Energy Allocation by Yellow-bellied Marmots

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Abstract

*Energy intake, daily energy expenditure (DEE), and energy available for production were determined for yellow-bellied marmots (*Marmota flaviventris*) at three study sites in the Elk Mountains of southwestern Colorado. Energy intake, estimated from tritiated-water turnover rates and the water and energy content of food plants, ranged from 3,283 kJ d^{-1} for two lactating females in July to 666 kJ d^{-1} for a yearling female in September. Maintenance, activity, and thermoregulatory components of DEE were estimated from time-budget data, estimated or measured activity costs, and heat-transfer theory. Not including energy allocated to production, DEE ranged from 1,017 kJ d^{-1} for a lactating female in July to 539 kJ d^{-1} for a female yearling in June. Time spent in the burrow accounted for 41%–60% of DEE; foraging, for 11%–51%; sitting on rocks by the burrow, for 1%–28%; and thermoregulation, for 1%–6%. Assimilated energy exceeded DEE for all but one animal studied; mass gains calculated assuming that assimilated energy in excess of DEE was available for production closely matched average measured mass gains of field animals.*

Introduction

Energy for growth, reproduction, or storage must be accumulated in excess of energy required for maintenance, thermoregulation, foraging, and other activities. Quantification of energy intake and expenditure of free-ranging animals is needed to evaluate how animals allocate available time and energy to accumulate additional energy. The influence of factors such as age, reproductive status, and weather on patterns of allocation, and the energetic

consequences of alternative behaviors and activity patterns, also need quantification. Energy expenditure by free-ranging animals often was estimated from time budgets and estimated activity costs (e.g., Wolf and Hainsworth 1971). Time budgets are easily quantified, but estimated energy costs of activity may be inaccurate (Karasov 1981). Accurate time-budget estimates of daily energy expenditure (DEE) are possible, however, using measured energy equivalents for various activities and heat-transfer theory to calculate thermoregulatory costs (Weathers et al. 1984; Buttemer et al. 1986). This study used such an approach to estimate DEE of yellow-bellied marmots (*Marmota flaviventris*). Values for DEE and estimates of energy intake calculated from water influx rates were then used to investigate the influence of age, reproductive status, and weather on energy demands, energy intake, and allocation.

Yellow-bellied marmots, large hibernating ground squirrels, typically inhabit montane areas with short growing seasons. In the Elk Mountains of southwestern Colorado, marmots have only 4–5 mo to reproduce, grow, and deposit fat for hibernation. High allocation to production is essential for juveniles to attain critical minimum mass needed to survive hibernation (Armitage, Downhower, and Svendsen 1976), and the size of fat stores may influence the reproductive success of females at high elevations where food is limited at the beginning of the active season (Andersen, Armitage, and Hoffmann 1976). Marmots differ from typical endotherms in allocating a high proportion of assimilated energy to production (Kilgore and Armitage 1978). Previous field and laboratory studies interpreted aspects of marmots' physiology and behavior as energy-conserving adaptations that promote high allocation to production: resting metabolic rates of marmots are lower than those predicted from allometric equations (Kilgore and Armitage 1978), and activity costs may also be low. Marmots spend more than 70% of the active season in their burrows (Travis and Armitage 1973; Frase 1983; this study), and much of their time aboveground is spent resting. Herbers (1981) termed them "lazy," but others (Travis and Armitage 1973; Frase and Hoffmann 1980) suggest that marmots conserve energy by basking, using solar radiation to supplement heat production for thermoregulation. The present study investigated these suggestions by quantifying energy intake and expenditure of free-ranging marmots, and compared patterns of energy intake and allocation among animals of different sex, age, and reproductive status.

Material and Methods

Study Sites

We studied marmots at three sites in the Elk Mountains of Gunnison County, Colorado: Marmot Meadow (MM) and Picnic (PIC) in July 1983, MM in June

1984, and MM and North Pole Basin (NPB) in September 1984. The MM and PIC sites, located on opposite sides of the East River at an elevation of 2,900 m, include talus slopes where the marmots maintained home burrows, an expanse of open meadow, and are bordered in part by forest (detailed description in Armitage 1974). At NPB, a 3-km-long hanging valley 10 km northwest of MM and PIC, burrows were located on the valley floor at an elevation of 3,400 m, within rock outcrops bordered by patches of open meadow and willow thicket (detailed description in Andersen et al. 1976).

Labeled Water

We injected marmots intraperitoneally with 1.0 mCi tritium per kg body mass. After a 3-h equilibration period, a blood sample was withdrawn from the femoral vein, flame-sealed in heparinized hematocrit tubes, and refrigerated. Animals were released at their home burrows and retrapped at 1–3-d intervals for additional blood samples. Body mass was measured at each recapture. Eleven marmots were studied: two adult females at MM and one adult female and one adult male at PIC in July 1983, one adult female and two yearling females at MM in June 1984, one yearling female and one male young at MM in September 1984, and one adult female and one male young at NPB in September 1984.

