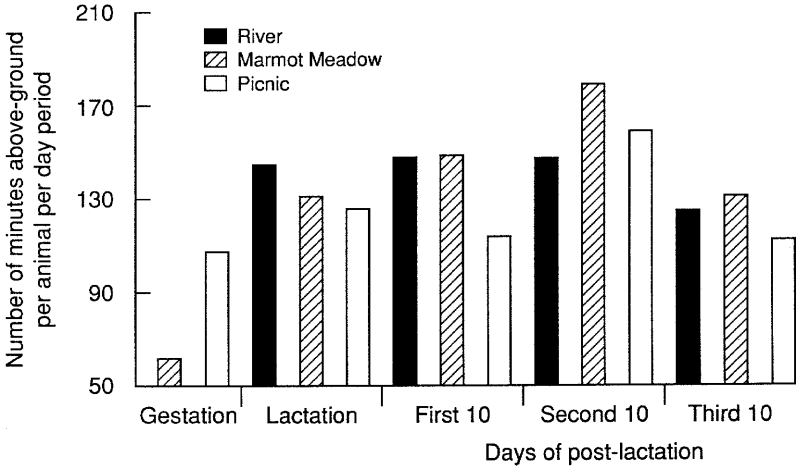

Fig. 3. — The average number of minutes above-ground per day-period for each season-period for three populations of yellow-bellied marmots. Total daily time may be calculated by multiplying the values by three.

Table 2.

The mean number of minutes each cohort was active for each season-period averaged across all day-periods. The season-period X cohort interaction was very highly significant (P = 0.0001).

Season-periods	Animal cohorts				
	Reproductive females	Nonreproductive females	Adult males	Yearlings	
				females	males
Gestation	69.0	137.1	148.6	159.6	114.6
Lactation	113.6	145.7	198.2	125.6	96.1
Post-lactation					
1st 10 days	150.0	124.8	165.9	136.0	119.2
2nd 10 days	189.4	112.0	183.1	132.5	125.1
3rd 10 days	144.1	116.1	135.4	110.8	47.5

Table 3.

The number of minutes spent above-ground for each cohort of yellow-bellied marmots. Means are averaged across day-periods and season-periods. The mean number of minutes active daily can be obtained by multiplying the mean values in the table by 3.

Animal cohort	Mean	SD
Reproductive females	130.0	67.4
Nonreproductive females	133.1	66.9
Adult males	175.6	63.9
Yearling females	137.5	80.5
Yearling males	107.1	64.7

extensive above-ground activity by the young and the increased time of reproductive females probably represents a form of maternal care. Further investigations of juvenile and adult time budgets are required to document this interpretation.

The amount of time active differed significantly among cohorts (P = 0.0001). The adult male at Picnic was significantly more active than all other cohorts and both cohorts of adult females and the yearling females were significantly more active than yearling males (Table 3). At both Picnic and River, the low values for male yearlings were because male yearlings spent less time sitting or lying (an average of 196 min for females and 134 min for male yearlings). A significant colony X cohort interaction (P = 0.0004) revealed that male yearlings were more active at River than at Picnic, probably a consequence of no adult male being present at River. Adult males harass yearling males who enter burrows to escape the adult males (Armitage 1974).

Foraging

The mean percentage of time allocated to foraging varied from 12% for the adult male at Picnic Colony to 22.6% for the reproductive females at Marmot Meadow. The mean number of minutes allocated daily varied from 37.5 for yearling females at Picnic to 94 min for the females at Marmot Meadow. Although the adult male allocated the least percentage of time, he allocated 63.9 min per day, the fourth highest of all cohorts. The high number of minutes occurred because the male spent more time above-ground than any other cohort.

All populations allocated both a significantly greater proportion of time and more minutes to foraging in the afternoon; least time was allocated during mid day at Picnic and River and in the morning at Marmot Meadow (Table 4, Fig. 4). The low allocation in the morning at Marmot Meadow probably occurred because the sun reaches this site later in the morning than at the other sites. A comparison across colonies of time foraging for adult females revealed that a significantly greater percentage of time was allocated in the afternoon than in the morning and more in the afternoon and morning than at mid day (P = 0.0013). In addition, there was a significant (P = 0.0015) colony X day-period interaction. There was little difference in the percentage time allocated to foraging in the morning, but more time was allocated at Marmot Meadow during mid day and less time at River in the afternoon (Fig. 4).

Table 4.

Significant effects from the GLM ANOVA. For each effect the left-hand column is the average frequency (% of time) and the right-hand column is the total time per individual. Colony symbols (P = Picnic, M = Marmot Meadow, R = River) indicate significance for that colony; one symbol, $P = 0.05$; two symbols, $P = 0.01$; three symbols, $P = 0.001$.

Behavior	Cohort		Day-period		Season-period		Cohort × day-period		Cohort × season-period		Day-period × season-period		Cohort × day-period × season-period	
Foraging	PP		PPP RRR M	PPP RR	RR PPP	RR PPP					PP	PPP		
Foraging-alert			R MMM	R	PPP RRR MMM	P RRR					R			
Foraging-vigilance	PP RRR	RRR	PP RRR	P PRR	RRR	P RRR	P RRR	RRR	PPP RRR	RRR	RRR	RRR	PP RRR	RRR
Locomotion	RR	PP	PP		PP R MM	PP R MM	RRR	RR	RR	RR	RRR	PPP R	R	
Lying		PPP	PPP MMM	PPP MM							PPP R			
Sitting		PPP R	RRR MMM	P RRR	PPP	PPP MM	PPP RR	RRR		PPP	RR	R		
Alert					PPP RRR MM	PPP RRR								
Vigilance	PPP RRR	PPP	R	RRR	MMM	M	R			RR	RR			
Out-of-sight	P	PPP	RRR	PP RRR	RR		RR							
Enter-burrow	PPP	PPP	P R MMM	PP MMM	PP	PPP	PPP	PPP	P	PPP		PPP	PPP	PPP
Grooming	PPP	PPP	PPP	PPP										RR
Social			P	P RR	MMM	R MMM		RR				RR		
Gathering-grass	PP					M			PP			M		R
Chirp	PPP		PPP	PP	PPP	P	PPP	PPP	PPP	P	PPP	P	PPP	PPP
Play	PPP	PPP	R		R	RR			R	RR				

At River and Picnic more time and a greater percentage of time were allocated to foraging during the gestation and lactation periods than during the post-lactation periods (Table 4, Fig. 5). At both colonies there was a marked decrease in foraging time in the third post-lactation period. As the season progressed, marmots at Picnic tended to decrease the percentage of time foraging in the morning and mid day day-periods whereas marmots at River decreased percentage of time foraging only at mid day. This pattern of decrease in percentage of time allocated to foraging was supported by an analysis across colonies of foraging by adult females. Foraging time decreased progressively from gestation through post-lactation (P = 0.026); the difference between lactation and the second-10-days post-lactation was statistically significant in pairwise comparisons. There was a highly significant day-period X season-period interaction at Picnic (Table 4). In the first-10-days post-lactation, foraging time was less in the morning than in the afternoon and in the third-10-days post-lactation, less time was spent foraging in the afternoon than during mid day or in the morning (Table 5). However, this interaction does not obscure the overall progressive decline in foraging as the season advanced and the reduced foraging time during mid day (Tables 4-5).

