

Body temperature patterns during hibernation in a free-living Alaska marmot (*Marmota broweri*)

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Marmota broweri is endemic to arctic Alaska. We implanted data loggers into one free-living subadult female in August 2007 to record body temperature (T_b). Seasonal heterothermy lasted for 224 days (10 September to 21 April). Midwinter torpor bout length (mean $\pm$ SD) was 13.91 ± 3.56 days and duration of interbout euthermia was 18.43 ± 2.55 hr. Unlike other marmot species, torpor entry during midwinter was consistently characterized by two distinct cooling rates differing by about 10-fold and separated by a transient temperature increase. Minimum hibernaculum temperature was -14.97 °C in February (7 month mean: -7.33 °C). Minimum T_b was 1.01 °C when defending a 15.5 °C thermal gradient. At least six animals emerged from the hibernaculum suggesting that communal hibernation may be a strategy to reduce metabolic costs while maintaining above-freezing T_b .

KEY WORDS: *Marmota broweri*, marmot, hibernation, body temperature, hibernaculum temperature, cooling rate, Arctic.

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INTRODUCTION

The Alaska marmot, *Marmota broweri*, was first recognized as a subspecies, *Marmota caligata broweri*, by HALL & GILMORE in 1934 from specimens collected by Native residents on the northwest coast of Alaska. Later, RAUSCH (1953) proposed a reorganization of the genus *Marmota* that described the Alaska marmot (*Marmota marmota broweri*) as a subspecies of the alpine marmot found in Europe. This reorganization was never fully accepted and the Alaska marmot was recognized as a unique species in 1965 when cytogenetic studies revealed it had $2n = 36$ chromosomes compared to *M. caligata*'s $2n = 42$ (RAUSCH & RAUSCH 1965) and *M. marmota*'s $2n = 38$ (RAUSCH & RAUSCH 1971). Since its specific recognition, very few studies have investigated either the ecology (RAUSCH & RAUSCH 1971, ALBERT 1977, RAUSCH & BRIDGENS 1989) or the physiology (WILLIAMS & RAUSCH 1973) of this arctic species.

M. broweri is endemic to northern Alaska, though its range has been misconstrued due to a lack of focused efforts to describe it (RAUSCH 1953, BARASH 1989, HOFFMANN 1999). Recently, GUNDERSON (2009) synthesized a current range map of *M. broweri* through analysis of museum specimens and extensive field surveys of potential habitats. Most populations of *M. broweri* occur in the Brooks Range, though some populations are found in the Kokrines Hills and Ray Mountains just north of the Yukon River in Alaska, which may function as a barrier between *M. broweri* and *M. caligata* (GUNDERSON 2009). Marmots were typically found on talus slopes 1000-1200 m in elevation with grassy meadows present for foraging (GUNDERSON 2009). This agrees with previous descriptions of *M. broweri*'s habitat (BEE & HALL 1956) and is consistent with the preferred habitats of most species of North American mountain marmots (ARMITAGE 2003). *M. broweri* utilize multiple summer burrows among talus (RAUSCH & RAUSCH 1971) but congregate in social groups of up to 12, but usually 7-8, animals in a single hibernaculum for winter hibernation (RAUSCH & RAUSCH 1971, RAUSCH & BRIDGENS 1989). The hibernaculum is usually situated in an exposed area of soil so the burrow plug, placed in mid September, will thaw and allow exit from late April to early May (RAUSCH & BRIDGENS 1989). Some evidence indicates *M. broweri* breed within the hibernaculum before spring emergence (RAUSCH & RAUSCH 1971, RAUSCH & BRIDGENS 1989).

Hibernation of *M. broweri* has only been cursorily investigated in three captive studies. An early study revealed that a captive colony of hibernating *M. broweri* tolerated CO_2 levels as high as 13.5% and O_2 levels as low as 4%, though levels were usually below 4% and above 15%, respectively (WILLIAMS & RAUSCH 1973). During that experiment, marmots in the artificial hibernaculum experienced ambient temperatures as low as -25°C . Marmots in an artificial den in Barrow, Alaska tolerated ambient temperatures as low as -13°C (ALBERT 1977), and there is a report of ambient temperatures during hibernation as low as -48°C while temperature probes in contact with the marmots frequently recorded -5°C (FOLK 1966).

