

2-1-2010

Latitudinal Differences in the Hibernation Characteristics of Woodchucks (*Marmota monax*)

Stam M. Zervanos

Pennsylvania State University - Berks

Christine R. Maher

University of Southern Maine, cmaher@usm.maine.edu

Jerry A. Waldvogel

Clemson University

Gregory L. Florant

Colorado State University

Follow this and additional works at: <http://digitalcommons.usm.maine.edu/bio-faculty>



Part of the [Biology Commons](#)

Recommended Citation

Zervanos, S. M., Maher, C. R., Waldvogel, J. A., & Florant, G. L. (2010). Latitudinal Differences in the Hibernation Characteristics of Woodchucks (*Marmota monax*). *Physiological & Biochemical Zoology*, 83(1), 135-141. doi:10.1086/648736

This Article is brought to you for free and open access by the Biological Sciences at USM Digital Commons. It has been accepted for inclusion in Faculty Publications by an authorized administrator of USM Digital Commons. For more information, please contact jessica.c.hovey@maine.edu.

Latitudinal Differences in the Hibernation Characteristics of Woodchucks (*Marmota monax*)

Stam M. Zervanos^{1,*}

Christine R. Maher²

Jerry A. Waldvogel³

Gregory L. Florant⁴

¹Department of Biology, Pennsylvania State University/Berks, P.O. Box 7009, Reading, Pennsylvania 19610-6009;

²Department of Biological Sciences, University of Southern

Maine, Portland, Maine 04104; ³Department of Biological Sciences, Clemson University, Clemson, South Carolina

29634; ⁴Department of Biology, Colorado State University, Fort Collins, Colorado 80523

Accepted 10/4/2009; Electronically Published 12/3/2009

ABSTRACT

There is little information on the phenotypic flexibility of hibernation characteristics within species. To address this issue, we observed differences in hibernation characteristics of three free-ranging populations of woodchucks (*Marmota monax*) distributed along a latitudinal gradient from Maine to South Carolina. Data from free-ranging animals exhibited a direct relationship between latitude and length of the hibernation season. As expected, woodchucks in the northern latitudes hibernated longer than those in the southern latitudes. Also, the length of interbout arousals decreased with increase in latitude, whereas the length of torpor bouts and the number of arousals increased. Thus, we observed phenotypic plasticity in hibernation characteristics based primarily on latitudinal temperature differences in each population. Further analysis revealed a direct relationship between latitude and total time spent in torpor. Maine animals spent 68% more time in torpor than South Carolina animals. However, total time spent euthermic did not differ among the three populations. The “cost-benefit” hypothesis of hibernation may help to explain these results. It assumes that hibernators avoid the physiological stress of torpor by staying euthermic as much as possible. Woodchucks in each population maximized time spent euthermic, utilizing torpor only at the level needed to survive winter hibernation and to commence reproduction in the spring.

Introduction

Hibernation in mammals can be defined as a voluntary seasonal hypometabolism that can be used to survive cold periods of food or water shortage (McNab 2002; Heldmaier et al. 2004). Although many characteristics of hibernation have been well studied, previous studies focus primarily on torpor patterns and energy expenditure in both lab and field settings (for reviews, see Davis 1976; Lyman et al. 1982; Carey et al. 2003; Geiser 2004; Heldmaier et al. 2004; Heller and Ruby 2004).

Surprisingly little information is available on the phenotypic plasticity of hibernation's characteristics under different environmental conditions. If the hibernation phenotype functions to conserve energy, then some or all of its characteristics should adapt to different or changing environments. That is, the amount of energy conserved during hibernation would depend on factors such as seasonal length, number and duration of torpor and arousal bouts, and thermoregulatory requirements of the hibernaculum (Wang 1989; Buck and Barnes 1999). Survival would depend on the ability to minimize energy expenditure by adjusting these characteristics to meet specific environmental conditions. Yet how fixed or flexible are various characteristics of the hibernation phenotype?