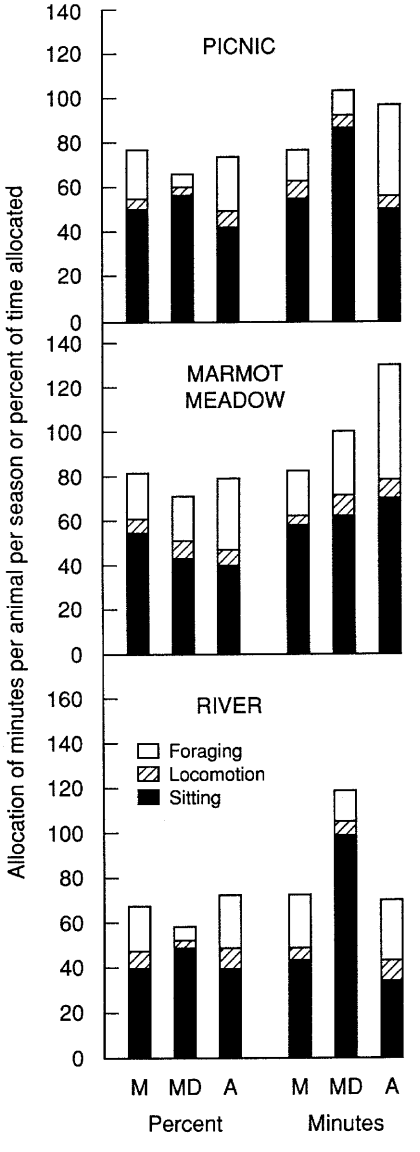

Fig. 4. — The allocation of time to foraging, sitting/lying, and locomotion for each day-period (averaged over all season-periods and cohorts) for each of the three colonies.

An important question is do reproductive females spend more time foraging than non-reproductive females? Only at Picnic were both reproductive and non-reproductive adult females present. However, the only significant difference among cohorts (Table 4) was that the reproductive females spent more time foraging than the adult male.

When foraging by adult females was compared across colonies, the percentage of time foraging was significantly greater at Marmot Meadow than at River and Picnic (P = 0.0007). The difference between reproductive and nonreproductive females was not statistically significant in the GLM but was significant in the GT2 pairwise comparison; reproductive females spent a greater percentage of time foraging than did nonreproductive females. The results of the

GT2 pairwise comparison are supported by the following argument. The females at Marmot Meadow allocated more minutes to foraging than did the females at River and Picnic (Fig. 6). Furthermore, the significant difference among colonies in the percentage time allocated to foraging makes sense because only reproductive females were present at Marmot Meadow and nonreproductive females were present at

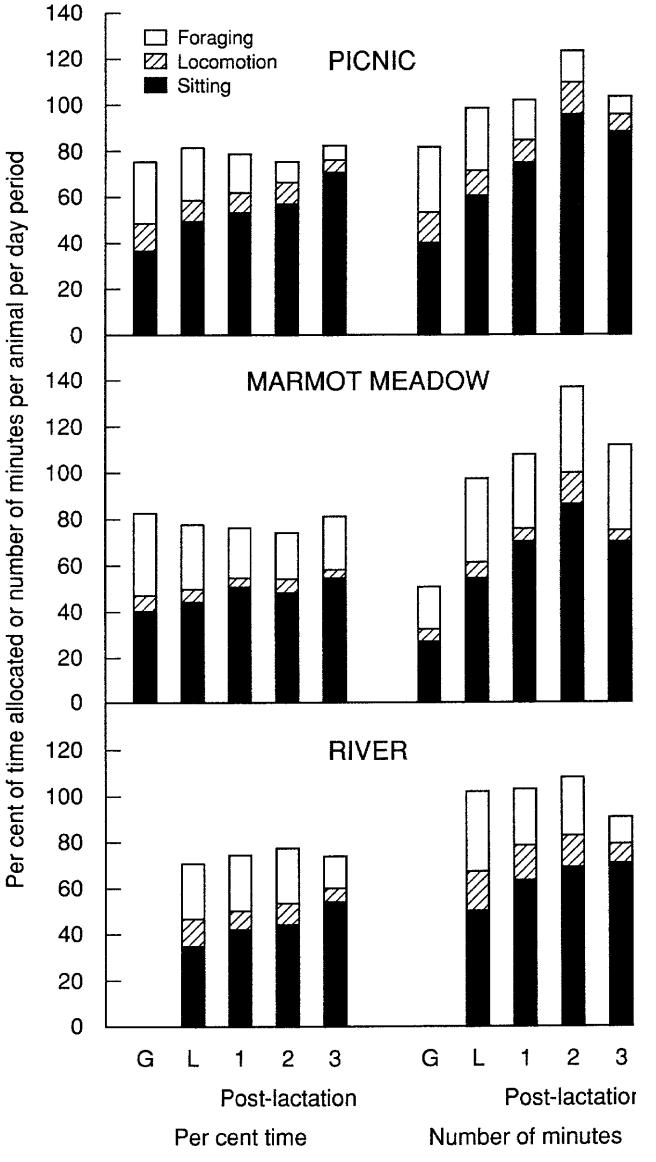

Fig. 5. — The allocation of time to foraging, sitting/lying, and locomotion for each season-period (averaged over all day-periods and cohorts) for each colony.

the other colonies. The failure to detect a difference in foraging time between reproductive and nonreproductive females at Picnic can be attributed to sampling error. For example, the behavior of two reproductive females was recorded only 7 and 44 times. They frequented areas where they were difficult to see; e.g., they were screened from view by willows or aspen. Thus, they were often missed when we censused. Sometimes an animal was seen returning from one of these areas and could then be assigned to the previous census as being present. However, we had no way of knowing how many females were missed at any given census; therefore, we did not attempt to develop or apply a correction factor to our census data. The under-representation of animals in the censusing effectively underestimates the time allocated to foraging. This underestimate probably did not affect other behaviors, such as sitting or lying, as the animals were easily seen during these behaviors. Because of probable sampling errors, further comparisons of adult females among colonies will focus on River and Marmot Meadow.

The difference in time allocated to foraging between the reproductive females at Marmot Meadow (28.8%) and the non-reproductive females at River (23.1%) is statistically significant ($P < 0.05$). Both populations after lactation decreased the percentage of time allocated to foraging except for the high value during the third-10-days post-lactation at Marmot Meadow (Fig. 5). However, the sample size at Marmot Meadow is small and this increase could be random sampling error.

