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Hibernation as a major determinant of life-history traits in marmots

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During the downward trend of Quaternary global temperatures, crown-group marmots evolved to occupy harsh, seasonal environments at high latitudes and elevations. Marmots evolved hibernation and large body size, which allowed them to cope with a long, cold season with low, stressful ambient temperatures when food was unavailable. Harsh conditions during a short active season frequently cause reproductive failure and reproductive skipping in marmots. Seasonal phenology is controlled by a circannual rhythm that directs metabolic changes and fat accumulation for hibernation and reproduction. Metabolism and water balance in marmots are adapted to the low environmental temperatures of hibernation. Thus, marmots are subject to heat stress from solar radiation and high ambient temperatures during the active season. Energy conservation characterizes metabolism in marmots throughout the annual cycle: metabolic rates are lower than predicted from body size and decline during the active season, metabolism is actively suppressed to enter torpor, and most of the time during hibernation is spent at low metabolism in deep torpor. Young typically require 2 or more of the short active seasons to reach reproductive maturity and are retained at home, which leads to sociality based on kinship. Competition within the social group is expressed primarily as reproductive suppression, which delays the age of 1st reproduction that in turn strongly affects demography. Early snowmelt due to global warming may enable marmots to colonize new habitats or increase population growth. However, climate change most likely will diminish the ability of marmots to mobilize sufficient energy resources in a drier, warmer active season, which will reduce both survivorship and reproduction.

Key words: circannual rhythm, energy conservation, harsh environment, metabolic consequences, reproductive consequences, sociality

There is no doubt that climate has affected the distribution and biology of mammals in the past and anthropogenic climate change currently impacts many mammalian species (McCain and King 2014). Essential to assessing the effects of climate change is knowledge of the critical features of a mammal's natural history, which links the organism to its environment (Tewksbury et al. 2014). Marmots may be susceptible to climate change because they have not evolved randomly with respect to climate (Davis 2005) and marmot distribution may track climate distribution (Armitage 2014). Hibernation is a life-history trait that may allow marmots to escape changes in climate and effectively expand their ecological niches (Liow et al. 2009). Hibernation is a component of sleep-or-hide behavior, which also includes the use of burrows to avoid unfavorable conditions. These mammals are underrepresented in the Red List Categories of the International Union for the Conservation of Nature, which suggests that they are less likely to be endangered (Liow et al. 2009). Sleep-or-hide species function at a metabolism lower than typical mammalian levels or are buffered from the changing physical environment. Statistical analyses indicate that sleep-or-hide behavior and geographic range but not body mass or diet contribute significantly to extinction risk (Liow et al. 2009). However, analysis of sleep-or-hide behavior does not consider how adaptation for hibernation may affect other life-history traits whose response to climate change could either increase extinction risk or cause a marked contraction of geographic range. Therefore, it is important to understand how the requirement of obligatory hibernation affects a range of life-history functions. In this context, I consider hibernation in marmots to be a keystone life-history trait that impacts critical areas of reproduction, metabolism, and sociality, analogous to the impact a keystone species has on its community (Paine 1995).

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Evolutionary History

Early evolution and Quaternary history.—The crown-group marmots originated in the late Miocene between 6 and 8 million years ago (mya) in western North America. There was at least 1 dispersal into Eurasia between 3 and 6 mya. Most species divergence occurred before the beginning of the Quaternary about 2.58 mya (Polly et al. 2015).

Extinct stem-group marmots most closely related to crown-group marmots were smaller; e.g., *Marmota minor* was about the size of *M. flaviventris* (yellow-bellied marmot), 1 of the smallest extant marmot species. Stem-group marmots occupied lower elevations; *M. vetus*, the geologically oldest member of this clade, lived in the wooded grasslands of the Great Plains of Nebraska. *M. minor* occupied warm, increasingly dry upland environments. The earliest members of the crown-group marmots transitioned from a low-elevation, nonseasonal environment to high elevation with seasonal precipitations but relatively warm temperatures (Polly et al. 2015).

Dispersion and speciation of marmots are limited to the northern hemisphere. Of the 15 currently recognized species, only *M. monax* (woodchuck), in the lowlands of eastern North America, and *M. bobak* (steppe marmot), in the Eurasian steppe, do not live at high elevations. Mean body mass at immergence into hibernation varies from about 3.0 to 6.4 kg (Armitage 2014). Mass at immergence is significantly related to head-and-body length; marmot species with a larger frame use significantly more mass during the hibernation period, the time between immergence and emergence aboveground (Armitage 1999). These species have a high cost in the pre-emergence time before emerging from the hibernation period when they become euthermic and may initiate reproduction (Armitage 1999). All marmot species are herbivorous; grasses and forbs in montane or alpine meadows are the major sources of energy (Armitage 2014).

Climate during the Quaternary was characterized as harsher, colder, and more seasonal than the earlier time period when marmots originated and was dominated by glacial–interglacial cycles. Despite considerable snow cover, marmots selectively inhabited higher elevations, which was associated with a likely contraction of geographic range (Polly et al. 2015). For example, *M. marmota* (alpine marmot) retreated from central Europe and became restricted to the higher Alps and *M. bobak* became extinct in the middle Rhine region (Kalthoff 1999).

Responses of marmots to Quaternary climate change.—One major response to increased seasonality was hibernation. Hibernation is the major mammalian mechanism for conserving energy during a season of either no food or food of low quality (Armitage 2014). Hibernation occurs in all 15 species of the monophyletic *Marmota*. The marmots, along with the ground squirrels, are well embedded in the Marmotini (Mercer and Roth 2003; Steppan et al. 2004). Given that the 1st true ground squirrel appeared in the late Oligocene (Black 1972), hibernation is likely an ancestral trait (Armitage 2008).

