ORIGINAL PAPER

Thermoregulatory changes anticipate hibernation onset by 45 days: data from free-living arctic ground squirrels

**Michael J. Sheriff · Cory T. Williams ·
G. J. Kenagy · C. Loren Buck · Brian M. Barnes**

Abstract Hibernation is a strategy of reducing energy expenditure, body temperature (T_b) and activity used by endotherms to escape unpredictable or seasonally reduced food availability. Despite extensive research on thermoregulatory adjustments during hibernation, less is known about transitions in thermoregulatory state, particularly under natural conditions. Laboratory studies on hibernating ground squirrels have demonstrated that thermoregulatory adjustments may occur over short intervals when animals undergo several brief, preliminary torpor bouts prior to entering multiday torpor. These short torpor bouts have been suggested to reflect a resetting of hypothalamic regions that control T_b or to precondition animals before they undergo deep, multiday torpor. Here, we examined continuous records of T_b in 240 arctic ground squirrels (*Urocitellus parryii*) prior to hibernation in the wild and in captivity. In free-living squirrels, T_b began to decline 45 days prior to hibernation, and average T_b had decreased 4.28 °C at the onset of torpor. Further, we found that 75 % of free-living squirrels and 35 % of captive squirrels entered bouts of multiday torpor with a single T_b decline and without previously showing short preliminary bouts. This study provides evidence that adjustments in the thermoregulatory component of hibernation begin far earlier than previously demonstrated. The gradual reduction in T_b is likely a component of the suite of metabolic and behavioral adjustments, controlled by an endogenous, circannual rhythm, that vary seasonally in hibernating ground squirrels.

Keywords Test drops · Torpor · Body temperature

M. J. Sheriff (✉) · B. M. Barnes
Institute of Arctic Biology, University of Alaska Fairbanks,
Fairbanks, AK 99775, USA
e-mail: mjsheriff@alaska.edu

B. M. Barnes
e-mail: bmbarnes@alaska.edu

C. T. Williams
Department of Biological Sciences, University of Alberta,
Edmonton, AB T6G 2R3, Canada

G. J. Kenagy
Burke Museum and Department of Biology,
University of Washington, Seattle, WA 98195, USA

C. L. Buck
Department of Biological Sciences,
University of Alaska Anchorage, 3101 Science Circle,
Anchorage, AK 99508, USA

Introduction

Hibernation is a physiological and behavioral strategy expressed by many mammals to survive unfavorable and unpredictable environmental conditions by decreasing energy intake and expenditure (Lyman et al. 1982). Hibernation in mammals typically lasts from late summer or autumn until late winter or spring. Torpor during hibernation is characterized by a regulated, substantial reduction in metabolic rate, core body temperature (T_b) and activity for days to several weeks at a time. Torpid metabolic rate is reduced to 2–30 % of basal levels and T_b falls from euthermic levels of ~32–42 °C to as low as −2.9 °C (Barnes 1989; Geiser and Ruf 1995). Across the hibernation season, bouts of torpor are interspersed with brief (<24 h) and spontaneous arousal episodes, during which animals rewarm to euthermic T_b and have metabolic rate > basal metabolic rate (Geiser 2004).

Hibernating mammals attain the low T_b associated with torpor by suppressing metabolism through a combination

of temperature-dependent and -independent mechanisms (Geiser 1988; Heldmaier and Ruf 1992; Buck and Barnes 2000; Tøien et al. 2011) in association with adjustments in their hypothalamic T_b set-point (Heller et al. 1977). However, even at low T_b, hibernating mammals maintain the ability to increase metabolism by means of thermoregulatory heat production to maintain constant T_b when ambient temperature is decreased below T_b set-point (Buck and Barnes 2000). Thus, low T_b during torpor is distinct from pathological hypothermia.

