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Phylogeny and Patterns of Energy Conservation in Marmots

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Summary

The monophyletic marmots (*Marmota*) live in a harsh environment characterized by seasonal food absence, low temperature, and precipitation as snow. Marmots may hibernate for up to 8 months; during their short active season they must reproduce, grow, maintain activity, and accumulate fat as the source of energy for hibernation. Mechanisms that reduce costs of maintenance thereby allocating more energy for growth and reproduction should be favored by natural selection. Phylogenetic analysis allows us to distinguish between ancestral traits that are expressed in all marmot species and independent evolutionary events. Hibernation, depressed metabolism to enter torpor, and seasonal decline in metabolism are ancestral traits; social thermoregulation, time spent in deep torpor, and efficient daily specific mass loss have evolved independently.

Introduction

The major reason for using phylogenetic analysis is to identify independent evolutionary events [1]. It is expected that closely-related species may inherit traits from a common ancestor and such traits would not represent independent evolutionary events. Hence, phylogeny can assist us in distinguishing between ancestral character states that may be shared by all species in a group from those character states representing divergent evolution. Phylogenetic analyses require a well-resolved phylogeny.

When a well-resolved phylogeny is not available, it may be possible to construct several working phylogenetic hypotheses based on existing taxonomies and other information as available. For example, the life history consequences of social complexity were examined for ground-dwelling sciurids using standardized independent

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Table 1. Variation explained by social complexity (adj. R^2). All R^2 values are statistically significant. ns = not significant

Life History Variable	*Raw Data*	*Corrected for Mass*	*Range for 5 Trees*
Percent females breed	0.58	—	0.24 – 0.41
Time to first reproduction	0.50	0.20	0.51 – 0.75
Average litter size	0.37	0.22	0.14 – 0.28
Survival to age 1	0.34	—	0.24 -- 0.36
Gestation time (days)	0.22	0	0.04 – 0.19 (3ns)
Lactation time (days)	0	0	0

contrasts calculated for each variable [2]. Five different partial working phylogenetic hypotheses were constructed. The variation in six life history variables explained by social complexity was determined for the raw data, the raw data corrected for body mass, and the data corrected for phylogeny (Table 1).

Two important points are evident in this analysis. First, the phylogenetic analysis did not eliminate any of the significant relationships between the life history variables and social complexity. The main effect was the reduction in the amount of variation (R^2) explained by the life history variable. This result is as expected as the introduction of another variable (phylogeny) in the analysis should reduce the amount of variation explained when only the raw data are considered. Second, the five phylogenetic hypotheses generated fairly consistent results. This pattern indicates that a plausible phylogenetic hypothesis may produce valid conclusions and a better resolved phylogeny will provide better estimates of the exact relationships between the variables being tested. This paper explores energy conservation and its relationship to phylogeny in the genus *Marmota.*

Methods

Marmots and marmot phylogeny

Marmots are large, ground-dwelling squirrels that typically live in alpine or montane environments in the northern hemisphere. Currently 15 species are recognized; nine in Eurasia and six in North America. Marmots adapted to environments characterized by a seasonal food shortage, low temperature, and precipitation as snow by hibernating in burrows for an average among species of 7.2 months [3]. Evidence that marmots live in a harsh environment that stresses energy acquisition and use is supported

by reproductive characteristics (annual reproduction, embryo re-absorption in cold Springs, patterns of fat accumulation), mass loss after emergence, home range area, mating before emergence, and reproductive skipping [4]. Mass loss after emergence, the need to gain mass for hibernation, and the requirement of allocating energy for reproduction suggest that natural selection would favor those marmots that can minimize the use of energy in maintenance in order to allocate more energy to reproduction.

Both parsimony and likelihood analyses of molecular sequence data produced a monophyletic phylogeny [5]. The then recognized 14 species are grouped into two major subgeneric groupings (Fig. 1). The exact relationships of three species, *M. monax*, *M. marmota*, and *M. broweri*, are unclear. All species, except the North American *M. monax*, are social. Thus, the phylogenetic analysis supports two evolutionary pathways leading to sociality (also see [6], for a similar conclusion). Although *M. monax* is more closely related to the Palearctic species, it may be a remnant of the earlier Nearctic phase of marmot radiation prior to the Palearctic invasion. This species apparently is the closest to the ancestral marmot.