Table 5.

Time (min) spent foraging by reproductive females at Picnic Colony.

Season-periods	Day-periods			
	Morning	Mid day	Afternoon	Total
Gestation	17.5	9.2	33.8	58.5
Lactation	16.9	7.8	27.9	52.6
Post-lactation				
1st 10 days	13.1	13.4	17.6	44.1
2nd 10 days	16.8	7.0	10.3	34.1
3rd 10 days	14.0	8.9	6.5	29.4
Mean	15.8	9.2	22.5	

Table 6.

Percentage of time allocated to lying by all cohorts at Picnic Colony.

Season-periods	Day-periods		
	Morning	Mid day	Afternoon
Gestation	9.2	21.6	7.9
Lactation	14.7	27.4	12.1
Post-lactation			
1st 10 days	7.7	25.7	3.9
2nd 10 days	8.6	23.7	3.3
3rd 10 days	28.1	12.8	10.2
Grand mean	11.0	21.6	6.1

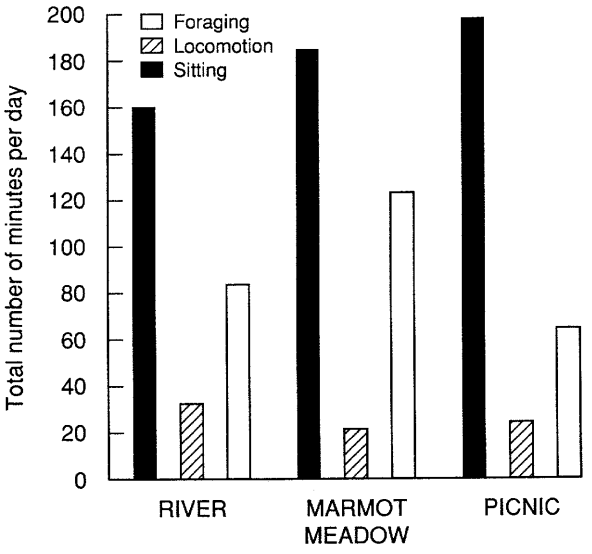

Fig. 6. — The amount of time allocated per day by adult females to foraging, locomotion, and sitting. Values are averaged over all season-periods.

Although the percentage of time spent foraging decreased at Marmot Meadow, the number of minutes spent foraging did not. The high number of minutes allocated to foraging was maintained because the females increased the number of minutes above-ground (Fig. 3).

The differences in foraging times between the reproductive females at Marmot Meadow and the non-reproductive females at River is consistent with patterns of seasonal mass-gain. All males and non-reproductive females gain mass rapidly through the period of lactation; during the first-10-days of the post-lactation period, the rate of mass-gain ceases and animals enter a period of mass stasis (ARMITAGE et al. 1976, ARMITAGE 1996). The period of mass stasis coincides with the period of reduced foraging (Fig. 5). By contrast, the reproductive females do not gain mass during lactation, but gain mass rapidly during the post-lactation periods (ARMITAGE et al. 1976, ARMITAGE 1996). The rapid increase in mass coincides with the continued high level of foraging at Marmot Meadow in the post-lactation period (Fig. 5).

Why did the females at Picnic not maintain a high level of foraging as predicted for reproductive females? In 1991, a drought occurred in the study area. The drought resulted in poor mass-gain by animals in the upper valley where Picnic is located (ARMITAGE 1994). Only three of 25 young and one of four reproductive females survived the hibernation of 1991-1992; a fourth female emigrated. We suggest that the drought reduced the quality of the vegetation, which was reflected in less foraging (= feeding) time. At Marmot Meadow, six of nine young and one of two females survived. Marmot Meadow is relatively flat and lies near the East River. Marmots can readily travel to moist areas near willows where plants remain

green. In general, Marmot Meadow appears to maintain healthy vegetation to a greater degree during drought than does Picnic, which is steep-sloped and much higher above the river.

Sitting and lying

These two behaviors were analyzed separately but are combined in the figures. These combined behaviors were never less than 40% of the above-ground activity and were as high as 60% (Figs 4-5). The mean number of minutes allocated daily varied from 110 for the yearling males at Picnic to 265 for the adult male at Picnic. At all study sites, the percentage of time and number of minutes allocated to sitting/lying increased seasonally until the final season-period when the number of minutes declined (Fig. 5). The decline in the final season-period coincided with the overall decline in above-ground activity (Fig. 3).

At Picnic, the significant animal X season-period interaction (Table 4) revealed that the adults allocated more minutes to sitting late in the season but the yearlings did not. Cohorts also varied in their allocation of minutes to sitting (Table 4). Reproductive females spent more time sitting than yearlings and non-reproductive females and adult males spent more time sitting than did yearling males. Marmots spent a significantly greater percentage of their time sitting late in the season than early in the season (Table 4). The significant animal X day-period interaction (Table 4) indicated that each cohort had a different pattern of sitting. The reproductive females spent a greater percentage of time sitting in the morning and afternoon and less at mid day whereas the non-reproductive female spent a greater percentage of time sitting at mid day and less time in the morning and afternoon. The adult male allocated the highest percentage of time to sitting in the morning and the lowest in the afternoon whereas the yearling female had a trend from highest in the afternoon to lowest in the morning. The yearling male also spent the lowest percentage of time sitting in the afternoon and essentially equal proportions of time at mid day and in the morning.

At Marmot Meadow, the reproductive females spent more minutes sitting (Table 4) during post-lactation than during gestation or lactation. The females allocated a significantly greater percentage of above-ground time to sitting in the morning period compared to the other two periods (Table 4).

At River, there was a highly significant cohort X day-period interaction for both the percentage of time and number of minutes allocated to sitting (Table 4). All cohorts allocated significantly more time to sitting during mid day than in the morning or afternoon (Fig. 4), but the difference was much less for the yearling male. The female cohorts also allocated a significantly greater percentage of time to sitting at mid day, but the yearling male allocated a smaller percentage of time to sitting at mid day than in the morning or afternoon.

A significantly greater percentage of time was allocated to lying (Table 4) at mid day at Picnic and at mid day and in the afternoon at Marmot Meadow. The number of minutes spent lying followed the same trend at both colonies. At River, the percentages were similar for the day-periods, but the number of minutes was greater (but not statistically significant) at mid day. At Picnic, the non-reproductive adult females and the adult male spent significantly more minutes lying than the reproductive females. The adult male also spent more time lying than did the yearling males. The highly significant interaction between day-period and season-period

(Table 4) occurred because in the third-10-days post-lactation period, more time was spent lying in the morning than at other times of the day (Table 6). However, this interaction does not exclude the highly significant affect of season-period because for all other season-periods, a greater percentage of time was allocated to lying during mid day (Table 6).