Tritium activity in water distilled from blood samples was measured at the University of Wisconsin—Madison by liquid-scintillation spectrometry. Total body water (TBW) was estimated from tritium activity in the initial blood sample according to the dilution method (Foy and Schnieden 1960). Tritium dilution commonly overestimates total body water measured by drying by 4%–5% (Foy and Schnieden 1960; Nagy et al. 1978; Nagy and Costa 1980). No animal in this study could be killed to obtain measured values; instead, an adjusted value for total body water was calculated as TBW/1.05.

We calculated rates of water influx of marmots maintaining constant body mass using equation (3) from Nagy and Costa (1980). We used Nagy and Costa's equations (4) and (6), for animals with linearly changing water volumes, for animals gaining mass. Mass gain in marmots is linear (Armitage et al. 1976).

Lean body mass was calculated as TBW/0.73 (Pace and Rathbun 1945; Holleman and Dieterich 1975). Body fat was calculated as the difference between total and lean body mass.

Body Temperature and Behavioral Observations

Body temperature (T_b) of all animals except the adult female at NPB was monitored with Telonics IMP/200/L temperature-sensitive telemetry trans-

mitters. Transmitters measured 5.8 × 2.0 cm and weighed 22–27 g when encased in a mixture of paraffin/elvax. We calibrated the transmitters individually in a water bath from 30–45°C; bath temperature was read to the nearest 0.1°C using a Bailey BAT-12 thermocouple thermometer previously calibrated against a Taylor Instruments mercury thermometer having a systematic error of 0.01°C. Pulse rate of the transmitters was linearly related to temperature over the calibration range.

Transmitters were implanted intraperitoneally in marmots anesthetized with Ketaset (ketamine hydrochloride, 1.0 mg/mL at a dosage of 1 mL/kg) diluted 1:1 with sterile physiological saline. Generally animals were released the day following surgery and behaved normally upon release. Marmots were recaptured at intervals beginning within a few days of surgery and always appeared healthy; incisions healed rapidly. In July 1983 and June 1984 transmitters were implanted several days to several weeks before beginning labeled water studies; in September 1984 transmitters were implanted within 24 h of beginning the studies.

We observed marmots from tree platforms (MM and PIC) or from behind natural blinds of willow (NPB) using 8 × 24 binoculars. Transmitter signals were received with a Telonics TR-1-20 receiver and a hand-held directional antenna. A Telonics TDP-2 digital data processor converted pulse rate to interpulse intervals (in milliseconds) that were recorded manually and later converted to body temperature using the calibration regression for each transmitter. When signal strength was too weak for decoder processing, 30 pulses were timed to the nearest 0.01 s instead. Body temperatures of animals studied in 1983 were recorded every 15 min (occasionally more frequently when an animal changed activity state) beginning before any animal emerged in the morning and continuing until the last animal entered its burrow at night. We have no evidence from 25 yr of marmot research that marmots are active aboveground at night. Location (burrow, rock, grass, or woods) and activity (sit, forage, or locomote) were recorded continuously for those animals whose location was known. During data analysis, locomotion associated with foraging was added to foraging time, and miscellaneous behaviors such as grooming, greeting, and play were pooled with sitting. Because daily activity patterns and body temperature cycles of these animals changed little over a few days, animals in 1984 were observed at different times over several days, and the observations were pooled to yield a composite daily record of activity and body temperature.

Microclimate Measurements

Microclimate data were recorded concurrently with behavior and body temperature. Solar radiation was measured with a Licor LI-200S pyranometer

TABLE 1

Water content (percentage) and energy content (kJ g⁻¹ wet weight)
of vegetation at study sites

	Marmot Meadow	Picnic	North Pole Basin
June	81.8, 3.37	. . .	. . .
July	79.8, 3.94	78.4, 4.38	. . .
August	68.5, 4.35	. . .	73.2, 4.95

sensitive to wavelengths between 400 and 1,200 nm. Net radiation was mea-
sured with a miniature Fritschen-type net radiometer. Air temperature at 10
cm and soil temperatures were measured with thermistor probes. Air tem-
perature probes were shielded with 15 × 9-cm sections of PVC tubing
painted flat white. Wind speed was measured between 0.5 and 1.0 m with
Rimco miniature cup anemometers. Wind speed at marmot height was cal-
culated later from wind profiles measured at the same sites. Output from
microclimate sensors was fed into a Campbell CR-21 micrologger that aver-
aged output every 15 min and stored the averaged values on cassette tape.
Microclimate data were later decoded from cassette tape using a Campbell
A235 interface and a decoding program.

Food Consumption and Energy Budgets

Food consumption was estimated from water influx rates. Marmots rarely
drink water in the field; hence, the main sources of water influx are pre-
formed water in food and metabolic water. Food consumption was calcu-
lated as the mass of vegetation that, through its water content and estimated
metabolic water production, would yield the measured water influx rates.
These calculations overestimate actual food intake somewhat because some
water influx occurs via respiratory and cutaneous surfaces and dew or rain-
water is sometimes consumed with vegetation.