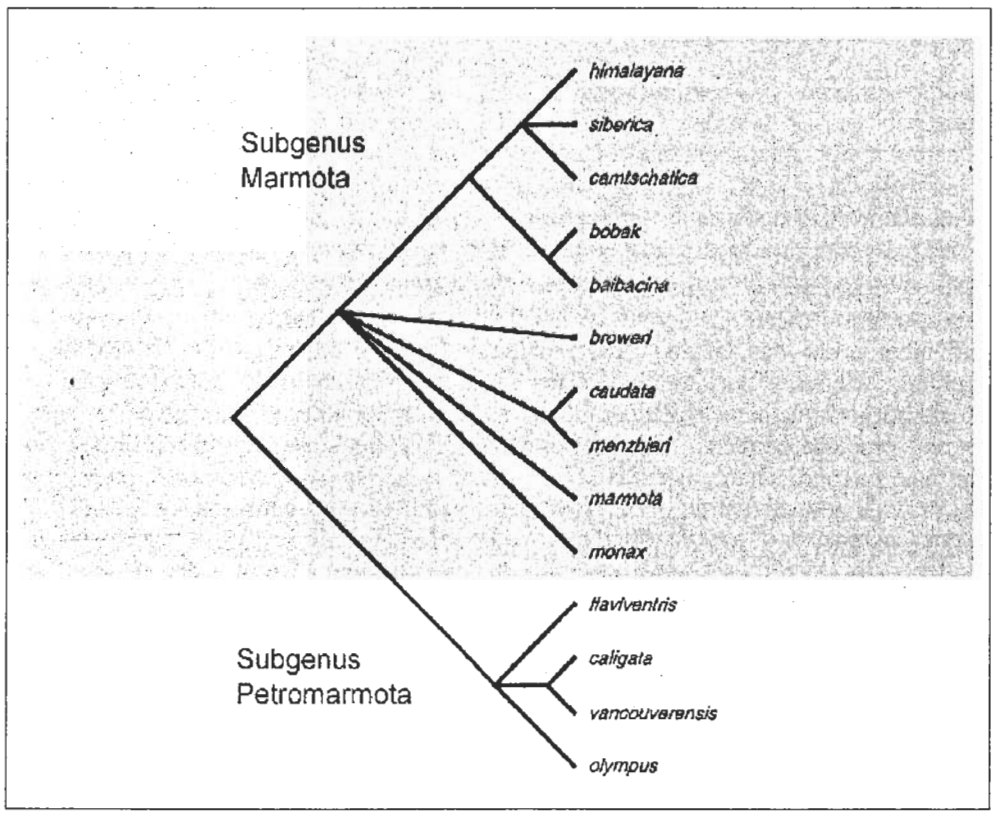

Figure 1. Phylogeny of Marmota. *Modified from [5].*

Table 2. Evidence for energy conservation

Mechanism	*References*
Circannual rhythm	[7], [8], [9], [10], [11]
Seasonal decline in metabolic rate	[7], [12], [13], [14], [15], [16], [17]
Seasonal decline in field metabolic rate	[17]
Metabolic rate lower than that predicted from body mass	[15]
Hibernation reduces metabolic rate	[14], [18], [19]
Metabolism depressed to enter torpor	[14], [20], [21]
Low daily specific mass loss (DML)	[14], [22]
Temperature independence during deep torpor	[14], [18], [19], [23]
Shrunken gastrointestinal tact	[24], [25]
Social thermoregulation	[23], [26]

Energy conservation

There is widespread evidence that the conservation of energy characterizes the biology of marmots (Table 2). Most of the research on energy conservation is of recent origin. Research generally focused on temperature regulation and water balance and hibernation was viewed as a problem in temperature regulation rather than a problem in energy conservation. Thus, research focused on the physiological and biochemical adjustments to hibernation rather than looking at hibernation as one of several processes directed to conserving energy in mammals coping with a seasonal shortage of food. There also was a general view that studying another species would not provide new advances; in other words, it would not be "cutting edge" science. As a consequence data are insufficient to do a phylogenetic analysis, but do provide evidence for identifying ancestral traits and independent evolutionary events. Data from the literature was used to relate mechanisms for energy conservation to marmot phylogeny.