Some characteristics of hibernation, such as the period of appetite suppression (Davis 1967, 1976) and dates of first torpor and last arousal during the hibernation season, appear to be fixed (Zervanos 2003). Other characteristics, however, such as torpor and euthermic bout duration, appear to be influenced by environmental factors such as body temperature (T_b) or ambient temperature (T_a ; Pivorun 1977; French 1982; Geiser and Kenagy 1988; Barnes and Buck 2000; Zervanos and Salisbury 2003; Dunbar and Tomasi 2006).

To further complicate the issue, daily torpor and seasonal hibernation may not be delineated clearly. For example, black-tailed prairie dogs (*Cynomys ludovicianus*) appear to demonstrate significant plasticity in the hibernation phenotype (Lehmer et al. 2006). Five of six colonies of prairie dogs remained active (with periodic, short, shallow torpor bouts) throughout winter. However, in the other colony, all monitored animals showed torpor patterns typical of mammalian hibernation. Finding no significant differences in body mass, stored lipids, and colony genetic composition, the authors attribute this expression of hibernation to drier environmental conditions that the colony experienced. Thus, limited water and food availability may trigger full expression of the hibernation phenotype. Woodchucks (*Marmota monax*) provide another example of plasticity in the hibernation phenotype; some woodchucks in a Pennsylvania population did not hibernate (Zervanos and Salisbury 2003). These studies indicate that the hibernation phe-

* Corresponding author; e-mail: smz1@psu.edu.

notype is flexible. To further investigate the adaptive plasticity of the hibernation phenotype, we undertook a field study of three woodchuck populations (*M. monax*) distributed along a latitudinal gradient.

Marmota monax is the most widely distributed of the six North American species of marmots. Its range extends from southeast Alaska through southern Canada and into the eastern United States as far south as Georgia, Alabama, and Arkansas (Lee and Funderburg 1982). The wide range of this species exposes populations to a variety of climatic conditions, from long cold winters and short mild summers in the north to relatively mild winters and hot summers in the south. Accordingly, hibernation lengths vary with climatic conditions. For example, in Quebec, Canada (68°21'W, 48°32'N), hibernation lasts for 167 d from mid-September to late March (Ferron 1996), while in southeastern Pennsylvania (75°22'W, 40°22'N), hibernation lasts for 114 d from early November to late February (Zervanos 2003). However, data from populations in the southern part of the woodchuck's range suggest that these animals do not hibernate (Grizzell 1955; Anthony 1962; Davis 1976). Because this conclusion is based only on anecdotal observations of year-round, aboveground activity, more conclusive data are needed to document the extent of phenotypic plasticity in this species.

Although separate field studies indicate that length of the hibernation season increases with latitude (Nevo and Amir 1964; Fowler and Racey 1990; Zervanos 2003), to date, no conclusive data from a single study support this idea. Also, no previous studies have described the latitudinal phenotypic plasticity of other hibernation characteristics, including torpor bout length, euthermic bout length, and frequency of bouts. We expected that woodchucks from more northern latitudes would hibernate longer and more deeply than those at more southern latitudes and that woodchucks in the southern population would hibernate infrequently.

Material and Methods

Study Sites

Our research was conducted at three study sites. The Maine site (ME) was located at Gilsland Farm Sanctuary in southeastern Maine (43°42'N, 70°14'W; elevation 10 m); the Pennsylvania study site (PA) was located at the Pieffer Farm of the Pennsylvania State University's Berks Campus in southeastern Pennsylvania (40°22'N, 75°22'W; elevation 85 m); and the South Carolina study site (SC) was located at Clemson University's Aquaculture Farm in western South Carolina (34°40'N, 82°50'W; elevation 45 m). All three sites contained open fields with abundant food resources and burrow sites. Mean annual precipitation was similar across sites (ME: 116.3 cm; PA: 114.7 cm; SC: 113.2 cm). Animals from each site were studied simultaneously over three hibernation seasons from October 2005 to March 2008.