Sitting and lying were combined for adult females and compared across colonies. Sitting/lying increased significantly throughout the season (P = 0.002) and in pairwise comparisons the percentage of time spent sitting/lying was greater during the last two season-periods (post-lactation) than during lactation. A significant cohort X season-period interaction (P = 0.0077) revealed that nonreproductive females increased sitting/lying more in late summer than reproductive females (Table 7).

There was no relationship between day-period and sitting/lying when day-period was treated as a main effect, but the day-period X cohort interaction (P = 0.04) and the day-period X colony interaction (P = 0.03) were statistically significant. Reproductive females spent about the same proportion of time sitting/lying at all day-periods (45.8-52.9%) whereas nonreproductive females spent much more time sitting/lying during the morning (59%) and mid day (60.4%) periods than during the afternoon (40.5%). The females at all colonies spent about the same proportion of time sitting/lying in the morning (53.5-55.8%) and in the afternoon (40.6-46.7%), but the females at Picnic spent far more time sitting/lying at mid day (58.9%) than the females at River and Marmot Meadow (42.9-47.9%).

Minor activities

Most of the remaining behaviors occupied 5% or less of the time budget (Table 8). For locomotion, the animals at Marmot Meadow allocated less time and the animals at River allocated the most minutes (Fig. 6). This pattern is consistent with habitat structure. At Marmot Meadow, the females live adjacent to the meadow where they forage and need travel only a few meters to begin foraging. At Picnic, some females live near foraging areas but others must travel many meters across the talus slope to reach a foraging area. At River, all animals must cross a deep and broad gulley and travel many meters to reach the prime foraging areas. However, when adult females were compared across colonies, there were no significant effects of colony, cohort, day-period, or season-period nor were any interaction terms significant.

Table 7.

The interaction between animal cohort and season-period for percentage time spent sitting/lying for adult females ($\bar{x}$ ± SD).

Season-period	Reproductive females	Nonreproductive females
Lactation	42.6 ± 13.0	52.4 ± 28.4
Post-lactation		
1st 10 days	53.3 ± 13.8	43.8 ± 21.0
2nd 10 days	54.1 ± 12.6	59.8 ± 21.2
3rd 10 days	57.9 ± 10.2	9.2 ± 9.5

At Picnic, adult males spent more minutes in locomotion than the other cohorts except for the non-reproductive female. The difference was significant in comparisons with the reproductive females and yearling males and nearly so with the yearling female. The high level of locomotion is consistent with male behavior, which includes patrolling his territory (ARMITAGE 1974).

At River, all interaction terms were significant (Table 4). Both percentage of time and number of minutes allocated followed the same trends. Adult females allocated similar amounts of time in each day-period whereas the yearling female allocated more time and the yearling male, the least time, to locomotion in the afternoon. Hence, there was no significant variation with day-period (Fig. 4). The adult and yearling females greatly reduced the time allocated to locomotion in the last season-period whereas the yearling male did not. Overall, there was a reduction in locomotion in the third-10-days post-lactation (Fig. 5). The highest allocation of time to locomotion in the morning occurred during lactation; to mid day, during the second-10-days post-lactation; and to the afternoon, during lactation and the second-10-days post-lactation.

Vigilance and alert were analyzed separately (Table 8), but are combined as vigilance in the figures. Combined values among cohorts ranged from 1.1 to 14.5% and 12.0 to 71.7 min per day.

All populations allocated a significantly greater percentage of time to alert during gestation and lactation and low or decreasing values during post-lactation. The same pattern in the number of minutes allocated occurred at River and Picnic, but not at Marmot Meadow.

At Picnic, the reproductive-female cohort allocated a significantly (Table 4) greater percentage of time to vigilance than the other cohorts; it also allocated significantly more minutes than yearling males and the yearling female and the adult male spent more time vigilant than the yearling males. At River, the adult and yearling females spent a significantly greater percentage of time vigilant than did the yearling males. The significant animal X day-period interaction (Table 4) was a consequence of the yearling male maintaining a higher percentage of vigilance dur-

Table 8.

Time allocated to minor activities. Values are ranges among animal cohorts.

Behavior	Percentage	Min per day
Locomotion	3.4-4.5	9.3-22.5
Alert	0.29-2.4	1.2-9.3
Vigilance	0.8-13.7	10.2-67.2
Foraging-alert	0.29-4.0	0.9-17.4
Foraging vigilance	0.04-0.75	0-2.4
Social	0.43-1.7	1.5-5.7
Investigation	< 1	3.0-9.0
Digging	≤ 0.5	< 4.5
Chirp	0-0.29	< 4.0
Grooming	0.83-3.4	5.7-8.8
Gathering grass	0-0.6	0.5-1.13
Play	0-2.2	1.34-3.0
Enter burrow	0.8-8.0	3.1-10.0
Out-of-sight	5.2-22.6	6.2-31.5

ing mid day than during the morning or afternoon whereas the other cohorts had similar values for each day-period or a high value for morning. The significant day-period X season-period interaction revealed that a greater proportion of time was spent vigilant in the afternoon than in the morning in the third-10-day period of post-lactation but the percentage of time spent vigilant in the morning exceeded that of the afternoon in the other season-periods. Finally, the number of minutes allocated to vigilance was significantly (Table 4) greater at mid day than in the morning or afternoon (Table 9). More time spent vigilant at mid day coincided with fewer animals being active at that time. The significant day-period X season-period interaction (Table 4) occurred as a result of a decrease in vigilance in the morning during mid summer and a large decrease in the afternoon during late summer (Table 9).

The high level of vigilance at River (Figs 7-8) may be a result of human traffic. Hikers frequented a road that ran along the east side of the habitat. Human activity was rare at Marmot Meadow and the animals at Picnic were more distant from human activity than the animals at River. The high mid day values may reflect the greater number of minutes of activity at River than at the other sites (Fig. 2); more above-ground activity provides more opportunities for vigilance.

At Marmot Meadow season-period significantly affected vigilance (Table 4). Both the percentage of time and the number of minutes allocated to vigilance were least during gestation and lactation and highest during post-lactation. High vigilance coincided with the time the young emerged. Furthermore, the two adult females, a mother and her daughter, were agonistic and occupied different burrow systems. Because infanticide may occur (ARMITAGE et al. 1979, BRODY & MELCHER 1985), increased vigilance may have represented defense against infanticide. The combined alert and vigilance will be referred to as wariness, which is defined as being watchful (ARMITAGE & CHIESURA CORONA 1994). The reproductive female cohort at Picnic allocated more time to wariness than the other cohorts. The yearling female at River had the highest wariness, especially in the number of minutes spent. The yearling participated in numerous social interactions and was chased by several adult females; thus, her high level of wariness was likely related to her social status.

At Picnic and Marmot Meadow, a greater proportion of time was allocated to wariness later in the day then earlier in the day (Fig. 7). More time was allocated to wariness at River than at the other sites. The high values of wariness at Marmot

Table 9.

The number of minutes allocated to vigilance by all cohorts at River Colony.