The 2nd major response was an increase in body size. Most current crown-group marmots are larger than the earliest members of the crown group (Polly et al. 2015). There are 3 major advantages to large body size. First, marmots may be too large for some predators. *M. flaviventris* vigorously chases long-tailed weasels (*Mustela frenata*) and the American marten (*Martes americana*) and *M. bobak* chases the red fox (*Vulpes vulpes*—Armitage 2003a).

Additionally, large body size increases the efficiency of energy use for hibernation. Energy (fat) stores scale directly with body mass, whereas energy use scales to mass$^{0.5}$ at hibernation temperatures (French 1986). Because marmots do not store food and rely entirely on body fat, increased metabolic efficiency is critical during the long hibernation period, which most frequently varies from 7 to 8 months in length (Armitage 2014).

Finally, large body size enables marmots to use herbaceous vegetation with a highly fibrous diet. Although marmots rarely ingest seeds, their teeth and simple digestive tract are characteristic of a seed eater, which puts marmots at a disadvantage in using a fibrous diet. Digestive efficiency increases with the retention time of food in the digestive tract. Retention time increases directly with the increase in body size; this retention time is about 24 h in marmots and at the size of marmots, digestive efficiency is equal to that of voles with a colonic separation mechanism (Hume et al. 1993). Hence, large size enables marmots to overcome the disadvantages of a simple gut and expand their food niche beyond seeds to include the forbs and grasses of their alpine and montane meadows (Hume 2003) and obtain the energy required for the active homeothermal season and the long heterothermal (hibernation) period (Armitage 2014). However, there is a cost to the lengthy retention time. Marmot species spend much of their time aboveground sitting or lying, which is widespread among animals (Herbers 1981). For example, *M. flaviventris*, on average, spends about 50% of the aboveground time sitting or lying and only about 15% of the time foraging (Armitage et al. 1996). Foraging time apparently is limited by the rate of digestion and absorption which, in turn, limits the rate of the acquisition of energy. Thus, the energy budget likely is physiologically constrained (Weiner 1992) as a consequence of the evolution of large body size to expand the food niche.

Hibernation Effects on Life-History Traits

Hibernation in concert with the harsh environment (Armitage and Blumstein 2002; Armitage 2014) and large body size impacts 3 major functions: reproduction, metabolism, and sociality—which impacts population dynamics (Fig. 1).

Reproductive Consequences

Reproduction is time limited; annual reproduction characterizes all marmot species. However, environmental stress in the harsh environment reduces the frequency of reproduction in most species of marmots. Cold spring weather and late snowmelt delay gain and may impose loss of body mass. For example, *M. caligata* (hoary marmot), *M. olympus* (Olympic marmot), *M. caudata* (long-tailed marmot), and other species may lose body mass for 2 or more weeks and *M. baibacina* (gray marmot) may

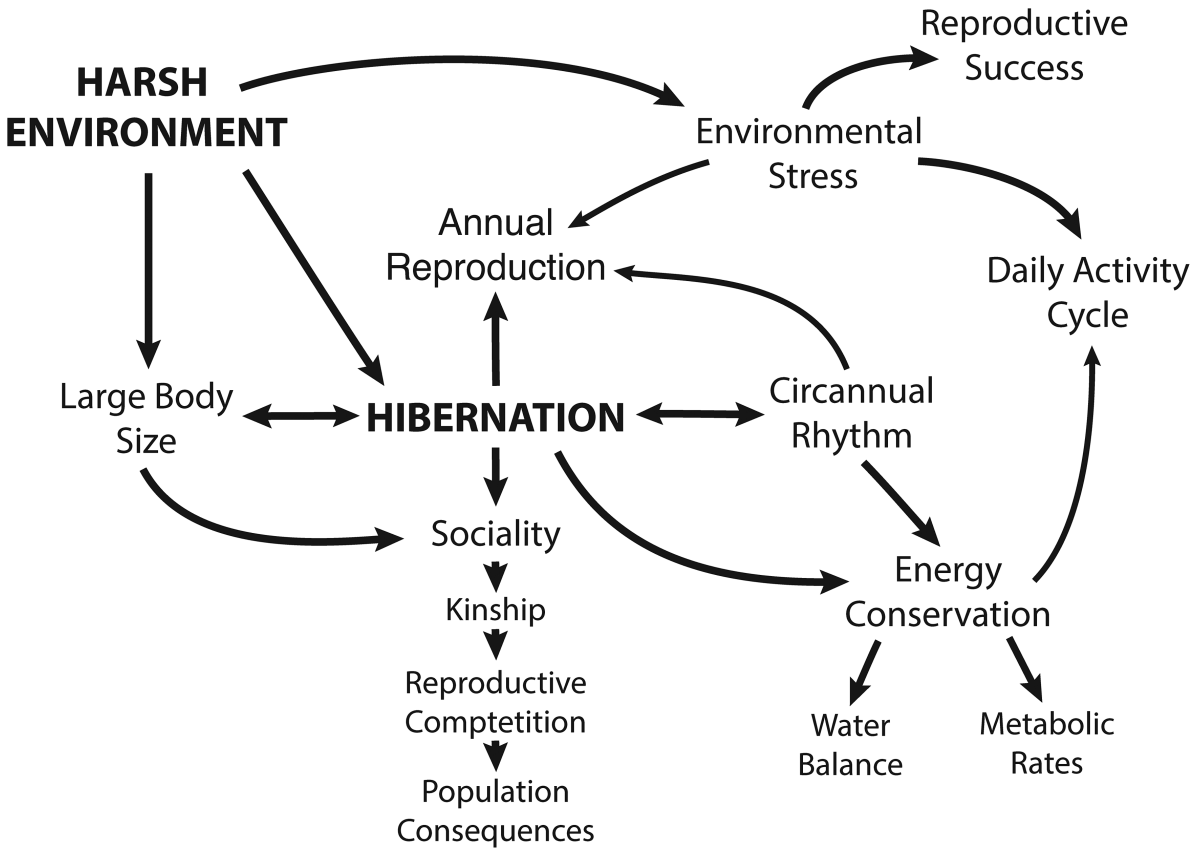

Fig. 1.—A diagram illustrating the effects of a harsh environment and hibernation on 3 sets of functional traits in marmots related to reproduction, metabolism, and sociality. Reciprocal interactions are indicated by 2-way arrows.