Field Studies

Temperature data loggers (iButtons; MAXIM, Dallas, TX) were used to monitor hourly T_b with a 0.1°C resolution from free-ranging woodchucks at each study site (3 females and 4 males in Maine; 6 females and 5 males in Pennsylvania; 4 females and 3 males in South Carolina). We captured animals in live traps (Tomahawk Live Trap, Tomahawk, WI; 81 cm × 25 cm × 30 cm) baited with lettuce or peanut butter and fresh apples. The data loggers were surgically implanted (intraperitoneal), as described by Van Vuren (1989), within 3 wk before each hibernation season and removed within 3 wk after the hibernation season ended. Body mass was measured during each procedure, and percent body mass loss was calculated using the difference between pre- and posthibernation values. In addition to the iButtons, implantable transmitters (model IMP/300/L; Telonics, Mesa, AZ) were used to track animal locations and movements. Each animal was used only once during the study. All procedures were approved by Institutional Animal Care and Use Committees at the University of Southern Maine (012605-01), Pennsylvania State University (20562), and Clemson University (06-ARC-066).

To monitor burrow temperatures at each study site, iButtons were placed in two to three separate burrow systems by taping a logger to a woodchuck's tail and allowing it to enter its burrow (as in Zervanos and Salsbury 2003). Although we could not verify the exact location of the data loggers, we are confident that the temperatures measured were representative of those experienced by the woodchucks. We base this conclusion on the logger distance from the entrance of 2–3 m and the fact that all the burrow temperatures decreased gradually, with no daily fluctuation over the entire winter season (Zervanos and Salsbury 2003; Zervanos et al. 2009). Ambient temperatures (T_a) were determined for the Maine location from a U.S. weather station within 4 km of the study site. In South Carolina, data loggers and min-max thermometers were used, whereas in Pennsylvania, an on-site weather station (model 900ET, Spectrum Technologies, Plainfield, IL) was employed.

Data Analysis

To eliminate prehibernation "test drops," only data from deep torpor bouts (≥ 24 h) were used in our analysis. We defined a deep torpor bout as the period of low stable $T_b < 20^\circ\text{C}$ (Waßmer and Wollnik 1997; Zervanos et al. 2009). Time of entry into torpor (end of euthermia) began when T_b fell to 30°C . Time of arousal from deep torpor (beginning of euthermia) began when T_b rose to 30°C . Torpor bout duration was defined as the time when T_b was $< 30^\circ\text{C}$ to when T_b rose to 30°C . Euthermic bout duration (e.g., interbout arousal period) was measured as the time between the end of one torpor bout and the beginning of the next bout.

Hibernation season was measured from the date of first torpor bout in autumn to the date of the last arousal from torpor in spring. First torpor was defined as the date and time when T_b reached 30°C during entrance into the first deep torpor bout.

Table 1: Comparisons of hibernation season characteristics among three latitudinally distributed populations of free-living woodchucks over a 3-yr period, 2005–2008

	Maine ($n = 7$)	Pennsylvania ($n = 11$)	South Carolina ($n = 7$)
Date of first torpor	291.1 ± 9.6^A	318.4 ± 16.1^B	346.3 ± 8.5^C
Date of last torpor	93.0 ± 13.2^A	60.1 ± 21.3^B	57.0 ± 16.9^B
Hibernation season (d)	166.9 ± 12.1^A	106.8 ± 24.1^B	75.7 ± 10.8^C
Number of torpor bouts	20.1 ± 1.6^A	14.8 ± 2.7^B	11.1 ± 1.5^C
Body mass loss (%)	33.3 ± 5.5	31.5 ± 2.9	$32.6 \pm .6$

Note. Data presented as mean \pm SD. Dates are reported in Julian calendar days. Different letters denote significant population differences within each characteristic ($P \leq 0.05$).