Season-periods	Day-periods			
	Morning	Mid day	Afternoon	Total
Lactation	10.6	15.0	14.1	39.7
Post-lactation				
1st 10 days	7.1	26.1	12.6	45.8
2nd 10 days	7.0	41.6	5.5	54.1
3rd 10 days	20.0	33.1	2.2	55.3
Grand mean	11.6	25.9	10.5	48.0

Meadow in the evening and at River during mid day coincide with high levels of activity at those times (Figs 3, 7).

Allocation of time to wariness remained high at River throughout the study (Fig. 8). Not only was human traffic higher at this site, but the resident animals were from different social groups. Agonistic behavior between members of the social groups could have contributed to the levels of wariness. Wariness was low at Picnic where all the adult females were descended from one female ancestor; most had the same father and were related by 0.5. In contrast to River, agonistic behavior among adult females was rare. High population density probably cannot account for the difference between River and Picnic as both colonies had high densities.

Foraging-alert was significantly affected by both day-period and season-period (Table 4). All populations allocated a greater percentage of time and more minutes to foraging-alert early in the season than during post-lactation.

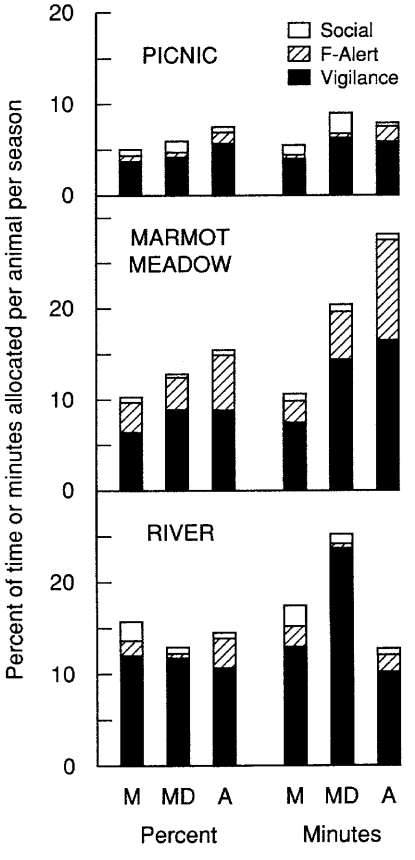

Fig. 7. — The allocation of time to social, feeding-alert (which includes feeding-vigilance), and vigilance (which includes alert) during each day-period (averaged over all season-periods and cohorts) for each colony.

At River, foraging-alert was significantly lower at mid day than in the morning and afternoon. A significant day-period X season-period interaction (Table 4) revealed that the lowest percentage of time allocated to foraging-alert in the morning occurred during the first two 10-day-periods of post-lactation and, at mid day, during the last two 10-day-periods of post-lactation.

All populations allocated significantly more time (Table 4) to foraging-vigilance in the afternoon. At River, all interactions were highly significant (Table 4). The non-reproductive adult females overall allocated more time to foraging-vigilance than the other cohorts and more foraging-vigilance occurred in the afternoon than in the other day-periods. The animal X day-period X season-period interaction can be attributed to the patterns expressed by the yearlings. The male had unusually high values during the second-10-days post-lactation and the female was observed foraging-vigilant only during mid day during the lactation period.

The combined foraging-alert and foraging-vigilance occurred more frequently (percentage and minutes) in the afternoon in all colonies (Fig. 7) and was low at mid day except at Marmot Meadow where the two antagonistic females lived. The combined behavior decreased late in the season in all colonies (Fig. 8). The trends in time allocation for foraging-alert, foraging-vigilance and the combined behaviors parallel the trends in foraging (e.g., Figs 4, 7). This pattern is not unexpected because these

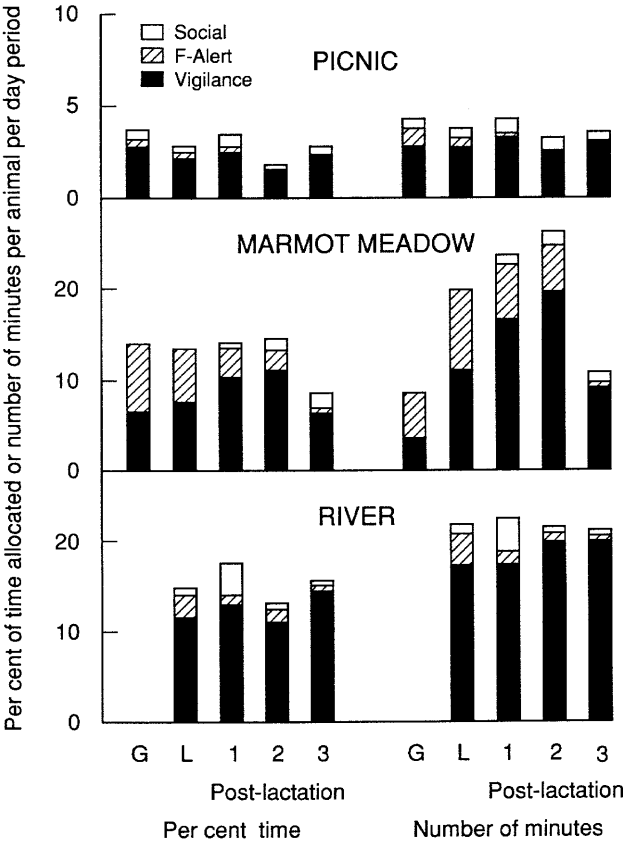

Fig. 8. — The allocation of time to social, feeding-alert (which includes feeding-vigilance), and vigilance (which includes alert) during each season-period (averaged over all day-periods and cohorts) for each colony.

behaviors occur while the animal forages and probably represent a regular proportion of foraging time.

Although social behavior has a prominent role in dispersal, recruitment, social organization, and reproductive success (ARMITAGE 1984, 1986a, 1991; DOWNHOWER & ARMITAGE 1981), little time was allocated to this activity (Table 8). At River where no adult male was present, the yearling male had high values (1.7%, 5.7 min per day); at Picnic where an adult male was present, the yearling-male cohort had low values (0.8%, 2.3 min per day). Social behavior occurred more often during lactation (Table 4, Fig. 7). The cohort X day-period interaction resulted primarily from the high values of the yearling male in the morning and of the other cohorts in mid day. High values also occurred at mid day at Picnic (Table 4, Fig. 7). At mid day marmots spend more time near their burrows; thus proximity may account for high values of social behavior at this time.

The effect of season-period was most pronounced at Marmot Meadow (Table 4). All social interactions occurred during post-lactation and all were between adult females and their young (Fig. 8). The social interactions were distributed throughout the day-periods (Fig. 7) and coincide with the increased time above-ground by the mothers and the increased time spent sitting/lying, which occurs at the burrow area. Most amicable social interactions occur at the burrow area (K.B. ARMITAGE unpublished data).