M. broweri is sympatric with *Spermophilus parryii* in the Alaskan Arctic. Soil temperatures of natural hibernacula of *S. parryii* decrease to as low as -23.4°C in winter (BUCK & BARNES 1999b), and animals defend a minimum

body temperature during hibernation no lower than -2.9°C both in the field (BUCK et al. 2008) and in captivity (BARNES 1989). Although *S. parryii* are solitary hibernators (BUCK & BARNES 1999b) and *M. broweri* hibernate in social groups (RAUSCH & RAUSCH 1971, RAUSCH & BRIDGENS 1989), they likely experience similar environmental temperatures. In the current study, we describe for the first time overwinter thermal conditions of a natural hibernaculum, the timing of hibernation, and pattern of body temperature regulation of a free-living *M. broweri*.

MATERIALS AND METHODS

Two colonies of *M. broweri* near the Toolik Field Station (TFS), $68^{\circ}38'\text{N}$, $149^{\circ}36'\text{W}$, were targeted for this study. Tomahawk® live traps (Tomahawk Live Trap, Tomahawk, WI) approximately $23 \times 23 \times 66$ cm were situated near burrow entrances or where animals had disappeared under rocks. Despite extensive trapping effort in early August 2007, no animals were captured from the larger colony. One animal, a young female estimated to be 1-2 years old, was captured at the smaller colony's hibernaculum through blocking the entrance so that the animal could only exit into a trap.

The captured marmot was transported to the lab at TFS and anesthetized with a $3 + 40$ mg/kg xylazine-ketamine cocktail injection (BEIGLBÖCK & ZENKER 2003) and maintained on a surgical anesthesia level using 1-5% isoflurane gas anesthesia. The marmot was weighed on an electronic balance to the nearest gram and 3 ml of blood was sampled from the femoral vein for other studies. Two TidBit Stowaway temperature loggers (Onset Computer Corporation, Bourne, MA), coated in Elvax (DuPont, Wilmington, DE) and weighing approximately 15 g each, were surgically implanted into the abdominal cavity (LONG et al. 2007). Two loggers were implanted to ensure that data would be collected even if one of the loggers failed. Briefly, an area approximately 15 cm^2 of the animal's abdomen was shaved and scrubbed. An incision of approximately 3 cm was made through the skin and subcutaneous adipose tissue was blunt dissected to reveal the linea alba where the abdominal cavity was opened with an incision and the data loggers were inserted to float freely in the peritoneal space. Muscles and skin were closed with absorbable and non-absorbable (respectively) interrupted sutures and the adipose tissue was closed with an absorbable continuous suture. Implanted loggers were pre-programmed to measure and record core body temperature ($T_b \pm 0.2^{\circ}\text{C}$) every 20 min. The animal was released at the site of capture within 12 hr of recovery from anesthesia.

We outfitted the hibernaculum site with two temperature-sensitive data loggers (Hobo Pro Series Temp Dual Component Temperature, Onset Computer Corporation, Bourne, MA) in late September 2007 after the burrow opening had been plugged from within with loose soil and cobble. The data loggers were pre-programmed to measure and record temperature at the depth of an attached thermistor probe and at the surface every hour ($\pm 0.2^{\circ}\text{C}$). The thermistor probes were fitted within 1.25 cm (inner diameter) cpvc pipe (BUCK & BARNES 1999b). One thermistor probe was placed into part of the hibernaculum through a hole in the soil left by a steel rod. The second probe was placed into the frozen burrow plug.