lose body mass and use body fat for 2 months following emergence from hibernation. Reproduction in some species affects gain of body mass. Reproductive female *M. baibacina* gain 525 g and *M. sibirica* (Siberian marmot) gain 414 g, whereas barren female *M. baibacina* gain 1,100 g and *M. sibirica*, 747 g by the time of immergence (Armitage and Blumstein 2002). As a consequence, only the barren females accumulate sufficient mass to reproduce the following year. Harsh vernal conditions, such as cold temperatures, cause the loss of up to 48% of the embryos in *M. caudata* and 25% in *M. baibacina*.

Because females cannot both reproduce and gain sufficient body mass for hibernation and reproduction the following year, reproductive skipping of 1 or more years characterizes reproduction of 10 marmot species. The largest marmot species, e.g., *M. vancouverensis* (Vancouver Island marmot) and *M. baibacina*, often skip ≥ 2 years. This relationship between body mass and skipping reproduction is another example of a trade-off; large body size enables these species to occupy their harsh environments but at a cost of a reduced frequency of reproduction (Armitage 2012).

As a consequence of the interaction between hibernation and the harsh environment, on average only 28% (*M. baibacina*) to 55% (*M. vancouverensis*) of adult females wean a litter each year (Armitage 2014). The 1 exception is *M. monax*, in which about 72% of the females wean litters each year. This higher frequency of reproduction is associated with a relatively short hibernation period; hence, a long active season of about 7.5 months provides more time for female *M. monax* to accumulate sufficient resources for hibernation and reproduction the following year.

One way that marmots can extend their active season and increase the probability of successful reproduction is to initiate reproduction as early as possible in the annual cycle. At least 6 species of marmots mate before emergence. Four species initiate prenatal development before emergence; young *M. caudata* and *M. camtschatica* (black-capped marmot) are about halfway through gestation at emergence. Birth may occur in *M. bobak* prior to emergence (Armitage 2014).

The ability to initiate reproduction before emergence raises the question of how these events are timed given that marmots occupy burrows that may be covered by several meters of snow and therefore are unlikely to receive information on weather or daylength. Timing resides in the endogenous circannual rhythm that drives food consumption, body mass, and metabolic rate (Davis 1976; Ward and Armitage 1981a). The rhythm may be demonstrated by the changes in body mass when marmots are maintained at constant photoperiod and temperature with food provided ad libitum (Fig. 2). Immergence and emergence are timed by the circannual rhythm; adult female *M. flaviventris* hibernating in the laboratory at 5°C spontaneously terminated hibernation (French 1990). *M. flaviventris* are prepared for torpor up to 3 weeks before immergence thus avoiding the likely catastrophic effects of trying to accumulate fat in the event environmental conditions turn stressful and palatable food rapidly declines (Armitage 2014). The early accumulation of body mass in preparation for hibernation does not increase the

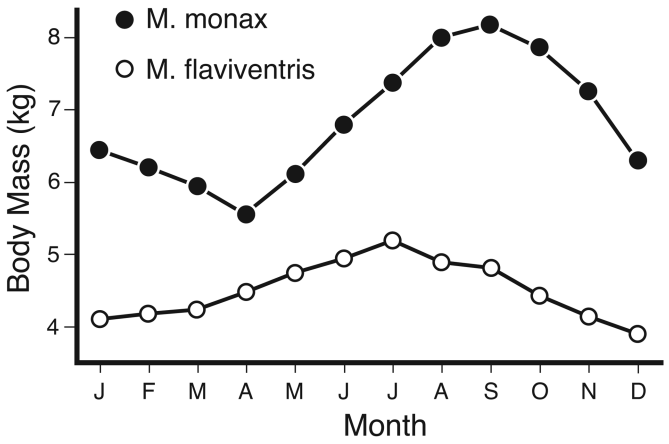

Fig. 2.—Circannual changes in body mass for laboratory populations of 2 species of marmots, *Marmota monax* from Pennsylvania (Davis 1976) and *M. flaviventris* from Colorado (Ward and Armitage 1981a). These changes in body mass occur under 12L:12D photoperiod at an ambient temperature of 20°C with food and water provided ad libitum, thus demonstrating the endogenous nature of the changes.

danger of predation which does not change over time for adults (Armitage 2014). The role of the circannual rhythm is evident in *M. flaviventris* provided with supplemental food in the field; juveniles ceased to gain body mass by 2 weeks before hibernation (Woods and Armitage 2003).

