Hibernation strategies and patterns in sympatric arctic species, the Alaska marmot and the arctic ground squirrel

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We compared patterns of core body temperature (T_b) change, including inter-individual synchrony, in 2 free-living arctic hibernators that differ in size and sociality, the Alaska marmot (*Marmota broweri*) and the arctic ground squirrel (*Urocitellus parryii*). We report overwinter T_b changes from 3 to 4 marmots from the same hibernaculum in each of 3 years and from 7 ground squirrels that hibernated at 2 nearby burrow sites in 1 year. Very close synchrony in the timing of torpor and arousal cycles in Alaska marmots indicates social hibernation and thermoregulation, while lack of synchrony in arctic ground squirrels further confirms solitary hibernation. The mean duration between the first and last marmot measured within the group to initiate an arousal was 3.7 ± 2.5 h and to recool to 30°C during torpor entrance was 5.7 ± 3.7 h. The minimum T_b recorded in marmots was 0.6°C and in ground squirrels was −2.0°C. Marmots entering torpor displayed an interrupted pattern of T_b change defined by 2 distinct rates of cooling, early and late during entry, that differed by 21-fold. Ground squirrels cooled in a continuous pattern, initially 3-fold slower than marmots during rapid cooling but 4-fold faster during slow cooling. Both species must minimize energy expenditure to survive long arctic winters; our results suggest that Alaska marmots do this through social thermoregulation, while arctic ground squirrels decrease T_b below freezing to minimize the difference between body and ambient temperatures.

Key words: Alaska marmot, Arctic, hibernation, *Marmota broweri*, synchrony, *Urocitellus parryii*

The Alaska marmot (*Marmota broweri*) and arctic ground squirrel (*Urocitellus parryii*) are sympatric species in the family Sciuridae that experience the extreme seasonality and harsh winter conditions of the Arctic, including soil temperatures at burrow depth that can reach minima of −15°C to −23.4°C (Buck and Barnes 1999b; Lee et al. 2009). Both species spend the majority of the year in hibernation, during which they reduce metabolic rate and body temperature (T_b) during torpor yet periodically rewarm to high, euthermic T_b levels for short intervals during spontaneous arousal episodes. The Alaska marmot is social and hibernates communally in family groups or harems in a common den (Rausch and Rausch 1971; Rausch and Bridgens 1989), while the arctic ground squirrel hibernates individually (Carl 1971; Armitage 1981).

Differences in sociality between marmots and ground squirrels have been suggested to influence their hibernation strategies, specifically that communal hibernation allows marmots to engage in social thermoregulation and thus maintain

higher minimum T_b during torpor than solitary ground squirrels (Arnold 1993). Ground squirrels reach very low T_b during torpor, as low as −2.9°C in the arctic ground squirrel (Barnes 1989). This strategy minimizes the thermal gradient, the difference between T_b and still lower ambient temperatures, in the hibernaculum, thus reducing energy expenditure during torpor. In contrast, huddling social thermoregulation reduces energy expenditure of individuals by decreasing overall thermal conductance due to a lower surface area-to-volume ratio and a larger thermal mass that is less affected by fluctuations in ambient temperature (Arnold 1988; Armitage and Woods 2003; Gilbert et al. 2010). Social thermoregulation thus reduces winter mortality and allows animals to begin spring activities in better body condition (Arnold 1990, 1993, 1995). Social thermoregulation is indicated by synchrony in patterns of T_b among individuals across successive cycles of torpor and arousal to euthermia (Arnold 1988). Loss of synchrony during social thermoregulation is energetically costly (Ruf and Arnold 2000;

Armitage and Woods 2003), suggesting that high levels of synchrony during hibernation may be critical for socially thermoregulating marmots exposed to challenging thermal conditions, just as minimal thermal gradients are critical to solitary ground squirrels (Buck and Barnes 2000).

Little is known about hibernation in the Alaska marmot (see Lee et al. 2009), but the arctic ground squirrel has been well studied and provides a valuable, sympatric reference group that experiences similar environmental conditions. To investigate the influence of social system on hibernation in these 2 related species in the Arctic, we recorded core T_b of animals with implanted temperature loggers and measured soil temperatures at burrow depth at each hibernaculum site to quantify the thermal gradient between core T_b and soil temperature. Our 1st objective was to determine whether free-living Alaska marmots trapped from the same hibernaculum utilized social thermoregulation during hibernation by assessing the degree of synchrony of torpor-arousal cycles among individuals. Our 2nd objective was to compare minimum T_b during torpor in Alaska marmots with those of arctic ground squirrels trapped from nearby burrow sites. Our final objective was to determine whether the interrupted cooling pattern observed in Alaska marmots (Lee et al. 2009) is typical of this species and compare their cooling rates and patterns to arctic ground squirrels.