The composition of marmot diets (Frase 1983), water and caloric content
of food plants (Kilgore 1972; Andersen and Armitage 1976; this study, table
1), and digestive efficiencies of marmots fed field diets (table 4 in Kilgore
and Armitage 1978) are known. Metabolic water production was estimated
using a conversion factor of 0.030 mL H_2O kJ⁻¹ metabolized (Schmidt-Niel-
sen 1979, p. 319). To simplify calculations, we assumed all digested food

was oxidized, even though some animals were growing or storing fat. Because metabolic water production is only about 10% of preformed water intake, the resulting error in estimation of food intake using this assumption is small compared to total food intake. Thus, measured H_2O influx $= V \times$ (mL H_2O/g food) $+ V \times$ (digestive efficiency) $\times$ (kJ g^{-1} food) $\times$ (0.030 mL H_2O kJ^{-1}) was solved for V, vegetation intake in g. Energy intake in kJ was calculated using reported energy content of food plants (Kilgore 1972; Andersen and Armitage 1976).

Energy budgets were constructed using time-budget data, estimates of the energetic cost of various activities, and heat-transfer theory to calculate thermoregulatory costs. Energy expenditure of marmots in their burrows was estimated as the minimum resting metabolic rate (RMR) of animals in metabolic chambers: 11.1 J g^{-1} h^{-1} for adult females and 16.9 J g^{-1} h^{-1} for yearling females and juvenile males (Kilgore and Armitage 1978; Melcher 1987). Air temperature of burrows remains near 10°C during summer (Kilgore and Armitage 1978), but insulation provided by nesting materials and huddling with other animals can modify the thermal environment sufficiently that animals are in thermoneutral conditions. Energy expenditure of animals aboveground was estimated using published estimates for the energetic cost of activity. Two activities, sitting (basking) on rocks near the burrow and foraging, accounted for nearly all time spent aboveground. Energy expenditure during sitting was calculated as 1.7 $\times$ RMR (Taylor, Schmidt-Nielsen, and Raab 1970). The metabolic cost of activity estimated from doubly labeled water studies of several mammalian species is 3 $\times$ RMR (Karasov 1981); this value was used for foraging animals.

The energetic cost of thermoregulation was calculated using standard operative temperature (T_{es}) (Bakken 1980). The value T_{es} specifies the temperature of a laboratory enclosure with standard convection conditions that would yield the same net heat flow experienced by the animal in its natural environment, thus incorporating the various heat flows into a single term (Bakken 1981). Thus, an animal's metabolic response to a given T_{es} can be equated to its response in a metabolic chamber at an air temperature the same as T_{es}. Hourly averages of microclimate data were used to calculate T_{es} using energy-budget equations from Bakken (1981) and Mahoney and King (1977) (Melcher 1987); a regression of metabolic rate on T_a for marmots in metabolic chambers (Ward 1980; Melcher 1987) was used to determine metabolic rate at T_a's equivalent to T_{es}; thermoregulatory costs were then calculated as the difference between minimum RMR and metabolic rate at the given T_{es}. Quantitative estimation of the contribution of heat produced during activity is difficult and is available for few species (Paladino and King 1984). We did not attempt to determine this relationship for marmots and

have not included estimates of heat production during activity in our calculations of thermoregulatory heat requirements; thus our calculations probably overestimate actual costs. Time spent in each activity was summed over hourly intervals, then multiplied by the energy cost estimated for that activity. Costs were summed for the duration of each study, then divided by the length of the study in days to give an average daily value for comparison with calculations based on tritium turnover rates, which are average values for each study period.

The difference between DEE and digested energy, minus energy lost in urine (Kilgore and Armitage 1978), was considered energy available for production. Production of nonreproductive or postreproductive animals 3 yr old or older was assumed to consist entirely of fat; that of yearlings in June and young in late summer, to be lean tissue (Kilgore and Armitage 1978). Energy retained as fat or lean tissue was calculated using efficiencies of 70% and 45% for fat and protein deposition, respectively (Garrett 1980). Production in kJ was converted to g using equivalents of 38.1 kJ g^{-1} for fat and 6.0 kJ g^{-1} for lean tissue (Kilgore and Armitage 1978), permitting comparison of estimates to measured growth rates of field animals (Armitage et al. 1976). Production of reproductive females includes growth and metabolism of young and was not estimated.

Results

Microclimate

Microclimate conditions were warmest at MM in July 1983, when skies were clear for most of the study period (fig. 1). Skies were overcast most afternoons during the PIC study, hence the lower temperatures and solar radiation. Skies were generally clear during September 1984; lower temperatures and solar radiation reflect seasonal changes in daylength and solar elevation. Wind speed at NPB was consistently high throughout the day, whereas wind speed at MM and PIC tended to peak at midafternoon. Lower wind speeds at PIC in July 1983 and at MM in September 1984 reflect the attenuating effect of increased vegetation height.