Results and Discussion

Seasonal decline in metabolism

There is strong evidence that basal metabolic rate is subject to natural selection

[27]. Previously we reported that BMR of yellow-bellied marmots was lower than that predicted from body-mass:metabolism equations [15]. However, evidence that metabolism shifts seasonally raises the question of what is the species-characteristic BMR. Thus, rather than trying to determine the relationship between body mass and BMR, I will focus on changes in metabolism during the annual cycle.

Seasonal changes in metabolic rate apparently are underlain by an endogenous circannual rhythm [10]. The changes in metabolic rate are associated with seasonal changes in body mass and food consumption [7], [8], [9], [10], [11]. In *M. monax*, metabolic rate increases after emergence from hibernation [14] and metabolism is lower in late summer than in the spring [7],[12]. In *M. flaviventris* [15], [16], [17] and *M. marmota* [13] metabolic rate declines throughout the active season. The thermoneutral zone (TNZ) of *M. marmota* shifts so that the lower critical temperature changes from about 10°C in July to about 0°C in September. The lower critical temperature for wild-caught *M. flaviventris* is 10°C, which is 5°C lower than that of marmots acclimated in the laboratory at 22°C [17]. There appears to be no clearly defined TNZ in *M. monax*. Oxygen consumption increases linearly at temperatures below 28.5°C. This difference between the TNZ's of *M. marmota* and *M. flaviventris* and that of *M. monax* suggests that the lack of a clearly-defined TNZ may be an ancestral trait that has undergone evolutionary change in the two major clades of the marmots. The mean summer burrow temperature of *M. monax* was 20.3°C [28] whereas that of *M. flaviventis* was 11.3°C [29]. Given that marmots spend up to 80% of their time in their burrows, possibly metabolic responses to environmental temperature evolved to reduce energetic costs of maintenance in those species that live at higher and colder elevations. Interestingly, *M. monax* is the only species that lives at lower and warmer elevations [3]. The field metabolic rate of *M. flaviventris* also declines seasonally which indicates that not only resting metabolism but also activity declines. Thus metabolic rate is highest during reproduction, which occurs shortly after emergence from hibernation and then declines as marmots prepare for immergence. As a consequence of this seasonal decline, more ingested energy can be shifted to energy storage in the form of fat [15]. The shift of energy from maintenance to growth results in a tissue growth efficiency much higher than that of non-hibernating mammals [29].

The seasonal decline of metabolism probably is an ancestral trait because it occurs in *M. monax*, the species that is nearest the "ancestral marmot", and in *M. flaviventris* and *M. marmota*, each of which lies in a different major grouping (see Fig. 1).

Hibernation

All species of marmots hibernate [3], [30]. Hibernation is characterized by a series of hibernation bouts (Fig. 2). Hibernation conserves energy; as compared to euthermic animals in winter, *M. monax* and *M. marmota* save about 43% and *M. flaviventris* saves about 83% [14] of the energy they would otherwise expend. It seems reasonable to conclude that hibernation evolved in an ancestral marmot.

Several characteristics of a hibernation bout lend themselves to evolutionary changes. First, we will examine the descent from euthermia to torpor. Originally, the decrease in metabolic rate was attributed to a decrease in body temperature [31]. More recently it has been proposed that the metabolic rate is suppressed actively and that body temperature decreases to a low level as a consequence [18]. The depression of meta-

Table 3. Stable metabolic rates during torpor

Species	*TNZ (°C)*	*Rate (mL $O_2 \cdot g^{-1} \cdot h^{-1}$)*
M. camtschatica	-2 to +2	0.024 to 0.035
M. marmota	5 to 15	ca 0.025 to 0.043
M. monax	4 to 10	0.0064 to 0.007
M. flaviventris	6 to 10	0.0065 to 0.0075

bolic rate and the lag in the decline in body temperature is clearly evident as a marmot enters hibernation (Fig. 2). This metabolic depression was observed in *M. monax* [14], *M. flaviventris* [21] and *M. marmota* [20]. The presence of this trait in both major groups and in the "near ancestor", *M. monax*, suggests that depression of metabolic rate when entering torpor is an ancestral trait.

Secondly, stable metabolic rate occurs over a wide temperature range during torpor (Table 3). The range may be wider than reported here because all species were not measured over the same range of temperatures. Interestingly, the metabolic rate for *M. camtschatica* is about the same as that of *M. marmota* even though the temperature range is lower. At 2°C, the metabolic rate of *M. marmota* [20], *M. flaviventris* [19] and *M. monax* [14] approximately doubles over that in the TNZ. *M. camtschatica* hibernates in permafrost [32]; the low TNZ is an example of an independent evolutionary event that enables this species to exist in a very harsh, cold environment.