Before entering hibernation, animals undergo a suite of major physiological changes. Rates of food consumption in many fat-storing species (such as ground squirrels) increase months before first torpor as animals increase body mass by adding both fat and lean components (Pengelley and Fisher 1963; Buck and Barnes 1999). Compared to the active season, hibernating animals have differential gene and protein expression (Carey et al. 2003; Yan et al. 2008), reduced cell division and proliferation (Carey et al. 2003), altered hormone secretion (Barnes et al. 1988; Kronfeld-Schor et al. 2000), a switch from carbohydrate-based to fat-based fuels (Carey et al. 2003; Dark 2005), and remodeling of certain organs (Arnold et al. 2011). However, despite extensive research on physiological adaptations expressed during hibernation, less work has been done to examine transitional states in thermoregulation. It has been hypothesized that short-term (3–4 days) thermoregulatory adjustments may occur during a series of 'test drops' prior to the first multiday torpor bout. Test drops are described as a step-wise series of short (<24 h) bouts of torpor with consecutively lower minimum T_b and complete arousal between torpor bouts. This is suggested to be due to a progressive resetting within hypothalamic regions that control T_b set-point and thermoregulation (Strumwasser 1958, 1960; Hammel 1967; Heller and Colliver 1974; Luecke and South 1972; Pivorun 1976; Lyman et al. 1982). Recently, it has been shown that 13-lined ground squirrels expressed irregular use of daily torpor prior to multiday torpor (Russell et al. 2010), and that Syrian hamsters exhibit a small decrease in subcutaneous temperature 5–16 days before their first torpor (Arai et al. 2005). However, these studies were conducted under laboratory conditions, and thermoregulatory patterns prior to hibernation in free-living animals are not well understood. Here we investigate patterns of T_b in arctic ground squirrels (*Urocitellus parryii*) prior to hibernation to assess changes associated with preparation for hibernation in both free-living and captive animals.

Materials and methods

Arctic ground squirrels were captured using Tomahawk live-traps (Tomahawk Trap Co.) baited with carrot near the University of Alaska Fairbanks' Toolik Field Station (68° 38″N, 149° 38″W) on the North Slope of Alaska. Animals brought into captivity were transported to Fairbanks and housed in laboratory cages within environmental chambers held at 18 °C and an 18 h light: 6 h dark photoperiod or in individual $1 \times 1 \times 2$ m soil filled outdoor enclosures at the University of Alaska Fairbanks (Barnes and Ritter 1993). Free-living animals were released to the site of capture <24 h after surgery. Between 1996 and 2010, prior to the first day T_b decreased <30 °C, we obtained data from 203 T_b-loggers (TidBit Stowaway model TBICU32-05+44, Onset Computer Corporation programmed to record core T_b ±0.2 °C at 20 min intervals) implanted abdominally in 141 different free-living ground squirrels (some squirrels were implanted multiple years; being implanted once or multiple times did not affect T_b changes or test drop probability). During this time we also obtained data from 75 T_b-loggers implanted in laboratory held ground squirrels, and in 2009 and 2010, we obtained data from 24 T_b-loggers implanted in ground squirrels from the outdoor enclosures. Details of surgical procedures are provided in Long et al. (2007). Loggers were implanted in free-living animals throughout the active season with most implants occurring in spring or summer; in captive animals, implant surgeries occurred only in autumn just prior to hibernation. Of the 141 implanted free-living squirrels, we obtained T_b records up to 60 days prior to entrance of hibernation in a subset of 43 individuals. In captive animals, long-term T_b records were not obtained since loggers were implanted near the beginning of hibernation.

In the field, squirrels entered hibernation between August and October. Ambient temperatures during the study ranged from August: $T_{ave} = 4.1$ to 10.7 °C, $T_{max} = 12.4$ to 25.6 °C, $T_{min} = -9.5$ to -2.1 °C; September: $T_{ave} = -4.7$ to 4.7 °C, $T_{max} = 8.8$ to 17.0 °C, $T_{min} = -26.5$ to -4.1 °C; October: $T_{ave} = -16.2$ to -5.4 °C, $T_{max} = -1.6$ to 14.3 °C, $T_{min} = -35.5$ to -21.1 °C (Environmental Data Center, Toolik Field Station, toolik.alaska.edu/edc). In the laboratory, squirrels were transferred to environmental chambers at 2 °C and a 6-h light: 18-h dark photoperiod in late August and September. In the outdoor enclosures, animals were exposed to ambient photoperiod and temperature and entered hibernation between August and October. Ambient temperatures in 2009 and 2010 were August: $T_{ave} = 12.0$ and 15.1 °C, $T_{max} = 29.3$ and 32.2 °C, $T_{min} = -0.4$ and 4.2 °C; September: $T_{ave} = 8.7$ and 8.4 °C, $T_{max} = 22.9$ and 21.1 °C, $T_{min} = -4.4$ and -9.2 °C; October: $T_{ave} = -0.4$ and -1.0 °C, $T_{max} = 14.8$ and 14.9 °C, $T_{min} = -10.7$ and -12.4 °C (The Alaska Climate Research Center, Geophysical Institute at the University of Alaska Fairbanks, climate.gi.alaska.edu). All procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee, and conducted under permits from the Alaska Department of Fish and Game.