The following spring (4-7 May 2008), five marmots including the implanted female were captured at the hibernaculum directly after emergence and were implanted with temperature data loggers (as above); loggers from the previously implanted female were explanted and replaced using a similar surgical procedure. At least one additional marmot, a yearling much smaller than the others, was seen at the burrow immediately after emergence.

The season of heterothermy, defined as the interval between when the animal first decreased $T_b < 30^\circ\text{C}$ and last increased $T_b > 30^\circ\text{C}$, is separated into bouts of torpor ($T_b < 30^\circ\text{C}$) alternating with arousal to intervals of euthermia ($T_b \geq 30^\circ\text{C}$; BUCK et al. 2008). Torpor bouts of low, stable T_b ($< 1^\circ\text{C}$ variation over 24 hr) were considered midwinter torpor bouts and were used in analyses. Rates of cooling ($^\circ\text{C/hr}$) following arousal were divided into two phases: rapid and slow. Rapid cooling rates are defined as an initial drop in T_b of $\geq 3^\circ\text{C}$ within 40 min from euthermic T_b until a transient temperature increase, after which slow cooling rates continued until $T_b \leq 5^\circ\text{C}$. Rewarming rates were calculated from low, stable T_b to 30°C to allow comparison with other species and T_b 10 to 30°C to estimate maximal rewarming rates. Mean and minimum hibernaculum soil temperature (T_s) were calculated from each timeframe of the associated phase of body temperature. Relationships between cooling rates, rewarming rates, mean torpid T_b , minimum torpid T_b , torpor bout duration and mean or minimum soil temperature were analyzed by linear regression ($\alpha = 0.05$). Means $\pm$ SD are reported. All animal use procedures were approved by the Institute of Animal Care and Use Committee of the University of Alaska Fairbanks (Protocol 07-34).

RESULTS

Patterns of body temperature

The marmot first entered torpor on 10 September 2007 and ended heterothermy 21 April 2008 for a total heterothermic season duration of 224 days during which the animal was torpid 87.5% of the time (Fig. 1). During midwinter, the animal displayed 11 torpor bouts averaging 13.91 ± 3.56 days and spent 95.2% of this time torpid. The 10 intervening euthermic intervals averaged 18.43 ± 2.55 hr in duration. Torpor bout duration was not related to either mean or minimum T_s ($F = 0.0058$, $P > 0.05$; $F = 0.1107$, $P > 0.05$, respectively).

Both mean and minimum T_b during individual midwinter torpor bouts decreased with decreasing mean T_s ($F = 17.91$, $P = 0.0022$, $R^2 = 0.67$; $F = 12.96$, $P = 0.0057$, $R^2 = 0.59$, respectively) and were even more strongly related to minimum T_s during the bout ($F = 23.70$, $P = 0.0009$, $R^2 = 0.72$; $F = 16.68$, $P = 0.0027$, $R^2 = 0.65$, respectively). Minimum T_b recorded was 1.01°C on February 9-10 when T_s was -14.10 to -14.53°C .

Minimum torpid T_b changed dramatically throughout the heterothermic season. Midwinter torpor bouts were preceded by seven early-winter torpor bouts of decreasing minimum T_b and followed by five late-winter torpor bouts of increasing minimum T_b . T_b during these early and late-winter torpor bouts was not stable, and bouts were truncated at relatively high T_b (Fig. 1).

Cooling and rewarming rates

Entry into torpor during midwinter was consistently characterized by two distinct rates of cooling (Fig. 2). The animal cooled rapidly until reaching T_b of $21.49 \pm 1.11^\circ\text{C}$, and then cooled much more slowly after a transient increase in temperature peaked at $22.75 \pm 1.23^\circ\text{C}$. The rate of rapid cooling was not affected by mean T_s ($F = 2.96$, $P > 0.05$) and averaged $-5.87 \pm 2.71^\circ\text{C/hr}$ (range:

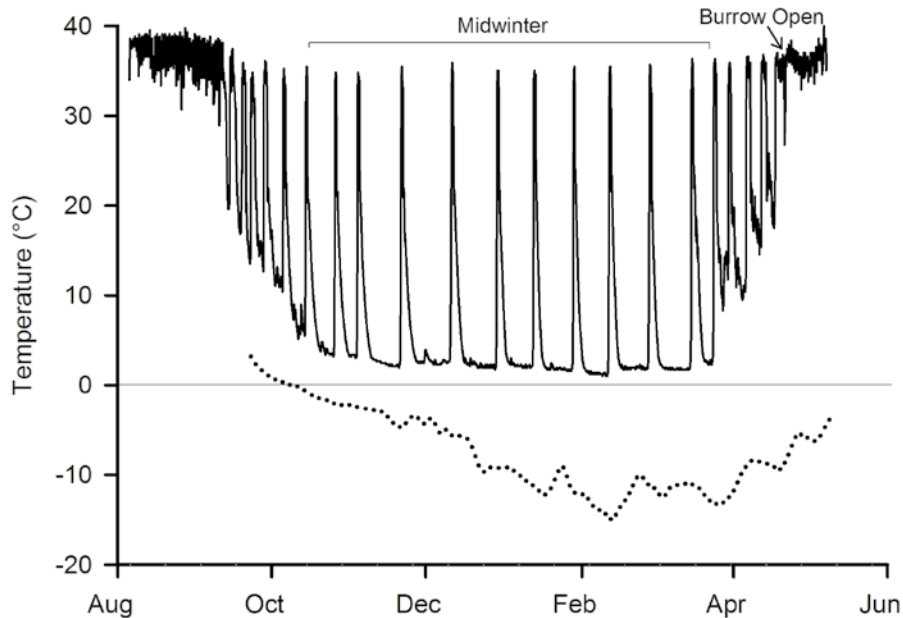


Fig. 1. — Body temperature (solid line) and associated soil temperature (dotted line) profile of a female Alaska marmot hibernating during winter 2007-2008. Horizontal bracket shows torpor and arousal bouts considered midwinter (torpor bouts of low, stable T_b with $< 1^\circ\text{C}$ variation over 24 hr). Arrow indicates date burrow was opened.

– 1.32 to – 11.21 $^\circ\text{C/hr}$). Slow cooling ranged from – 0.18 to – 0.43 $^\circ\text{C/hr}$ and was significantly related to mean T_s ($F = 26.00$, $P = 0.0006$, $R^2 = 0.74$).

Rates of rewarming from stable T_b to 30 $^\circ\text{C}$ and T_b 10 to 30 $^\circ\text{C}$ were not related to mean T_s ($F = 0.24$, $P > 0.05$; $F = 0.04$, $P > 0.05$, respectively). Rewarming from stable T_b to 30 $^\circ\text{C}$ averaged 3.26 ± 0.48 $^\circ\text{C/hr}$ (range: 2.37 to 4.20 $^\circ\text{C/hr}$) whereas rates from T_b 10 to 30 $^\circ\text{C}$ averaged 6.04 ± 1.46 $^\circ\text{C/hr}$ (range: 4.54 to 8.58 $^\circ\text{C/hr}$).

Soil temperatures

Soil temperature at the hibernaculum averaged -7.33 ± 4.53 $^\circ\text{C}$ from 22 September 2007 to 9 May 2008. Minimum soil temperature was – 14.97 $^\circ\text{C}$ in February. From 22 September-20 April, the temperature of the soil plug averaged -11.80 ± 6.19 $^\circ\text{C}$ with a minimum of – 25.42 $^\circ\text{C}$. The temperature of the soil plug became erratic on 21 April, indicating the opening of the burrow and exposure to air, which was visually confirmed on 23 April (last seen closed 23 March). Three interspersed temperatures measured from the soil plug a few hours prior to exposure to air were unusually high (+ 8 to 11 $^\circ\text{C}$) as compared to surface temperature (about – 6 $^\circ\text{C}$); these spikes in temperature likely reflect the influence of marmot T_b as the animal(s) worked to open the plug.