Body Temperature and Activity

Body temperature varied with activity state (fig. 2). The T_b's of foraging animals were typically 1–2°C higher than resting T_b's, but rarely exceeded 40°C. Nighttime T_b's averaged 1°C lower than T_b's of animals resting in their burrows during the day. Daily range of T_b was similar for all animals, with
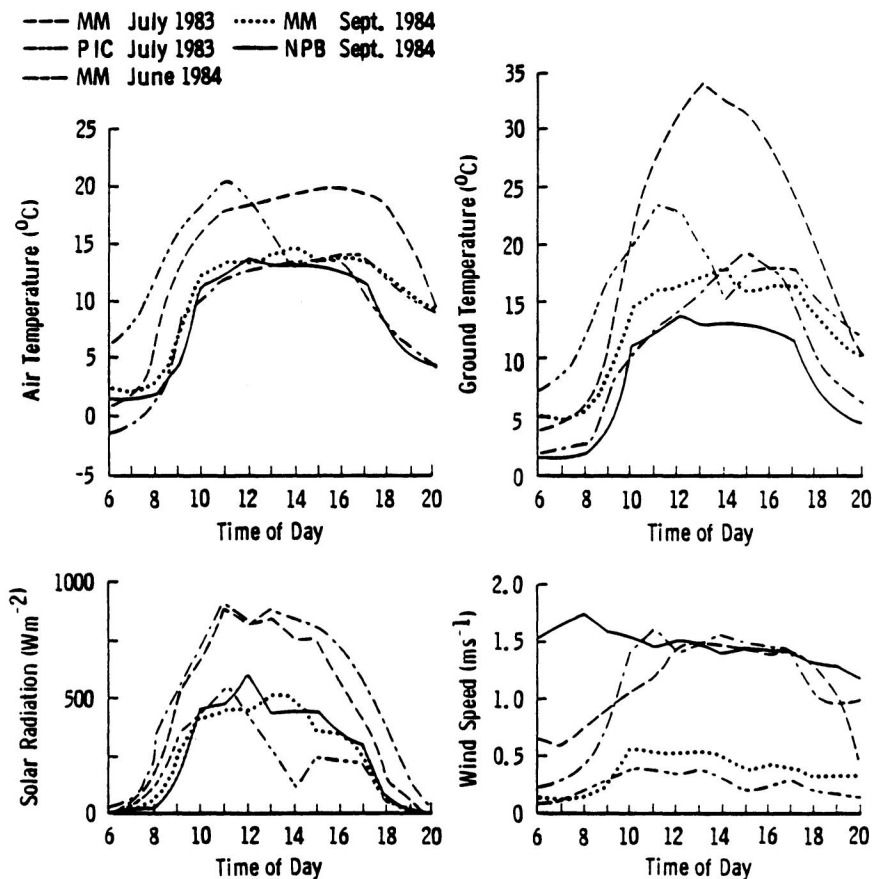
Fig. 1. Microclimate conditions during labeled water studies at Marmot Meadow (MM), Picnic (PIC), and North Pole Basin (NPB).

lows averaging 36.6°C and highs 39.8°C (Melcher 1987). Marmots did not use solar radiation as a supplemental heat source to elevate T_b in the morning. The T_b's generally rose before animals left their burrows; adults often emerged before direct sunlight reached the burrow area. No animal entered hibernation or underwent prehibernation test drops in T_b during this study.

Marmots spent most of their time belowground (table 2). Young and yearlings spent 16.1 h d^{-1} in their burrows; adults, 18.3 h d^{-1}; the difference between these means probably is biologically significant ($P = .057$, Mann-Whitney U test). The timing of aboveground activity also differed among age classes. Adults emerged earliest, usually between 0600 and 0700 hours in June and July. Yearlings and young typically emerged 1–1.5 h after the adults and usually entered their burrows for the evening earlier than adults. All animals immerged by dusk. Yearlings and young spent more time aboveground at midday than did adults, which accounts for their greater daily time
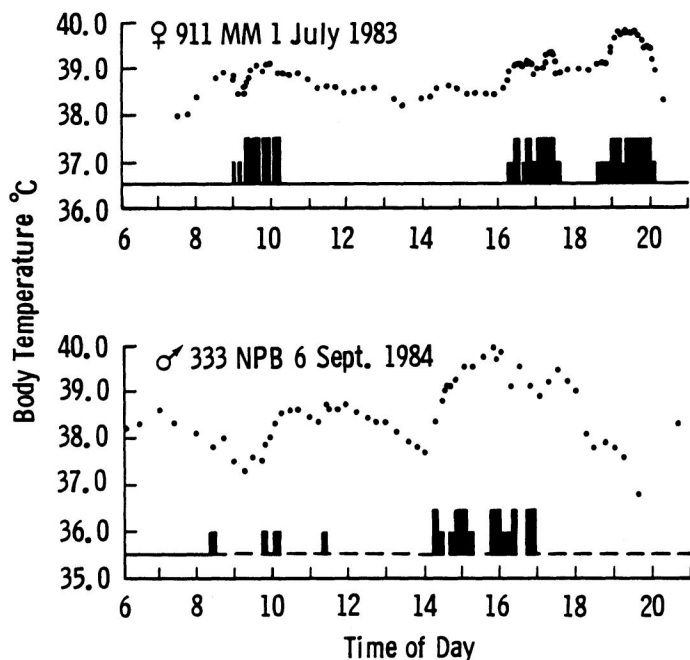
Fig. 2. *Body temperature of adult female 911 at Marmot Meadow on July 1, 1983, and young male 333 at North Pole Basin on September 6, 1984. Symbols below plotted temperatures indicate activity: solid horizontal line indicates animal in burrow; broken horizontal line indicates animal's location uncertain; lower vertical bar indicates animal sitting on rocks aboveground; higher vertical bar indicates animal foraging.*