Final arousal was defined as the date and time when T_b reached 30°C during the last arousal.

We generated mean values for each animal; thus, each animal was represented once in the data analysis. Within each population (ME, PA, SC), we analyzed hibernation characteristics in separate repeated-measures three-way ANOVAs where sex, year, and body mass were designated as main effects in a general linear model. We also examined differences among populations using ANOVA. All ANOVA and post hoc tests (Tukey) were performed using Minitab statistical software (release 13 for Windows; Minitab, State College, PA). Regressions were performed using Statistics 9 (Analytical Software, Tallahassee, FL). Significance was assigned based on probability of $\alpha < 0.05$. Means are reported \pm SD.

Results

At each location, mean burrow temperatures during the three hibernation seasons did not differ significantly (ME, $P = 0.51$; PA, $P = 0.26$; SC, $P = 0.22$). Thus, at each location, data from the 3-yr study period were combined. Winter (November–February) burrow temperatures averaged $4.2^\circ \pm 0.2^\circ\text{C}$ in Maine, $7.3^\circ \pm 0.4^\circ\text{C}$ in Pennsylvania, and $12.4^\circ \pm 0.5^\circ\text{C}$ in South Carolina. Over the same period, T_a averaged $-5.9^\circ \pm 2.6^\circ\text{C}$ in Maine, $3.2^\circ \pm 1.0^\circ\text{C}$ in Pennsylvania, and $9.8^\circ \pm 2.1^\circ\text{C}$ in South Carolina.

For each location, we found no statistically significant re-

lationships between dates of first and last torpor, length of hibernation season, number of torpor bouts, body mass loss, and sex, body mass, or year. Thus, we combined all animals from each location into the three population groups (Tables 1, 2). Hibernation characteristics among the three populations revealed overall differences in seasonal duration and torpor bout patterns (Fig. 1). The three populations differed significantly in dates of first and last torpor (first torpor: $F = 23.55$, $df = 2$, $P = 0.002$; last torpor: $F = 7.16$, $df = 2$, $P = 0.003$), length of hibernation season ($F = 33.25$, $df = 2$, $P = 0.001$), and number of torpor bouts ($F = 14.07$, $df = 2$, $P = 0.001$). As expected, ME woodchucks entered torpor earlier and emerged from torpor later than the other populations. SC Woodchucks entered torpor later than either of the other populations, while PA woodchucks were intermediate (Table 1). PA and SC animals did not differ, however, in dates of last torpor. Thus, ME animals hibernated longer than PA and SC animals (Table 1). The number of torpor bouts also differed among the three populations, such that ME woodchucks experienced the highest number of bouts and SC woodchucks the lowest number. Body mass loss (%) did not differ among populations ($P = 0.28$; Table 1); animals of equal immergent body mass at each of the three locations (means: ME = 3.4 ± 0.4 kg, PA = 3.7 ± 0.8 kg, SC = 3.6 ± 0.7 kg) showed hibernation mass losses that were not significantly different from each other.

Table 2: Comparisons of torpor and euthermic bout characteristics among three latitudinally distributed populations of free-living woodchucks over three hibernation seasons, 2005–2008

	Maine ($n = 7$)	Pennsylvania ($n = 11$)	South Carolina ($n = 7$)
Torpor bout length (h)	184.6 ± 18.9^A	148.8 ± 31.3^B	117.3 ± 30.1^C
Euthermic bout length (h)	28.3 ± 2.5^A	37.9 ± 8.5^B	59.4 ± 11.8^C
Torpor body temperature ($^\circ\text{C}$)	$10.1 \pm .9^A$	12.4 ± 1.6^B	$14.5 \pm .9^C$
Lowest body temperature ($^\circ\text{C}$)	$5.3 \pm .5^A$	8.2 ± 2.4^B	11.8 ± 2.0^C
Euthermic body temperature ($^\circ\text{C}$)	$35.8 \pm .2$	$35.8 \pm .5$	$36.1 \pm .2$

Note. Data presented as the means of each mean for each animal \pm SD. Torpor T_b represents the mean over the entire hibernation season, while lowest T_b indicates the mean of the lowest T_b reached by each animal during the hibernation season. Different letters denote significant population differences within each characteristic ($P \leq 0.05$).

