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We measured the time budgets of yellow-bellied marmots to determine what constraints limited energy acquisition and whether trade-offs occurred among the behaviors. Therefore, we focus on which behaviors form a consistent pattern among marmot populations, the degree of phenotypic plasticity in the time allocated to the behaviors, and the biotic and abiotic factors associated with variations in time allocations. Time budgets for 14 behaviors were recorded at six sites in the Upper East River Valley in western Colorado over two active seasons. Data were analyzed for cohort, day-period and season-period, and for interactions among the main effects. Sitting and vigilance, accounting for 63% of aboveground activity, are strongly associated with wariness, the need for marmots to monitor the presence of conspecific and predatory intruders. Foraging accounts for 15% of daily activity. These three activities are the major contributors to time budgets at all sites. Radiation, acting as a thermal constraint, greatly reduces activity during mid-day when radiation is intense. Sitting is the only major behavior to increase at mid-day, presumably to maintain wariness. Time allocations change little over the season-periods and foraging does not significantly increase in the weeks prior to hibernation. Young generally are less vigilant, often spend less time sitting and forage less than adults, but generally allocate more minutes to investigation. Time is a seasonal but not a daily constraint. Thermal constraints reduce overall daily activity, and digestive constraints limit foraging time. Sitting provides a reservoir of time that can be drawn upon when needed for other behaviors such that costly trade-offs are not evident. Time allocations for an activity may differ among sites; these differences and most significant differences, whether for cohort, day-period or season-period, are associated with the behaviors of a particular age/sex group, such as high time allocation to investigation by immigrant males.

KEY WORDS: sitting, vigilance, foraging, phenotypic plasticity, day-period, season-period, cohort, *Marmota flaviventris*, abiotic factors, constraints.

INTRODUCTION

Energy acquisition is a major activity of all animals that forms the essential component of a time budget. Because time is limited, time spent in one activity reduces the time available for other activities, thus leading to a trade-off in the amount of time available for any activity (Pianka 1988). For example, time spent interacting with other individuals is a cost in energy expenditure and reduces the time available for foraging and other activities (Kryazhimskiy & Maklakov 2013). However, many animals spend a large proportion of their active time in resting (Herbers 1981), which raises the question of what constraints (Karasov 1986), if any, limit energy acquisition or the time allocated to other activities.

Time is a major influence on the biology of the 15 species of marmots. Time constraints in conjunction with large body size underlie marmot sociality, affect the age of maturity and reproductive strategies and truncate annual population growth (Armitage 2014). During the short average active season of 4.8 months, marmots must reproduce, grow and prepare for an average hibernation period of 7.2 months. Prolonged snow cover reduces the amount of time available seasonally (Armitage 2013a), and decreases reproductive success and increases mortality during hibernation (Armitage 1994, 2013b).

These reproductive and survival costs to fitness suggest that time has a major impact on the accumulation and storage of energy by marmots. Therefore, marmots should be highly efficient processors of energy. The costs of maintenance should be reduced so that more energy is available for growth and reproduction. Energy costs of yellow-bellied marmots (*Marmota flaviventris)* are minimized by a rapid decline from euthermy to deep torpor and spending over 85% of the time in torpor during hibernation (Armitage et al. 2003), and by energy conservation during the active season (Armitage 2004a).

The physiological adaptations that increase energy efficiency would be inadequate to increase reproductive success if marmots were limited in energy acquisition. Thus, we predict that foraging will be the major activity when marmots are aboveground during the active season. The amount of time expended in foraging may be limited by thermal or digestive constraints (Karasov 1986) or by behavioral (e.g., competition, mating, predator detection) factors. Herein, we describe how yellow-bellied marmots allocate time among 14 behaviors; how these behaviors vary among sites and animal cohorts (age/sex classes), during the day and over the active season; and what factors, such as weather, may act as constraints on energy acquisition. Although we interpret some of the variation in relation to the behaviors of certain animal cohorts, these interpretations are based on associations between behaviors and known behavioral patterns, not direct cause and effect measurements.

METHODS

Time budget measurements were conducted in the Upper East River Valley, Gunnison County, Colorado, USA, in the vicinity of the Rocky Mountain Biological Laboratory, from 28 May through 4 September 1992 and from 7 June through 10 September 1993. Yellow-bellied marmots emerge from hibernation in early to mid-May and wean young from late June to mid-July. All marmots at the study sites were trapped, sexed and weighed. At first capture, a marmot received a uniquely numbered Monel metal tag in each ear for permanent identification. Each

year, each marmot was marked with a non-toxic fur dye for visual identification. The mark was lost during the summer molt; therefore, marmots were re-trapped and re-marked after molting.

Study populations

Six sites were used; two (Boulder and Stone Field) were satellite sites (Svendsen 1974), and the remaining sites were colonial. The study sites are described and pictured in Armitage (2014). Population numbers and age/sex composition varied among sites within a year and within sites between years. Not all marmots at a site were included in the study; marmots were selected to represent the diversity of age, sex and reproductive status (Table 1).

Behaviors and sampling procedures

Based on our earlier study (Armitage et al. 1996), we recorded 14 behaviors (Table 2). Animals were observed with binoculars or spotting scopes from blinds or automobiles 50 or more meters beyond the site boundary. Observation periods ranging from 3 to 7 hr varied from day to day so that marmot activity throughout the day was sampled. The day was divided into 3 day-periods: morning (from first emergence until 10:00), mid-day (10:00–16:00) and afternoon (16:00 until immergence). The number of hours in each day-period represents the available time for aboveground activity; available time in the morning and afternoon varied with changing day length. Over the summer, morning and afternoon time-periods averaged about 3 hr each, and this average was used in the data analysis. Thus, the total available time was the sum of hours for each day-period; e.g., 12 hr.

Table 1.

Marmots used in the time-budget analysis. Sample size (*n*) in parentheses.

Site	Year	Marmots used
River	1992	Four adult, non-reproductive females (48) and an adult male (4) Reproductive female (5) and female young (34) from a different matriline added in late summer
		Reproductive female (5) and female young (34) from a different matriline added in late summer
	1993	Two males (45); two reproductive (110) and two non-reproductive (99) females; three yearling females (139) from a different matriline
Marmot Meadow	1992	One adult male (25) and one non-reproductive adult female (27)
Picnic	1992	A reproductive female (83) an adult female who lost her litter (62), one adult male (56), one male (17) young and three female (71) young
	1993	Two adult males (90) and an adult female (65) who lost her litter
Boulder	1992	An adult male (2), a reproductive female (33), and one female (32) and three male young (92)
North Picnic	1993	Two adult males (18), two non-reproductive adult females (15), one immigrant yearling female (9)
Stone Field	1992	A reproductive female (30), and one female (26) and four male (69) young
	1993	One female (23) and three male (61) yearlings – the same individuals from 1992

Table 2.

Description of the behaviors recorded during observation bouts.

Sitting	Stationary, sitting on haunches or reclined on the substrate
Foraging	Head down, eating; movement between eating bouts recorded as run/walk
Vigilance	Head up while sitting or walking, or sitting upright on the haunches and surveying the surroundings
Run/walk	Movement from one location to another
Out of sight	Aboveground, not visible as animal moves into dense or high vegetation, or behind boulders, or into a gully or low depression
Enter burrow	Marmot enters a burrow while being monitored and is not visible; may remain in burrow during remaining bout time
Groom	Scratching or chewing at some part of the fur or body, usually while sitting; includes allo-grooming where one marmot grooms another
Foraging-alert	Vigilance expressed while foraging and chewing food
Investigation	Apparent sniffing of ground, vegetation or rocks in the immediate environment; may include cheek rubbing (Armitage 1976, 2014)
Social	Greeting, flight or chase (Armitage 1962, 2014); includes sex-grasp (Armitage 1974)
Play	Variety of motor patterns, including grapple, mouth-spar, chase/flee (Jamieson & Armitage 1987)
Dig	Scratching the substrate with the forefeet or excavating dirt from a burrow
Gathering grass	Pulling at grass, usually dried, with the mouth, and carrying it into a burrow (Armitage 2003c)
Chirp	The high-pitched alarm call (Armitage 2014)

The amount of time a site was sampled varied with our assessment of the potential new information we would gain. For example, at Marmot Meadow, observations ceased after 29.5 hr when the two adults expressed typical activity patterns (Armitage et al. 1996). Likewise, the simple population structure at North Picnic required only 48 hr of observations. By contrast, the presence of competing males at Picnic in 1993 elicited 96.5 hr of observations. Because of the need to focus observations at the critical times at a site (e.g., when an immigrant or young appeared), not all sites were observed in every season-period.

Focal animal sampling was used for recording activity (Altmann 1974). We chose the first animal that we could find and recorded its activity for 30 sec using a Psion hand-held computer, from which the data were downloaded into a computer for analysis. When the bout was finished, another marmot was located and the bout was repeated. If another marmot could not be located, the same animal as in the previous bout was observed. These recordings were interspersed with scan sampling every 10–15 min when the location of each animal was recorded for measuring the amount of space overlap among age/sex groups and of individuals of different degrees of relatedness (Armitage 1984, 1986a, 1989).

Weather variables

During a study of energy flow in marmot populations (Kilgore & Armitage 1978), Marmot Meadow was monitored to examine the effects of five weather variables on daily activity. The variables were net radiation (ergs/m^2/sec), ambient temperature (°C), relative humidity (%), cloud

cover (%) and wind speed (m/min). The number of marmots active and the weather variables were recorded every 30 min in the morning from 07:00 until 12:00, and in the afternoon from 16:00 until 20:00. Starting and finishing times varied as day length decreased over the summer. Three adults were monitored from 21 June until 15 September 1969; four yearlings from 21 June until 2 August (when the last yearling disappeared), and four young from 16 July (time of weaning) until 15 September. These previously unpublished data are included because they test the effects of thermal constraints on the variation in day-period activity.

Data analysis

The number of observations per behavior and the total number of observations were tallied for each animal for each day-period at each site. Mean values (number of minutes) for each behavior for each marmot were calculated for each day-period; thus, each animal contributed only one data point for each day-period in the statistical analysis. The percentage of time (the number of minutes for a behavior divided by the total minutes of activity) allocated to each behavior was calculated. We also determined average bout length, the number of seconds spent in a behavior before the marmot switched to a different behavior. The total number of minutes, the percentage of time, and mean bout length for each behavior were sorted into groups based on cohort (see Table 1 for cohort composition), day-period, day and site.

Because seasonal phenology between up-valley and down-valley sites may differ by as much as 21 days (Van Vuren & Armitage 1991), seasonal events were standardized to the reproductive cycle rather than to the Julian day. The season was divided into nine season-periods (SPER): gestation (30 days, SPER 1), lactation (25 days, SPER 2) and seven 10-day post-lactation periods (SPER 3–9). Thus, data were grouped for each site by cohort, day-period and season-period. These three main effects and all possible interactions were analyzed with a general linear model, GLM ANOVA analysis of variance (SAS Institute, Inc.) Multiple comparisons of means (GT2 method with a Bonferroni correction, Sokal & Rohlf 1981) were performed to determine which levels within the main effects and interactions differed significantly. The analysis was repeated with the non-significant interactions removed to increase the power of the test; these results are used in this report. For the main effects, cohorts were compared over all season-periods and day-periods, day-periods were compared over all cohorts and season-periods, and season-periods were compared over all cohorts and day-periods.

Three analyses were performed for each behavior. One compared the estimates of total time (min) spent per individual for each cohort; the others compared the actual transformed average frequencies (percentage of time) and the bout length for each cohort. Because so many analyses were run, only those that were significant in both GLM ANOVA and GT2 multiple comparisons are recorded. Not all statistically significant results are described in the following discussion because no plausible biological interpretation was available in many instances, and we focus on interpreting the plausible reason for differences. Significance possibly was affected by small sample size, especially for minor activities where many zeros occurred.