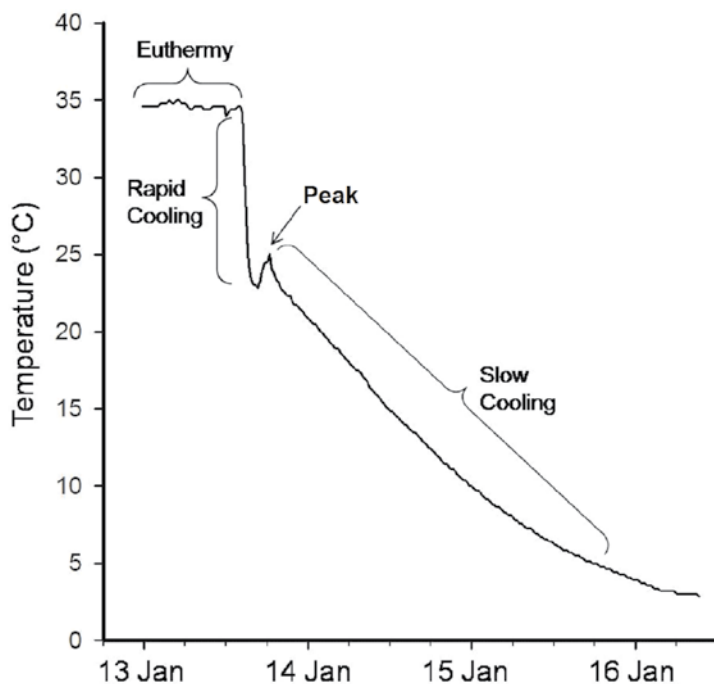


Fig. 2. — Detail of body temperature during entrance into torpor of a female Alaska marmot during January 2008 to illustrate consistent, distinct rates of cooling.

Temperatures at the snow-ground interface averaged -14.59 ± 10.48 °C with a minimum of -42.03 °C.

Body mass

The female marmot weighed 3.094 kg on 5 August 2007 and 2.055 kg when recaptured after emergence on 7 May 2008. During this time, including 17 days of euthermy at emergence, the animal lost 1.039 kg, 33.6% of her initial body mass. Four other marmots were captured at emergence only: two non-reproductive, young males (2.22 kg and 2.77 kg), one adult breeding female (2.85 kg), and another young female (2.16 kg).

DISCUSSION

Here we present the first description of overwinter body temperature patterns of a free-living *M. broweri* and associated soil temperatures of the hibernaculum, which demonstrate that *M. broweri* defends a large thermal

gradient between T_b and T_s while maintaining above-freezing body temperatures during torpor. *M. broweri* displays an apparently atypical change in cooling rates during torpor entrance that, for at least this marmot, is consistent throughout midwinter. Whether this pattern is manifest for others within the species has yet to be determined. Torpid T_b decreases in sequential torpor bouts in the fall and shows a mirrored increase in the spring, but the extent to which social dynamics influence this pattern are unknown.

Most species of marmot that have been studied naturally hibernate at ambient temperatures above freezing (ARNOLD et al. 1991, FERRON 1996, FLORANT et al. 2000) and may not be capable of hibernating in sub-freezing temperatures. ORTMANN & HELDMAEIR (2000) demonstrated that *M. marmota* spontaneously arouse from torpor when ambient temperatures decrease below -0.5°C . However, *M. camtschatica* from arctic Russia, where soil temperature at nest level can decrease to -22°C , hibernated in captivity at ambient temperatures of -5°C and displayed minimum rectal temperatures of 0.9°C (VASIL'EV 2000). *M. broweri* are also able to hibernate in freezing temperatures as shown by the hibernaculum soil temperatures recorded in this study. Measured T_s should closely approximate ambient temperatures in the hibernaculum. We think that the thermistor probe was positioned in part of the burrow system because the steel rod used to make a hole for the probe plunged through 'open space' about 1 m below the soil surface. This space was about 20 vertical cm and was underlain by permafrost. Thus, the patterns of T_s we report probably represent ambient temperatures experienced by the marmot. Burrows of *S. parryii* are at similar depth and exhibit similar patterns of soil temperatures (BUCK & BARNES 1999b) and hibernating *M. broweri* in artificial hibernacula tolerate similar temperatures (ALBERT 1977). In our study it is unlikely the thermistor probe was in contact with the marmots as the temperature recordings show no influence of body temperature.