Fig. 1 Core body temperature (T_b) of a free-living arctic ground squirrel 62 days before heterothermy (first T_b decline <30 °C). *Arrows* denote the day prior to first heterothermy, *asterisk* denotes the first significant decline in T_b 45 days prior to heterothermy. *In-set* shows truncated T_b record for a free-living animal that exhibited preliminary torpor prior to multiday torpor
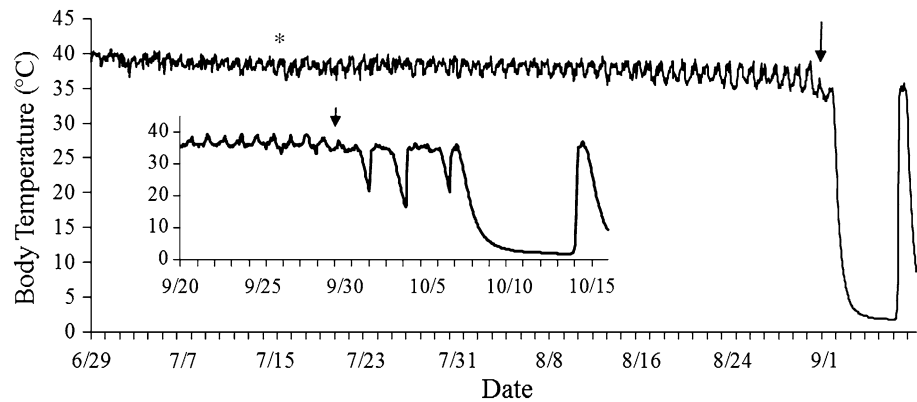
We defined stages of the heterothermic season as in Buck et al. (2008). Specifically, the heterothermic season began the first day an animal's T_b declined <30 °C, the duration of torpor was defined as the interval when T_b was <30 °C, and we distinguished multiday torpor from preliminary torpor (test drop) by the duration of the bout (Fig. 1). If T_b was <30 °C for <24 h we considered it a preliminary torpor bout and if T_b remained <30 °C for >24 h we considered it a multiday torpor bout (Pivorun 1976; Geiser 2004). A t test for dependent samples was used to compare the change in T_b of free-living squirrels every 5 days from day 60 to day 0 to determine when the first decline occurred and to compare the difference between active season T_b (day 60) with T_b the day before animals T_b first declined <30 °C. To maintain the family-wise error rate, we applied a Bonferroni correction and thus used a P value of 0.004. Average daily T_b was calculated each 5th day, i.e., average of day 60, 55, 50, etc; daily minimum and maximum was the lowest and highest T_b reached each 5th day. We did not have long-term pre-hibernation records of T_b for captive squirrels. We used a z test with a Yates correction to compare the proportion of free-living, laboratory or enclosure-held squirrels that underwent preliminary torpor and Kruskal–Wallis rank sum tests with Dunn's method pairwise comparisons to compare the duration and number of all preliminary bouts occurring before the onset of multiday torpor in squirrels that had at least one preliminary bout. A t test for dependent samples was used to compare the duration and minimum temperature reached of the last preliminary torpor bout to the second last. We found no difference among years, or between ages or sexes for any of the comparisons ($P > 0.05$). All statistics are presented as mean ± SD unless otherwise specified.

Results

All free-living arctic ground squirrels significantly decreased T_b in advance of the first day when T_b decreased <30 °C (Fig. 2). Average daily T_b declined by 4.3 ± 1.1 °C from day 60 pre-heterothermy (ph) until 1 day ph ($t_{42} = 24.55$,

$P < 0.0001$); the first significant decline from average summer values occurred on day 45 ph ($t_{42} = -25.73$, $P < 0.0001$). Daily minimum T_b declined 3.8 ± 1.3 °C from day 60 ph until 1 day ph ($t_{42} = 19.17$, $P < 0.0001$); the first significant decline in minimum summer values occurred on day 45 ph ($t_{42} = -3.55$, $P = 0.001$). Daily maximum T_b declined 4.7 ± 1.8 °C from day 60 ph until 1 day ph ($t_{42} = 17.17$, $P < 0.0001$); the first significant decline in maximum summer values occurred on day 40 ph ($t_{42} = 3.48$, $P = 0.001$).