The circannual rhythm introduces phenotypic plasticity in the phenology of hibernation and reproduction (Williams et al. 2014). Hibernation is characterized by torpor bouts that are terminated by arousal when marmots abandon torpor and become euthermic. Arousals occur more frequently early and late in the hibernation period, as seen in *M. marmota* (Heldmaier et al. 1993a) and *M. flaviventris* (Florant et al. 2000; Armitage and Woods 2003), when euthermic, marmots presumably detect external cues that either initiate emergence or reentry into torpor. Female *M. flaviventris* that emerge earlier in the spring wean their young earlier and effectively increase the length of the active season (Armitage 2014). This plastic response for emergence time can have a strong demographic response and exemplifies one way that hibernation affects population dynamics. Early emergent juveniles and adults increased body mass, were larger at hibernation, and had increased survivorship. The resulting decline in adult mortality was the major driver of population increase. From 1976 to 2001, population increased at the rate of 0.56 marmots/year; from 2001 to 2008, a period of earlier emergence, population increased at the rate of 14.2 marmots/year (Ozgul et al. 2010).

Snow cover is a major environmental determinant of the length of the hibernation period. In Gunnison County, Colorado, snowmelt on average occurs about 40 days later in North Pole Basin than in the East River Valley (Table 1). Late snowmelt, which causes a longer hibernation period (decreasing energy reserves), negatively affects reproductive success; far fewer females successfully wean a litter and a greater proportion fail reproduction at the site with the longer hibernation period (Armitage 2013a).

Table 1.—The effect of the presence of snow cover on reproductive success of female *Marmota flaviventris* at 2 elevations in Gunnison County, Colorado. The lower elevation (< 3,000 m) area of the Upper East River Valley is about 10 km to the southwest of the higher elevation (> 3,300 m) area of North Pole Basin. Reproductive condition was determined by nipple development (Armitage and Wynne-Edwards 2002). Failed reproduction refers to females whose nipple development indicated that reproduction was initiated, but no young were weaned. Nonreproductive refers to females whose nipples provided no evidence of reproduction. Female year refers to 1 female for 1 year. Data compiled from Armitage (2013a).

	Lower elevation (East River Valley)	Higher elevation (North Pole Basin)
Julian day of snowmelt	140	182
Female reproductive success		
Weaned a litter (%)	50.4	19.3
Failed reproduction (%)	6.7	23.0
Nonreproductive (%)	42.9	59.7
n (female years)	919	119

Physiological Consequences

Energy use.—The effects of hibernation on reproduction indicate that the central effect is on energy utilization. Energy required for maintenance—including for hibernation, foraging, temperature regulation, locomotion, social behaviors, etc.—may be so great that energy needed for reproduction may be insufficient for 1 or more years. Thus, one expects that marmots should evolve ways to reduce the cost of maintenance so as to shift more energy into production, which includes both the accumulation of fat reserves and the formation of offspring.

Several lines of evidence support the proposition that maintenance costs are reduced throughout the annual cycle. In *M. flaviventris*, values of observed metabolic rates range from 46.3% to 86.3% of rates predicted from body-size equations (Armitage and Salsbury 1992). In energy budgets of yellow-bellied marmots, about 23% of the energy is allocated to growth and 77% to maintenance (Kilgore and Armitage 1978), in marked contrast to the 98% allocation of energy to maintenance typical of homeotherms (Humphreys 1979).

The reduction in maintenance energy is achieved, in part, by a seasonal decline in metabolic rate. The seasonal decline was observed both in the laboratory in *M. marmota* and in the field in *M. flaviventris* (Fig. 3). The seasonal decline also is observed in mass-specific field metabolic rates of *M. flaviventris* (Armitage 2004), which means that overall metabolic activity, not just resting metabolism, declines. This seasonal decline probably is instrumental in the relatively high allocation to growth in the energy budget.

The seasonal decline in metabolic rate is evident in the circannual rhythm in captive *M. flaviventris* (Ward and Armitage 1981a; Armitage 2014). As a consequence of the circannual rhythm, resting euthermic metabolism is lower during the hibernation period than during the summer, which produces some energy servings.

One measure of energy costs during hibernation is specific daily mass loss (DML) expressed as mg day^{-1} g immergence mass^{-1}. Three patterns of specific DML are evident among

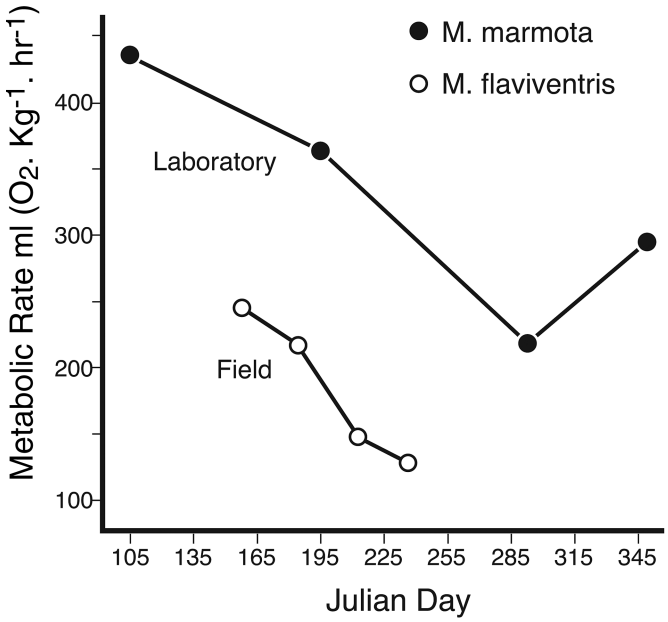

Fig. 3.—Seasonal decline in metabolic rates for 2 species of marmots. Julian Day 195 is July 15. Data for laboratory *Marmota marmota* calculated from Ortmann and Heldmaier (1992). Data for field *M. flaviventris* extrapolated from Armitage (2004).