The young female marmot demonstrated body temperature patterns typical of deep hibernators, i.e. multi-day torpor bouts with spontaneous interbout arousal intervals, but the extent of hibernation was more extreme in ambient temperature, duration, T_b depression, and torpor bout length than has been recorded in other species of marmots in the field (Table 1). The hibernation duration and intervals were more similar to those of *S. parryii* hibernating in the same area under similar conditions (Table 1).

In studies of communal hibernation in the European marmot, the energetic savings of each animal hibernating communally depends on the least efficient member of the group: synchrony of torpor bouts among members is necessary for hibernation to save enough energy for animals to survive (ARNOLD 1988). At least six *M. broweri* exited the hibernaculum in the spring, suggesting that *M. broweri* hibernate in social groups as has been previously reported (RAUSCH & RAUSCH 1971, RAUSCH & BRIDGENS 1989). Though we don't know the T_b patterns of the nest-mates of the study animal, arousals initiated before attaining a stable and minimum T_b are likely at least in part a result of passive warming from other animals increasing T_b during arousal. Although bouts of torpor in *S. parryii* are shorter at the beginning and end of the heterothermic season, truncated multi-day torpor bouts at high T_b are not seen in *S. parryii* (BUCK et al. 2008). Short torpor bouts at relatively high T_b dur-

Table 1.

Comparison of hibernation parameters among *M. breweri*, *M. monax*, *M. marmota* and *S. parryii*.

Measurement	<i>M. breweri</i> (f) ¹	<i>M. monax</i> (Penn) ²	<i>M. marmota</i>	<i>S. parryii</i> (f)
Heterothermy start	10 Sept ^a	31 Oct-4 Nov ^a	24 Sept- 3 Oct ^{3b}	13 Aug- 11 Sept ^{5b}
Heterothermy end	21 April ^a	1-5 Mar ^a	7-13 April ^{3b}	18 April- 13 May ^{5b}
Hibernation Duration	224 d ^a	121.8±1.83 d (f) ^a	186-201 d ^b	227 d (juv) ^{6a} 245 d (ad)
Torpor Bout Length (midwinter)	13.91±3.56 d ^c	8.04±0.32 d ^d		17.6 d ^{6e}
Interbout Arousal Length (midwinter)	18.43±2.55 hr ^c	56.0±7.4 hr ^d		15.6 hr ^{6e}
Minimum T _b	1.01 °C	6.5 °C	~7.8 °C ⁴	-2.9 °C ⁷
Minimum T _a	-14.97 °C	6.3 °C	> -0.5 °C ⁴	-23.4 °C ⁸
Potential thermal gradient (T _b -T _a)	15.98 °C	0.2 °C	~8.3 °C	20.5 °C

T_a = ambient temperature; juv = juvenile; ad = adult; ^a based on dates of heterothermy; ^b based on dates of immergence and emergence; midwinter defined as ^c period of torpor bouts reaching low, stable T_b with < 1 °C variation in 24 hr; ^d middle third of hibernation season, and ^e period between first and last two multi-day torpor bouts; "f" denotes measurements of females; ¹ This study; ² ZERVANOS & SALSBUURY 2003; ³ ARNOLD et al. 1991; ⁴ ORTMANN & HELDMAIER 2000; ⁵ BUCK & BARNES 1999a; ⁶ BUCK et al. 2008; ⁷ BARNES 1989; ⁸ BUCK & BARNES 1999b.

ing early hibernation in *M. breweri* may be described as "test drops" proposed to 'reset' hypothalamic T_b set-points (FLORANT & HELLER 1977). This hypothesis for the functional significance of these torpor bouts, however, would not explain the mirrored pattern at the end of hibernation. In spring, the incremental increases in T_b over sequential torpor bouts may be due to disturbance from a male that has attained euthermy to undergo spermatogenesis (BARNES 1996).