RESULTS AND DISCUSSION

Weather variables

The environmental variables were correlated and the correlations varied somewhat with the time period (Table 3). Temperature and radiation were positively correlated; both increased steadily during the morning hours and decreased steadily after the high value at 16:00. Temperature may remain high and then decrease rapidly after 19:00. Thus, the PM correlation was lower than the AM correlation. Temperature

Table 3.

Correlation matrix for five weather variables extracted from a stepwise multiple regression to determine which weather variables significantly affected the activity of adult marmots for two daily time periods from 1 June to 15 September. AM = 07:00 to 12:00; PM = 16:00 to 20:00. The correlation matrix for yearling marmots was very similar.

	Temperature		Relative humidity		Cloud cover		Wind speed	
	AM	PM	AM	PM	AM	PM	AM	PM
Radiation	0.594**	0.353**	−0.654**	−0.457**	−0.077	−0.048	0.636**	0.349**
Temperature			−0.863**	−0.702**	0.292**	0.008	0.370**	0.410**
Relative humidity					−0.036	0.034	−0.541**	−0.460**
Cloud cover							−0.252*	0.066

Note: *P = 0.05, **P = 0.01.

sometimes remained low until 11:00 or later and seldom reached 20 °C; however, temperatures could reach 25 °C or higher in the PM.

Relative humidity, negatively correlated with radiation and temperature, was high in the early AM, then generally decreased as radiation and temperature increased. Relative humidity remained low until late PM (19:30); then usually increased rapidly. Relative humidity decreased significantly as wind speed increased (Table 3).

Cloud cover was negatively related with radiation; it was variable, often with no cloud cover, in the AM; higher values often occurred late in the morning and in the PM, but may have decreased in the late PM. Some days had high levels of cloud cover all day.

Wind speed was variable, generally low in the early morning, then increasing, but often with periods of relative calm. It was variable in the afternoon and often decreased in the late PM. This pattern of wind speed accounts for its positive correlation with radiation and temperature.

Time spent active: season-period

The total number of minutes active aboveground was low for season-periods 1, 8, and 9 and high, with some fluctuations, for season-periods 2 through 7 (Fig. 1). Because only one site was observed during season-periods 1 (Stone Field, 1993) and 9 (River, 1993), the low values could be the result of sampling error. However, low values for SPER 1 were reported previously; the low values for SPER 9 are consistent with the late-season decline in activity (Armitage et al. 1996). Also during SPER 1, vegetation may be scant, snow cover may persist and weather may be stormy (Svendsen 1974; Van Vuren & Armitage 1991). These environmental conditions reduce aboveground activity.

Six behaviors – sitting, foraging, vigilance, out of sight, run/walk and foraging-alert – accounted for 88–98% of the minutes of activity (Table 4). This pattern varied little among the nine site-years (a site-year is one site in one year), which is reflected in the relatively consistent rank order of the activities. The mean value for percentage of time for the six activities is 92%. However, these behaviors accounted for only 44–53% (mean = 48%) of the available time during the diurnal period.
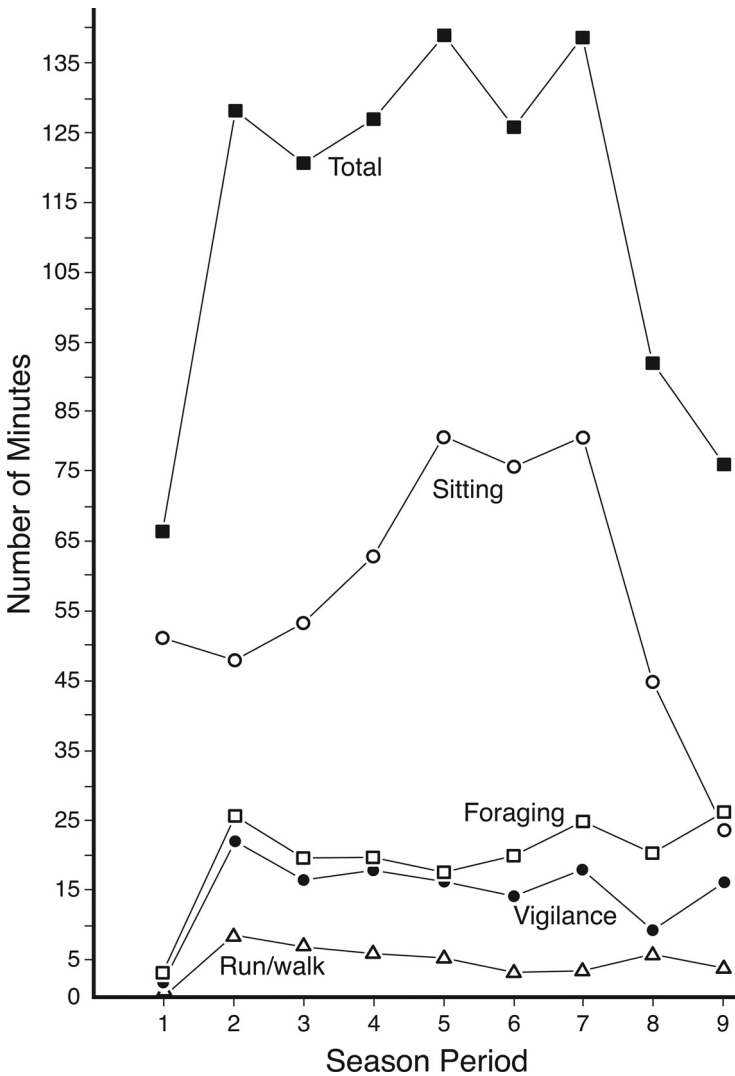
Fig. 1. — The number of minutes allocated to aboveground activity and to four major behaviors for nine season-periods. Data for each season-period are averaged over all cohorts and day-periods.

The much greater allocation of minutes to vigilance than to foraging at North Picnic, in contrast to the general pattern (Table 4), was associated with an unstable population. Unrelated marmots immigrated into the site at various times during the summer. Social behavior of unrelated marmots is primarily agonistic (Armitage 2014). Consequently, individuals allocated greater time to vigilance in order to monitor the location of conspecific antagonists.

At River in 1992, both vigilance and social had significant season-period effects (Table 5). More time was allocated to vigilance than to foraging, which slightly decreased the overall ranking (Table 4) of foraging and increased the ranking of

Table 4.

Time spent (total minutes and percentage of time) in the six most active behaviors for each site observed in 1993. Values are means averaged over all season-periods, day-periods and animal cohorts, and are reported to the nearest whole number. The number in parentheses is the mean rank order for five sites in 1992 and four sites in 1993.

Behavior	Sites									
	Picnic		River		North Picnic		Stone Field		Mean	
	Min	%	Min	%	Min	%	Min	%	Min	%
Sitting (1.1)	191	48	157	44	180	46	224	59	188	49
Foraging (2.1)	70	16	64	18	48	13	61	14	61	15
Vigilance (2.8)	54	14	51	14	93	22	19	5	54	14
Out of sight (4.2)	19	6	20	6	37	10	14	5	23	7
Run/walk (5.2)	21	5	18	5	20	6	8	2	17	5
Foraging-alert (5.6)	6	2	7	2	4	1	7	3	6	2
Total	361	91	317	89	382	98	333	88	349	92
% of AT	50		44		53		46		48	

Note: Min = total number of minutes; % = total percentage; AT = available time.

vigilance. Our field notes revealed that social interactions between a new immigrant male and the resident females were higher early in the season (0.207/female/hr) when vigilance was also greater. A new male frequently approaches a female and grasps (sex-grasp) her, similar to reproductive behavior (Armitage 1965). Females typically rebuff the male and are alert to his presence. This male behavior declines markedly (0.024/female/hr) or is absent after about mid-July (Armitage 1974).

Clearly, total activity and those of the major behaviors vary over the nine season-periods (Fig. 1); this pattern is expressed in the large number of significant season-period effects on virtually all activities (Table 5). Because the curves in Fig. 1 appeared to be highly similar, Pearson correlations were measured among the behaviors, and a multiple regression analysis revealed the contributions of the six variables to total minutes and percentage of time of activity. Minutes allocated to sitting, vigilance and out of sight were significantly correlated with total minutes, and other activities had high correlation coefficients (Table 6). The contributions of the six variables to total minutes is expressed in the following equation:

$$\text{Total minutes} = 10.1 + 0.352 \text{ foraging} + 0.980 \text{ sitting} + 1.45 \text{ vigilance}$$
$$+ 0.891 \text{ foraging-alert} + 0.594 \text{ out of sight}$$
$$+ 2.17 \text{ run/walk} \left[P = 0.001, \text{R}^2\text{-adj} = 99.8\% \right]$$

Sitting and vigilance are the most significant contributors to total minutes of activity (Table 7).

The mean values for the percentage of time allocated to the behaviors (Table 8) vary similarly to the values for the number of minutes allocated in each season-period (compare Fig. 1 and Table 8). The correlations between number of minutes and percentage of time allocations for each behavior are significant for all behaviors (Table 6). This

Table 5.

Significant effects for the number of minutes spent in a behavior in 1992 and 1993. Significance is reported only for those analyses when both the GLM ANOVA and the GT2 multiple comparisons were significant. Site abbreviations (B = Boulder, M = Marmot Meadow, N = North Picnic, P = Picnic, R = River, S = Stone Field) indicate levels of significance for that site; one letter, $P = 0.05$; two letters, $P = 0.01$; three letters, $P = 0.001$. Abbreviations for 1993 are in bold. Chirp is not included because there were no significant effects.

Activity	Cohort	Day-period	Season-period	Cohort by day-period	Cohort by season-period	Day-period by season-period	Cohort by day-period by season-period
Sitting	**RR**	BB M PPP **P** RR **RRR** S **SS**	PP **PP** RR **RRR** SSS **SSS**	**SS**	NN **RRR**	P **RRR SSS**	**R**
Foraging	B PPP **P**	B MM N **PP** SSS	BBB PPP SSS RRR **RRR**			SS	
Vigilance	BB M S	BB R	B N PP **PPP RRR** RRR SS			**P** R	**R**
Run/walk	SS	PPP R	N PPP RRR **RRR**	**RR**	**RR**	**RRR** S	
Out of sight		PPP	P RRR **R S**		**RR**	BBB	
Enter burrow	R	PPP RRR **RR**	PPP **PPP** RRR		RRR	PPP **PP** RRR	
Groom	P **PP**	PP	RRR				PP
Foraging-alert	P **R** S	B M PP **R** SSS **S**	B N PP **PP** RRR **RR** S S	**RR**		**RR**	**R**
Investigation	**R RRR**	BBB NNN PPP R **RRR**		NNN **RRR**	NNN	NNN PP	NNN
Social	B S	B R S	BB N RRR SSS	P			PP
Play	**SSS**	**RRR**	**RRR SSS**	**RRR**	R **SSS**	**RRR**	
Dig	**RR**	**R**		**RR**			
Gathering grass		**R**	**R**	**RR**	**R**		**RR**

Table 6.

Correlation coefficients among major variables contributing to variation in the number of minutes and percent time allocated to season-period activity and the total minutes of activity. n = 9 season-periods, P = 0.05*, P = 0.01**, $P_{0.05sig}$ = 0.666, $P_{0.01sig}$ = 0.798. Correlations for minutes are in bold; correlations for percent time are in italics. For example, both minutes and percentage of time sitting are negatively correlated with foraging, but only percentage of time is significant. Correlation between number of minutes and percentage of time for an activity is recorded in the line in italics along the diagonals.