We also found that preliminary torpor bouts are not required before multiday torpor (Fig. 1). Only 25.6 % of free-living ground squirrels underwent preliminary torpor prior to expressing multiday torpor, compared to 66.7 % of squirrels in the outdoor enclosures ($z = 3.92$, $P < 0.001$) and 64.5 % of squirrels in the laboratory ($z = 5.78$, $P < 0.001$; Fig. 3a). There was no difference in the proportion of animals exhibiting preliminary torpor between outdoor enclosure and laboratory conditions ($z = -0.004$, $P = 0.996$). Of animals that exhibited preliminary torpor bouts, we found a significant difference in the number of preliminary bouts ($H = 12.20$, $P = 0.002$; Fig. 3b) and average duration of each preliminary bout ($H = 36.99$, $P < 0.0001$; Fig. 3c) among the three groups. Free-living squirrels averaged 1.84 fewer preliminary bouts than squirrels held in the outdoor enclosure ($P = 0.0003$) and 1.82 fewer than squirrels held in the laboratory ($P = 0.051$). Conversely, preliminary torpor bouts lasted on average 6.27 h longer in the field than in the laboratory ($P < 0.0001$) and 5.16 h longer in the outdoor enclosures than in the laboratory ($P = 0.001$); there was no difference between field squirrels and those in the outdoor enclosures ($P = 1.00$). In free-living squirrels, there was no difference in the duration of ($t_{15} = 1.09$, $P = 0.30$) or minimum T_b between ($t_{15} = -1.99$, $P = 0.067$) the last and second last preliminary bout (Fig. 4).

Discussion

We found that average daily T_b of free-living arctic ground squirrels began to decline 45 days prior to their first expression of preliminary or multiday torpor (Fig. 2).

Fig. 2 The daily average (**a**), daily minimum (**b**), and daily maximum (**c**) body temperature of free-living arctic ground squirrels ($n = 43$) during the 60 days preceding entrance into hibernation. *Solid black line* represents mean $\pm$ SD; the *light gray lines* represent the range. The *equation* represents the best-fit function of the decline in T_b. *Asterisk* denotes first significant decrease in body temperature from day 60 ($P < 0.004$)
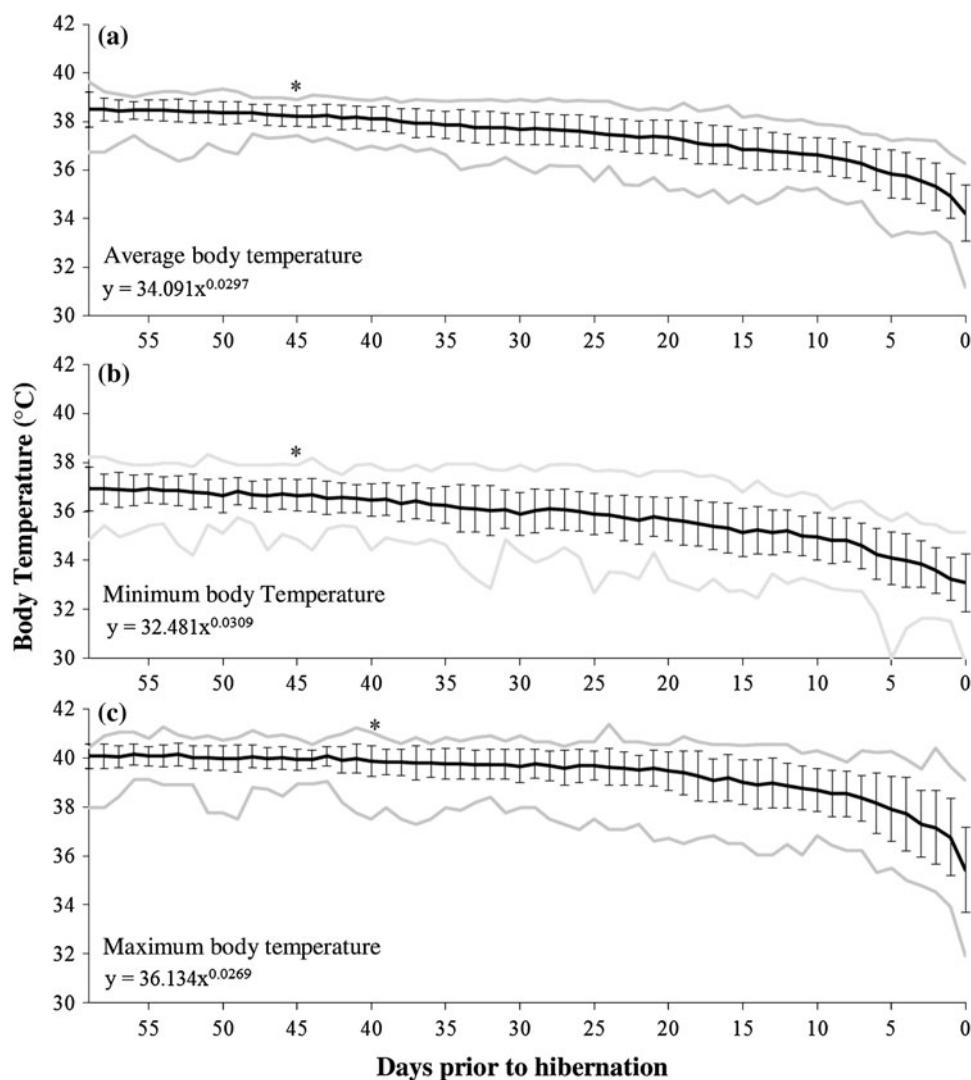
Levels of T_b are relatively dynamic over this time as average, maximum, and minimum daily T_b values all steadily declined prior to the onset of torpor. Other studies also provide evidence that small mammalian hibernators undergo thermoregulatory changes weeks, and not days, prior to hibernation. In a population of free-living marmots, Arnold et al. (2011) found that T_b began to decline 14 days prior to hibernation. Arai et al. (2005) found that captive Syrian hamsters significantly decreased T_b 5–16 days prior to hibernation, and animals that did not decrease T_b did not enter hibernation. Similarly, Christian and Geiser (2007) found that free-living sugar gliders that entered torpor lowered resting T_b in the preceding 3 days, while those that did not enter torpor did not lower T_b. In laboratory held 13-lined ground squirrels, Russell et al. (2010) describe a transition period between the active and hibernation seasons when torpor use was extensive, even while animals were held at room temperature and long photoperiod. However, the duration and minimum T_b reached was