Thirdly, the amount of time a species spends in different phases of the hibernation bout can affect the energetic costs of hibernation. Recall that *M. flaviventris* saves considerably more energy during hibernation than *M. monax*. The metabolic rate of these two species during torpor does not differ (Table 3). Total bout metabolism of *M. flaviventris* is about 60% less than that of *M. monax* (Table 4). However, *M. flaviventris* spends more time in deep torpor, less time euthermic, reaches deep torpor

Table 4. Comparison of hibernation characteristics

	M. flaviventris	*M. monax*
Bout metabolism (mL $O_2 \cdot g^{-1} \cdot h^{-1}$)	0.023	0.038
Percent time: deep torpor	77.3	66.6
Percent time: euthermy	7.2	14.4
Time to deep torpor (h)	23.2	33.4
Mean time spent torpid (h)	90.5	69.3

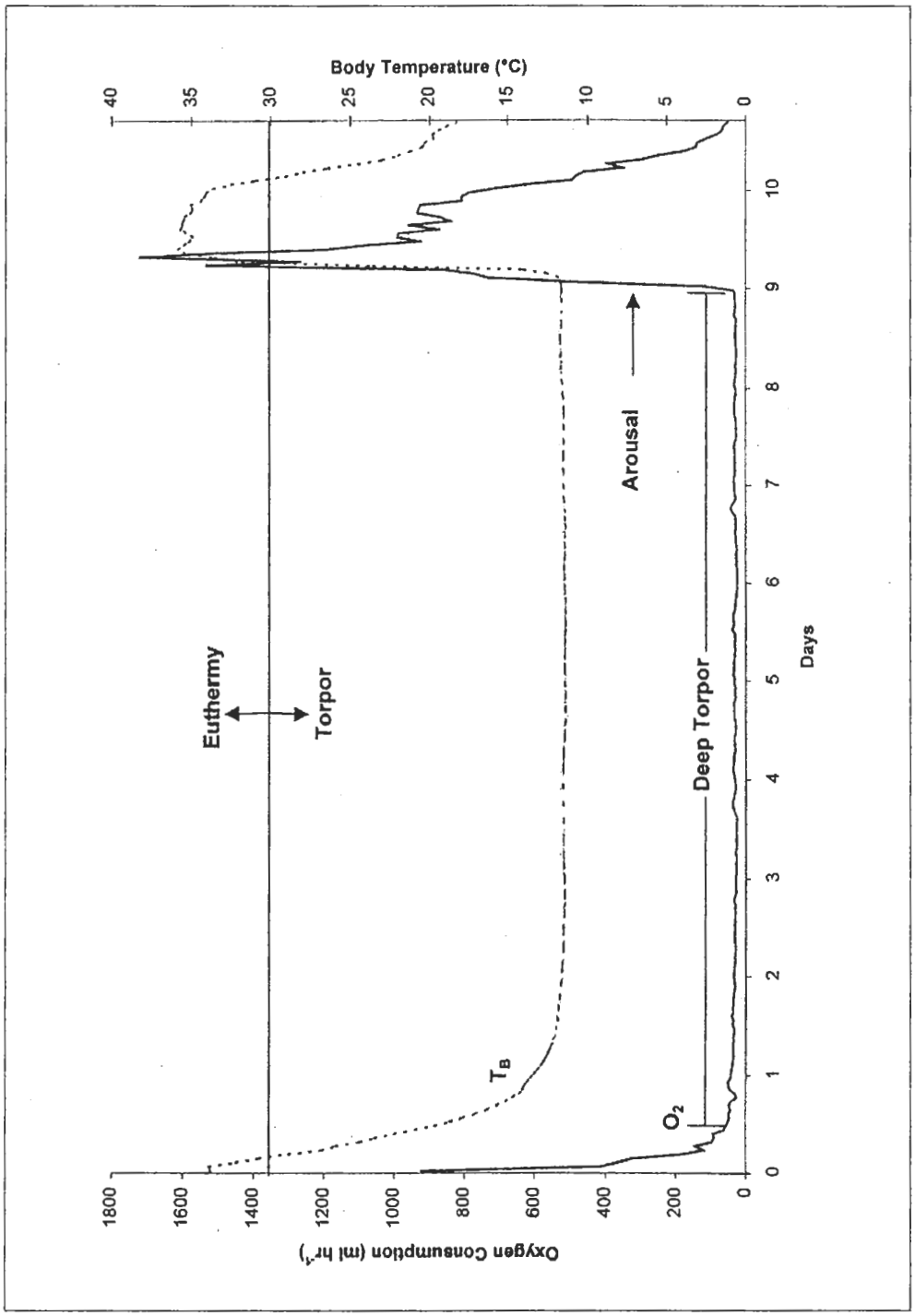

Figure 2. A typical hibernation bout of M. flaviventris. *From [19].*

more quickly, and as a consequence spends more time in the low energy expenditure stage of torpor and thus has higher energy savings than *M. monax*.