	Sitting	Foraging	Vigilance	Run/walk	Foraging-alert	Out of sight
Sitting	*0.728**	*−0.909***	*−0.615*	*−0.694**	*−0.368*	*−0.099*
Foraging	**−0.102**	*0.707**	*0.508*	*0.487*	*0.067*	*0.023*
Vigilance	**0.156**	**0.843****	*0.920***	*0.509*	*0.399*	*0.141*
Run/walk	**−0.036**	**0.591**	**0.740***	*0.730**	*0.296*	*0.505*
Foraging-alert	**−0.197**	**0.581**	**0.722***	**0.766***	*0.669**	*−0.255*
Out of sight	**0.318**	**0.482**	**0.728***	**0.867****	**0.550**	*0.680**
Total minutes	**0.751***	**0.497**	**0.794***	**0.560**	**0.381**	**0.765***

Table 7.

The partial values for multiple regressions for the contributions of six major behaviors to the total minutes and the total percentage of time expended by yellow-bellied marmots.

Behavior	Partial P	
	Minutes	% time
Sitting	0.001	0.047
Foraging	0.105	0.108
Vigilance	0.017	0.133
Run/walk	0.058	0.128
Foraging-alert	0.235	0.164
Out of sight	0.255	0.048

relationship indicates that marmots keep the proportion of time allocated to an activity fairly constant, but that some variation occurs.

The contributions of the six variables to the total percentage of time is expressed in the following regression:

$$\text{Total percentage of time} = 16.1 + 0.881\% \text{ sitting} + 0.84\% \text{ foraging} + 0.318\% \text{ vigilance} + 0.904\% \text{ run/walk} + 1.67\% \text{ foraging-alert} + 1.02\% \text{ out of sight } [P = 0.065, R^2\text{-adj} = 91.2\%]$$

Sitting and out of sight make the most significant contributions to total percentage of time (Table 7).

Sitting was clearly the dominant activity. The number of minutes allocated to sitting is not significantly correlated with their allocation to the other five variables (Table 6, first

Table 8.

Mean values for percent of time allocated by season-period for six behaviors from four sites for 1993.

Activity	Season-periods									Mean
	1	2	3	4	5	6	7	8	9	
Sitting	66.1	39.3	40.9	49.8	52.8	57.5	58.9	41.1	29.2	48.4
Foraging	6.9	18.1	17.1	14.8	12.3	13.3	15.2	22.3	29.3	16.6
Vigilance	2.0	15.0	14.2	13.3	13.7	10.4	11.5	10.1	13.4	11.5
Run/walk	1.7	5.8	10.0	4.9	3.2	3.1	3.0	6.6	5.0	4.8
Out of sight	3.8	7.1	7.3	7.7	4.4	3.7	6.5	10.8	1.4	5.9
Foraging-alert	1.3	3.1	3.0	1.1	3.5	0.8	1.1	0.8	2.4	1.9
Total	81.8	88.4	92.5	91.6	89.9	88.8	96.2	91.7	80.7	89.1

column). However, the percentage of time allocated to sitting is negatively correlated with the percentage of time for all other behaviors, and the correlations with foraging and run/walk are statistically significant while the correlation with vigilance is nearly significant (Table 6, top row). None of the other correlations of percentage of time between two behaviors is significant. This pattern of correlations suggests that sitting is a key behavior and that time allocated to other behaviors comes from time not used sitting. The relationship is especially strong between sitting, foraging and run/walk; obviously, when not sitting a marmot is likely to be traveling to or from a foraging area, foraging or moving within a foraging area. Although foraging-alert and out of sight can occur only when not sitting, the percentage of time allocated to these activities depends on the local environmental conditions (e.g., presence of shrubs or other tall vegetation) during foraging.

Sitting and vigilance were closely related. Earlier observations indicated that marmots are wary while sitting (Armitage & Chiesura-Corona 1994). For example, the heart rate of a sitting marmot increases at the approach of a conspecific, which indicates the sitting marmot monitors its environment (Armitage 2003a). In general, the heart rates of sitting marmots were significantly greater than those of the same marmots while in their burrows. Elevated heart rates are consistent with a basic level of wariness; heart rates during vigilance increased as much as 20%. Elevated heart rates probably prepare the marmot for action, such as fight or flight (Nelson 1995: 71). Behaviorally, vigilance seems to be an enhancement of a general wariness. Combined, vigilance and sitting accounted on average for 63% of aboveground activity (Table 4) and may exceed 80–90% at a site during peak summer activities such as during lactation and when adults and young rapidly gain mass (Armitage & Chiesura-Corona 1994).

Foraging is a critical activity that varies seasonally because of the behavioral patterns of particular cohorts. All cohorts allocate about the same percentage of time to foraging because sufficient mass gain is critical for surviving the subsequent hibernation (Armitage 2014). Adult males and non-reproductive females typically complete mass gain by early August, but mass gain by the reproductive females continues for at least an additional 12 days (Armitage 1996). At Picnic in 1993, the significant cohort effect (Table 5; see also Table 11) was because the reproductive female allocated both more minutes and a greater percentage of time to foraging than the adult male. The same pattern of greater allocation to foraging by adult females occurred in 1992. In 1993 at

Table 9.

Time spent (number of minutes for all behaviors) as a percentage of minutes available (% Avail) for the three day-periods for four sites for 1993. Values are means averaged over all season-periods and animal cohorts, and are reported to the nearest whole number. Minutes available are: Morning = 180, Mid-day = 360, Afternoon = 180.

| Sites | Day-periods | | | | | | Daily total |
| | Morning | | Mid-day | | Afternoon | | |
	Min	% Avail	Min	% Avail	Min	% Avail	Min
Picnic	126	70	129	36	122	70	377
River	94	52	140	39	108	60	342
North Picnic	137	76	137	38	119	66	393
Stone Field	116	64	149	41	112	62	377
Mean	118	66	139	39	115	65	372

Note: Min = number of minutes active aboveground.

River, the minutes allocated to foraging in SPER 8 was unusually high (25.8 min, compared to a mean of 14 min for the two previous periods), probably because yearlings were sampled at that time and yearlings spend more time feeding than the other cohorts (Armitage & Chiesura-Corona 1994) and forage for a longer time during the summer (Armitage et al. 1996).

Time spent active: day-periods

The number of minutes and the percentage of time allocated to 13 of the 14 behaviors were significantly affected by day-period (Tables 5 and 11). The number of minutes spent active varied little among the three day-periods (morning, mid-day, afternoon); however, the percentage of time active was considerably less in mid-day than in the morning and afternoon (Table 9). Time spent active at River in the morning was much less than that at the other sites, probably because some observation days coincided with periods of light morning precipitation which reduced activity.

The pattern of activity over the day-periods varied among the six major activities (Table 10). Sitting was more frequent at mid-day than in the morning or afternoon, whereas foraging occurred more often in the morning or afternoon than at mid-day. Vigilance was lowest at mid-day, probably because sitting contributed much more to wariness. Also, vigilance typically occurs prior to foraging and during movement. Less time foraging would lead to less time vigilant.

Vigilance

The interpretation of variation in time spent vigilant is complicated by significant interactions for minutes (Table 5) and for bout length (Table 12). At Picnic, the day-period peak of vigilance varied over the SPER (Fig. 2); variation in bout length varied similarly. The consistent level of both minutes and bout length throughout the day in

Table 10.

Contributions of the six major behaviors to time spent (minutes and percentage of time) at each of the 3 day-periods. Values are means averaged over all season-periods and cohorts and the four sites for 1993.

Activity	Day-periods					
	Morning		Mid-day		Afternoon	
	Min	%	Min	%	Min	%
Sitting	57.8	48.9	76.6	55.1	53.3	46.3
Foraging	20.5	17.3	16.3	11.7	23.8	20.7
Vigilance	17.4	14.7	18.9	13.6	17.8	15.8
Out of sight	6.6	5.6	8.5	8.5	7.5	6.5
Run/walk	6.1	5.2	6.5	4.7	4.3	3.7
Foraging-alert	1.6	1.4	1.5	1.1	2.6	2.3
Totals	110	93.1	128.3	94.7	109.3	95.3
% of AT	61.1		35.6		60.7	

Note: Min = number of minutes; % = percent time in that activity; AT = available time.

Table 11.

Significant effects for the percentage of time allocated to a behavior for major behaviors for four sites in 1993. Only those variables significant in both the GLM ANOVA and GT2 multiple comparisons are included. Site abbreviations (N = North Picnic, P = Picnic, R = River, S = Stone Field) indicate levels of significance for that site; one letter, $P = 0.05$; two letters, $P = 0.01$; three letters, $P = 0.001$.

Activity	Cohort	Day-period	Season-period	Cohort by season-period	Day-period by season-period
Sitting		PPP	P RRR	R	
Foraging	PP	PP			
Vigilance			PP NN RRR SS		PP R
Run/walk	N	SS	N	R	P
Out of sight	NN		SS	R	
Foraging-alert	R	SS	NN PP RR		PPP RR SS

SPER 2 was associated with the presence of an intruder. The low level of vigilance in the morning for both minutes and bout length in SPER 6 occurred during a period of morning rain and heavy overcast. Alarm calls were frequent during mid-day in SPER 6 and 7. High levels of vigilance in the afternoons in SPER 4 and 5 were associated with the presence of two adult males in conflict. The pattern of the percentage of time allocated to vigilance was similar to that for the number of minutes (Fig. 2), but the occurrence of several major quantitative differences indicates that the time allocated to vigilance is conditional and determined by environmental circumstances. Also, the increase or decrease in vigilance was a consequence of increasing or decreasing bout length.

Table 12.

Significant effects for bout length for the four sites in 1993. Site abbreviations (N = North Picnic, P = Picnic, R = River, S = Stone Field) indicate levels of significance for that site; one letter, $P = 0.05$; two letters, $P = 0.01$; three letters, $P = 0.001$.

Activity	Cohort	Day-period	SPER	Cohort by day-period	Cohort by SPER	Day-period by SPER	Cohort by day-period by SPER
Foraging	P	R	RRR PP	PP		RR	PP
Vigilance	N		RR P N			P SS	
Run/walk		SS	RRR		R	RR SS	
Foraging-alert	RRR	RRR	RRR PPP SS	RRR	RRR P	RRR P SS NN	RRR
Investigation	RRR	RRR	RR PP S	RRR NN			
Gathering grass				R	R		
Social			N				

Note: SPER = season-period.
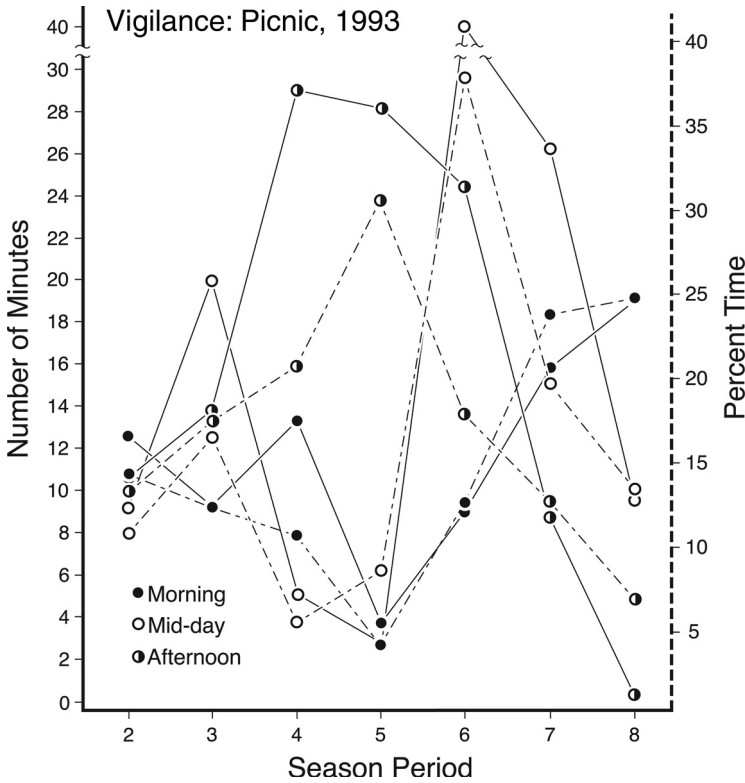
Fig. 2. — The number of minutes and percentage of time allocated to vigilance for each day-period in relation to the season-period at Picnic Colony. Data for each season period are always averaged over all cohorts. Morning = emergence until 10:00; mid-day = 10:00–16:00; afternoon = 16:00 to immergence.