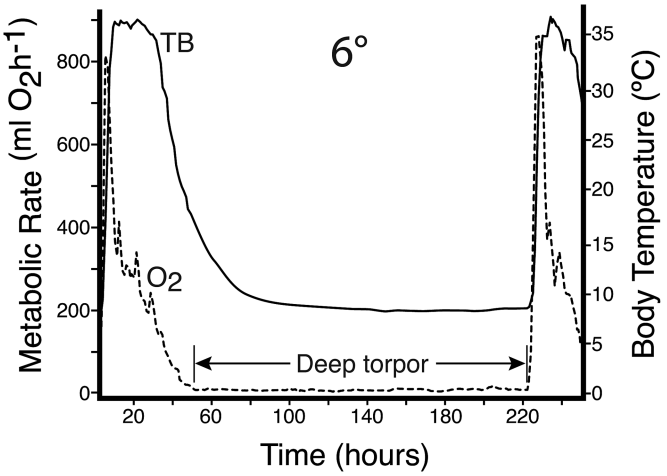

Fig. 4.—Metabolic rate (O_2—dashed line) and body temperature (T_B—solid line) during a torpor bout for a hibernating 2.4 kg young male *Marmota flaviventris* at an environmental temperature of 6°C. Note that the decline in oxygen consumption precedes that of body temperature and that oxygen consumption reaches its minimum about 40 h before body temperature does. No spiking of metabolic rate is evident during deep torpor when mean mass-specific metabolism = 0.0053 ml O_2 g^{-1} h^{-1}.

marmot species. The 1st (DML = 1.94) combines large size with a relatively short hibernation period, as in *M. monax*. The 2nd (DML = 0.94 to 1.06) I designate as high efficiency and occurs in *M. flaviventris*, *M. olympus*, and *M. vancouverensis*. The 3rd occurs in species, such as *M. marmota*, in which social thermoregulation occurs and specific DML varies depending on the composition of the hibernating group. For an adult *M. marmota* hibernating singly DML = 1.95, which indicates low physiological efficiency. Specific DML decreases to 1.6 for a territorial pair without offspring, then increases to 1.82 with offspring (Armitage 2008, 2014).

Energy is conserved during entrance into torpor by suppressing metabolism (Lyman 1958; Heldmaier et al. 1993b; Woods et al. 2002), which declines to a low steady state (deep torpor). The reduction in metabolic rate causes body temperature (T_B) to decline passively and reach its low steady state many hours later (Fig. 4). Spikes in metabolic rate indicate that the decrease in T_B is an actively regulated process (Wang and Lee 2000). T_B (mean ± *SD*) of *M. flaviventris* varies with environmental temperature (T_E). At T_E = 6°C, T_B = 8.99 ± 0.52 (n = 10); at T_E = 4°C, T_B = 6.99 ± 0.53 (n = 5); and at T_E = 2°C, T_B = 5.93 ± 0.61 (n = 5). At 6°C and 4°C, $T_B - T_E$ = 2.99°C and increases to 3.93°C at T_E = 2°C (K. B. Armitage, pers. obs.). This pattern suggests that *M. flaviventris*, on average, increases metabolism sufficiently to maintain a minimal T_B at about 6°C.

By allowing T_B to vary passively, marmots and other hibernating sciurids regulate metabolic rate by maintaining a minimal steady-state oxygen consumption (deep torpor) over a range of environmental temperatures (Table 2). When exposed to low-temperature stress, *M. flaviventris* increases mean metabolic rate (Fig. 5). This increase does not occur by increasing steady-state metabolism to a higher and more costly level, but results from "spiking," periodic increases in oxygen consumption (Fig. 5) to maintain body temperature (Heldmaier et al. 1993a, 1993b; Karpovich et al. 2009). Spiking rather than increasing steady-state metabolism to a higher level indicates that marmots attempt to regulate metabolism at a consistent minimum (energy conservation) when responding to the requirement of regulating body temperature.

Minimal oxygen consumption and major energy savings occur during deep torpor (Fig. 4). Energy savings may be expressed as the amount of energy expended compared to the amount of energy that would have been expended if the marmot maintained euthermy (Heldmaier et al. 1993a). Energy savings vary from about 83% for *M. flaviventris* to about 43% for *M. marmota* and *M. monax*. This difference occurs because *M. flaviventris* spends 77.3% of bout time in deep torpor compared to 66.3% for *M. monax*, and *M. monax* spends 14.4% and *M. flaviventris* only 7.2% of bout time in euthermy (Armitage et al. 2003).

Table 2.—Range of environmental temperatures where minimal metabolism is maintained in hibernating Marmotini, including 2 species of ground squirrels. The temperature ranges for *Marmota monax* and *M. flaviventris* may be wider as oxygen consumption was measured only at the recorded range.

Species	Temperature range (°C)	Reference
Marmota flaviventris	6 to 10	Armitage et al. (2003)
M. marmota	8 to 11	Heldmaier et al. (1993a)
M. monax	4 to 10	Armitage et al. (2000)
Callospermophilus lateralis	0.6 to 12	Heldmaier et al. (1993b)
Urocitellus parryii	0 to 12	Barnes and Buck (2000)