highly variable and animals alternated between bouts of torpor >24 h and bouts <24 h. Over time, animals tended toward maximizing time spent torpid, suggesting that animals were readjusting thermoregulatory mechanisms to enhance expression of torpor as they progressed through a fall transition period. We suggest that our findings provide evidence that thermoregulatory preparations for multiday torpor in arctic ground squirrels begin several weeks before hibernation. This view is consonant with the role proposed for endogenous, circannual rhythms in the mechanisms of ongoing, year-round adjustments in appetite, energy intake and expenditure, and body mass (Pengelley and Fisher 1963; Körtner and Geiser 2000).

Previously, we described behavioral and physiological changes occurring in free-living arctic ground squirrels throughout their active season that are linked to changes in T_b. Williams et al. (2011) showed that average female T_b decreases 0.5–1.0 °C during gestation and abruptly increases 1–2 °C on the day of parturition in both captive
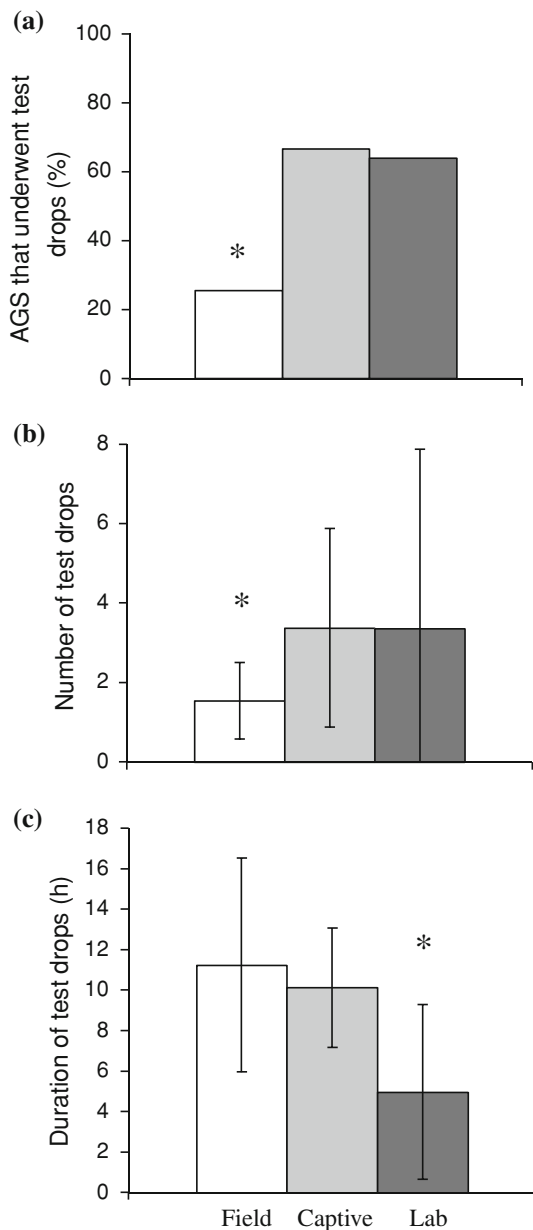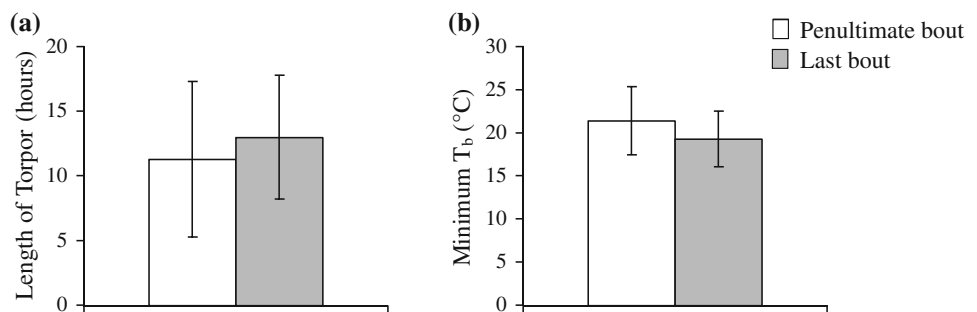
Fig. 3 The proportion (**a**), number (**b**), and duration (**c**) of preliminary torpor bouts (test drops) in free-living ($n = 52$), captive (held in outdoor enclosures; $n = 16$) and laboratory-caged ($n = 48$) arctic ground squirrels. Mean $\pm$ SD, *asterisks* denote significant difference ($P < 0.005$)

and free-living squirrels. Males end heterothermy and achieve high T_b for several weeks prior to emergence from hibernation as a requirement for testis growth and spermatogenesis (Barnes 1996), and only upon emergence from hibernation does their T_b begin to fluctuate in daily rhythms (Sheriff et al. 2011; Williams et al. 2011). Other studies have also indicated that physiological changes occur throughout the active season, which likely play a role in preparation for hibernation. In a recent review, Florant and Healy (2011) discuss how hormonal, enzymatic and neuronal mechanisms that control changes in feeding behavior throughout the active season may play a role in preparation for hibernation. Delehanty and Boonstra (2011) and Sheriff et al. (2012) found that free-cortisol levels in arctic ground squirrels significantly decrease following breeding. Given the catabolic nature of cortisol and its ability to stimulate hepatic gluconeogenesis, animals may decrease cortisol as they increase fat stores and lean body mass prior to hibernation. Thus, in hibernating animals thermoregulatory and physiological changes in preparation for hibernation appear to be occurring over the broader course of the active season.