The complexity of vigilance, and its conditional expression, is evident in the cohort by day-period by season-period significant interaction at River (Table 5). Bout length was significantly greater during lactation (SPER 2), when both minutes and percentage of time allocated to vigilance were high and social interactions were numerous (0.211/ad female/hr compared to 0.036/ad female/hr in SPER 6). Otherwise there was no relationship between bout length and the other variables, other than a general seasonal decrease. Two major social groups, or matrilines (Armitage 1991, 2014), were present. Conflict, especially between adults of one matriline and yearling females of the other, typified social behavior. Conflict throughout the summer was characterized by the yearlings becoming alert to or fleeing the presence of the adults. Thus, both the adults and the yearlings were on the lookout for each other. Their interactions also were affected by where in the site the marmots were active. At times the adults and yearlings were active in areas distant or out of sight of each other and the observer. In SPER 3, observations focused on the major areas where the yearlings and a male were active; adult females were not included. By contrast, in SPER 5, observations occurred in an area where only the adult females were present (Fig. 3). The two immigrant males, present from SPER 3 through the summer, wandered widely, harassed both the adult and yearling females, and tended to avoid each other. For example, in SPER 6 and 8 when both males were present, they had the highest level of vigilance (Fig. 3). The adult females were highly vigilant in SPER 4 and 5 when the young were active (also see Armitage & Chiesura-Corona 1994).

At North Picnic, a significant three-way interaction (Table 12) revealed that the bout length of the adult female was especially high in the morning in SPER 2, when three unknown transients were present and social interactions, especially agonistic by
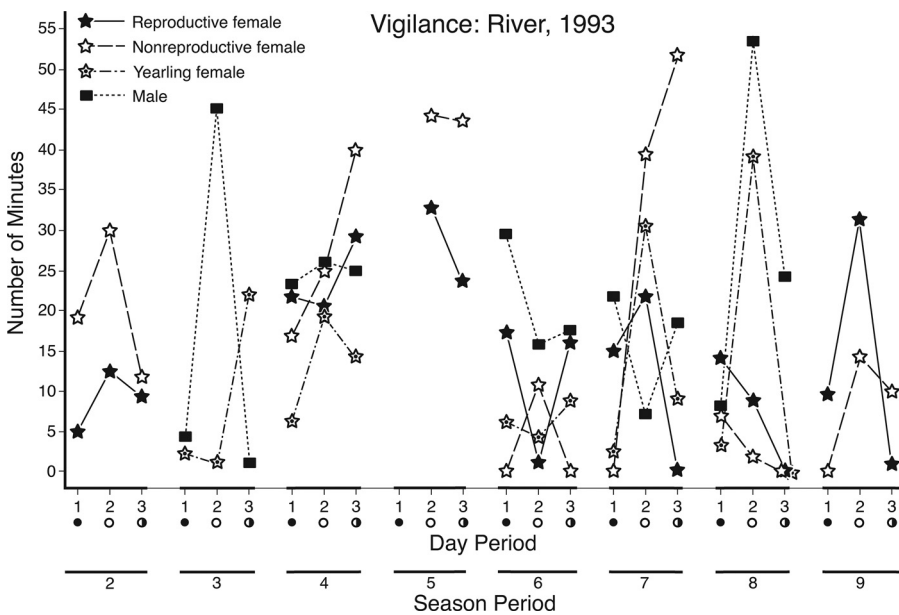

Fig. 3. — The significant three-way interaction (cohort by day-period by season-period) for the allocation of minutes to vigilance at River Colony.

the adult male, were numerous. The longer bout length at this time also coincided with a high but statistically insignificant number of minutes spent vigilant.

We conclude that vigilance varied over the summer as a consequence of the locations, movements and activities of the cohorts coupled with their tendency to keep track of their conspecifics. Bout length decreased or increased as overall vigilance decreased or increased. Weather also affected vigilance; when the weather was cool, cloudy and rainy in the afternoon of SPER 8, overall activity and vigilance by all cohorts were low (Fig. 3).

Sitting

Although sitting clearly occurred more often at mid-day than in the morning or the afternoon (Table 10), its expression is strongly affected by interactions: season-period with cohort and with day-period, cohort with day-period for total minutes (Table 5), and cohort with season-period for percentage of time (Table 11). There was no significant variation in bout length at any site. During some season-periods, sitting occurred more frequently during other day-periods. At Stone Field in 1993, early in the season, the yearlings, especially the female, allocated more time to sitting (about 68 min) in the afternoon than at mid-day (about 53 min). Late in the season the pattern was typical; about 182 min at mid-day, when the male yearlings spent more time sitting compared to about 98 min in the morning and 62 min in the afternoon.

At River, sitting was always more frequent at mid-day, but values varied considerably among season-periods and day-periods (Fig. 4). The high value for mid-day during SPER 5 coincided with the high level of vigilance by the adult females when agonistic behavior between the adults and yearling females (0.625/animal/hr) was unusually high (Armitage 1962, 1975). Associations between agonistic behavior (high in SPER 7) and sitting suggest that marmots may increase wariness and vigilance (Fig. 3) during periods of social conflict.

Adult females allocated many minutes to sitting in SPER 5 (Fig. 5) when vigilance also was high (Fig. 3). This relationship is consistent with the interpretation that wariness (sitting + vigilance) increases during social conflict. The percentage of time and the number of minutes allocated to sitting are correlated (Table 6), but percentage of time may increase when minutes decrease (SPER 6, Fig. 5). From SPER 5 to SPER 6, the minutes allocated to foraging, sitting, run/walk and vigilance decreased; percentage of time decreased also except for sitting, which increased (Fig. 5). This pattern indicates that some minimal level of wariness was maintained and required an increased percentage of time when activity overall decreased. There is no obvious environmental explanation for the different patterns of sitting in late summer (Fig. 5).

Run/walk

Run/walk on average varied little over day-periods (Table 10), but was significantly affected by interactions among the variables (Tables 5 and 11). High run/walk at River was associated with the adult females in SPER 5 and with yearling females and the male in SPER 8 (Fig. 6), and with high levels of vigilance by these cohorts (Fig. 3). Similarly, the high values for run/walk in SPER 3 (Fig. 6) coincided with a high level of vigilance at mid-day by the male and in the afternoon by the yearling females (Fig. 3). Minutes allocated to vigilance and to run/walk were significantly
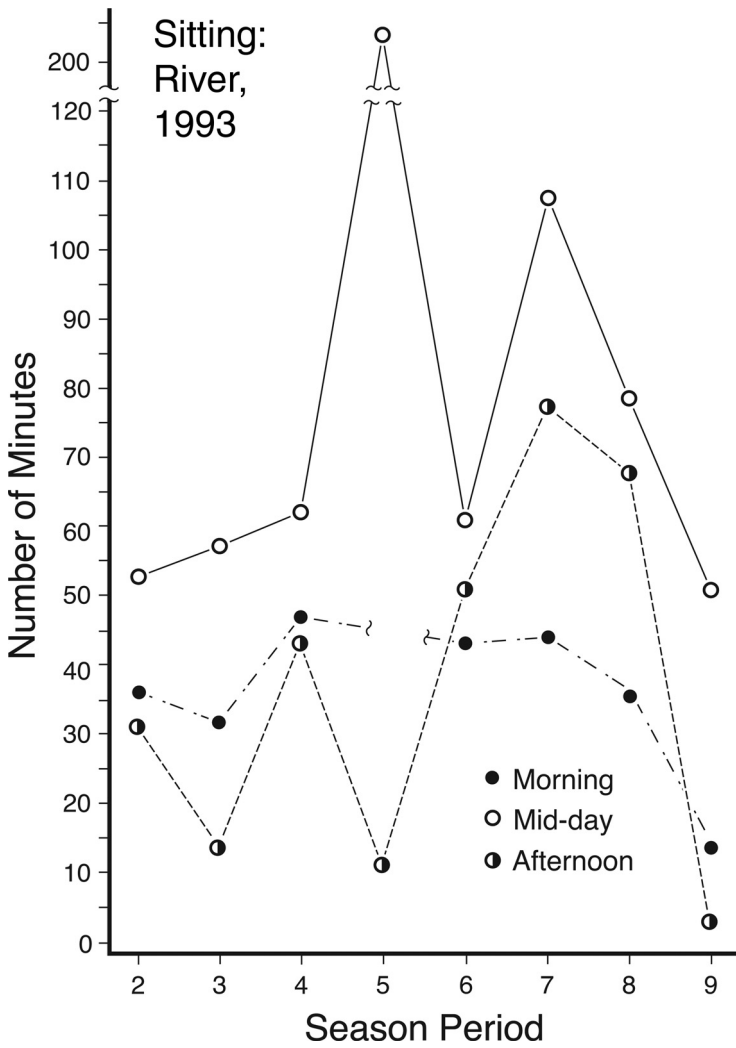
Fig. 4. — The number of minutes allocated to sitting for each day-period in relation to season-periods at River Colony.

correlated (Table 6), which indicates that a situation (presence of predator or con-specific) that enhances vigilance also increases movement; e.g., running to a burrow or perch.

The percentage of time allocated to run/walk at River was affected by a cohort by season-period interaction (Table 11). Run/walk peaked for all cohorts and day-periods in SPER 3 and generally declined over summer, except for a mid-day peak in SPER 8 associated with the male and an afternoon peak in SPER 9 associated with the non-reproductive females (unpublished data). These peaks at River in percentage of time indicate that activities associated with increased wariness extract a greater proportion of daily activity.
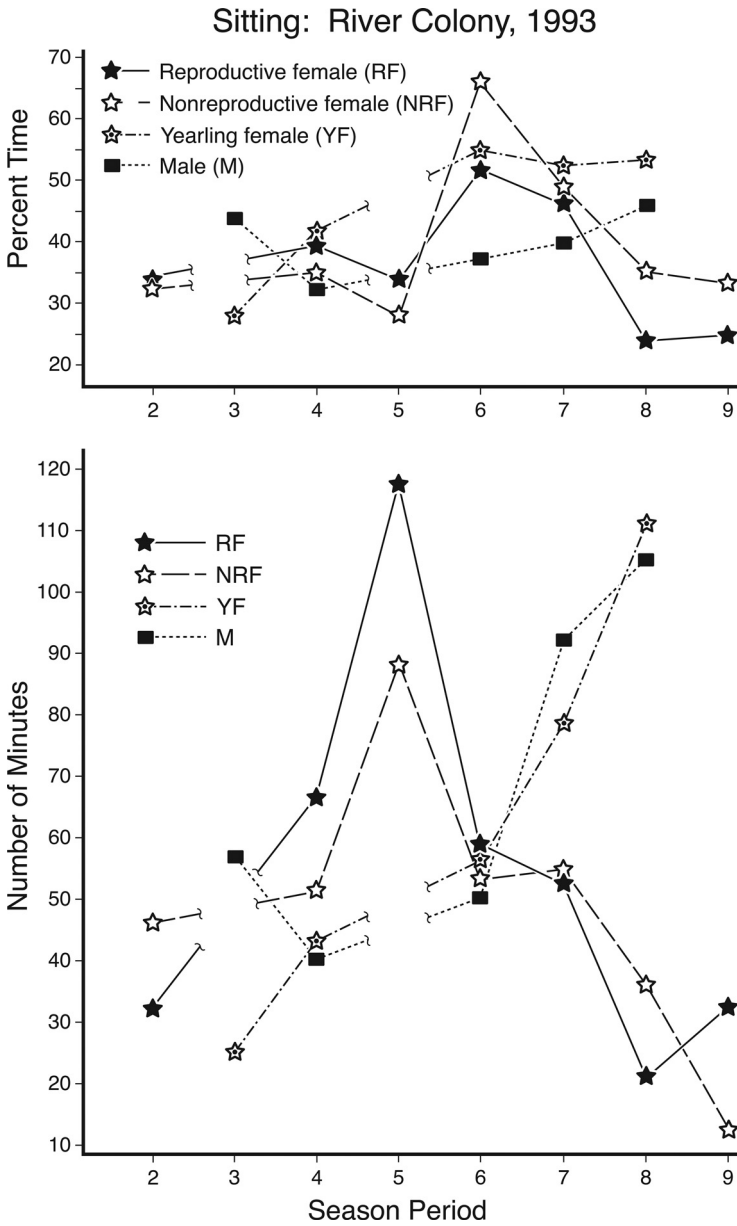
Fig. 5. — The relationship between number of minutes (lower) and percentage of time (upper) for sitting for four cohorts as related to season-periods at River Colony.