aboveground. Daily emergence and immergence times shifted seasonally with changes in the time of sunrise and sunset. In September, animals usually emerged after 0900 at MM, and after 0930 at NPB.

Foraging and sitting account for most of the marmots' time aboveground. The proportion of aboveground time spent foraging varied greatly among individuals, ranging from 0.18 for yearling 278 at MM in June 1984 to 0.96 for young 333 at NPB in September 1984.

Body Water Content and Water Influx Rates

Body water content exceeded 70% for five animals and exceeded 60% for all but two of the remaining animals (table 3). Because lean tissue is approximately 73% water (Holleman and Dieterich 1975), lean body mass can be estimated from the water content of each animal and body fat estimated as the difference between total and lean mass. Lean animals have the highest

TABLE 2

Time and energy budgets of individual yellow-bellied marmots

Study Date	Animal	Burrow		Sitting		Foraging		Thermo-regulation DEE
		Time	DEE	Time	DEE	Time	DEE	
July 1983	f 254	77	56	9	11	14	31	2
July 1983	f 911	80	60	8	10	12	26	4
July 1983	f 573	66	41	15	16	19	37	6
June 1984	f 966	64	41	19	21	17	32	6
June 1984	f 278	73	55	22	28	5	11	6
Sept. 1984 ...	m 84	74	52	8	9	18	38	1
Sept. 1984 ...	m 333	71	43	1	1	28	51	5

Note. Values are percentage of 24 h and percentage of DEE spent in each activity. m = male; f = female.

body water content; most animals in this study had little body fat. The two animals with lower body water and hence greater body fat, yearling 966 at MM in September and adult female 335 at NPB, were studied in fall when fat stores should have neared their peak. Body water content of the two young studied in September indicated almost no fat stores. Rapid fattening is essential for these animals to reach the critical minimum mass needed to survive hibernation (Armitage et al. 1976).

Water influx varied with age (body size), reproductive status, season, and site (table 3). Mass-specific water influx of free-ranging marmots was up to five times greater than influx of laboratory-housed animals (Ward and Armitage 1981). Marmots meet most of their water needs through preformed water in food and metabolic water, rarely drinking free water in the field. Because water influx in the field is linked to food intake, high influx results from both higher water content of food and greater food intake. The reproductive females and adult male in July 1983 and yearlings in June 1984 had the highest mass-specific water influx. Both reproductive females produced litters and probably were lactating during the labeled water studies. Water influx of nonreproductive female 254 and postreproductive female 335 was about half that of the lactating females. Water influx of one of the reproductive females, 911, measured in June 1984 while she was pregnant, was about 70% of that measured while she was lactating. Water influx was lowest for animals studied in September at the end of the growing season, particularly at MM.

TABLE 3

Body water, body fat, and water influx of individual yellow-bellied marmots

Study Date	Site	Animal	Mass (kg)	Body Water (%)	Body Fat (%)	Water Influx (mL kg^{-1} d^{-1})
July 1983	MM	f 254 (A nr)	2.3	64	12	161
July 1983	MM	f 911 (A lt)	2.4	67	8	294
June 1984	MM	f 911 (A pg)	2.6	75	. . .*	201
July 1983	PIC	f 573 (A lt)	2.4	62	15	289
July 1983	PIC	m 891 (A)	2.7	69	6	257
June 1984	MM	f 966 (Yl)	.9	75	. . .*	323
Sept. 1984	MM	f 966 (Yl)	2.1	51	30	54
June 1984	MM	f 278 (Yl)	.9	70	4	281
Sept. 1984	MM	m 84 (Yg)	1.0	73	. . .*	85
Sept. 1984	NPB	m 333 (Yg)	1.2	75	. . .*	179
Sept. 1984	NPB	f 335 (A pr)	2.6	59	19	122

Note. A = adult; Yl = yearling; Yg = young; nr = nonreproductive; lt = lactating; pg = pregnant; pr = post reproductive; m = male; f = female; * = body fat content too low to be measurable. MM = Marmot Meadow; PIC = Picnic; NPB = North Pole Basin.