Historically, thermoregulatory and T_b adjustments that anticipate hibernation were thought to occur during a short time interval through a series of test drops. Strumwasser (1958) measured the brain temperature of captive California ground squirrels and found that before displaying extended torpor, squirrels entered into and aroused from torpor on a daily basis several times with each succeeding bout being longer in duration and terminating at a lower temperature. He argued that each subsequent minimum temperature reached was a critical point, and that temperature regulating mechanisms were being informed of the state of an animal's physiological preparations for multiday torpor. Our results show that in arctic ground squirrels shallow, preliminary bouts of torpor are not required for multiday torpor to occur. Only 25 % of field squirrels exhibited preliminary torpor compared to 66 % of captive squirrels held outdoors and 65 % of those held in the laboratory (Fig. 3). Furthermore, we found no difference in duration or in minimum T_b reached between the last and second to last preliminary torpor bout (Fig. 4). In a study of

Fig. 4 The duration (**a**) and minimum body temperature (T_b) (**b**) of the penultimate and last preliminary torpor bout preceding multiday torpor in free-living arctic ground squirrels. Mean $\pm$ SD, $n = 15$

captive and free-living Anatolian ground squirrels, Gür et al. (2009) found that only 62 % of squirrels exhibit preliminary torpor bouts prior to multiday torpor, although they did not distinguish between captive and free-living animals. In our study, T_b patterns of squirrels where not different regardless of whether animals entered hibernation early (August) or late (October) or in different years, suggesting absolute differences in ambient temperature are not drivers of T_b pattern differences among free-living and captive squirrels. However, the increased propensity of captive animals to exhibit short preliminary bouts of torpor early in hibernation may be due to sensitivity to disturbances that occurs in captive conditions, or the lack of normal cues or inability to use available seasonal environmental cues, such as the rate of changes in day length, light intensity, and ambient temperature that are likely used by free-living animals to synchronize and coordinate endogenous circannual physiological changes in anticipation of hibernation.