At North Picnic, run/walk varied seasonally (Tables 5 and 11). Both percentage of time (9.5%) and minutes (14.3) were about 3 times greater in SPER 2 than in the other season periods (means of 3.5%, 4.1 min). The high value coincided with a new
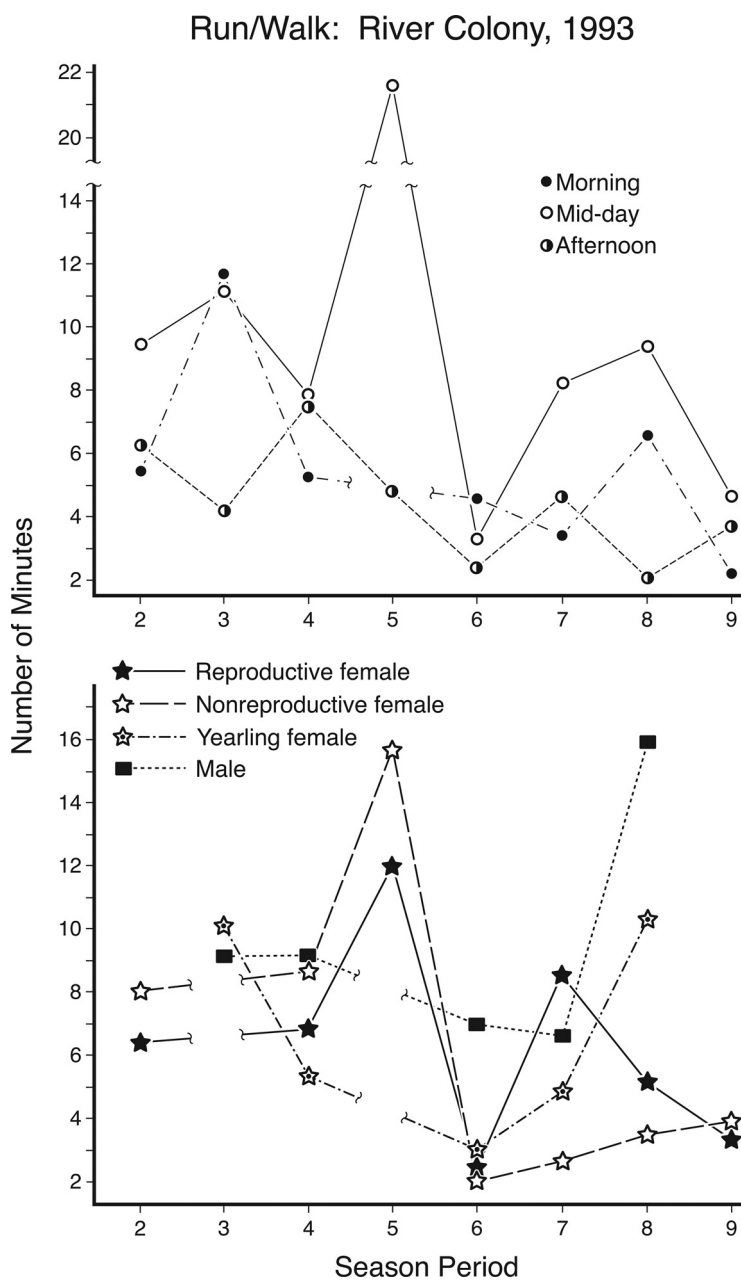
Fig. 6. — The number of minutes allocated by day-period (upper) and by cohort (lower) to run/walk in relation to season-periods at River Colony.

male immigrant and the resident male eventually moving to an adjoining site. Adult males move around in the site in response to the presence of another male (Armitage 2014). A male may be seeking or avoiding the other male.

At River and Stone Field, bout length varied significantly (Table 12). The high levels of run/walk at River in SPER 5 (Fig. 6) are associated with long bouts by the adult females and with long bouts at mid-day. Similarly, the high level of run/walk in SPER 8 coincides with longer bout length by the male and with relatively long bouts in the morning and mid-day. Both the yearling females and the male had long bouts in SPER 3, when the time allocated to run/walk was high (Fig. 6). At Stone Field, longer bout lengths were associated with longer bouts in the morning in SPER 5 and in the afternoon in SPER 2. Overall, the general pattern indicates that the time allocated to run/walk was determined by bout length and not by the number of bouts.

Foraging-alert

Foraging-alert occurred most frequently in the afternoon (Table 10). These average values conceal considerable variation among sites; e.g., foraging-alert varied significantly with day-period at Picnic in 1992, but not in 1993, and at River in 1993, but not in 1992 (Table 5). Bout length varied significantly (Table 12); at Picnic the reproductive female tended to have longer bouts early in the season, with the peak value in SPER 3 when the young had emerged and with declining bout lengths thereafter. The male had relatively short bout lengths in mid-season and long bout lengths late in the season, especially in SPER 8 and 9. The seasonal decline by the reproductive female was similar to seasonal patterns at North Picnic and Stone Field; bout length was longest during SPER 2 and shorter the rest of the season.

Both bout length (Table 12) and the number of minutes (Table 5) allocated to foraging-alert at River were significantly affected by the three-way interaction. Foraging-alert was significantly correlated with vigilance and run/walk (Table 6), and the curves for vigilance and foraging-alert are similar. For example, the male allocated many minutes to foraging-alert and vigilance at mid-day in SPER 3, and the yearling females had high values for both activities for the morning of SPER 7 (Figs 3 and 7). Bout length most often was longest in the morning and declined during the subsequent day-periods for most cohorts for most season-periods. A striking exception was the male who had a short bout length at mid-day when total minutes allocated to foraging-alert was the highest recorded for the summer. Bout length increased by about seven-fold in the afternoon when values for foraging-alert remained high. In SPER 8, the yearling females greatly increased the total minutes spent in foraging-alert from morning to mid-day to afternoon (Fig. 7), but bout length did not increase between mid-day and afternoon, which suggests that the increase in foraging-alert resulted from increasing the number of bouts. This pattern suggests that the minutes allocated to foraging-alert may be a function of either bout length or the number of bouts.

Although there is a high correlation between foraging and foraging-alert (Table 6), it does not reach statistical significance. Variation in foraging-alert is affected by where in the home range foraging occurs. Hoary marmots foraging near the home talus looked up less frequently than marmots feeding more distantly from the talus (Holmes 1984a). Yellow-bellied marmots were foraging-alert more often at the edge of the colony than at the colony center (Armitage 1962). Vigilance is also affected by group size; yellow-bellied marmots in California spent about 10.2% of foraging time looking up and looked up less often when feeding in groups (Carey & Moore 1986). These patterns emphasize
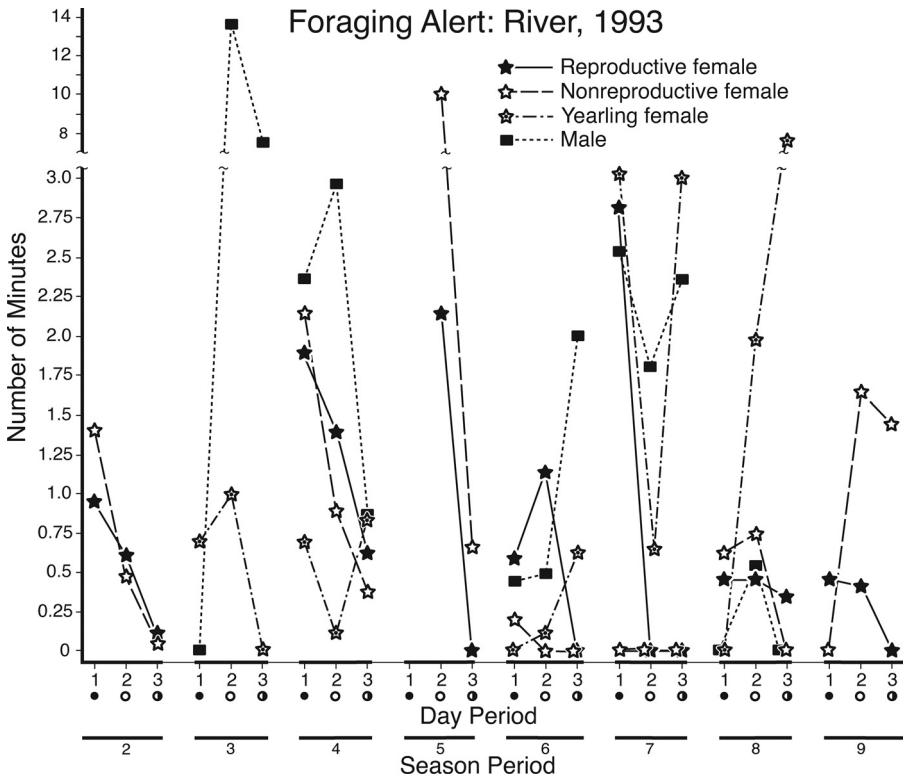
Fig. 7. — The significant three-way interaction (cohort by day-period by season-period) for the number of minutes allocated to foraging-alert at River Colony.

that vigilance while foraging is plastic and that heightened vigilance, whatever the cause, is expressed in all of those activities that contribute to overall wariness.

Foraging

Mean time allocated to foraging in 1993 varied little between morning and afternoon (Table 10). However, morning and afternoon time allocations may vary among sites. At Picnic, the minutes spent foraging were significantly greater in the afternoon (Table 5) because the reproductive female foraged more at that time than in the morning. However, the percentage of time foraging did not differ between morning and afternoon (18.9–20.9%) and was unusually low at mid-day (9.3%), as was the number of minutes (15.6 vs 21.5 in morning and 30.9 in the afternoon). The sun shines directly on Picnic during mid-day, which probably reduced the time spent foraging. At Marmot Meadow in 1992, significantly less time (Table 5) was spent foraging in the morning (8.6 min, 7.3% time) than at mid-day (18.0 min, 8.8%) or afternoon (28.3 min, 22.6%). The sun strikes Marmot Meadow later in the morning than at Picnic (the sites are on opposite sides of the East River Valley); thus, marmots at Marmot Meadow initiate activities later and forage mainly in the afternoon. At Boulder, which receives

direct sun in the morning and is strongly shaded in the afternoon, significantly (Table 5) more time (36.7 min, 27.3% time) was allocated to foraging in the morning than in the afternoon (18.0 min, 23.8% time).