MATERIALS AND METHODS

Animals.—We studied Alaska marmots (*M. broweri*) and arctic ground squirrels (*U. parryii*) living in the northern foothills of the Brooks Range, Alaska, near the Toolik Field Station of the University of Alaska Fairbanks (68°38′N, 149°36′W). Marmots were captured from a single hibernaculum using livetraps (Tomahawk Live Trap, Hazelhurst, Wisconsin; approximately 23×23×66 cm) during fall 2007 and early spring 2008–2011. We caught marmots by barricading the entrance of their earthen burrow (Rausch and Rausch 1971) with rocks and the open end of the trap so that animals could only exit the burrow by entering the trap; only a subset of animals known to be in the burrow were captured. Only 1 animal could be captured at a time and its capture discouraged other animals from coming above ground. We ended trapping based on considerations to allow the long-sequestered animals opportunity to forage and also to avoid recapture. We recovered data from the single Alaska marmot implanted for the 2007–2008 winter (a female), 4 of 5 marmots implanted for the 2008–2009 winter (3 females, 1 male; Fig. 1), 3 of 4 for the 2009–2010 winter (3 females), and 3 of 6 for the 2010–2011 winter (1 female, 2 males; 5 loggers were recovered but 2 failed). Two females were represented in 3 years; all other individuals were represented in only 1 year. We caught no more than 6 marmots in any year, but we resighted most marked animals as well as several unmarked individuals that were using the burrow in successive years. Ground squirrels (*n* = 7) were captured using livetraps (15×15×48 cm) baited with carrot after their emergence from hibernation in spring 2009 at 2 distinct burrow sites that had multiple openings. We assume the tunnels at each site were connected in 1 burrow system (Gaglioti et al. 2011); thus, these few ground squirrels were selected from a long-term study due to their potential to have hibernated within the same burrow chambers. The marmot and ground squirrel hibernacula sites were 5 km apart.

Ground squirrels that had been captured and marked during the active season of their birth year (determined by body mass—Buck and Barnes 1999a) were considered juveniles through the end of their 1st hibernation. Marmot age (yearling, 2-year-old, adult) was estimated by body mass relative to adult body mass according to Arnold (1995). Among the 7 arctic ground squirrels, 3 of 6 females and the male were juveniles hibernating for the 1st time, whereas no 1st-hibernation marmots are represented.
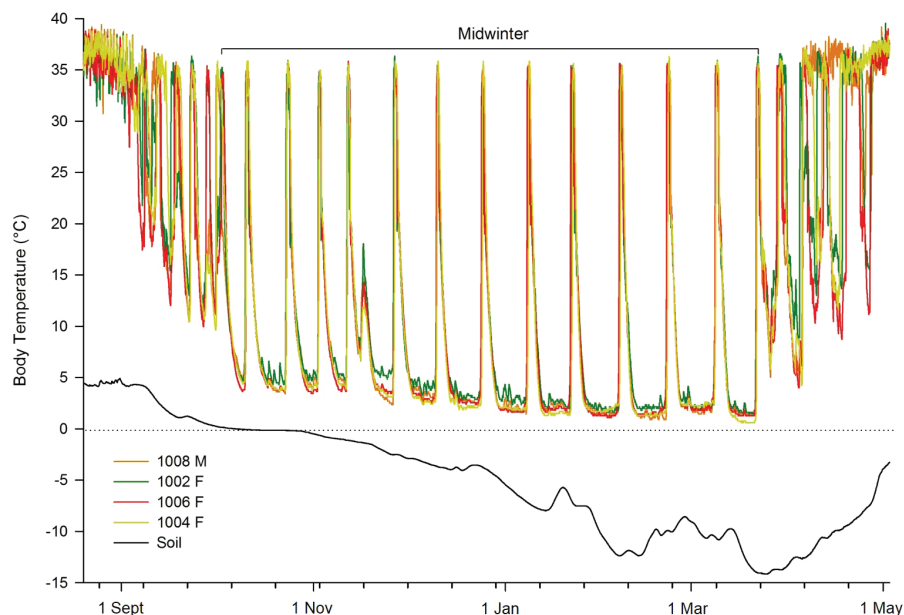

Fig. 1.—Season of heterothermy for 4 adult Alaska marmots hibernating together: body temperatures (colored lines) and soil temperature (black line) during winter 2008–2009. Midwinter is the period corresponding to low, stable T_b (< 1°C variation in 24 h).

Surgical procedures.—Captured animals were transported to the animal holding facility at the nearby Toolik Field Station. Anesthetized individuals were weighed to the nearest gram with an electronic balance and uniquely marked with small metal ear tags. Temperature loggers were shrink-wrapped, coated 3-times using Elvax-Paraffin (Minimitter, Bend, Oregon), and gas sterilized with ethylene oxide. Data logger package weight was ~15 g. Marmots were anesthetized with an intramuscular injection of 3 + 40 mg/kg xylazine–ketamine cocktail (Beiglböck and Zenker 2003) and maintained on a surgical level by gas anesthesia (0.5–1.5% isoflurane in oxygen). Squirrels were anesthetized for the duration of surgery with gas anesthesia (3–5% isoflurane in oxygen). Abdominal surgery on marmots and squirrels was performed as described in Lee et al. (2009). Briefly, we shaved and scrubbed a small area of the animal's abdomen before making a longitudinal midline incision of ~2–3 cm through the skin and peritoneum and into the abdominal cavity. After a data logger was inserted into the peritoneal space, muscle, peritoneum, and skin were closed separately with absorbable (internal) and non-absorbable sutures (skin). Animals were held until full recovery from anesthesia and inspected for the integrity of stitching before being released at their burrow site. All animal procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (protocols 06-06, 09-16, and 07-34) and followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Body temperature.—Temperature loggers (custom range 32K Stowaway TidBit, Onset Computer Corporation, Bourne, Massachusetts) were calibrated at 0°C and 37°C (Long et al. 2007). We programmed loggers to record core T_b (± 0.2°C) every 20 (2007–2009) or 34 (2010) min. During heterothermy, animals alternated between torpor (defined as $T_b < 30$°C) and brief arousal episodes ($T_b > 30$°C—Buck et al. 2008; Karpovich et al. 2009). For all animals, we determined minimum T_b during steady-state torpor, number and duration of steady-state torpor bouts and arousal episodes, and the number of torpor bouts that did not reach a stable T_b. Sequential bouts of stable T_b during torpor (< 1°C variation over 24h) defined the midwinter season in marmots. For comparisons between species, we used data from torpor bouts in ground squirrels coincident with the midwinter bouts of marmots in the same year (3 October 2008 to 24 March 2009).