Other studies of T_b patterns show that animals can begin multiday torpor in a single, simple temperature decline (Geiser and Kenagy 1988; Michener 1992; Geiser 2004). The short preliminary torpor bouts displayed early in the hibernation season do not resemble daily torpor physiologically and metabolically, and it has been demonstrated that preliminary bouts involve metabolic rates that are more similar to those of multiday torpor (Song et al. 1997; Geiser and Brigham 2000). Thus, we suggest that rather than being preparatory, brief preliminary torpor bouts of <24 h prior to multiday torpor are a continuum of torpor patterns associated with hibernation.

In conclusion, we found that average T_b of free-living squirrels begins to decline up to 45 days before the first day of torpor, indicating that changes in thermoregulation begin earlier than previously recognized. We also found that free-living animals can enter multiday torpor in a single, simple T_b decline without exhibiting preliminary bouts of torpor <24 h. We suggest that short shallow, preliminary bouts of torpor that occur prior to multiday torpor may physiologically and metabolically resemble multiday torpor and are simply part of a continuum of torpor patterns associated with hibernation. Thus, future studies investigating the complex physiological changes that occur prior to hibernation need to commence much earlier in the active season.

References

Arai S, Hanaya T, Sakurai T, Ikeda M, Kurimoto M (2005) A novel phenomenon predicting the entry into a state of hibernation in Syrian hamsters (*Mesocricetus auratus*). J Vet Med Sci 67:215–217

Arnold W, Ruf T, Frey-Roos F, Bruns U (2011) Diet-independent remodeling of cellular membranes precedes seasonally changing body temperature in a hibernator. PLoS ONE 6:e18641

Barnes BM (1989) Freeze avoidance in a mammal: body temperatures below 0 °C in an Arctic hibernator. Science 244:1593–1595

Barnes BM (1996) Relationships between hibernation and reproduction in male ground squirrels. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold: tenth International Hibernation Symposium. University of New England Press, Armidale, pp 71–80

Barnes BM, Ritter D (1993) Patterns of body temperature change in hibernating arctic ground squirrels. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological, and molecular mechanisms. Westview Press, Boulder, pp 119–130

Barnes BM, Kretzmann M, Zucker I, Licht P (1988) Plasma androgen and gonadotropin levels during hibernation and testicular maturation in golden-mantled ground squirrels. Biol Reprod 38:616–622

Buck CL, Barnes BM (1999) The annual cycle of body condition and hibernation in free-living arctic ground squirrels. J Mammal 80:430–442

Buck CL, Barnes BM (2000) Effects of ambient temperature on metabolic rate, respiratory quotient, and torpor in an arctic hibernator. Am J Physiol Regul Integr Comp Physiol 279:R255–R262

Buck CL, Breton A, Kohl F, Toien O, Barnes BM (2008) Overwinter body temperature patterns in free-living Arctic squirrels (*Spermophilus parryii*). In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: hibernation, torpor, and cryobiology. Proceedings of the 13th international hibernation symposium. Pietermaritzburg, pp 317–326

Carey HV, Andrews MT, Martin SL (2003) Mammalian hibernation: cellular and molecular responses to depressed metabolism and low temperature. Physiol Rev 83:1153–1181

Christian N, Geiser F (2007) To use or not to use torpor? Activity and body temperature as predictors. Naturwissenschaften 94:483–487

Dark J (2005) Annual lipid cycles in hibernators: integration of physiology and behavior. Annu Rev Nutr 25:469–497

Delehanty B, Boonstra R (2011) Coping with intense reproductive aggression in male arctic ground squirrels: the stress axis and its signature tell divergent stories. Physiol Biochem Zool 84:417–428

Florant GL, Healy JE (2011) The regulation of food intake in mammalian hibernators: a review. J Comp Physiol B doi: 10.1007/s00360-011-0630-y

Geiser F (1988) Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition. J Comp Physiol B 158:25–37