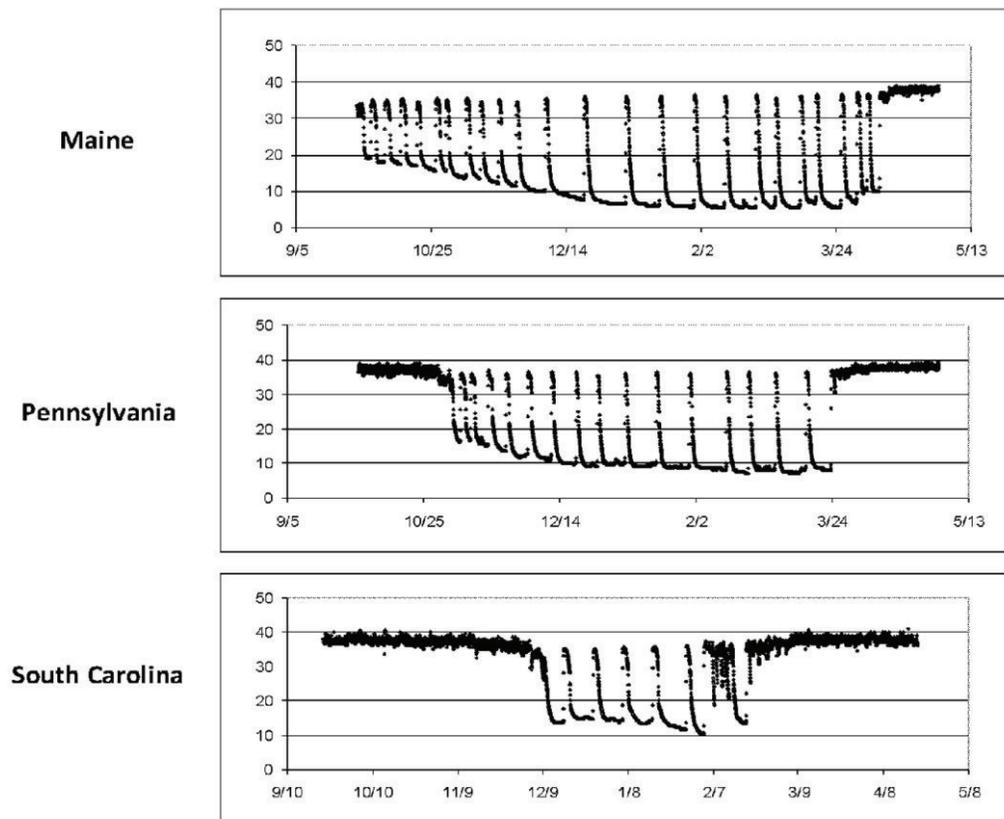


Figure 1. Typical torpor patterns of woodchucks from the three study locations. Plots represent data collected from females during the 2006–2007 hibernation season. Body temperatures ($^{\circ}\text{C}$) are shown on the Y-axis, and dates are indicated on the X-axis.

Comparison of hibernation bouts (Table 2) indicated that the three populations differed significantly in length of torpor bouts ($F = 7.82$, $df = 2$, $P = 0.003$) and euthermic bouts ($F = 14.54$, $df = 2$, $P = 0.001$). ME animals had longer torpor bouts and shorter euthermic bouts than the other two populations (Table 2). SC animals had the shortest torpor bouts and the longest euthermic bouts, with PA animals falling almost halfway between SC and ME animals (Table 2). During torpor, T_b also varied with populations ($F = 7.31$, $df = 2$, $P = 0.004$), and ME animals experienced the lowest T_b (Table 2). Euthermic T_b , however, did not differ ($P = 0.47$; Table 2). No significant interactions were found between the characteristics in Table 2 and sex, age, or year.