M. breweri appears to have a strategy for entering torpor that differs from the uninterrupted pattern of decrease in body temperature typical of *S. parryii* (KARPOVICH et al. 2009), *M. marmota* (ARNOLD 1988, ORTMANN & HELDMAIER 2000), *M. monax* (ZERVANOS & SALSBUURY 2003), and *M. flaviventris* (WOODS et al. 2002). In *M. breweri*, T_b drops rapidly (- 5.87 °C/hr) from euthermic body temperatures during arousal to an average of 21.5 °C, at which point cooling slows dramatically to an ambient temperature-related rate less than - 0.43 °C/hr after a small 1.2 °C temperature increase (Fig. 2). Rapid cooling may be the result of a strategy to quickly dump heat as metabolic rate is suppressed (ORTMANN & HELDMAIER 2000, WOODS et al. 2002) and may be achieved by behavioral means, i.e., animals may be separated in the hibernaculum in a position to expose maximal surface area. As body temperatures approach 20 °C, the marmots likely still have some motor capability (FOLK 1966), and they may then move (causing the small temperature increase) to huddle together (ARNOLD 1988) causing a decrease in cooling rates

by reducing surface area for heat loss and increasing thermal mass. Alternatively, T_b may fall passively with the initial drop of metabolic rate until reaching a certain temperature, at which point animals may increase metabolic rate as they initiate thermoregulatory heat production to slow the rate of T_b decline. Results from captive animal studies with simultaneous measurement of T_b and metabolic rate of animals are necessary to mechanistically understand the significance of the change in rate of cooling.

Marmots, like other mammalian hibernators, increase mass rapidly during the summer active season prior to hibernation (ARMITAGE 2003). *M. flaviventris* attains peak body mass in August (WARD & ARMITAGE 1981) and marmots may maintain mass up to 5 weeks before immergence (ARMITAGE 2003) as forage senesces and their gastrointestinal tract reduces in both function and mass in preparation for hibernation (HUME et al. 2002). In our study, the marmot may have been near maximal body mass when captured in the fall 36 days prior to becoming heterothermic. When captured in the spring, the animal had been euthermic for 17 days. There was no evidence of feeding during this time: snow covered possible forage, marmots did not exit the burrow between 23 April and their capture 4-7 May, and no fecal material was seen from any animal brought into the lab. Marmots may need at least a week after hibernation to rebuild their gastrointestinal tracts to be able to digest forage, but rebuilding in the spring also depends on ingestion of food (HUME et al. 2002). If we assume the animal was at peak body mass in August, she lost 33.6% of her body mass during hibernation, which is similar to mass losses in several other marmot species and less than losses of 46-53% in *M. caligata* and *M. olympus* (ORTMANN & HELDMAIER 2000, ARMITAGE 2003). This unexpectedly low mass loss could indicate that the animal was not at peak body mass in August as increased metabolic costs of maintaining a larger thermal gradient (BUCK & BARNES 2000) should be reflected by increased mass loss over winter. Alternatively, *M. broweri* may be more efficient during hibernation than other species. Possible increases in efficiency could be due to increased insulation, lower metabolic rates during torpor, or a combination of factors.

M. broweri did not display subfreezing T_b even under a 15.5 °C thermal gradient, suggesting that they may not be able to physiologically tolerate $T_b < 0$ °C. These marmots may use communal hibernation as a strategy to reduce the metabolic costs of hibernating against the large thermal gradient they experience. The distinct cooling rates should be further investigated by a combination of metabolic rate and T_b measurements and behavioral observations. Also, possible means of increased efficiency of *M. broweri* should be explored to learn more about how this species can withstand the extreme environment it inhabits.

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