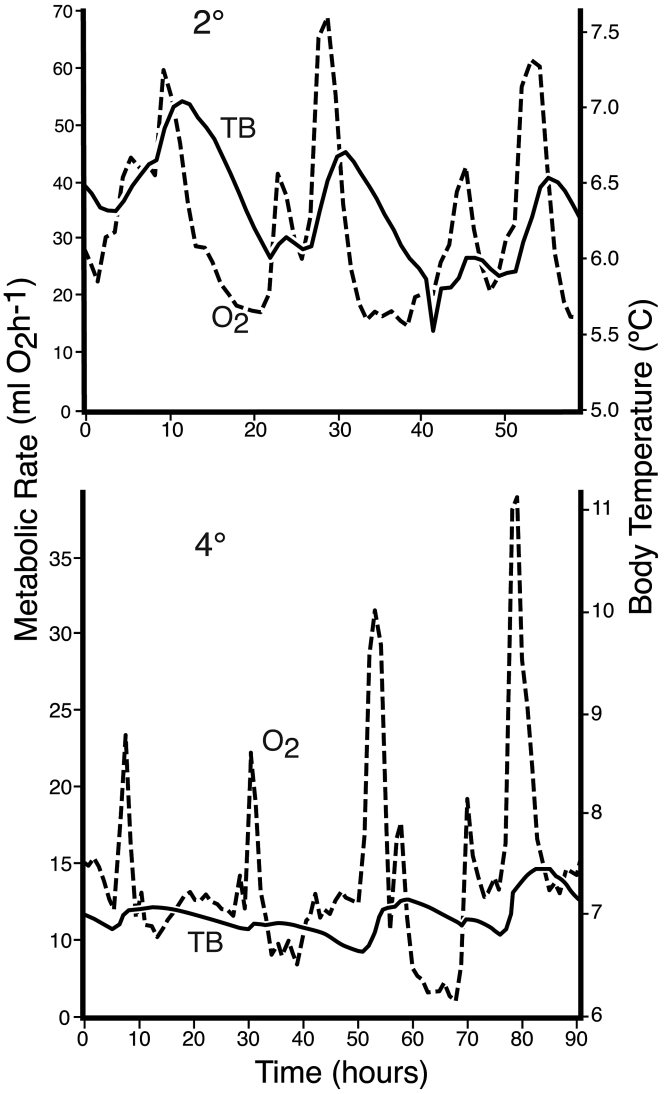

Fig. 5.—Spikes in oxygen consumption (O_2—dashed line) during deep torpor for the same young male marmot as in Fig. 4. Deep torpor mean mass-specific metabolism = 0.0061 ml O_2 g^{-1} h^{-1} at ambient temperature of 4°C and 0.0122 at 2°C. Spiking increased by about 50% at 2°C compared to 4°C and both were greater than at 6°C shown in Fig. 4. Note the differences in time span for torpor in Figs. 4 and 5.

These differences in deep torpor and euthermy raise the question of why *M. monax* does not increase energy savings by decreasing the time spent euthermic. Deep torpor appears to have negative physiological effects, including reduced immunocompetence and increased oxidative stress (Bieber et al. 2014). Thus, hibernators with sufficient energy stores should spend less time in torpor in order to reduce the negative effects of torpor (Humphries et al. 2003). *M. monax* with a larger body mass spends more time at a higher body temperature and less time in torpor as a proportion of the heterothermal period (Zervanos et al. 2014). *M. monax* spends only as much time in torpor as necessary to survive hibernation and to emerge with sufficient energy reserves for initiating reproduction (Zervanos et al. 2014). Possibly other species of marmots with much longer hibernation periods must maximize their time in torpor and minimize time euthermic in order to survive hibernation and have some chance at reproduction and, as a consequence, pay the costs of torpor.

Considerable evidence indicates that mortality during hibernation is the 2nd major source of mortality after predation for *M. flaviventris* (Schwartz et al. 1998). Some hibernation mortality can be attributed to the lack of time to prepare for hibernation when weaning occurs relatively late. The survivorship rate of reproductive females who weaned a litter after mid-July was 0.55 and that of the young was 0.28 (Armitage 2014) compared to the overall population average of 0.71 for adult females and 0.53 for young (Oli and Armitage 2004). Some mortality during hibernation is associated with parasitism (Armitage 2014). This mortality is related in part to poor growth during the active season (Arnold and Lichtenstein 1993; Van Vuren 1996). To what degree mortality due to disease may be a cost of torpor requires further research.

Water conservation.—As far as is known, marmots have no access to water during hibernation, and therefore they must conserve water. Conductance (a measure of heat, thus energy, loss) is reduced and is only 82.5% of that predicted from body size in *M. flaviventris* (Armitage et al. 1990). Low conductance saves energy by reducing both dry heat loss and evaporative water loss; < 10% of heat loss is by evaporation at environmental temperatures of 20°C or lower. *M. flaviventris* also forms a highly concentrated urine (Ward and Armitage 1981b). There is no need for additional water during hibernation; metabolic water formed at T_E 5°C to 15°C meets the requirements of evaporative water loss (Armitage et al. 1990).

Conservation of water as an adaptation for hibernation comes with a trade-off: marmots have a reduced capacity to increase conductance under heat stress and are highly sensitive to environmental temperatures ≥ 20°C. The inability to mobilize water for evaporative heat loss is not a consequence of lack of water. Mass-specific water influx of free-ranging *M. flaviventris* was as much as 5 times greater than water use by laboratory marmots provided water ad libitum (Melcher et al. 1989).

Activity and heat load.—Marmots avoid temperature stress by adjusting the amount of time they are active aboveground. On average, *M. flaviventris* is active for 74% of the time from sunrise to 10:00 h, for 43% from 10:00 to 16:00 h, and 64% from 16:00 h to sunset (Armitage et al. 1996). This activity pattern in midsummer in both *M. flaviventris* and *M. monax* produces a bimodel activity cycle with minimal activity during the day when environmental temperatures are relatively high. Early and late in the active season the activity cycle is unimodel with peak activity at midday when temperatures are warmer and with low activity when temperatures are cooler (Armitage 2014).