Foraging bout length at River varied significantly (Table 12). Bout lengths generally were shorter in the morning and longest at mid-day or in the afternoon early in the summer. But in SPER 7–9, the longest bout lengths occurred during mid-day with shorter bouts in the morning and afternoon. Time spent foraging was high during SPER 8; the mornings were frequently cool and rainy, which shifted more time foraging to mid-day with the associated longer bouts.

At Picnic, bout length was affected significantly (Table 12) by a three-way interaction. The female had long mid-day bouts in SPER 4 and 7; the male had long bouts in the morning in SPER 5 and the afternoon of SPER 6. Generally, when the bout of the female was long, that of the male was short. Bouts for both adults were relatively short for all day-periods during SPER 2 and 3, and usually longer in all day-periods late in the season. The long bouts of the adult female at mid-day occurred when mornings were cool and overcast with ground fog.

These descriptions of bout lengths from two colonies demonstrate that time allocations vary among sites. These differences are partly attributable to different population structures. The similar pattern of long mid-day bouts emphasizes the effects of weather patterns on time budgets.

Minor activities

Minor activities are so designated because, as a group, they contributed, on average, about 23 min or 6.5% to daily activity (Table 13). However, these activities have important roles in marmot biology. Chirp was not recorded at two sites and

Table 13.

Time spent (total minutes and percentage of time) in the minor behaviors for four sites observed in 1993. Values are means averaged over all season-periods, day-periods and animal cohorts.

| Activity | Sites | | | | | | | | | |
| | Picnic | | River | | North Picnic | | Stone Field | | Mean | |
	Min	%	Min	%	Min	%	Min	%	Min	%
Chirp	0.8	0.23	0.1	0.02	0	0	0	0	0.2	0.06
Dig	0	0	0.8	0.2	0	0	1.5	0.4	0.6	0.15
EB	5.5	1.6	9.8	3.6	5.3	1.6	15.7	3.7	9.1	2.6
GG	0.7	0.2	0.6	0.21	0	0	0	0	0.3	0.1
Groom	5.0	1.1	5.6	1.5	3.5	0.9	13.0	4.5	6.8	2.0
Investigation	2.3	0.6	2.3	0.7	3.3	0.7	1.6	0.5	2.4	0.6
Play	0	0	0.9	0.23	0	0	5.3	1.6	1.6	0.46
Social	0.7	0.2	2.6	0.7	0.7	0.2	4.1	0.9	2.0	0.5
Total	15.0	3.9	22.7	7.2	12.8	3.4	41.2	11.6	23.0	6.5

Note: Min = total number of minutes; % = percentage of time in that activity; EB = enter burrow, GG = gathering grass.

was rare at the other sites. Chirp occurs primarily when intruders penetrate a site, and reproductive females call more frequently than other cohorts, especially after young are weaned (Blumstein et al. 1997). Reproductive females called more frequently than other cohorts at River, but the large number of zeroes in the data precludes statistical significance. Adult males may call more frequently than other cohorts, especially when a predator, such as the badger (*Taxidea taxus*), repeatedly invades a site (Armitage 2004b). However, at Picnic, an adult male called more often than the other residents, especially during the morning in SPER 3, when mule deer (*Odocoileus hemionus*) and coyotes (*Canis latrans*) frequently were present. Marmots frequently 'chirp' when deer are present (Armitage 2003b); the alarm-calling apparently represents the marmot 'telling' the predator that it has been detected (Armitage 2014). This instance of a high rate of male chirps exemplifies the variation in time-budget allocations depending on the local situation.

The time allocated to dig was significantly affected by cohort, day-period and a cohort by day-period interaction at River (Table 5). Dig occurred primarily in mid-day or the afternoon by all cohorts except the reproductive female. Most dig was mainly maintenance of existing burrows (Armitage 2003c). The frequent dig by males is consistent with an immigrant cleaning an existing burrow; the frequent dig by the yearling females is associated with their frequent change of activity centers and occupying different burrows during the summer.

Enter burrow varied widely because it depends on when a marmot responds to either a disturbance, such as a predator or antagonistic conspecific, or the completion of some activity; e.g., foraging, by entering a burrow. For seven of the nine site-years, values were higher at mid-day than during the other day-periods. The differences sometimes reached significance (Table 5). In the other two site-years, enter burrow in the afternoon was greater than or identical to mid-day; the time for enter burrow was never highest in the morning. This pattern occurs because marmots enter their burrow during mid-day to escape heat stress or in the afternoon when aboveground activity is terminated. Enter burrow varied widely over season-periods at all sites; maximal values usually occurred in SPER 1 and 3 – early in the season when inclement weather was more likely. There was no pattern in the frequency of enter burrow among animal cohorts; one significant effect occurred at River (Table 5) when non-reproductive, adult females had more than double the values of the other cohorts.

Gathering grass varied significantly only at River (Table 13); there was a significant day-period by season-period interaction (Fig. 8). In SPER 2, the reproductive females spent more time in the morning and afternoon and the non-reproductive females at mid-day. High levels of gathering grass by reproductive females during lactation is typical (Armitage 2003c). The high values for yearling females late in the season probably reflect the preparation of a nest for hibernation. The percentage of time allocated to gathering grass was characterized by a day-period by cohort significant interaction (Fig. 9). Reproductive females spent a larger percentage of time in morning and afternoon, non-reproductive females spent a larger percentage at mid-day and yearling females increased gathering grass from morning to mid-day to the peak in the afternoon. Reproductive females had significantly (Table 12) longer bout lengths when the number of minutes was greater in the morning and afternoon during lactation.

There was little significant variation in time allocated to groom (Table 5). Adult males groomed significantly more often in 1993 at Picnic. An adult male participated in all cases of allo-grooming. Males also groom after male:male interactions (Armitage
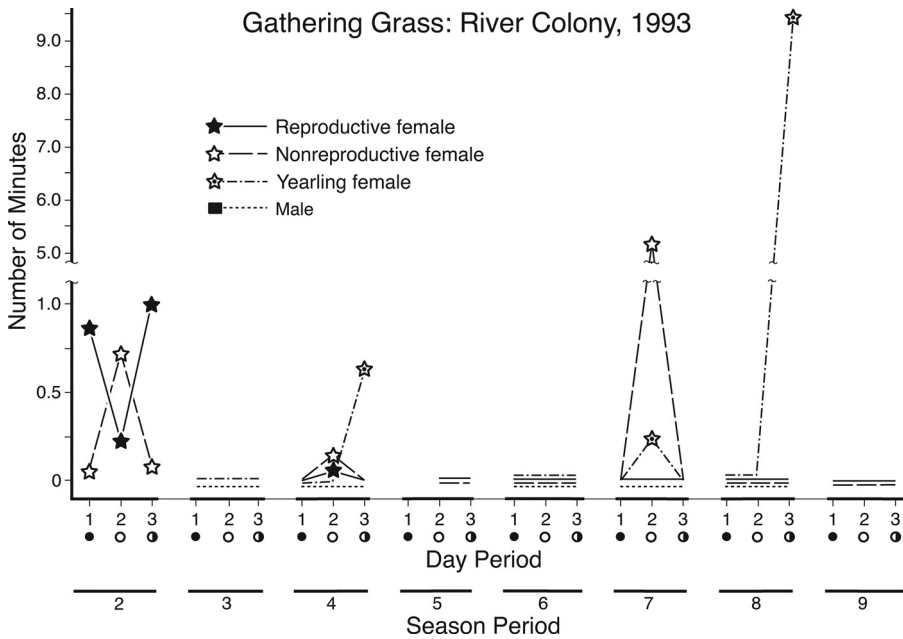
Fig. 8. — The significant three-way interaction (cohort by day-period by season-period) for the number of minutes allocated to gathering grass at River Colony.

2014); the two males at Picnic were in conflict, especially in SPER 2 when grooming occurred at its highest frequency.

At River in 1993, the yearling females spent significantly more time in investigation than the adult females, but not than the male. The cohort by day-period interaction revealed that the yearling females and the reproductive female investigated more during mid-day when the non-reproductive females and males allocated the fewest minutes to investigation; the males allocated the most time in the morning. Bout length was significantly (Table 12) affected; the reproductive female had a longer bout at mid-day, but the yearling females had their shortest bouts at mid-day and their longest bouts in the morning and afternoon when they spent fewer minutes investigating. Similarly, the male had the longest bout during mid-day when he allocated the fewest minutes, and the bout length of the non-reproductive females coincided with the total number of minutes spent. Thus, variation in the number of minutes spent in investigation involved changes in both bout length and the number of bouts.

Both the number of minutes (Table 5) and bout length (Table 12) allocated to investigation significantly varied at North Picnic. The low time spent in investigation during SPER 2 is associated with two adults familiar with the site and each other. An adult male and female immigrant and a yearling female immigrant in SPER 4 (Fig. 10) had high values of investigation, but in different day-periods. The time allocated to investigation by the yearling female was a direct function of bout length; i.e., long bout length at mid-day and short bout length in the morning and afternoon. The same relationship between minutes and bout length occurred in the adult females: high values in the morning and zero values in mid-day and afternoon.
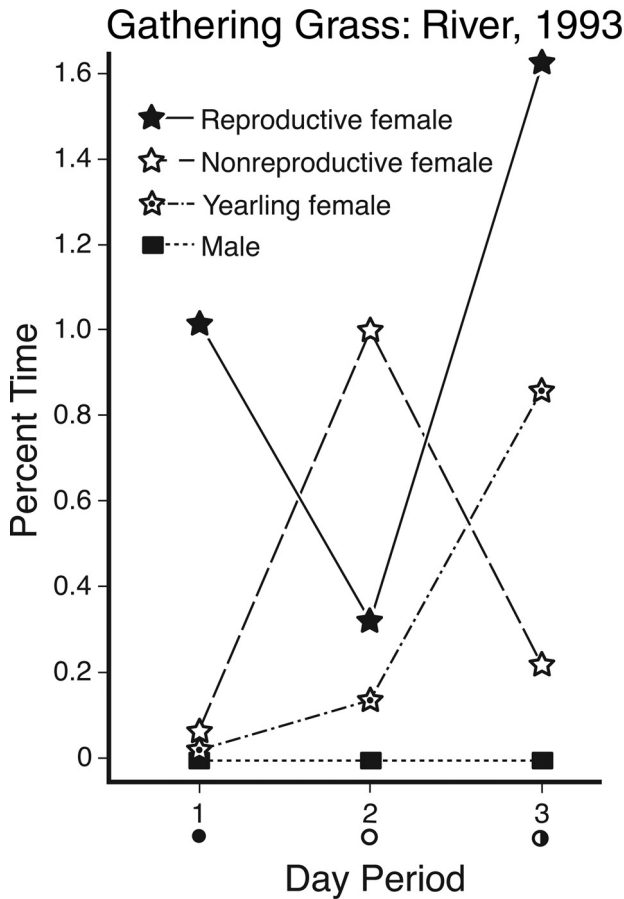
Fig. 9. — The percent time allocated to gathering grass by four cohorts as related to day-period at River.

Investigation was highest for an immigrant male in SPER 5 when he engaged in considerable cheek-rubbing where an unknown transient marmot was active. The relationship between the number of minutes and bout length is more complex for the adult males, in part, because two different males were present and their social environments differed. Overall, bout length was shortest in the morning, increased at mid-day, and was longest in the afternoon.