We summed all the time spent in torpor during all torpor bouts and found that ME animals spent a total of $3,365.9 \pm 273.9$ h in torpor, whereas PA animals spent $1,789.8 \pm 498.9$ h and SC animals spent $1,188.9 \pm 168.4$ h in torpor (Fig. 2). These differences were significant ($F = 31.50$, $df = 2$, $P = 0.006$). Regression analysis revealed a significant linear relationship between burrow temperature (latitude) and total time spent in torpor ($F = 45.70$, $r^2 = 0.66$, $P = 0.001$). However, the total time spent euthermic did not differ among the three populations ($F = 0.79$, $df = 2$, $P = 0.466$). Mean total time spent euthermic for ME animals was 493.7 ± 68.2 h, whereas

PA animals were euthermic for 488.1 ± 124.4 h and SC animals for 566.3 ± 155.1 h (Fig. 2).

Discussion

As predicted (Davis 1976; Ferron 1996; Zervanos 2003), we found a direct relationship between latitude (or burrow temperature) and length of the hibernation season, such that hibernation season lengthened with latitude. This is the first study to conclusively document that length of the hibernation season increases with latitude and that woodchucks in the southern part of their range hibernate. We also demonstrated latitudinal differences in torpor and euthermic bout lengths and the number of arousals. Torpor bouts increased with increased latitude, which may be related to burrow temperatures and, in turn, to T_b experienced during hibernation (Pivorun 1977; French 1982; Geiser and Kenagy 1988; Barnes and Buck 2000; Zervanos and Salsbury 2003; Dunbar and Tomasi 2006). This strategy of longer torpor bouts with decreasing T_b would result in greater energy savings, and our results are compatible with this concept. Interbout arousal length decreased with increasing latitude, whereas the number of arousals increased. French (1982) found that ground squirrels (*Spermophilus beldingi* and *Spermophilus lateralis*) exhibit longer interbout arousals after experiencing

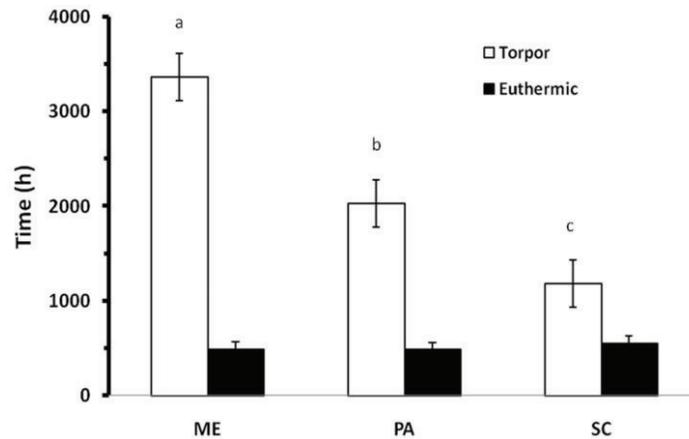


Figure 2. Total amount of time spent in torpor or euthermic in relation to population latitude, over a 3-yr period (ME, $n = 7$; PA, $n = 11$; SC, $n = 7$). Error bars represent \pm SD.

higher T_b during torpor and suggested that this increase in euthermic period is related to the time necessary to eliminate the greater “metabolic imbalances” that occur at higher torpor T_b . This hypothesis could explain the longer euthermic bouts observed in the southern populations during our study. The greater number of arousals in the ME population could simply be related to the longer hibernation season. If we divide length of the hibernation season by number of arousals, we find that “frequency of arousals” decreases with increasing latitude (ME = every 8.8 d, PA = every 7.8 d, and SC = every 7.2 d). More frequent arousals may be needed to reestablish the required metabolic balance at higher temperatures. Although the “metabolic imbalance” hypothesis can be applied to our results, other explanations are possible, including sleep balance, memory maintenance, reproductive development, immunity defense, and gene expression (Boyer and Barnes 1999; Buck and Barnes 2000; Carey et al. 2003). To date, reasons for interbout arousals during hibernation remain unclear.