Synchrony.—We analyzed synchrony in T_b during midwinters 2008–2009, 2009–2010, and 2010–2011. Animals were considered synchronous if all individuals in the group from which we recovered loggers overlapped in time spent at high T_b during arousal episodes. Synchrony of change in T_b was measured at 2 points: as the time between when the first and last animal initiated arousal (defined as the first of 3 consecutive increases in T_b measurements) and the time between when the first and last animal decreased T_b below 30°C during reentry into torpor (time determined by interpolating between measurement intervals). We also generated correlation coefficients between T_b patterns of each pair of hibernating individuals (see "Statistical Analyses").

Cooling and Rewarming Rates.—Rates of cooling and rewarming were calculated during midwinter. Rapid cooling rates were calculated from $T_b = 30$°C to 24°C and slow cooling rates from $T_b = 19$°C to 6°C to avoid the transient temperature increases that seem to be common in cooling Alaska marmots (these data; Lee et al. 2009). Rewarming rates were calculated from arousal initiation to $T_b = 30$°C for comparison between marmots and ground squirrels. We also calculated rewarming rates from 10°C to 30°C for comparison with another social species, the alpine marmot (Ruf and Arnold 2000).

Soil temperature.—Soil temperature was recorded by temperature loggers (Hobo Pro, Onset Computer Corporation, Bourne, Massachusetts) programmed to measure and record soil temperature (± 0.2°C) every hour at approximately −1 m (approximate burrow depth defined by the depth of the permafrost—Buck and Barnes 1999b) via a thermistor probe within a sand-filled plastic pipe (Lee et al. 2009). Minimum soil temperatures were subtracted from minimum T_b of animals at each location during each year to calculate maximum potential thermal gradients.

Statistical analyses.—To create a measure of synchrony similar to the only other quantified measure of synchrony in marmots (Ruf and Arnold 2000), we generated Pearson correlation coefficients. Each individual animal's T_b measurements during midwinter were correlated to every other individual of the same species in the same year in the same burrow system by aligning the data as close as possible by date and time (all data aligned within 20 min). Correlation coefficients were then *z*-transformed and differences were tested by a nonparametric Mann-Whitney analysis as the data failed to meet the assumptions of a parametric test. Rates of cooling and rewarming were compared between species using *t*-tests based on an average rate of each type for each individual from the winter of 2008–2009. Minimum T_b was compared between species using a *t*-test. Durations of torpor bouts and arousal episodes were compared between species using *t*-tests based on the mean for each squirrel ($n = 7$) and the mean of a randomly selected marmot from each year ($n = 4$) to avoid a potential confounding effect of synchrony. One data logger implanted in a female arctic ground squirrel failed in January; only intact torpor and arousal bouts prior to logger failure are included in data presented. Values are reported as mean ± *SD*.

RESULTS

Synchrony.—Marmots hibernating in the same hibernaculum displayed a large amount of overlap in time spent at high T_b during arousal episodes, and this led to a high degree of synchrony in their patterns of T_b during midwinter each year: marmots ($n = 11$ over 3 winters) initiated arousals within 3.7 ± 2.5 h and recooled below 30°C within 5.7 ± 3.7 h of each other (Figs. 1 and 2; Table 1). Even during an unusual partial arousal in November 2008, the animals' patterns of T_b remained synchronized (Fig. 1). Marmots did not exhibit synchrony at either the
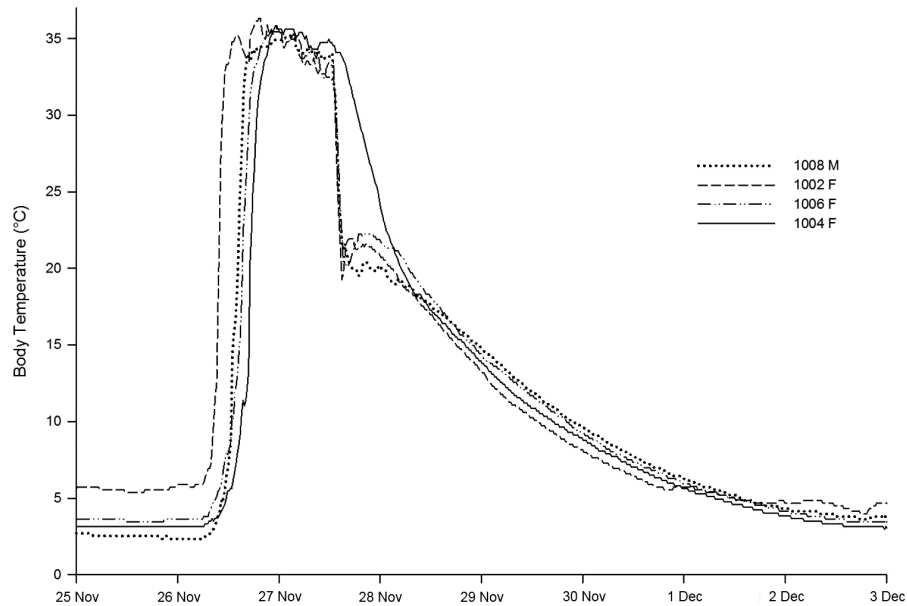
Fig. 2.—An example of synchrony among body temperatures of 4 free-living adult Alaska marmots during arousal and return to torpor in winter 2008–2009. Marmot 1004 F (solid line) was identified as the breeding female and typically cooled last in a continuous pattern, unlike the interrupted cooling curve typical of other Alaska marmots.