Food Consumption and Energy Budgets

Because food consumption was estimated from water influx rates, variation among animals parallels variation in water influx (table 4). Estimated energy intake ranged from 317 kJ kg^{-1} d^{-1} for yearling 966 in September 1984 to 1,441 kJ kg^{-1} d^{-1} for female 573 in July 1983. Estimated energy intake of adults depended in part on reproductive status. Average estimated energy intake of lactating females 911 and 573 in July 1983 was 3,283 kJ d^{-1}, nearly identical to intake of a captive lactating female, 3,203 kJ d^{-1} (Melcher 1987), and double the intake of nonreproductive female 254. The only animal studied in both June and September, yearling 966, consumed 75% less food in September. Young 84 at MM in September 1984 consumed less than half as much as young 333 at NPB during the same period. Feeding rate ranged from 1,494 kJ h^{-1} for female 911 to 101 kJ h^{-1} for male young 84 in September.

Because DEE estimates used time-budget data to calculate activity costs, DEE was calculated only for animals for which continuous behavioral observations were available. Estimates of DEE ranged from 539 kJ d^{-1} for yearling 278 in June 1984 to 1,017 kJ d^{-1} for adult female 573 in July 1983 (table 5). Time spent in the burrow accounted for the majority of DEE, followed by

TABLE 4

Food consumption of individual yellow-bellied marmots estimated from water influx rates and the water and energy content of food plants

Study Date	Animal	Food Consumption (kJ kg^{-1} d^{-1})	Calculated Feeding Rate (kJ h^{-1})	Field/ Lab Intake
July 1983	f 254	711	468	.79
July 1983	f 911	1,295	1,095	1.45
June 1984	f 911	764	1,494	1.40
July 1983	f 573	1,441	747	1.61
July 1983	m 891	1,268	. . .*	1.11
June 1984	f 966	1,209	208	1.28
Sept. 1984	f 966	317	. . .*	.49
June 1984	f 278	1,054	463	1.11
Sept. 1984	m 84	422	101	.39
Sept. 1984	m 333	1,044	208	.96
Sept. 1984	f 335	762	. . .*	1.13

Note. Feeding rate was calculated as energy intake per unit foraging time. Lab intake was calculated from values reported in Kilgore and Armitage (1978). m = male; f = female; * = insufficient observations of animal to determine feeding rate.

foraging (table 2). Costs of thermoregulation were low, ranging from 1% to 6% of DEE (table 2). Because thermoregulatory costs were low, the amount of time spent active and the type of activity were the major modifiers of DEE for animals of any given age (size) class and reproductive status.

The DEE estimates include resting metabolism, activity, and thermoregulatory costs; energy intake in excess of DEE was assumed available for production. Estimated production for the yearlings at MM in June and young 333 at NPB in September 1984 was close to average mass gain of free-ranging marmots (table 5). Production estimated for female 254 was about half of average field values; food intake of 254 was also lower than predicted from ad lib. intake of captive animals (table 4). Actual energetic costs of pregnancy and lactation are unknown, but food energy allocated to reproduction can be estimated as the difference between DEE and assimilated energy because reproductive females apparently devote all extra energy intake to production of young and do not begin to deposit fat until the young are weaned.

TABLE 5

Estimated DEE and production of individual yellow-bellied marmots

Study Date	Animal	Energy Assim- ilated (kJ d^{-1})	DEE (kJ)	Energy for Produc- tion (kJ)	Estimated Produc- tion (g)	Measured Produc- tion (g)
July 1983	f 254	1,266	878	388	7.1	12.6
July 1983	f 911	2,460	856	1,604	. . .	. . .
July 1983	f 573	2,739	1,017	1,722	. . .	. . .
June 1984	f 966	762	636	126	9.5	15.4
June 1984	f 278	720	539	181	13.6	15.4
Sept. 1984	m 84	357	593	−236	. . .	. . .
Sept. 1984	m 333	1,047	673	374	28.1	29.3

Note. Measured production values are averages measured for field animals by Armitage et al. (1976) and Andersen et al. (1976). Production was not estimated for lactating females 911 and 573.

Discussion

Maintenance, activity, and thermoregulation typically constitute most of an endotherm's DEE (Karasov 1981; Weathers et al. 1984). Energy for growth, reproduction, or storage must be acquired in excess of these costs, by increasing energy intake and/or minimizing costs. Marmots need high allocation to production to deposit sufficient fat for hibernation (Armitage et al. 1976), and female reproductive success may depend partly on fat stores remaining after hibernation (Andersen et al. 1976).

Marmots in the East River valley consume only 0.8%–3.1% of aboveground primary production (Kilgore and Armitage 1978); increased food consumption could seemingly meet the demands of production. Available foraging time, food quality, and food-processing rate may, however, set an upper limit to energy intake. Growth rates of laboratory-housed young fed Purina Lab Chow ad lib. exceeded the highest measured field growth rates by more than 50% (Melcher 1987), indicating higher potential production rates than are attained by field animals. Young Richardson's ground squirrels (*Spermophilus richardsoni*) from field populations similarly took longer to reach adult mass than did laboratory-housed animals (Bintz and Strand 1983).