Overall, investigation occurred more often when marmots were recent residents at a site. Investigation appears to function to familiarize a marmot with its surroundings. It may be especially important for assessing the activity of other marmots. Marmots commonly cheek-rub, a means of scent-marking objects in their home range. These scent-marks may be sniffed by other marmots who may respond by cheek-rubbing the same object, thus announcing their presence, or by moving out of the area (Armitage 2014). Thus, through investigation a marmot gains information about other marmots and chooses an appropriate reaction.
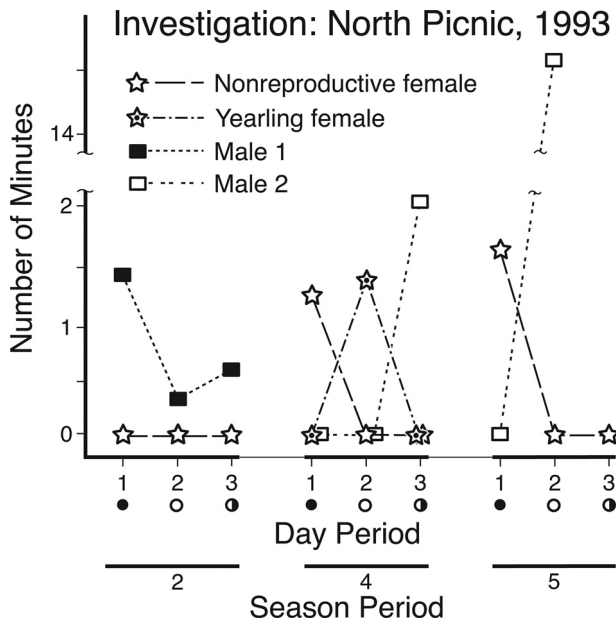
Fig. 10. — The significant three-way interaction (cohort by day-period by season-period) for the number of minutes allocated to investigation at North Picnic. Male 1 = the original resident; Male 2 = new immigrant. There were no observations in season-period 3.

Play rarely involves an adult yellow-bellied marmot, but is frequent among young (Nowicki & Armitage 1979) and yearlings (Jamieson & Armitage 1987). At both Stone Field and Boulder, young allocated significantly more time (minutes and percentage of time) and had longer bouts in the AM and males played more and had longer bouts than females, which characterizes play of young yellow-bellied marmots. Play is higher in the morning because young congregate at the burrow after emergence before beginning foraging and again when returning from foraging. Play peaked in SPER 4 when young were fully active, and declined thereafter.

Play was especially frequent by yearling males in SPER 2, and also high in SPER 1 and 5 (Fig. 11). Play by yearling females was low. Play occurred significantly more often in the morning, declined in late summer and was not observed in SPER 6. The more frequent play by males and the seasonal decline characterizes yearling play (Jamieson & Armitage 1987).

Although social behavior has a critical role in dispersal (Armitage et al. 2011), in establishing cohesiveness among members of female groups, in conflict both within and between matrilineal groups and in reproductive success (Armitage 1977, 2014), little time was allocated to this essential activity (Table 13). The few significant effects in time allocation (Table 5) were associated primarily with changes in population composition. Social bout length varied significantly only at North Picnic (Table 12) where bout lengths were longer in SPER 2 than in SPER 4. Long bout length was associated with frequent sex-grasp, chase and greeting between the male, the resident adult female, and two immigrant females.
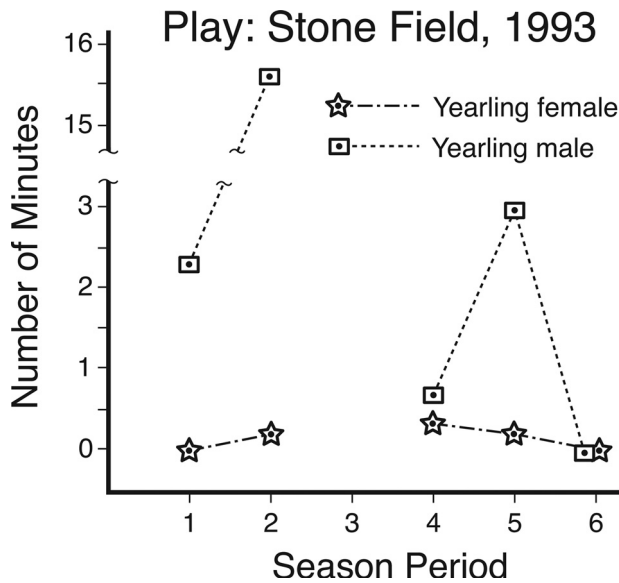
Fig. 11. — The number of minutes allocated to play by two yearling cohorts as related to season-period at Stone Field satellite site. No observations occurred in season-period 3.

At Picnic in 1992, time allocated to social was high in SPER 3–6 when young were active aboveground. Young had the highest values; the reproductive female also had high values as she had many interactions with the young. Social interactions were more likely when the marmots emerged and were near the burrow; thus, social activity was highest in the morning until late summer, when cold, rainy mornings delayed emergence and more minutes were spent social in mid-day, and to a lesser degree in the afternoon.

More minutes were allocated to social activity at River in 1992 during SPER 2, when the four adult females (a mother and her three littermate daughters) engaged in frequent social interactions (0.286/hr/female). Social activity decreased after lactation (0.133/hr/female), but was high in SPER 4 primarily because of amicable (0.202/hr/yg) behavior among the young. In addition, sex-grasp was high because of a new immigrant male (Armitage 1974). Social decreased in SPER 6 (none among adults); social behavior typically declines in late summer (Armitage 2003d, 2014). The immigrant effect also occurred at North Picnic, where the adult male frequently sex-grasped an immigrant adult female. Social in 1992 was high at Boulder and Stone Field in SPER 4 because of high activity among the young. These examples demonstrate that the presence of a particular age-group significantly affects a behavior.

Significant differences in social during the day varied among the three sites where young were recorded. At Stone Field, social was lowest mid-day when young were less active and allocated more time to sitting. By contrast, social was highest mid-day at River because sex-grasp occurred more frequently at that time, and inclement weather late in the summer reduced morning activity and increased mid-day activity. At Boulder, time allocated to social was almost identical in the morning and mid-day and decreased markedly in the afternoon, possibly because foraging was relatively frequent and enter burrow was high.

The percentage of time allocated to social at Stone Field in 1993 was higher at mid-day early in the season when social was low in the morning. The percentage of time spent social in the morning increased to a peak in SPER 5, then declined in SPER 6 when peak social occurred at mid-day. The peak in SPER 5 coincides with the high level of play by the yearling males (Fig. 11). Social behavior is a play-associated behavior pattern that occurs at a lower frequency than the major play motor-patterns (Jamieson & Armitage 1987). The relationship between social and play is another example of how time allocated to one activity affects the time related to another activity.

Behavior of the young

Other than play, activities of young yellow-bellied marmots seldom differed significantly from those of other cohorts. However, consistent trends in differences between young and adults coupled with statistical significance for seven activities (Table 14) support the interpretation that activities of young differed quantitatively from those of adults.

Time allocated to sitting did not differ significantly among these cohorts. However, young spent fewer minutes sitting than adults at three sites. Young may sit less because young spend less time than adults aboveground. Young at River spent 89.7%, and at Stone Field 87.3%, of the time aboveground that adults spent, probably because young emerge later in the morning and immerge earlier in the afternoon than adults (Melcher et al. 1990).

Table 14.

Behaviors for which young differ significantly from the other cohorts for the number of minutes allocated at four sites in 1992. See Table 5 for levels of significance.

Activity	Site	Pattern of difference
Vigilance	Boulder	Young less than the adult female; young males less than the young female
	Stone Field	Young males much less than the young females and the adult females
Foraging-alert	Stone Field	Young much less than adult female
	Picnic	Young much less
Foraging	Boulder	Young more than the adult female
	Picnic	Young male less than all others; young females less than the adult female
Run/walk	Stone Field	Young males less than all others
Social	Boulder	Young more social than adult female
	Stone Field	Adult female more social; young females especially low
Investigation	River	Young females much more than the adults
	Picnic	Young male much more than all the other cohorts
Enter burrow	River	Young females much less than adults

Overall, young were less vigilant than adults (Table 14). At all four sites, young spent less time foraging-alert and less time vigilant. Young also allocated a smaller percentage of time to vigilance, and young males were less vigilant than young females except at Stone Field. The lower level of vigilance by young probably explains why reproductive females increase wariness after young are weaned (Armitage & Chiesura-Corona 1994).

Time spent foraging in relation to adults varied at the four sites. Young allocated fewer minutes and less percentage of time to foraging than adults at River and Picnic, and more time than adults at Boulder (Table 14). At Stone Field, all cohorts allocated almost identical percentages of time to foraging, and the young spent slightly fewer minutes foraging than the adult female. The general trend is for young to forage less than adults. This difference likely is related to body size; young weigh < 600 g when adults weigh > 2000 g. Obviously young require less food and spend less time foraging than adults. Young require energy for growth and fat accumulation and might have greater mass-specific food requirement than adults, but such intake has not been measured.

Generally, young spent fewer minutes than adults in run/walk and males allocated fewer minutes than females; the difference was statistically significant at Stone Field (Table 14).

The time spent social varied among the sites. At Picnic, the young male was more social (total minutes and percentage of time) than all other cohorts. The young allocated more minutes to social than the adult male or non-reproductive females; the reproductive females spent a greater percentage of time social than the young females. At River, young females were the least social, but the reproductive female, who spent most of her time in an area that could not be viewed from our most-used viewing site, was infrequently observed. These differences in time allocations to social may be attributed to variation in individual behavior. For example, at Boulder (Table 14), the young usually congregated at the burrow site under a large boulder and this close proximity could lead to more social contact. At Stone Field, young were more dispersed and social behavior that included the adult female was more likely as young interacted more with her than with each other. Also, at River, the young were weaned unusually late so that there was much less time for social behavior to occur (0.157/hr/yg), whereas adult females had a high rate of social interactions (0.385/hr/female) from early June through mid-July. Although the frequency of social behavior by adults decreased after the young were weaned, the rate for the entire summer (0.242/hr/female) for adult females exceeded that of the young females.

Young allocated more time to investigation than other cohorts (Table 14). At Boulder and Stone Field, the young allocated more minutes to investigation than the adult female (not statistically significant). Thus, the general pattern is for young to investigate more than the other cohorts. This pattern probably represents part of the process whereby the young familiarize themselves with their new, aboveground environment.

Young entered a burrow significantly less than adults only at River (Table 14), but generally young entered less than other cohorts.

Influence of weather variables

The multiple regression of five weather variables was statistically significant only for the number of active adult and yearling marmots in the AM. For adults, radiation, cloud cover and wind speed were significantly correlated with the number of active marmots; these variables plus temperature and relative humidity were significantly

Table 15.

Correlation matrix for five variables and the number of marmots active aboveground for three age groups. AM = 07:00 to 12:00; PM = 16:00 to 20:00. For adult marmots in the AM, temperature did not enter the model, and relative humidity made a small contribution (< 0.01) to R^2; in the PM wind speed did not enter the model, and radiation and temperature made small contributions to R^2. For yearling marmots in the AM, wind speed and temperature made small contributions to R^2; in the PM, relative humidity made a small contribution to R^2. For young in the AM, radiation did not enter the model, and temperature made a small contribution to R^2; cloud cover made a small contribution to R^2 in AM and PM.

| Weather variables | Marmot age groups | | | | | |
| | Adult | | Yearling | | Young | |
	AM	PM	AM	PM	AM	PM
Radiation	−0.335**	0.241*	−0.939**	−0.284	0.017	0.279*
Temperature	−0.111	0.091	−0.293*	−0.083	−0.024	0.067
Relative humidity	0.172	−0.086	0.308*	0.075	0.046	−0.380**
Cloud cover	0.229*	0.244*	0.304*	0.060	−0.006	−0.042
Wind speed	−0.357*	0.116	−0.366**	0.227	0.111	0.109
Multiple R	0.515**	0.391	0.697**	0.618	0.199	0.499
n	96	73	61	29	61	48

Note: *P = 0.05, **P = 0.01.

correlated with the number of active yearlings. All of these weather variables contribute to the thermal influences on marmot activity.