Table 1.—Parameters of heterothermy of Alaska marmots during midwinter. Animals were considered in torpor when body temperature (T_b) < 30°C and in an arousal episode when T_b > 30°C. Synchrony is the time between the first and last loggered animal to reach a defined threshold. F represents females and M represents males. Means are expressed ± *SD*.

Parameter	2008–2009 (3F, 1M)	2009–2010 (3F)	2010–2011 (1F, 2M)	All Years (*n* = 11)
# Torpor bouts[a]	13	11	11	
# Arousal episodes[a]	12	10	10	
Torpor bout length[a] (d)	12.23±0.06	15.59±0.02	14.49±0.14	13.81±3.19
Arousal episode[a] (h)	20.5±0.7	21.0±0.3	23.5±2.8	21.2±5.0
Synchrony—Cooling at 30°C (h)	7.3±2.6[b]	3.8±2.5	5.6±4.9	5.7±3.7
Synchrony—Warming from torpor (h)	5.5±3.0	3.1±1.6	2.2±1.0	3.7±2.5

[a] Midwinter: defined in marmots as period when T_b reaches low and stable levels.
[b] Does not include 1st cooling into midwinter: marmots had not coordinated cooling yet (synchrony = 30.5 h).

beginning or end of the hibernation season. Group synchrony began 28–35 days after individuals began heterothermy and ceased 14–37 days before individuals ended heterothermy. In early spring (beginning 23 March–6 April), males warmed and maintained high T_b (> 30°C) for 18–32 days, but each subsequently decreased T_b to < 30°C on 2–4 occasions within the last 4–19 days before ending heterothermy for the season. While males were euthermic prior to ending hibernation, females continued to be heterothermic but did not attain steady torpor (Fig. 3). During midwinter, the average z-transformed correlation coefficient of T_b patterns among pairs of marmots hibernating in the same burrow over all 3 winters was 1.978±0.264 (*n* = 12 pairwise comparisons) with a range of 1.551–2.410.

Arctic ground squirrels captured from 2 burrow sites (3 females at 1 site, 3 females and 1 male at the other) in spring 2009 did not display synchrony in T_b patterns across the hibernation season as evidenced by lack of consistent overlap in time spent at high T_b (Fig. 4 shows the most "synchronous" arousal episode). Ground squirrels captured at the burrow site with 4 animals initiated arousals at least 100.6 h apart and recooled

below 30°C as they reentered torpor at least 102.8 h apart. The male ended heterothermy and maintained euthermic T_b 20–32 days before the females resumed high T_b. All females maintained regular torpor bouts when the male was at high T_b (Fig. 4). During midwinter, the average z-transformed correlation coefficient of T_b patterns among squirrels within the 1st burrow was −0.052±0.016 (*n* = 3 pairwise comparisons) and within the 2nd burrow was 0.060±0.063 (*n* = 6 pairwise comparisons). Squirrels in the 1st burrow (*n* = 3) had body temperatures more correlated to soil temperature than each other (z-transformed: 0.170±0.023). Synchrony differed between marmots and ground squirrels (*U* = 108.00, *P* < 0.001).

Cooling rates.—Individual Alaska marmots cooled at 2 distinct rates when entering torpor (Fig. 5; Table 2). An initial rapid rate from T_b of 30°C to 24°C averaged −5.2±3.0°C/h over 2.5±2.1 h for all animals in all years. Cooling was interrupted around T_b 20–22°C, then T_b increased briefly or remained stable before marmots resumed cooling at a slower cooling rate of −0.25±0.08°C/h. In contrast, arctic ground squirrels cooled in a continuous pattern at an average of −1.7±0.3°C/h
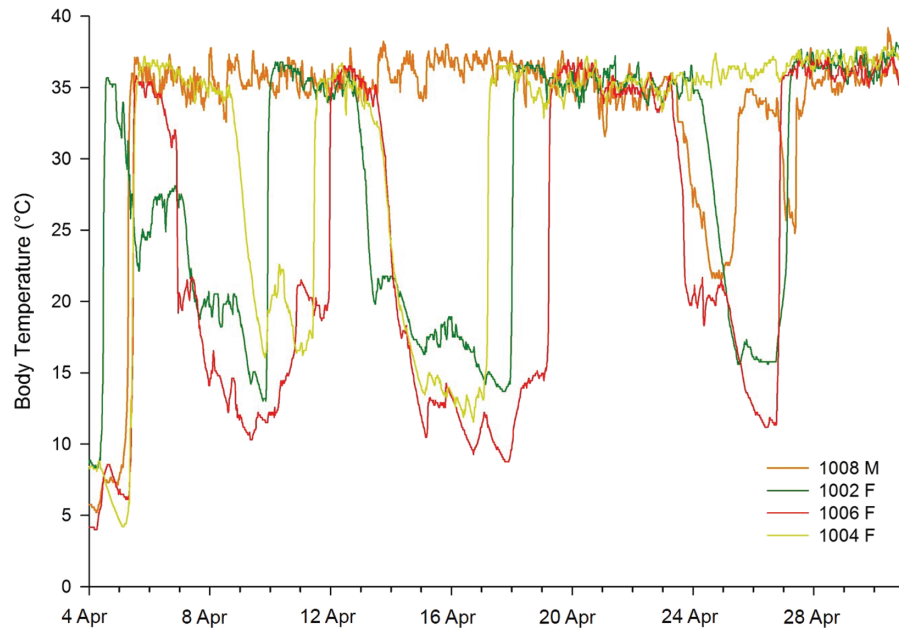
Fig. 3.—End of heterothermy for 4 Alaska marmots in spring 2009. Marmot 1008 M, a male (orange line), returned to high body temperature and females correspondingly lost synchrony and did not return to steady torpor. The male cooled below 30°C twice after maintaining high body temperature for 18 days, but the individual assumed to be the breeding female, 1004 F (yellow line), remained at high body temperature during the other animals' last drop below 30°C.
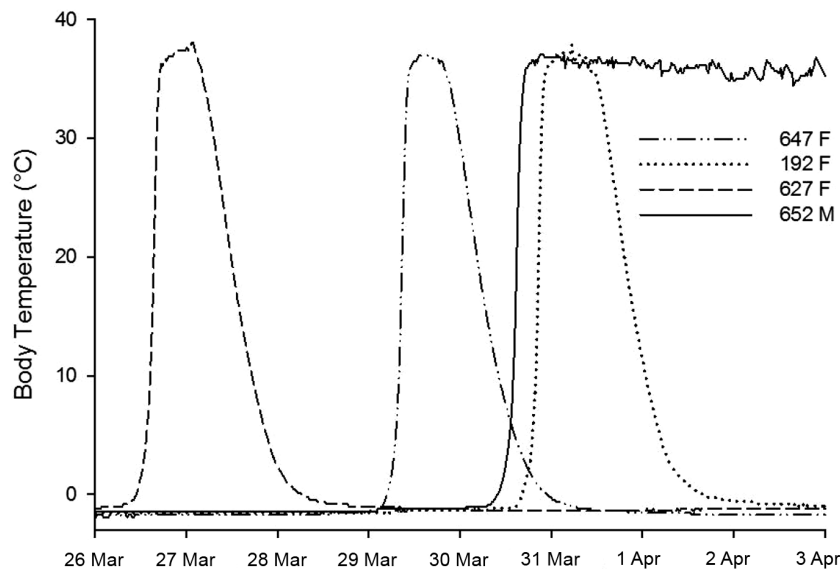