Previous studies suggested that energy-conserving mechanisms may complement increased energy intake: low resting metabolic rates (RMR) (Kilgore and Armitage 1978) and short activity periods (Travis and Armitage

1973; Frase 1983). Using the ratio of field metabolism (DEE) to RMR as a basis to compare marmots to other mammals indicates energy expenditure by marmots is indeed low. The ratio of DEE (excluding costs of production) to RMR averaged 1.4 for the three adults for which DEE was calculated (911 and 254 at MM and 573 at PIC in July 1983), lower than four other mammals reported in Karasov (1981), and at the lower end of the range of 1.4–5.7 for 19 species of rodents (King 1974). The most complete set of data currently available for comparison is Nagy's (1987) compilation of field metabolic rates (FMR). Our values are not directly comparable to Nagy's, since his values for FMR were obtained from doubly labeled water measurements and thus include all energetic costs incurred by the animals, whereas our values for DEE are sums of indirect estimates of the energetic costs of maintenance, activity, and thermoregulation. For those animals either growing or deposit-ing fat, estimated costs of production can be added to DEE, producing values that can be compared to predictions from Nagy's equations. Our values fall within the lower end of the range bracketed by the 95% confidence limits for a marmot-sized herbivore. However, the range of values included within the 95% confident limits is very broad; more meaningful comparisons will be possible only when data are available for a greater number of species. Low DEE of marmots chiefly reflects low RMR. The DEE of animals in Sep-tember may be even lower than the values calculated here from RMR of captive marmots in July (Kilgore and Armitage 1978); standard metabolic rates of laboratory-housed marmots decreased over the active season and in September were about 20% lower than July (Ward and Armitage 1981).

Short growing seasons and high mortality rates among marmots that fail to accumulate sufficient fat for hibernation appear to have selected for an energy-conservative life-style. Within that constraint, how do energy de-mands vary among animals of different sex, age, and reproductive status, and are differences in energy demand reflected by differences in behavior or patterns of energy allocation?

Energy Demand

Energy demand can be estimated given the energy intakes and DEEs calcu-lated in this study and daily energy requirements for growth and fat deposi-tion predicted from average field growth rates. Total energy demands were highest for reproductive females. Average energy intake of lactating females 911 at MM and 573 at PIC in July 1983, 3,283 kJ d^{-1}, nearly doubled that of nonreproductive female 254 at MM in July 1983 or postreproductive female 335 at NPB in September 1984. Food intake of up to 200% of nonreproduc-

tive intake was recorded for other reproductive rodents (Grodzinski and Wunder 1975).

Male territoriality may be as energetically expensive as female reproduction. Energy intake of male 891 nearly equaled that of the lactating females. Male 891 did not gain mass during the study and was observed too infrequently to estimate DEE from time-budget data, but he ranged over a large area at PIC and probably had high activity costs. An adult male spent a higher proportion of its aboveground time foraging than any adult female studied by Frase (1983). The annual energy budget of male golden-mantled ground squirrels (*Spermophilus saturatus*) equaled that of females (Kenagy 1987), and the energetic requirements of Scottish red deer stags were similar to those of lactating hinds (Clutton-Brock, Guinness, and Albon 1982).

Young and yearlings require energy for both lean tissue growth and fat deposition. To support average field growth rates of 15.4 g d^{-1}, yearlings in early summer require 205 kJ d^{-1} to produce lean tissue. Energy available for production in June 1984 was 181 kJ for yearling 278 and 126 kJ for yearling 966. To support average field growth rates of 29.3 g d^{-1}, male young in NPB require 391 kJ if they are building lean tissue, and 1,595 kJ if they are depositing fat. Young 333 at NPB had 374 kJ available for production. To support average growth rates of 16.8 g d^{-1}, production by male young in the East River valley requires 224 kJ if they are adding lean tissue, and 914 kJ if they are depositing fat. Energy expenditure of male young 84 exceeded energy intake. Neither 333 nor 84 had measurable quantities of fat; 84 did not survive hibernation; the fate of 333 is unknown.

Energy Intake

Energy intake can be increased by increasing either time spent foraging or feeding rate while foraging. Foraging costs are higher than those of sitting aboveground or resting in the burrow; maximizing feeding rate therefore minimizes foraging cost, but calculated feeding rate (energy intake per unit time spent foraging) varies widely even among animals at a given site and time. Reproductive females have the highest calculated feeding rates (table 4), presumably to meet high energy demands. At MM in June 1984, the calculated feeding rate of reproductive female 911 was three times that of yearling 278, and seven times that of yearling 966. Mass-specific intake by the yearlings exceeds that of 911, however, because the yearlings spent more time foraging. Calculated feeding rates are lowest in September, when plant water and nitrogen content decrease (Frase 1983), perhaps indicating longer search times needed for preferred plants or plant parts. Young marmots in the East River valley nearly double the proportion of their above-

ground time spent foraging in late summer (Frase 1983). Food quality at NPB in September is somewhat higher than in the East River valley and may account partly for the higher energy intake per unit foraging time of young 333. Longer foraging bouts require additional energy expenditure for foraging but may also be necessary to maintain high growth rates once the young begin to deposit fat. Young Richardson's (Bintz and Strand 1983) and Belding (Morton, Maxwell, and Wade 1974) ground squirrels, and presumably young marmots, postpone fattening until a certain lean mass is reached. The energy content of 1 g of fat is about six times that of lean flesh; hence, once the animal begins to deposit fat, food intake must increase for growth rate to remain constant. Adult males and nonreproductive females have the option of accumulating most of their fat supply early in the season before food quality declines.