Although activity is closely related to air temperature, the heat load that marmots encounter is better characterized by standard operative temperature, which integrates air temperature, radiation, and convection into a single index that is used to establish thermal equivalence between laboratory and outdoor environments. An animal's metabolic response to a given standard operative temperature can be equated with the response at

the same temperature experienced by the marmot in a metabolism chamber (Melcher et al. 1989, 1990). Aboveground activity is reduced when standard operative temperature is high, but activity time may be increased as the marmot allows its body temperature to increase from a mean of 36.6°C to as much as 40°C (Melcher et al. 1990).

Heat transfer through fur depends on fur structure, fur spectral properties, and the thermal environment. Heat transfer is most sensitive to solar radiation; heat gain at midday can be up to 10 times basal heat production on the portion of the marmot's surface receiving the direct solar radiation (Armitage 2009). A model integrating structure and spectral properties of fur successfully predicted metabolic rates for environmental temperatures below 20°C, but not at higher temperatures (Armitage 2009). *M. flaviventris* spends most of its life at environmental temperatures < 12°C, the temperatures characteristic of burrows (Kilgore and Armitage 1978). Burrow temperatures of *M. flaviventris* correspond closely with the lower end of the thermoneutral zone (Armitage 2004). Thus, properties of fur appear to be adapted to the relatively low temperatures of burrows, where annually *M. flaviventris* spends about 80% of its time. The adaptation of fur properties for the low-temperature environment of hibernation saves considerable energy but imposes heat stress at high ambient summer temperatures.

Social Consequences

A multivariate analysis of life-history traits of 18 species of ground-dwelling squirrels revealed that sociality index, calculated from the sex and age structure of social groups, was best explained by age of 1st reproduction and the age at which adult body mass was reached, both of which were highly correlated with mean body mass (Armitage 1981). Large size plus the short growing season reduce the time that young have to grow to reproductive maturity and to accumulate fat for their 1st hibernation. As a consequence, the young of all species of marmots, except *M. monax*, remain in their natal area for their 1st hibernation. For many species of marmots, e.g., *M. olympus*, *M. bobak*, and *M. marmota*, young may not disperse before they are 2 years old or older. Retention of young in the natal area leads to sociality, the formation of social groups based on kinship (Armitage 2007). At least 4 social systems are recognized; the social systems based on family structure characteristically delay reproductive maturity to 3 years old and dispersal from the natal area may be delayed beyond the age of reproductive maturity (Armitage 2014).

A major consequence of marmot sociality is reproductive competition within the social group. *M. marmota* forms an extended family social group consisting of an adult, territorial pair, subordinate adults, yearlings, and young. Only the territorial pair reproduces; subordinate adult males and adult females are reproductively suppressed by their con-genders (Arnold and Dittami 1997; Hackländer et al. 2003). Suppression is a function of social rank, not reproductive status; subordinate females also fail to wean litters in years when the dominant female fails to breed (Arnold 1990).

In *M. flaviventris*, reproductive suppression mainly delays age of 1st reproduction (Table 3). Two-year-olds (the age of maturity) are less likely to reproduce under several conditions: when older females are present (G test for goodness of fit, $G = 15.5$, $P < 0.001$); when the mother is present compared to when she is absent ($G = 5.9$, $0.025 > P > 0.01$); and when the older female is reproductive (14.5% of cases—$G = 3.37$, $0.1 > P > 0.05$) than when she is nonreproductive (30.3% of cases—Armitage 2003b). However, a 2-year-old is more likely to breed if the older female is her mother than if the older female is an aunt or sister ($G = 4.5$, $0.05 > P > 0.025$).

Similarly, females that do not reproduce at 2 years of age are more likely to reproduce at 3 years of age if no older adult is present (Table 3—$G = 5.74$, $0.025 > P > 0.01$). Whether the older female is the mother or some other relative does not affect the likelihood of breeding ($G = 0.003$, $P > 0.9$). Although females whose age of 1st reproduction is 4 years are less likely to reproduce if an older female is present (Armitage 2003b), the difference is not statistically significant ($G = 1.26$, $P > 0.1$). When age of 1st reproduction was 5 or 6 years, no older female was present and all females reproduced (Table 3).

Sociality acting through reproductive suppression affects population dynamics of *M. flaviventris*. An analysis of the contributions of annual juvenile survival, annual adult survival, fertility, and age of 1st reproduction to demography of *M. flaviventris* found that population dynamics of marmots was driven primarily by changes in reproductive parameters; i.e., fertility and age of 1st reproduction, with changes in juvenile survival having a secondary role and adult survival, an insignificant role (Oli and Armitage 2004). Fertility and age of 1st reproduction are strongly affected by reproductive suppression that occurs within matrilines (Armitage 2003b).

Hibernation affects demography indirectly through a chain of events associated with sociality (Fig. 1) for which the significance becomes apparent by comparing the demography of 2 species of the Tribe Marmotini, *M. flaviventris* and *Callospermophilus lateralis* (golden-mantled ground squirrel). The 2 species live and hibernate in the same area in the East River Valley in Colorado; thus, any differences between the 2 species cannot be a consequence of their living in different geographic areas. There is no evidence to support reproductive suppression in the smaller asocial *C. lateralis* (Kneip et al. 2011) in contrast to its major role in the large social *M. flaviventris*. The contrast between these 2 species emphasizes the

Table 3.—Reproductive suppression in adult female *Marmota flaviventris* as shown by reproductive success when older adult females were present or absent. The numbers in bold are the numbers of marmots for whom that age was potentially the age of 1st reproduction. The number of those females whose mothers were present is shown in parentheses. Modified from Armitage (2003b).