Clearly, torpor conserves energy, whereas euthermia and arousal consume energy. Yet the similarity in percentage of body mass loss (31.5%–33.3%) among all three populations suggests a close relationship between energy conservation and consumption that results in comparable mass (energy) loss during the hibernation season. Similar to woodchucks, arctic ground squirrels (*Spermophilus parryi*) hibernating in colder burrows lose the same mass during hibernation as those in warmer burrows (Buck and Barnes 1999). This occurred even though burrow temperatures for the two groups of ground squirrels were much lower and differed more (-8.9° and -18.8°C) than those experienced by any woodchuck in our study. To explain similarities in mass loss in our study, we examined differences in temperature conditions among the three populations.

Compared to PA and SC populations, ME woodchucks experienced lower mean burrow temperatures, which would have required more energy expenditure. However, ME animals reduced energy expenditure by staying in torpor longer, both in terms of torpor bout length and total time spent in torpor.

That is, although the hibernation period was significantly longer for the ME population, most of it was spent torpid. Because torpor consumes little energy, if the total time spent torpid is greater and the total time euthermic is the same over the entire hibernation season, then the ME population would save even more energy than the PA and SC populations and thus lose less body mass. However, three other factors need to be considered: total energy expenditure during torpor, total energy expenditure of arousals, and total energy expenditure during interbout arousals.

Energy expenditure during torpor reflects the differential between T_b and burrow T_a . Hibernators attain the lowest metabolic rate and the longest torpor bouts at an optimal range of T_b and T_a (Heldmaier et al. 2004). Within the T_b range of 4° – 12°C , woodchucks exhibit the lowest and relatively constant metabolic rate (0.013 – 0.014 mL $\text{O}_2/\text{g}/\text{h}$; Armitage et al. 2000). Likewise, for alpine marmots (*Marmota marmota*), metabolic rate is constant when T_b is between 7° and 16°C (Heldmaier et al. 2004). Above and below this optimal range, metabolic rates tend to increase (Geiser and Kenagy 1988; Barnes and Buck 2000; Buck and Barnes 2000). Woodchucks significantly increase metabolic rates below $T_a = 4^\circ\text{C}$ in order to regulate $T_b > 5^\circ\text{C}$ (Armitage et al. 2000). Although we could not determine the exact positions of our burrow temperature loggers, the only location where burrow temperatures dropped below 4°C was in the ME population (mean = 2.6°C for January and 1.6°C for February). The lowest ME T_b observed during these low burrow temperatures was 5.3°C . Thus, the ME woodchucks may have incurred additional energetic costs during these colder periods.

Interbout arousals and time spent euthermic consume major amounts of energy. At a T_a of 6.0°C , woodchucks from the same PA population spent 13.8% of the energy expended during hibernation for arousals (0.229 mL $\text{O}_2/\text{g}/\text{h}$) and 57.6% for euthermia (0.141 mL $\text{O}_2/\text{g}/\text{h}$; Armitage et al. 2000). However, the colder the T_a , the greater the thermal gradient (T_a to T_b differential), and thus animals must expend more energy to

arouse and to maintain euthermy. Again, due to the greater thermal gradient, ME animals would have incurred additional energetic costs for arousals and euthermy.

On the basis of mass loss, all three populations experienced similar energy costs during hibernation, which suggests that the total energy used during hibernation represents a balance among the energy used for torpor, euthermy, and arousals. That is, each population devotes a different percentage of the hibernation season to torpor, euthermy, and arousals, and these trade-offs result in similar energy losses. The trade-offs would depend on the length and severity of the hibernation season.