The thermal influences on marmot activity were modeled using standard operative temperatures (T_{es}). T_{es} incorporates microhabitat characteristics, such as ambient temperature, wind speed and solar radiation, and integrates them into a temperature measurement equivalent to the temperature a marmot would experience in a metabolism chamber (Melcher et al. 1990). The effect of wind speed, i.e., convection, is complex; wind speed reduces T_{es} over the tops of rocks, where marmots may sit, in comparison to T_{es} in the meadow where marmots forage. The correlations between wind speed and marmot numbers (Table 15) probably reflect the high correlations between radiation and wind speed (Table 3). The positive correlation of the numbers of adults and yearlings active with cloud cover (Table 15) is a consequence of the negative relationship between cloud cover and radiation (Table 3), which reduces T_{es}. Thus, marmots may spend more time foraging on cloudy than on sunny days (Travis & Armitage 1972). High T_{es} decreases time spent foraging (Melcher et al. 1990), thus reducing foraging during mid-day, except when cool and cloudy mornings, which occurred often in 1993, allowed marmots to spend more time foraging in mid-day. By contrast, marmots increase sitting during mid-day, in part because wind may enhance convective heat loss and reduce T_{es} where marmots sit (Melcher et al. 1990). Also, when marmots sit in the sun, they angle their bodies to reduce the amount of direct radiation by sitting or lying on the shady side of a rock (Armitage 2009a).

The decreased mid-day activity of marmot populations as a consequence of thermal stress is expressed in a well-known bimodal daily activity cycle with peak

numbers of marmots in the morning and afternoon. Early and late in the season the daily cycle is unimodal with a mid-day peak of activity (Armitage 1991, 2014).

Although the multiple regressions for the number of adults and yearlings active in the PM were not significant, radiation and cloud cover were significantly correlated with the number of active adults (Table 15). Both radiation and the number of adults declined, especially in the late PM. The number of active adults is affected by non-weather factors. Marmots may cease activity once foraging is completed, and territorial males generally are active later in the afternoon than are other cohorts (Armitage et al. 1996). The yearlings received agonistic behavior from the adults. Space overlap between the yearlings and the two adult females averaged 19%, compared to 34% between the two adult females. Thus, yearlings modified their activity to avoid the adults, and this behavior probably affected the relationship between activity and weather in the PM.

The number of active young was not significantly related to the weather variables; the multiple regression was statistically insignificant for both AM and PM (Table 15). In the AM, neither radiation nor temperature was a significant variable. In the PM, relative humidity was negatively and radiation positively correlated with the number of active young (Table 15).

Young generally emerge later in the morning than adults when radiation and T_{es} are increasing, thereby avoiding low, stressful T_{es}. In general, young used relatively more of the high-T_{es} time whereas adults used relatively more of the low-T_{es} time (Melcher et al. 1990). As a consequence, young generally are more active after T_{es} and radiation have increased, whereas adults initiate activity at low T_{es} and decrease activity as T_{es} and radiation increase, thus accounting for the lack of correlation between radiation and the number of active young, and the negative correlation between radiation and the number of active adults in the morning (Table 15).

In the PM, young generally immerge earlier than adults; thus, young are active when radiation is relatively high, which accounts for the positive correlation between radiation and the number of active young (Table 15). The significant negative correlation between the number of young and the relative humidity is surprising because we know of no data relating relative humidity to marmot metabolism. This correlation may result from the relationship between relative humidity and other weather variables. During the time young were active, relative humidity was negatively correlated with temperature ($r = -0.638$, $P = 0.01$) and radiation ($r = -0.509$, $P = 0.01$). As relative humidity increased, radiation and temperature decreased, and both of these would decrease the number of active young. Thus, relative humidity may have acted as a surrogate for the effects of temperature and radiation. The key point is that young time their daily active cycle to avoid the most stressful T_{es} periods (Melcher et al. 1990).

GENERAL CONCLUSIONS

Although time-budget differences among sites were not statistically analyzed, site differences are clearly evident in the patterns of significance for the analyzed variables (see Tables 5, 11 and 12). Most of this variation can be attributed to diverse cohort structure (e.g., presence of immigrants) and environmental variables (e.g., presence of predators, weather patterns, site aspect). Site differences and variation among cohorts, day-periods and season-periods indicate considerable phenotypic plasticity in time budget allocations. Phenotypic plasticity characterizes many responses to environmental variability (Armitage 2014; Maldonado-Chaparro et al. 2015).

Some of the variation in time allocation among cohorts may be a consequence of age (e.g., young), and of individual behavioral phenotypes. Play and social behavior of yearlings (Armitage & Van Vuren 2003), amicable behavior among young (Armitage 1982b) and social behavior of adults (Svendsen & Armitage 1973; Armitage 1986b) are significantly affected by individual behavioral phenotypes. It seems plausible that time allocations to other behaviors could be similarly affected, and this possibility should be the subject of future research.

However, within the broad framework of plasticity, a consistent pattern of time allocations is evident across sites and years. Sitting, foraging, vigilance and run/walk account for more than 80% of aboveground activity, a pattern evident in other time-budget studies (Armitage & Chiesura-Corona 1994; Armitage et al. 1996) that can be considered a characteristic feature of yellow-bellied marmot biology. Wariness is the behavior that integrates these activities into a consistent pattern, as wariness dominates the most important activities of sitting and vigilance and is expressed during foraging as foraging-alert.

It seems reasonable that wariness would be strongly associated with sitting, which raises the question: why do marmots allocate half of their aboveground time to this activity, when they are exposed to thermal constraints? Their general watchfulness indicates that marmots remain aboveground in order to monitor for possible intruders. The watchful marmot can act to prevent competitive conspecifics from exploiting resources in the marmot's home range. More importantly, the marmot remains watch-ful for predators. The underground marmot cannot know if a predator, such as a coyote, is positioned near the burrow entrance to await an emerging marmot. Successful predation was observed when a coyote lay in ambush and attacked and captured a yearling marmot after it emerged in the afternoon (Armitage 1982a). The danger when emerging is evident in the cautious and slow process coupled with vigilance when a marmot emerges (Armitage 2014).

Foraging must provide the energy and essential nutrients required for mainte-nance and reproduction. Time may be a major constraint that prevents marmots from meeting nutritional requirements. A seasonal time constraint is evident; some species of marmots of large body size with a short active season usually are unable to reproduce, accumulate sufficient energy reserves for hibernation, and reproduce the next season; i.e., reproductive skipping occurs for as much as 2 or 3 years (Armitage & Blumstein 2002). A seasonal time constraint is imposed by the length of time of snow cover. Prolonged snow cover in the spring reduces the reproductive frequency of individuals, decreases litter size, delays the time of weaning and reduces the proportion of females reproducing (Johns & Armitage 1979; Van Vuren & Armitage 1991; Armitage 2013a). By contrast, a longer growing season results in increased survival, increased reproduction and rapid population growth (Ozgul et al. 2010).

Despite seasonal time constraints, yellow-bellied marmots maintain about the same allocation of time to foraging throughout the summer; clearly there is no increase in time prior to hibernation (Fig. 1). There may be a decrease in feeding (ingestion of plant food) coupled with an increase in search time. Earlier in the summer when plant productivity is high (Kilgore & Armitage 1978, Frase & Armitage 1989), yellow-bellied marmots feed almost constantly; e.g., when foraging in a meadow with abundant cinquefoil (*Potentilla gracilis*), a highly used food plant (Armitage 1979). In late summer, many food plants undergo senescence and many are unpalatable (Armitage 2003e). At this time, marmots were observed feeding on fruits of elderberries (*Sambucus pubens*). They spent considerable time manipulating the branches to reach the berries. Hence,

more foraging time was spent seeking than eating. By contrast, average daily foraging time of golden-mantled ground squirrels (*Spermophilus saturatus*) increased steadily during the active season as the squirrels increased the amount of fungus in their diet (Kenagy et al. 1989). For neither species is daily foraging time-limited. The ground squirrels on average spent 65% and yellow-bellied marmots 49% (Table 4) of above-ground time sitting.

Time spent foraging responds to food abundance. The Siberian marmot (*M. sibirica*) allocated significantly less time to foraging in a site with much greater biomass and more forbs than in a site with lower biomass and fewer forbs (Buuveibaatar & Yoshihara 2012). The hoary marmot (*M. caligata*) concentrated foraging in areas of greatest food abundance even though the area was more distant from the burrow area (Holmes 1984b). Likewise, yellow-bellied marmots in California spent more time feeding in areas of high plant biomass (Carey 1985). However, black-capped marmots (*M. camtschatica*) spent much less time foraging in areas with rich vegetation compared to areas of low-quality vegetation (Tokarsky 1996). Most likely, the greater time in food-poor areas represented increased search time, as in the case of golden-mantled ground squirrels. Such differences were not evident in this study because all yellow-bellied marmots foraged in meadows with plant biomass ranging from 247 to 350 g/m^2, about 5 times greater than the biomass reported for *M. sibirica* (Armitage 2009b).

Food consumption, hence foraging time, is controlled by an endogenous circannual rhythm (Ward & Armitage 1981); consumption decreases markedly leading up to hibernation (e.g., Couch 1930). Juvenile yellow-bellied marmots cease growth for 2 weeks or more before hibernation (Armitage et al. 1996; Lenihan & Van Vuren 1996), even when abundant supplemental food is provided (Woods & Armitage 2003).

All age-classes of yellow-bellied marmots cease mass gain for several weeks before hibernation (Armitage et al. 1996, 2014). Feeding during this period of mass stasis may function to maintain rather than increase body mass. Marmots may delay hibernation because of the negative effects of torpor (Bieber et al. 2014). However, marmots probably delay hibernation as early hibernation would initiate a decrease in fat reserves while food is available. Delaying hibernation conserves energy that could be critical for survival and reproduction the following year. The circannual cycle prepares marmots to anticipate immergence, the timing of which depends on local conditions, such as plant senescence or snowfall (Andersen et al. 1976).

Thermal constraints, especially mid-day radiation, limit potential foraging time. Marmots can make short-term foraging bouts when T$_{es}$ is high, but cease foraging when body temperature nears 40 °C (Melcher et al. 1990). The alpine (*M. marmota*, Sala et al. 1992) and Olympic (*M. olympus*, Barash 1973) marmots also spent more time at rest than feeding; thus, we conclude that thermal constraints do not limit energy acquisition because time can be shifted from resting to foraging.

Marmot dentition and their simple digestive tract are best suited for a diet of seeds and are disadvantageous for an herbivorous diet (Hume 2003). The large body size with its larger absolute gut capacity relative to metabolic rate offsets the disadvantage of the simple gut and achieves a high digestive efficiency (Kilgore & Armitage 1978; Hume 2003). The high digestive efficiency is derived from a mean retention time of digesta in the gut of more than 24 hr (Hume et al. 1993). Marmot foraging time likely is constrained by the time required for food processing (Weiner 1992), and much of the time spent sitting is time spent digesting.

We conclude that the major components of the time budget of the yellow-bellied marmot are directed toward energy acquisition, and processing and maintaining wariness for possible intruders. Time (length of the active season) acts as major constraint

on overall marmot activity and curtails energy acquisition. Digestive constraints limit daily energy acquisition; thermal constraints play a minor role. Time spent in one behavior does not impose a trade-off in the amount of time available for other behaviors because time allocations are flexible, not fixed. In general, the variations in time allocation to various activities indicate that considerable phenotypic plasticity characterizes marmot activity. This plasticity allows marmots to adjust time budgets in response to environmental factors such as weather patterns and conspecific activity either during day-periods or season-periods. Finally, our results indicate that extensive knowledge of the life history, including physiology, behavior and demography, is essential for interpreting time budget allocations.

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