Fig. 4.—Body temperature change in 4 arctic ground squirrels captured at the same burrow site upon emergence from hibernation in spring 2009. Squirrel body temperatures are independent of each other, and the females are not affected by the male's return to high body temperature.

over temperatures corresponding to the rapid cooling segment of marmots and $-0.97 \pm 0.29°C/h$ from 19°C to 6°C, corresponding to the slow cooling segment. Rapid and slow cooling rates significantly differed between species (rapid: $t = -4.48$, $P = 0.0015$; slow: $t = 14.69$, $P < 0.0001$).

One female marmot in the 2008–2009 hibernation season cooled in a continuous pattern, similar to the ground squirrels, during 9 of 13 midwinter cooling bouts and was usually the last of the sampled animals to recool, often reaching low T_b before or with the others in the group (Fig. 2). This animal was likely the breeding female of the colony based on her size and

prominent teats. One other female cooled continuously during 2 bouts in 2008–2009 and a 3rd-winter female cooled continuously once during 2009–2010; neither of these females showed evidence of previous lactation.

Minimum T_b.—The minimum T_b recorded in individual female and male marmots was 0.6°C and 0.9°C, respectively. The minimum T_b in female and male arctic ground squirrels was $-2.0°C$ and $-1.6°C$, respectively. Mean minimum T_b significantly differed between marmots ($1.2 \pm 0.3°C$) and squirrels ($-1.7 \pm 0.2°C$; $t = -18.78$, $P < 0.0001$). Marmots experienced maximum potential thermal gradients between body and
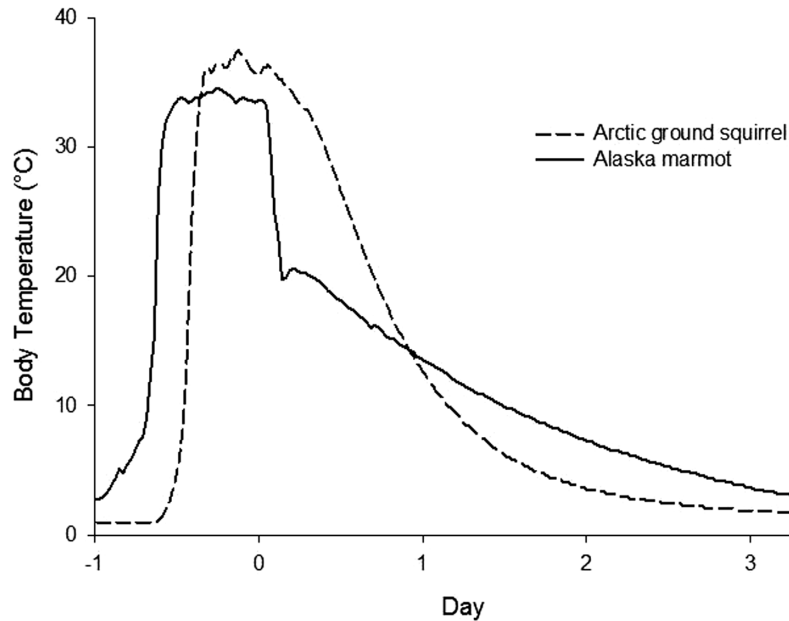
Fig. 5.—An arctic ground squirrel male and an Alaska marmot male demonstrate different cooling patterns from an arousal episode (continuous and interrupted, respectively). Interrupted cooling of marmots during the rapid cooling phase was 21-times faster than during the slow cooling phase. Data were assigned a time of 0 at the beginning of cooling during the arousal.

Table 2.—Characteristics of heterothermy in Alaska marmots and arctic ground squirrels hibernating in the Arctic. Heterothermy began with 1st body temperature (T_b) < 30°C and ended with final return to T_b > 30°C; torpor duration is days T_b < 30°C, euthermic phase of the arousal episode = hours T_b > 30°C. Means are expressed ± SD.