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66:239–274

Geiser F, Brigham RM (2000) Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). J Comp Physiol B 170:153–162

Geiser F, Kenagy GJ (1988) Torpor duration in relation to temperature and metabolism in hibernating ground squirrels. Physiol Zool 61:442–449

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966

Gür MK, Refinetti R, Gür H (2009) Daily rhythmicity and hibernation in the Anatolian ground squirrel under natural and laboratory conditions. J Comp Physiol B 179:155–164

Hammel HT (1967) Temperature regulation and hibernation. In: Fisher KC, Dawe AR, Lyman CP, Schonbaum E, South FE (eds) Mammalian hibernation III. Elsevier, Amsterdam, pp 86–96

Heldmaier G, Ruf T (1992) Body temperature and metabolic rate during natural hypothermia in endotherms. J Comp Physiol B 162:696–706

Heller HC, Colliver GW (1974) CNS regulation of body temperature during hibernation. Am J Physiol 227:583–589

Heller HC, Colliver GW, Beard J (1977) Thermoregulation during entrance into hibernation. Pflügers Archiv 369:55–59

Körtner G, Geiser F (2000) The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. Chronobiol Int 17:103–128

Kronfeld-Schor N, Richardson C, Silvia BA, Kunz TH, Widmaier EP (2000) Dissociation of leptin secretion and adiposity during prehibernation fattening in little brown bats. Am J Physiol Regul Integr Comp Physiol 279:R1277–R1281

Long RA, Hut RA, Barnes BM (2007) Simultaneous collection of body temperature and activity data in burrowing mammals: a new technique. J Wildl Manage 71:1375–1379

Luecke RH, South FE (1972) A possible model for thermoregulation during deep hibernation. In: South FE, Hannon JP, Willis JR, Pengelley ET, Alpert NR (eds) Hibernation and hypothermia, perspectives and challenges. Elsevier, New York, pp 577–605

Lyman CP, Willis JS, Malan A, Wang LCH (1982) Hibernation and torpor in mammals and birds. Academic Press, New York

Michener GR (1992) Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. Oecologia 89:397–406

Pengelley ET, Fisher KC (1963) The effect of temperature and photoperiod on the yearly hibernating behavior of captive golden-mantled ground squirrels (Citellus lateralis tescorum). Can J Zool 41:1103–1120

Pivorun EB (1976) A biotelemetry study of the thermoregulatory patterns of Tamis striatus and Eutamias minimus during hibernation. Comp Biochem Physiol 53:265–271

Russell RL, O'Neill PH, Epperson LE, Martin SL (2010) Extensive use of torpor in 13-lined ground squirrels in the fall prior to cold exposure. J Comp Physiol B 180:1165–1172

Sheriff MJ, Kenagy GJ, Richter M, Lee T, Tøien Ø, Kohl F, Buck CL, Barnes BM (2011) Phenological plasticity: variation in annual timing of hibernation and breeding in two nearby populations of arctic ground squirrels. Proc Roy Soc B 278:2369–2375

Sheriff MJ, Wheeler H, Donker SA, Krebs CJ, Rupert P, Hik DS, Boonstra R (2012) Mountain-top and valley-bottom experiences: the stress axis as an integrator of environmental variability in arctic ground squirrel populations. J Zool doi: 10.1111/j.1469-7998.2011.00888.x

Song X, Körtner G, Geiser F (1997) Thermal relations of metabolic rate reduction in a hibernating marsupial. Am J Physiol Regul Integr Comp Physiol 273:R2097–R2104

Strumwasser F (1958) Factors in the pattern, timing and predictability of hibernation in the squirrel, Citellus beecheyi. Am J Physiol 196:8–14

Strumwasser F (1960) Some physiological principles governing hibernation in Citellus beecheyi. Bull Mus Comp Zool 124:285–320

Tøien Ø, Blake J, Edgar DM, Grahn D, Heller HC, Barnes BM (2011) Hibernation in black bears: independence of metabolic suppression from body temperature. Science 331:906–909

Williams CT, Sheriff MJ, Schmutz JA, Kohl F, Tøien Ø, Buck CL, Barnes BM (2011) Data logging of body temperatures provides precise information on phenology of reproductive events in a free-living arctic hibernator. J Comp Physiol B 181:1101–1109

Yan J, Barnes BM, Kohl F, Marr TG (2008) Modulation of gene expression in hibernating arctic ground squirrels. Physiol Genomics 32:170–181