Among investigation, digging, chirp, and grooming, significant patterns occurred for chirp and grooming. At Picnic, significantly high values of chirp occurred during late post-lactation (Table 4). It is worth noting that the number of minutes allocated to chirp more than tripled at Marmot Meadow after the young emerged. High variances and small sample size probably preclude statistical significance.

At Picnic the reproductive females groomed more than yearlings and the non-reproductive female, but not significantly more than the adult male (Table 4). The adult male groomed significantly more than the non-reproductive female. The Picnic animals groomed significantly more during mid day than during the afternoon or morning.

At Picnic, reproductive females allocated a significantly greater percentage of time to gathering-grass than did all other cohorts (Table 4). This activity occurred primarily during gestation and lactation prior to young emergence. At Marmot Meadow, the reproductive females allocated more minutes to gathering-grass during lactation and the second-10-days post-lactation than at other season-periods. The high value during the second-10-days post-lactation occurred almost entirely at mid day, which accounted for the significant day-period X season-period interaction (Table 4). By contrast, during lactation gathering-grass occurred approximately equally throughout all day-periods. Only during lactation was gathering-grass observed in the morning.

Play did not occur at Marmot Meadow as the only cohort was the reproductive females. At Picnic, the yearling males played significantly more than the other cohorts except for the yearling female. Neither the non-reproductive female nor the adult male played; play by the reproductive females was rare and occurred only in the morning during lactation. Although the yearling female played more than all cohorts except the yearling male, the differences were not statistically significant. Given that adults rarely play and that yearlings frequently play (ARMITAGE 1962, JAMIESON & ARMITAGE 1987), the differences are likely biologically significant. Play was highest in the morning (1.0 to 1.3%), but the day-period effect was statistically significant only at River (Table 4). Play occurred at a higher frequency early in the season (0.88 to 1.2%); no play was observed in late post-lactation. The season-period effect was statistically significant at River (Table 4). The significant cohort X season-period interaction occurred because the yearling female did not play after the first-10-days post-lactation whereas the male yearling had high play activity during lactation and the second-10-days post-lactation. The pattern of seasonal play is consistent with an earlier report that play rarely occurs after mid July (JAMIESON & ARMITAGE 1987).

At all colonies, animals were observed to enter their burrows more at mid day than during the morning or afternoon (Table 4). This pattern is consistent with the thermal environment in which yellow-bellied marmots live. The standard operative temperature frequently exceeds the upper limit of their thermoneutral zone from late morning to mid afternoon on clear days (MELCHER et al. 1990). Thus, during high standard operative temperatures, marmots reduce their above-ground activity and are more likely to be seen entering their burrows.

At Picnic, there was one major departure from the general pattern. Yearling males were likely to enter their burrows just as frequently in the morning and afternoon as in mid day. Because yearling males enter their burrows to avoid the adult male, this avoidance behavior is likely to occur at any time animals are above-ground.

The adult male at Picnic spent more minutes out-of-sight than any other cohort (Table 4). The male wandered more widely than did members of other cohorts and was more likely to move into or behind tall vegetation where he could not be seen. Out-of-sight was significantly affected by day-period at Picnic and River (Table 4). Animals were likely to move out-of-sight during mid day when thermal stress is greatest. Marmots often moved behind rocks or bushes into shady areas at this time.

Major patterns of time allocation

Two behaviors, sitting/lying and foraging, account for more than half of above-ground activity for all animal cohorts at all colonies throughout the active season (Figs 9-10). Furthermore, except at River during lactation, the time allocated to sitting/lying exceeded the time allocated to foraging. Similarly, adult *M. marmota* spend a greater percentage of above-ground time at rest than feeding (SALA et al. 1992) as does *M. olympus* (BARASH 1973). The large amount of time spent inactive characterizes many species and the inactivity was characterized as laziness (HERBERS 1981).

The large amount of time allocated to laziness suggests that energy budgets of marmots are not constrained by time. For example, at Picnic, marmots could double the number of minutes allocated to foraging by reducing sitting/lying by as little as 6% or as much as 47%, depending on the season (Fig. 9). Possibly energy acquisition is limited physiologically by the rate of food processing, in particular, the digestive capacity of the gut (WEINER 1992).

Time spent vigilant or alert also does not seem to constrain energy intake. Time spent in these behaviors (Fig. 8) can readily be recovered by a modest decrease in sitting/lying. At most, this reallocation would require a maximum of 18 to 54 min per day, depending on the colony. However, vigilance and alert also occur during sitting/lying, locomotion, grooming, etc.; thus, the time needed to compensate for time lost foraging would be much less than the maximum.

CAREY & MOORE (1986) reported that *M. flaviventris* in California spent about 10.2% of foraging time on vigilance. We did not determine with what behaviors alert and vigilance were associated. However, during many foraging bouts, only foraging-alert and foraging-vigilance were recorded. On average, the combined foraging-alert and foraging-vigilance varied from 4.2% (Picnic) to 16% (Marmot Meadow) of foraging time. These values are in the same order of magnitude as those reported by CAREY & MOORE and differences between California and Colorado marmots and among Colorado colonies represent local conditions. If time spent in vigilance or alert were critical, marmots could always use foraging-alert or foraging-vigilance exclusively and effectively eliminate costs of vigilance/alert.

Several authors report marmots can reduce the time spent on vigilance by activities such as foraging in areas with a high density of refuges or by foraging in a group (HOLMES 1984, CAREY & MOORE 1986). However, arguments for reducing vigilance assume that time is limiting and that marmots need to conserve time for

other activities. But we suggest that time is not limiting (see above). Marmots adjust vigilance according to prevailing conditions. There is no reason for marmots to engage in behaviors if they are unnecessary. Thus, it makes just as much sense to state that marmot behavior is characterized not by reducing vigilance but by increasing vigilance when conditions so require. That marmots adjust behavior to the current situation is exemplified by changes that occur during post-lactation when young are above-ground. Reproductive females increase the amount of time above ground, decrease the percentage of time foraging, but increase the number of minutes foraging, allocate more time to sitting/lying, especially in the morning, and spend more time in vigilance.

The activity pattern of the adult male and reproductive females differs (Fig. 9). During gestation and lactation, the adult male spent many more minutes above-ground than the reproductive females. Much of the difference is accounted for by sitting/lying and minor activities, especially locomotion. This period of the year is when the highest rates of intrusion by non-resident males occurs (SALSBURY & ARMITAGE 1994) and the high level of male activity probably represents territorial defense. The male maintained a high level of above-ground activity during post-lactation and female activity increased to about the same level, primarily by increasing sitting/lying. This increase coincides with the emergence of young and probably represents defense of young. *M. marmota* increases vigilance after young emerge (SALA et al. 1992). Sitting/lying is part of a general wariness by marmots (ARMITAGE & CHIESURA CORONA 1994); thus increasing sitting/lying increased vigilance.