	Alaska marmots			Arctic ground squirrels		
	Females ($n = 8$)	Males ($n = 3$)	All ($n = 11$)	Females ($n = 6$)	Male ($n = 1$)	All ($n = 7$)
Heterothermy start[a]	4 Sept (24 Aug–10 Sept)	9 Sept (24 Aug–17 Sept)	5 Sept (24 Aug–17 Sept)	9 Sept (29 Aug–22 Sept)	3 Oct	16 Sept (29 Aug–3 Oct)
Heterothermy end[a]	16 Apr (10–27 Apr)	9 May (27 Apr–12 May)	22 Apr (10 Apr–12 May)	28 Apr (19 Apr–1 May)	30 Mar	25 Apr (30 Mar–1 May)
Heterothermy duration (d)	228.0±6.2	237.7±7.2	230.7±7.6	229.7±6.5	177.7	221.0±22.0
Torpor bout length[b] (d)	13.87±3.09	13.65±3.49	13.81±3.19	16.74±2.70	16.98±3.82	16.77±2.86
Euthermic phase of arousal episode[b] (h)	20.6±3.7	22.9±7.3	21.2±5.0	13.2±2.0	20.3±4.5	14.2±3.5
# Torpor bouts[b]	11–13	11–13	11–13	10–11	10	10–11
# Arousal episodes[b]	10–12	10–12	10–12	9–10	9	9–10
# Irregular bouts, start of heterothermy[a]	7 (5–10)	4 (4–8)	7 (4–10)	0 (0–1)	0	0 (0–1)
# Irregular bouts, end of heterothermy[a]	3.5 (2–5)	4 (4–5)	4 (2–5)	0 (0–3)	0	0 (0–3)
Minimum T_b (°C)	1.2±0.4	1.1±0.2	1.2±0.3	−1.7±0.3	−1.6	−1.7±0.2
Minimum T_{soil} (°C)[c]	−12.4±2.5	−12.2±2.8	−12.4±2.5	−17.3±0.7	−16.7	−17.3±0.7
Maximum gradient ($T_b − T_{soil,}$ °C)[d]	13.5±2.1	12.6±2.1	13.2±2.0	15.4±0.6	15.1	15.4±0.6
Rapid cooling rate (30°C to 24°C; °C/h)	−5.1±3.2	−5.5±2.5	−5.2±3.0	−1.8±0.2	−1.5±0.2	−1.7±0.3
Slow cooling rate (19°C to 6°C; °C/h)	−0.26±0.07	−0.25±0.08	−0.25±0.08	−1.00±0.29	−0.79±0.25	−0.97±0.29
Rewarming rate (Torpor to 30°C; °C/h)	2.8±0.7	2.9±0.7	2.9±0.7	5.0±0.9	4.4±0.3	4.9±0.9
Rewarming rate (10°C to 30°C; °C/h)	5.8±1.7	6.3±2.0	5.9±1.8	10.5±1.3	11.8±0.9	10.7±1.3

[a] Expressed as median (range).

[b] Midwinter: defined in marmots as period when T_b reaches low and stable levels; defined in arctic ground squirrels as the same timeframe within hibernation as marmots for the year squirrels were captured (includes torpor bouts spanning from 3 Oct to 24 Mar).

[c] Marmots: 4 years at 1 burrow; squirrels: 1 year at 2 burrows.

[d] Calculated as mean of (minimum T_b of an individual − minimum T_{soil} at that individual's burrow that year).

surrounding soil during steady-state torpor of $13.2 \pm 2.0°C$ over 4 years. During the winter of 2008–2009, the maximum potential gradients were similar for the species (marmots: $15.1 \pm 0.4°C$; ground squirrels: $15.4 \pm 0.6°C$; Table 2).

Rewarming rates.—Rates of rewarming significantly differed between species (rewarm to 30°C: $t = 9.26$, $P < 0.0001$; rewarm 10–30°C: $t = 6.54$, $P < 0.0001$). Marmots rewarmed from torpor to T_b of 30°C at a rate of $2.9 \pm 0.7°C/h$. From 10°C to 30°C, their warming rate was $5.9 \pm 1.8°C/h$. Ground squirrels rewarmed from torpor to T_b of 30°C at an average rate of $4.9 \pm 0.9°C/h$ and from 10°C to 30°C at $10.7 \pm 1.3°C/h$.

Characteristics of heterothermy.—The seasonal timing of the beginning, end, and total duration of heterothermy (~230 d) was similar for male and female marmots and female arctic ground squirrels (Table 2). Mean torpor bout length for individual squirrels was longer than for marmots (1 individual marmot per year to avoid confounding synchrony), and duration of the euthermic phase of arousal episodes ($T_b > 30°C$) in ground squirrels was shorter than in marmots ($t = 4.39$, $P = 0.0017$; $t = -4.26$, $P = 0.0021$, respectively; Table 2). The number of stable torpor bouts and arousal episodes during midwinter was comparable between marmots and squirrels, but marmots displayed 2–10 irregular torpor bouts (i.e., animal did not reach low, stable T_b) at the beginning and end of heterothermy. Only 1 female squirrel experienced an irregular bout at the beginning of heterothermy and another female experienced 3 irregular bouts at the end.