Age (year)	Older adults present			Older adults absent			
	2	3	4	2	3	4	5–6
Weaned a litter	**20** (15)	**14** (8)	**4** (4)	**33**	**25**	**19**	**11**
Nonreproductive	**82** (41)	**29** (16)	**8** (3)	**36**	**18**	**10**	**0**
Percentage weaning	19.6	32.6	44.4	47.8	58.1	65.5	100

importance of the combination of large body size and hibernation in determining specific life-history responses of marmots.

Conclusions and Perspectives

Marmots have adapted to seasonality in a harsh environment by increasing body size and hibernating (Fig. 1). This adaptive response imposed a major constraint on marmot life history: a shortage of time. Time constraints limit reproductive frequency, delay the age of maturity, and underlie sociality. Although social groups are based on kinship, reproductive competition within a group affects population growth or decline. Perhaps the major effect of time is the limitation on energy acquisition. Sufficient energy must be stored primarily as fat in order to survive hibernation. Only energy in excess of that needed for hibernation can be used for growth and reproduction. The major marmot response to the time-limited active season imposed by hibernation is conservation of water and energy which primarily reduces energy used in maintenance during both the active and hibernation periods. The annual pattern of energy acquisition and use is tightly coupled with the circannual rhythm (Fig. 1).

Because marmots are adapted to low environmental temperatures, they are susceptible to heat stress which may be associated with summer dryness. Drought reduces the rates of mass gain and increases mortality, especially of young and of reproductive females (Armitage 1994; Lenihan and Van Vuren 1996). A shift of snow cover from a lower to a higher elevation resulted in a decrease in the population of *M. menzbieri* (Menzbier's marmot) because the foraging vegetation deteriorated due to increased dryness (Armitage 2013b, 2014). In effect, the availability of mainly dry vegetation shortens the active season while increasing maintenance metabolism by increasing resting metabolic rate (Armitage 2014). Thus, energy acquisition may be insufficient to support hibernation and mortality may increase.

Climate change is associated with extreme weather events whose impacts primarily affect the length of the active season. Plant biomass increases as snow melts and it peaks in late July or early August before declining in late summer (Armitage 2014). Plant quality decreases as plant senescence progresses, and many plant species that are abundant in late summer are not used as food plants by marmots (Armitage 2003c). Apparently, the active season of marmots is lengthened by starting earlier in the spring and not by extending the season in late summer. As described previously, several years of early snowmelt enabled *M. flaviventris* to emerge and wean young earlier in the season, which increased survival and reproduction, and population growth increased (Ozgul et al. 2010). However, prolonged snow cover in the spring 2 years later resulted in mortality of about 50% of the adults and 80% of the young and reduced reproduction in the following summer (Armitage 2013b). At North Pole Basin in Colorado, when snow cover lasted into mid-July, there was no reproduction and no survival of young from the previous year (Woods et al. 2009). Similar responses to late snowmelt were reported for *M. olympus* (Griffin et al. 2007), *M. caligata* (Karels and Hik 2003), *M. vancouverensis*, *M. camtschatica*, and *M. marmota* (Armitage 2014).

Marmots have limited response to the major threats of climate change—seasonal dryness and prolonged vernal snow cover. Both evolutionary and plastic responses (Boutin and Lane 2014) have occurred in populations of *M. flaviventris*. In captive marmots, lowland-xeric populations have lower metabolic rates than montane-mesic populations. The lowland populations use only half as much water daily, form a more concentrated urine, and are more capable of losing heat by evaporation (Armitage 2014). These differences occurred when both populations were maintained under the same conditions in the laboratory, suggesting they probably are genetic. The semiarid *M. flaviventris* is smaller than their montane-mesic conspecifics; smaller size is an adaptation to heat stress. A reduction in size has occurred in other marmot populations during global warming over the past 10,000 years; recent *M. sibirica* is smaller than marmots from the middle and late Pleistocene, such as *M. nekipelovi* (Erbaeva 2003), and late Pleistocene *M. marmota* is smaller than geologically older individuals in the same cave sequence (Aimar 1992). It is unclear at what rate evolutionary changes in body size and physiology can occur nor are effects of these changes on hibernation and other life-history traits known, in part because extensive studies of semiarid populations of marmots are lacking.

Plasticity in the circannual cycle allows for some adjustment to climate changes. The annual cycle and hibernation are obligate and probably genetic, but the timing of immergence and emergence is plastic (Armitage 2005). For example, the low-elevation *M. flaviventris* in eastern Oregon emerge in early March and immerge in July. When marmots from a higher elevation site (which emerge in early May and immerge in September) were translocated into enclosures at the low-elevation site, their phenology shifted to conform to the phenology of the local population. Plasticity in phenology could enable marmots to survive as they shift their phenology with changing climatic patterns. However, the shift in phenology will be inadequate to ensure survival if resources during the active season are inadequate to sustain the obligatory hibernation.

In the short term, climate-change warming and early snowmelt could increase the habitat available for marmot colonization. For example, *M. caudata* and *M. olympus* do not occupy what appears to be suitable habitat because prolonged snow cover produces an active season that is too short to allow marmots to meet their energy requirements (Armitage 2013b). Marmots may respond to long-term warming associated with increased aridity by shifting their elevational distribution upwards (Armitage 2014). If increased aridity also occurs at higher elevations, some marmot populations are likely to go extinct. Extinction is more likely in those species living at high elevations with a relatively small geographic range, such as *M. olympus*, *M. vancouverensis*, and *M. menzbieri*. Species with a large geographic range, such as *M. flaviventris*, *M. monax*, and *M. bobak*, are likely to persist into the foreseeable future, although some local populations likely will go extinct (Armitage 2013b).

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