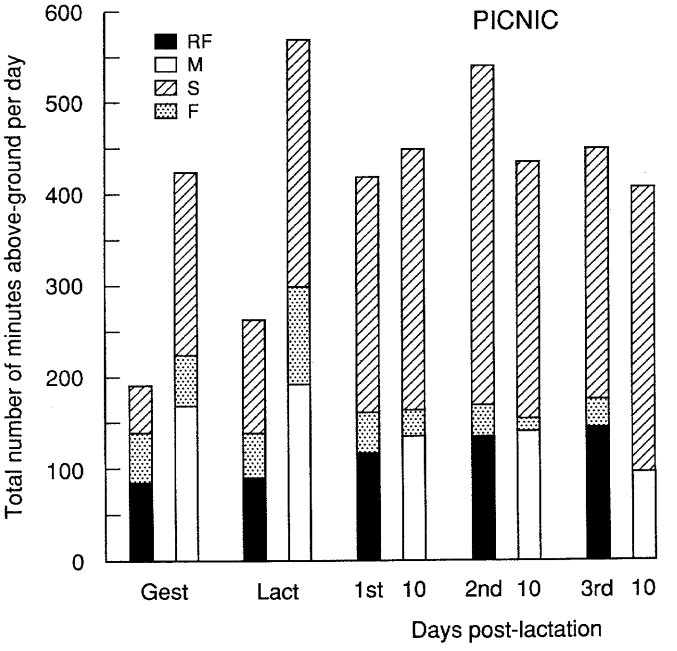

Fig. 9. — The total amount of time allocated to above-ground behaviors at Picnic Colony for each season-period. RF = reproductive females, M = male, S = sitting and lying combined, F = foraging. Solid bars (open or filled) include all behaviors except sitting/lying and foraging.

Because River and Marmot Meadow were similar in the total time spent above-ground (Fig. 1), time allocation of reproductive females (Marmot Meadow) and non-reproductive females (River) can be compared. Both groups spent about the same amount of time above-ground and foraging during lactation (Fig. 10). During post-lactation, the females at Marmot Meadow maintained high levels of foraging whereas the non-reproductive females at River progressively decreased the number of minutes allocated to foraging. Similarly at Picnic, the reproductive females maintained a steady allocation of minutes to foraging throughout post-lactation whereas the foraging time of the male decreased (Fig. 9). Foraging time also decreased in late summer in *M. marmota* (SALA et al. 1992). Adult males and non-reproductive females complete mass-gain by early post-lactation; reproductive females remain stable or lose mass during lactation and increase mass through the first 45 days of post-lactation (ARMITAGE 1996). Thus, mass-gain and time allocated to foraging are related. Interestingly, mass-gain is completed and foraging decreases well before the onset of hibernation, which begins in late August or early September.

Variation explained

The amount of variation explained by the three treatment effects (cohort, day-period, and season-period) and their interactions varied widely among behaviors and among colonies (Table 10). For 45 of the 100 R^2 values, 40% or more of the

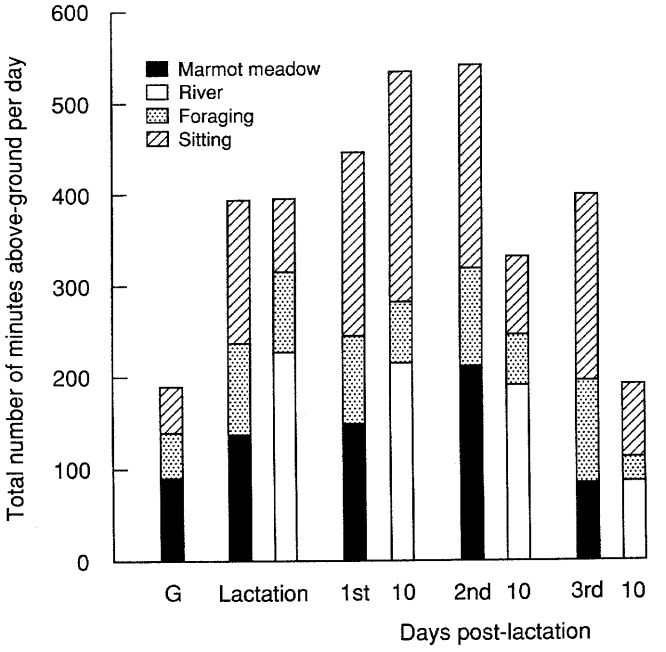

Fig. 10. —The total amount of time allocated to above-ground behaviors for each season-period at Marmot Meadow and River. Only the adult females are included. Solid bars (open or filled) include all behaviors except sitting and foraging. Sitting includes sitting and lying. G = gestation.

variation was explained by the treatment effects. These results emphasize the impact of seasonal and daily changes on the behaviors of a hibernator, as previously described for foraging, foraging-alert, foraging-vigilance, locomotion, sitting, and lying, among others. Cohort significantly affected behaviors less often than day-period or season-period (Table 4), which suggests that those behaviors of high occurrence; e.g., sitting/lying, were common to all members of a cohort. By contrast, significant effects of cohort on minor activities occurred primarily at one colony (Table 4). For many of the minor activities; e.g., investigation, digging, grooming, chirping, the analysis typically explained less than 30% (19 of 28) of the variation. Both foraging-alert and foraging-vigilance, although infrequent behaviors, usually had relatively high R^2s (Table 10). Because these behaviors occurred when marmots were foraging, their expression would be mainly influenced by the same factors that influenced foraging.

Two important factors that affect the time budget, individual variation within cohorts and weather, were not included. Individual differences likely affect all of the behaviors. For example, some individuals are more likely to chirp than others (K.B. ARMITAGE unpublished data), locomotion is affected by the location of an individual's burrow in relationship to its foraging area, and individuals vary widely in the frequency of social behaviors (ARMITAGE 1965, 1986b).

Weather is an important factor affecting time budgets (MELCHER et al. 1990, LOUGHRY 1993). Some weather effects are included in the analysis of day-period; reduced activity at midday is primarily a consequence of thermal stress (MELCHER et al. 1990). However, cloudy, windy, cool, and rainy weather affected behavior, but these factors were not quantified.

Species characteristics and comparisons

Some significant relationships were common to the three colonies of marmots. These common patterns reflect either species characteristics or common environmental influences. All populations allocated more time to foraging in the afternoon. More time was allocated to foraging-alert, alert, and locomotion during gestation and lactation than during post-lactation. More time was allocated to foraging-vigilance in the afternoon. The increase in foraging-vigilance cannot be attributed to the increase in foraging in the afternoon because marmots increased the percentage of time; i.e., a greater proportion of time was allocated to this behavior. The seasonal decline in foraging should also be included; more recent time budgets taken later in the season revealed that foraging by reproductive females also declines prior to hibernation (K.B. ARMITAGE unpublished data). The remaining significant relationships can be attributed to specific age-sex cohorts (e.g., yearling, reproductive females) or to habitat differences.