DISCUSSION

Our findings from 2 hibernating rodent species overwintering in the same arctic environment indicate that the social systems of marmots and ground squirrels have facilitated different strategies to survive months of extreme cold (Arnold 1993). Alaska marmots exhibit a high degree of synchrony in T_b change during hibernation, strongly suggesting that they huddle together during communal hibernation (Arnold 1988); this minimizes heat loss through social thermoregulation (Gilbert et al. 2010) and allows them to maintain above-freezing T_b in the face of a large thermal gradient between body and soil. In contrast, arctic ground squirrels do not hibernate communally (Carl 1971; Armitage 1981), which is further evidenced in this study by a lack of inter-individual synchrony in T_b patterns. Instead, they allow T_b to decrease below the ice nucleation point of their tissues (Barnes 1989) and thereby minimize the thermal gradient and rate of heat loss. Further, marmots usually demonstrated a unique interrupted cooling pattern with 2 distinct rates of cooling during entrance to torpor, as was noted previously from the record of a single individual (Lee et al. 2009). The rapid cooling phase in marmots was 3-times faster than the comparable range of cooling in squirrels and may reflect individuals cooling apart before they engage in a group.

Alaska marmots in this study seem to be more synchronous in the timing of arousal episodes than were alpine marmots (*M. marmota*), the only other communally hibernating species for which synchrony has been quantitatively investigated (Ruf and Arnold 2000). Synchrony coefficients (correlation coefficients that have been *z*-transformed) in a large number of free-living alpine marmots averaged 1.167 ± 0.028 (Ruf and Arnold 2000), while those for our smaller group of free-living Alaska marmots averaged 1.978 ± 0.264. While these values may not be directly comparable, for reasons of potential differences in statistical analyses and timeframes of measurement, other measures also indicate a highly synchronous pattern within Alaska marmots. Four adult free-living Alaska marmots initiated arousal from torpor within less than half the time arousals were initiated in a group of 4 captive alpine marmots, which included 2 juveniles (Fig. 2 in Arnold 1988). Groups of monitored alpine marmots also contained individuals that passively warmed after initiating arousal, as indicated by irregular patterns of T_b in contrast to a continual increase (Arnold 1988; Ruf and Arnold 2000), while Alaska marmots that we monitored only rarely showed evidence of potential passive warming (Fig. 2). In addition, the alpine marmots took 4-times longer for all 4 animals to cool to a T_b of 30°C than the mean of 4 Alaska marmots when entering torpor (Fig. 2 in Arnold 1988). Greater synchrony in Alaska marmots may be essential to hibernating under arctic conditions that include a much larger defended thermal gradient (up to 16°C at minimum T_b) than that experienced by alpine marmots: alpine marmots rarely experience sub-freezing burrow temperatures (Arnold et al. 1991) and do not maintain torpor below ambient temperatures of −0.5°C in the laboratory (Ortmann and Heldmaier 2000). The need for synchrony in extreme conditions may also help explain why marmots experiencing the harshest conditions and shortest growing seasons are the most social (Barash 1974; Arnold 1993).

The loss of synchrony among marmots at the end of heterothermy may be due to preparation for breeding by males. Male ground squirrels cannot undergo spermatogenesis at low T_b (Barnes et al. 1986), which is why male arctic ground squirrels end heterothermy 2–3 weeks earlier than females (Table 2; Barnes 1996; Buck and Barnes 1999a; Sheriff et al. 2011). If relationships between T_b and establishing spermatogenesis are the same in *Marmota*, male marmots should have also attained high T_b to prepare for breeding. The period during which male marmots maintained high T_b toward the end of heterothermy corresponds to the loss of group synchrony. While males were at high T_b, females did not reach low, stable T_b, likely due to the body heat of the males influencing female torpid T_b. Reproductive male ground squirrels do not reenter torpor (Barnes et al. 1986), but interestingly, all 3 male marmots became heterothermic again after the extended euthermic period, with 2–4 additional torpor bouts before they emerged from their den, suggesting that these individuals were no longer reproductively competent upon coming above ground. Because Alaska marmots have been known to breed underground before emergence from hibernation (Rausch and Rausch 1971; Rausch and Bridgens 1989), the euthermic period may include both spermatogenesis and mating, after which male marmots reenter torpor, perhaps to conserve energy until emergence.

Asynchrony at the beginning of heterothermy cannot be attributed to euthermy of the males, but it may be that juveniles, or other individuals for which we do not have T_b records, were

at high T_b after marmots became sequestered in their hibernaculum and thus influenced T_b patterns of the group. Juvenile alpine marmots impair synchrony, which contributes to the increased cost of hibernation in groups that include young (Arnold 1993, 1995; Ruf and Arnold 2000). Young marmots do not reach their adult size during their first, short summer (Armitage 1981; Arnold 1993). In this study, a young marmot emerged from its 1st hibernation with only a third of the body mass of an adult (Table 3), while 4 ground squirrels emerged from their 1st hibernation with body masses near ($75\pm2\%$) those of adults. Yearling female ground squirrels are also sexually mature (Armitage 1981; Sheriff et al. 2011), but Alaska marmots likely mature at 3 years, leading to younger marmots remaining with the family group for multiple winters and potentially affecting group synchrony (Arnold 1995). However, juvenile alpine marmots cannot successfully hibernate without social thermoregulation (Arnold 1995), so the cost of impaired synchrony is a tradeoff for juvenile survival.

Both species investigated in this study conserve considerable energy in arctic conditions by substantially reducing metabolic rate and levels of T_b and thus the gradient between T_b and ambient temperature during winter (Geiser 2004), with arctic ground squirrels reducing T_b to levels on average 2.9°C less than the minimum T_b in marmots. Lower T_b during torpor conveys a distinct energetic advantage (Barnes 1989), and the lower T_b of arctic ground squirrels may offset, in part, their lack of social thermoregulation as solitary hibernators. Arctic ground squirrels also exhibit longer torpor bouts and shorter arousal episodes than marmots, which also leads to energy savings. While larger hibernators tend to have longer arousal episodes than smaller hibernators (Ruf and Geiser 2014), in social marmots this may be a consequence of disturbance by conspecifics, or it may be that the energy saved through social thermoregulation has alleviated the selective force for lengthening torpor.