These differences in bout characteristics are expressed in daily specific mass loss (DML as mg·day $^{-1}$·g $^{-1}$ immergence mass). DML is 0.94 for *M. flaviventris* and 1.94 for *M. monax* [14]. DML for *M. monax* increases to 2.18 in Canada where hibernation is about a month longer [33] than in Pennsylvania, which indicates that there has been no selection for increased energetic efficiency in *M. monax* at higher latitudes.

However, energy-saving mechanisms leading to low DML apparently evolved in one of the major sub-groups of the *Marmota* (Fig. 3). The high values of DML in *M.*

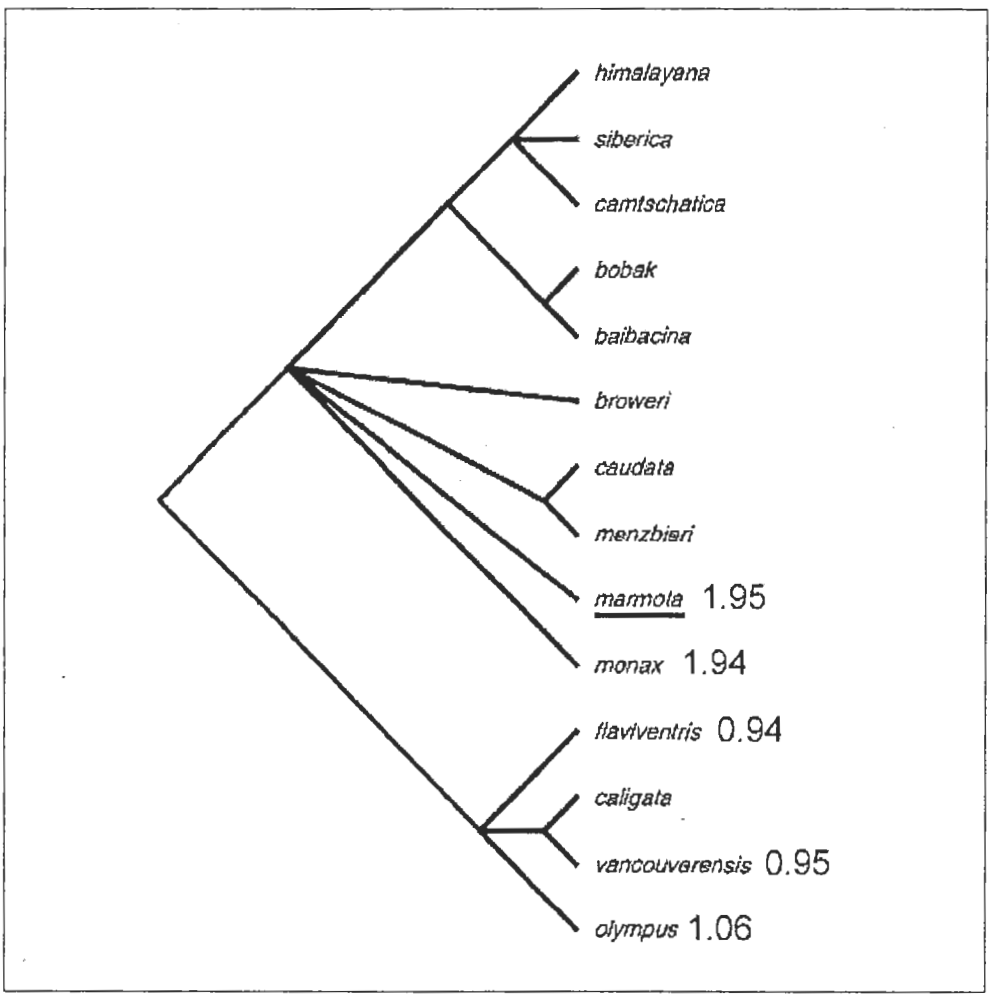

Figure 3. Marmot phylogeny with DML values. M. marmota *with known social thermoregulation is underlined. The phylogeny is from [5]. DML values:* M. monax, M. flaviventris, M. marmota *from [14];* M. vancouverensis *from [22];* M. olympus *values calculated from date provided by Sue Cox Griffin.*