As with yellow-bellied marmots (Table 8), social behavior among other ground-dwelling sciurids occupies a small proportion (usually < 5%) of the time budget (*Spermophilus elegans*, ZEGERS 1981; *S. tridecemlineatus* and *S. spilosoma*, STREUBEL 1975 cited in ZEGERS 1981; *S. beldingi*, MORTON 1975; *S. columbianus*, BETTS 1976; *S. beecheyi*, LEGER et al. 1983; *Cynomys ludovicianus*, LOUGHRY 1993).

The amount of time allocated to foraging varies widely (Table 11). For some species, more time is allocated to foraging late in the summer than early in the summer; e.g., *S. saturatus* and *S. beldingi*. Other species decrease the time spent foraging in late summer, e.g., *S. elegans*, *M. marmota*, reproductive female *C. ludo-*

Table 10.

R^2 values from the GLM ANOVA for the 17 behaviors recorded in the time budget

	Colonies					
	River		Marmot Meadow		Picnic	
Behavior	Percentage	No. of min	Percentage	No. of min	Percentage	No. of min
Foraging	0.498	0.412	0.379	0.479	0.482	0.622
Sitting	0.497	0.658	0.502	0.264	0.433	0.518
Lying	0.354	0.277	0.396	0.378	0.479	0.486
Locomotion	0.581	0.499	0.392	0.495	0.316	0.371
Alert	0.442	0.399	0.367	0.273	0.353	0.327
Vigilance	0.499	0.458	0.459	0.405	0.452	0.286
Foraging-alert	0.494	0.385	0.466	0.353	0.355	0.243
Foraging-vigilance	0.791	0.778	0.287	0.299	0.399	0.307
Social	0.353	0.433	0.551	0.454	0.452	0.286
Investigation	0.251	0.269	0.307	0.226	0.233	0.229
Digging	0.288	0.207	0.171	0.216	0.117	0.111
Chirping	0	0	0.233	0.255	0.638	0.430
Grooming	0.333	0.348	0.152	0.081	0.422	0.306
Gathering-grass	0.579	0.486	0.286	0.435	0.374	0.236
Play	0.406	0.415			0.303	0.294
Enter-burrow	0.263	0.259	0.471	0.465	0.529	0.571
Out-of-sight	0.414	0.434	0.367	0.503	0.307	0.269

vicianus. There also may be considerable variation among age-sex cohorts; e.g., *S. columbianus* and *M. flaviventris*. Locomotion usually occupies < 15% of the above-ground activity, but varies widely among species (Table 11).

The large-bodied herbivores, the marmots, allocate less time to foraging than nearly all of the smaller-bodied herbivores (Table 11). Because of their larger size, marmots should have greater total energy requirements and would be expected to allocate more time to foraging than the smaller species. However, foraging time does not necessarily measure ingestion rate. Quite possibly the quality and quantity of food varies widely. Marmots generally live in food-rich habitats; yellow-bellied marmots ingest less than 4% of the available primary production and have a production efficiency about 7 times greater than that of non-heterothermic mammals (ARMITAGE 1991). The small-bodied species may spend more time foraging because their habitats are not as rich as those of marmots. Information on the importance of food quality and quantity on foraging time is seriously lacking. Animals in poorer habitats may spend more time searching, thus we need to know ingestion rates. The length of time required to process ingested food needs to be determined. Marmots may be restricted to food-rich habitats because a long gut-retention time precludes the rapid processing of low quality food; thus, nothing is gained by increasing foraging time. Smaller species with higher mass-specific metabolic rates may process food more rapidly and may gain by increasing foraging time. However, it would seem that all members of the Marmotini may have similar physiologies; thus, it is more likely that the differences in foraging time are related to the distribution and abundance of nutritious food.

The widest variation occurs in behaviors, such as sitting or lying, recorded as inactive, and in vigilance. Some of the variation can be attributed to the way in which behaviors are recorded. For example, vigilance or alert are recorded when an animal has its head up or sits bipedally on its hind legs. When yellow-bellied marmots sit or lie, they are wary (ARMITAGE & CHIESURA CORONA 1994). When some activity catches their attention, they may lift their head or assume the upright position. But many times they sit in a position with the head at an angle so that the observer cannot distinguish between sitting and alert. Probably the high values for *S. columbianus* and *C. ludovicianus* represent the recording of any sitting behavior as alert. The absence of vigilance in *S. saturatus* occurred because the authors recorded all inactive behaviors (non-locomotion or non-foraging) as sitting. If vigilance and inactive are combined in order to remove the ambiguity of the degree of alertness for the same species for which one or both behaviors were recorded, the combined values equal or exceed the percentage of time allocated to foraging for five of them (Table 11).

Another factor that makes comparisons among species difficult is that not all studies were made throughout the day or throughout the day for the entire study period. Often the study period does not include the entire active season. Although a species may increase the percentage of time foraging in late summer, if the time above-ground decreases, the animals may actually be foraging less than earlier in the summer. For example, female *M. olympus* spent about 37% of the above-ground time feeding in June and in August. However, the time above-ground in August was 18% less than in June (BARASH 1973); thus, Olympic marmots spent less time feeding late in the summer. The amount of time spent above-ground by *S. columbianus*, *M. flaviventris*, and *M. marmota* decreases in late summer and this decrease is reflected in fewer minutes spent feeding by most cohorts of *M. flaviventris* (e.g., Table 5).

Finally, nearly all studies of ground-dwelling sciurids report reduced activity during mid day in summer when temperatures are high. During late summer when air temperature is low in the morning and afternoon, activity may shift toward mid day; e.g., *M. marmota* (PERRIN et al. 1992, SALA et al. 1992), *C. ludovicianus* (LOUGHRY 1993), and *S. columbianus* (BETTS 1976).

Table 11.

The percentage of time allocated to major above-ground behaviors for adult ground-dwelling sciurids. Vigilance includes behaviors recorded as alert or vigilance. Inactive includes sitting and lying.

Species	Foraging	Vigilance	Inactive	Locomotion	Reference
S. saturatus	11-28	—	65	3	KENAGY et al. (1989)
S. columbianus	49-74	24	< 2	< 5	BETTS (1976)
S. beldingi	42-72	—	10	15	MORTON (1975)
S. beecheyi	70	12.8	4.5	4.7	LEGER et al. (1983)
S. elegans	36	18	17	14	ZEGERS (1981)
S. tridecemlineatus	42	12	—	—	STREUBEL (1975)
S. spilosoma	46	15	—	—	STREUBEL (1975)
C. ludovicianus	62-74	19-28	—	—	LOUGHRY (1993)
M. marmota	30	6	44.8	13.9	SALA et al. (1992)
M. olympus	26-37	1-5	46-55	< 5	BARASH (1973)
M. flaviventris	12-23	1-15	40-60	3.4-5.1	This study

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