In addition to saving energy, communal hibernation allows marmots to breed underground before they can access the surface (Rausch and Rausch 1971; Barash 1989; Rausch and Bridgens 1989), thus maximizing the time available for development of the relatively large young during the brief growing season. Breeding in our study likely happened when the breeding female returned to high T_b while a male was euthermic in early spring, after which the male returned to torpor but the breeding female did not (Fig. 3). If marmots did not hibernate communally, the development time for their young would be shorter or they would be at greater risk of predation by not plugging the burrow entrance during hibernation. Solitary ground squirrels in this region do not plug their hibernacula (BMB, CLB, FK, TNL, pers. obs.); instead, males emerge in search of mates in spring well before a plug would thaw to allow exit.

Smaller hibernators rewarm faster than larger hibernators, but this relationship may not hold at low ambient temperatures (Geiser and Baudinette 1990). Thus, differences in rates of warming and cooling between arctic ground squirrels and Alaska marmots that faced similarly low ambient temperatures may be due to factors beyond body mass, including social thermoregulation, but unfortunately these factors could not be disentangled in this study. Solitary ground squirrels rewarmed about 1.7-times faster than marmots as they heated a smaller mass (0.545 ± 0.080 kg), and social Alaska marmots warmed 2.7-times faster than the slightly larger alpine marmots hibernating together from 10°C to 30°C (Ruf and Arnold 2000). In contrast, Alaska marmots typically had a body mass about 4-times greater than that of arctic ground squirrels, but they cooled 3-times faster at the beginning of torpor entrance. Arctic ground squirrels decrease metabolic rate prior to and during cooling (Karpovich et al. 2009) and cool in a continuous pattern similar to alpine marmots (Ruf and Arnold 2000), but Alaska marmots seem to be enabling increased rates of heat loss at the initiation of a torpor bout. After a transient T_b increase during entrance to torpor that we believe represents when marmots form a huddle, Alaska marmots resumed cooling at 0.25-times the rate of the arctic ground squirrels over the same temperature range, which would be expected considering the larger thermal mass and reduced surface area of the grouped animals. We previously proposed a behavioral mechanism in which Alaska marmots increased heat loss by exposing surface area (in contrast to arctic ground squirrels that curl themselves into a tight ball at the beginning of torpor entrance) before joining the huddle while still ambulatory (Lee et al. 2009). In addition, peripheral tissues of marmots may

Table 3.—Alaska marmot body mass (kg) at first capture in spring. Arctic ground squirrel mass ranged from 0.449 to 0.631 kg with a mean of 0.545 ± 0.080 kg.

	Animal ID								
	Females					Males			
	Breeding								
Year	1002	1006	1004	1010	1016	1000	1008	1012	1014
2008	2.156	2.055[a]	2.847			2.770	2.222		
2009	2.365[a]	2.210[a]		1.732[c]			2.402[a]		
2010	2.497[a]	2.285[a]	2.834[a]	2.171[a]				2.630	2.130
2011	2.568[a]	2.642[b]	2.815[b]		0.779[d]			2.504[a]	2.853[a]

[a] Data recovered at this capture.

[b] Failed T_b logger recovered.

[c] Animal judged to be 2 years old at first capture.

[d] Animal judged to be a yearling at first capture; all not otherwise indicated are adults ≥3 years old.

remain vasodilated during the early reentry phase of torpor, thus further facilitating heat loss before joining the huddle. In this study, we found that the breeding female of the colony usually entered torpor last and cooled continuously instead of in the interrupted cooling pattern typical of the other marmots, indicating that interrupted cooling is not obligatory in Alaska marmots, yet she reached low T_b at approximately the same time as the others. This animal may be part of regulating the synchrony of the group or serve as the focal point of the huddle which the others join.

We were unable to recover loggers from all implanted marmots, and we were also unable to implant every marmot that hibernated in the hibernaculum during each winter (Table 3). We have no data from juveniles, and we were unable to confirm an individual as the territorial male. More animals were present than monitored each year: we caught unmarked animals from the hibernaculum every spring and observed several unmarked individuals around the hibernaculum in summer 2009. Thus, our results may show a higher degree of synchrony than the synchrony of all animals in the hibernaculum. Animals during the winter from which we have 4 T_b records were less synchronous than animals in years from which we have only 3 T_b records, but in this case the additional animal was determined to be a breeding animal and was typically the last to enter torpor. Therefore, most other, unmarked adults may fall within the patterns of the animals for which we have data. Our findings are also limited as they are from a single group over multiple years and thus represent a small number of animals that were likely related.

In summary, we have shown that the high-latitude Alaska marmot, which experiences even greater thermal challenges than the high-altitude alpine marmot, demonstrates the most synchronous T_b patterns known among communally hibernating animals. Synchronous change in T_b is likely an adaptation to minimize energetic costs while utilizing social thermoregulation, and it contrasts with the patterns of hibernation observed in sympatric arctic ground squirrels, which hibernate individually even in close proximity to conspecifics. Alaska marmots typically display a unique, interrupted cooling pattern which has not been previously observed in hibernators, but they may also cool continuously like other hibernating mammals. Further research is needed to better understand the benefits and mechanisms associated with this unique cooling pattern.

ACKNOWLEDGMENTS

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