marmota and *M. monax* probably reflect the ancestral state and the low values in subgenus *Petromarmota* represents an independent evolutionary event that occurred in this clade.

By contrast, social thermoregulation evolved in the other major clade, the subgenus *Marmota* (Fig. 3). A typical social group of *M. marmota* consists of a dominant male and female, the territorials, a variable number of non-reproductive adults, the subordinates, and yearlings and infants [3]. Social thermoregulation reduces mortality of infants [26]. Adults increase their energy expenditure by warming infants. This thermoregulatory cost increases mass loss; the DML of territorials hibernating without offspring is 1.60; with offspring DML is 1.82. The cost of the presence of infants with the territorials can extend to causing mortality of the entire group, especially in hibernacula of low-quality [26]. The presence of subordinate adults reduces winter mortality; subordinates lose more mass when hibernating with potential full sib infants (DML = 1.74), but lose less mass if infants are not present or are less than full sibs (DML = 1.57). Because other species in subgenus *Marmota* have a similar social organization, it is likely that social thermoregulation occurs in all those species in which subordinate adults hibernate with the dominant pair. For example, in *M. camtschatica*, oxygen consumption of individuals in a group of three averaged 0.0147 mL $O_2 \cdot g^{-1} \cdot h^{-1}$ whereas the mean of two individuals was 0.0328 mL $O_2 \cdot g^{-1} \cdot h^{-1}$ [23]. By contrast, there was no significant difference in *M. flaviventris* in a group (0.034 mL $O_2 \cdot g^{-1} \cdot h^{-1}$) or singly (0.035 mL $O_2 \cdot g^{-1} \cdot h^{-1}$; values calculated from [34]).

One should note that the DML of *M. marmota* hibernating in groups without infants is less than that measured for individuals, but remains about 38% higher than the average DML of the *Petromarmota* group. I conclude that social thermoregulation evolved in those marmot species that delay dispersal beyond maturity which facilitates the formation of large groups of varied ages and sizes that hibernate in a common hibernaculum [3], [30]. Group hibernation is a necessary but insufficient condition for social thermoregulation. Probably all species of marmots, except *M. monax*, hibernate to some extent in groups, but the age groups most involved in social thermoregulation do not occur in the social groups of the subgenus *Petromarmota*. Thus members of this clade evolved mechanisms that increase metabolic efficiency rather than the social mechanisms of the other major clade.

During hibernation the gastrointestinal tract of *M. marmota* and *M. broweri* is greatly shrunken [24], [25]. The gastrointestinal tract is one of the most metabolically intense organs of the vertebrate body in terms of energy utilization. Reduced size obviously reduces energy expenditure, but this saving has not been quantified. *M. marmota* does little or no feeding during the first two to three weeks after emergence [35] and we have observed a similar pattern in *M. flaviventris*. If this delayed feeding is associated with a shrunken digestive tract, then a reduced tract may characterize marmot hibernation and be an ancestral trait. Only additional research on this topic can resolve this issue.

Conclusions

Traits that conserve energy are numerous and widespread in marmots. These traits are related to hibernation, which is universal among the monophyletic *Marmota* and

which probably evolved in an ancestral marmot. The use of phylogeny allows us to determine ancestral traits, such as the depression of metabolism during entry into torpor and the seasonal decline in metabolism. Phylogeny also revealed independent evolutionary events, such as social thermoregulation in one major clade and increased energetic efficiency in the other major clade. Neither of these traits occurs in the species most likely to be closely related to the ancestral marmot.

The analysis of the role of phylogeny in the evaluation of energy conservation is at an early stage. Many more marmot species need to be investigated in order to determine the generality of the traits described here, to determine which traits are ancestral and to perhaps find additional evolutionary events.

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