Because fat deposition is delayed by lean tissue growth in young and by pregnancy and lactation in reproductive females, these animals appear to compensate by extending the active season, rather than by accelerating fattening (Bintz and Strand 1983). Reproductive Richardson's ground squirrels hibernate after adult males, and young immerge last (Michener 1977). In several years of observations in September, young marmots immerged last. Marmots at NPB typically emerge in spring 2 wk after animals in the East River valley and often are active in fall after all marmots at lower elevations immerged (Armitge et al. 1976).

The physical environment may limit energy intake by restricting available foraging time through midday heat stress that limits aboveground activity. High solar radiation and T_a at midday impose a high heat load and additional heat production during activity causes T_b to rise rapidly (fig. 2). Marmots return to their burrows if T_b approaches 40°C. Because large animals are more tightly coupled to the radiant environment, midday heat loads are higher on adults than young, and adults usually retreat to their burrows while juveniles often remain active.

Energy Expenditure

One possible means to reduce energy expenditure is to minimize activity costs. With estimated costs of 1.7 × RMR and 3 × RMR for sitting aboveground and foraging, respectively, the duration and type of aboveground activity are the major modifiers of DEE for animals of a given age, sex, and reproductive status. Activity costs range from 36% of DEE for 911 at MM in July 1983 to 53% for 966 at MM in June 1984 and 573 at PIC in July 1983. Reproductive female 911 and young in September spent a smaller proportion of their aboveground time sitting than did the other animals. Unless an

animal increases feeding rate, foraging activity cannot be reduced without decreasing food intake, but decreasing time spent sitting aboveground reduces activity costs and permits more energy allocation to production.

In addition to low RMR and activity, another option for energy conservation is minimizing thermoregulatory costs. On most days, thermoregulatory heat production is needed only if animals are active aboveground early in the morning or after sunset; on average, thermoregulation constitutes only 1%–6% of the marmots' DEE (table 2). Predicted heat loss during the coldest hours required only a small thermoregulatory increment by adults but exceeds the highest rates of heat production measured for juveniles. Young avoid large thermoregulatory expenditure by emerging 1–1.5 h later than adults and immerging earlier in the evening. Because marmots appear to adjust the timing of aboveground activity to coincide with microclimate conditions requiring little thermoregulatory heat production, differences in thermoregulatory costs between animals, study sites, and times are minimized. The animals with the highest thermoregulatory costs, yearlings 966 and 278 at MM in June 1984, probably were best able to accommodate these costs, having both higher quality forage than the young in September and the entire summer to deposit fat.

Another thermoregulatory option, nighttime hypothermia, is used limitedly. Because marmots used metabolic heat production rather than solar radiation to elevate T_b in the morning, the cost of rewarming partially offsets energy saved by nighttime hypothermia. Because marmots do not conserve energy by basking, the function served by time spent inactive on rocks near the burrow remains unknown. Marmots may sit aboveground while processing food after foraging; periods of aboveground inactivity may also serve some social function, such as exclusion of conspecifics from an individual's home range, or may be important for predator surveillance.

Thermoregulatory costs for all animals potentially could be much greater. For example, male young 333 at NPB expended 36 kJ for thermoregulation on September 6, 1984. If this animal had been active aboveground during that day's coldest daylight hours, thermoregulation would have required at least 83 kJ. The difference, 47 kJ, is equivalent to about 3.5 g lean tissue, or about 12% of the average daily mass gain measured for NPB juveniles (Andersen et al. 1976). Based on similar calculations, female 254 at MM could have spent 89 kJ for thermoregulation, more than five times her estimated actual expenditure. The energetic savings would be sufficient to deposit an additional 1.4 g fat. Energetic savings may be particularly critical at the end of the growing season and at high elevation.

Because the timing of peak energy demand varies with age and reproductive status, ability to accumulate additional energy may be affected by factors

that vary over the active season, such as food quantity and quality or weather. These factors may determine in part the energy-conserving options available to any given animal. The high energy demands of pregnancy and lactation and short active season make energy conservation most crucial for reproductive females and their young, and these animals appear to respond by minimizing energy expenditure when possible. In general, marmots respond to the energetic demands of their environment by limiting aboveground activity to times of favorable microclimate conditions, and to the energetic demands of growth and reproduction by increasing feeding rate or length of foraging bouts, or by extending the active season.

Acknowledgments

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