Why would energy expenditures be the same across populations, even when the length of the hibernation season varies? For example, SC animals have a short hibernation season but have long euthermic bouts and short torpor bouts. They could stay torpid longer and save even more energy. The ME and PA populations could spend more time torpid and less time euthermic. Yet the total time spent euthermic did not differ in the three populations. One explanation may lie in the concept of “cost-benefit”; that is, the benefits of energy conservation and the costs of metabolic depression during hibernation may be trade-offs that explain the number of arousals and length of torpor and euthermic bouts (Humphries et al. 2003). This hypothesis assumes that hibernators avoid the physiological stress (see Carey et al. 2003 for types of stress) of torpor by staying euthermic as much as possible and still emerge with enough energy to survive and reproduce in the spring.

Our results indicate a direct relationship between total amount of time spent in torpor and latitude. To survive the longer and colder hibernation season, ME animals need to utilize torpor to a greater extent than PA and SC animals. The benefit of staying euthermic is therefore balanced with the cost of conserving energy through torpor. The maximum energetic cost of hibernation may approach one-third of mass loss. Thus, animals within each population may maximize the time spent euthermic, utilizing torpor only at the level needed to survive the hibernation season at their particular location, while utilizing only one-third of their fat reserves. This strategy requires changes in the hibernation characteristics. For the ME population, this means longer torpor bouts and more, but shorter, interbout arousals. For the SC populations, this means shorter torpor bouts and fewer, but longer, interbout arousals. As discussed earlier, these differences in bout lengths could be the result of T_a during torpor.

Are these hibernation characteristics fixed or plastic within a given population? Fenn et al. (2009) examined changes in hibernation characteristics under constant conditions, using captive woodchucks from the same three populations as in our study. Captive animals were maintained at a constant T_a of 5°C over one hibernation season, and yet they continued to display differences reflecting their population of origin with some notable changes. The captive ME animals, maintained at a higher T_a than that experienced in their wild state, responded by shortening the length of their torpor bouts compared to their free-ranging counterparts, whereas PA animals, maintained at an

average T_a similar to that experience in their wild state, exhibited torpor bouts similar to those of the free-ranging PA animals in our study. The captive SC animals increased torpor bout length in response to a lower T_a than that normally experienced in the wild. These results indicate plasticity in torpor bout length, which is not unexpected because, as stated previously, torpor bout length and T_a are inversely related. However, these differences in torpor bout length, under constant temperature, may indicate that previous climate exposure influences the direction and degree of the response. Plasticity was also seen in torpor T_b in response to temperature conditions. For example, the captive animals from SC lowered their torpor T_b to 5.8°C compared to 14.5°C for the free-ranging SC animals in our study. Notably, the number of torpor bouts remained the same as those in the wild. Also, as in the wild, the length of hibernation and total time in torpor were longest for the ME captive animals and shortest for the SC animals, whereas total time euthermic was the same in all three captive groups. Thus, these characteristics of hibernation seem to be more fixed and perhaps genetically based.

Our results suggest a degree of plasticity in the expression of the hibernation phenotype in response to different climatic conditions experienced on a latitudinal gradient. This plasticity allows animals to adjust energy utilization to changing environmental conditions. However, further studies are needed to better understand the relative influences of genetic versus environmental factors on differences in hibernation phenotypes.

Acknowledgments

We wish to extend a special thanks to J. K. Brown at Penn State University/Berks and A. Fenn at Colorado State University for their dedicated assistance during this study. We thank the staff at the Maine Audubon Society for permission to work at Gillsland Farm Sanctuary. We are grateful to C. Radding, DVM, for volunteering her time and facility to implant devices into Maine woodchucks and to A. Baird, S. Long, K. Regan, and J. Wright for assistance in the field. At Clemson University we wish to thank S. Davis, S. Miller, K. Becraft, G. Richards, C. Worthington, C. Clark, and R. Hawkins for their assistance during the South Carolina portion of the study. Funding was provided to S.M.Z. by a Pennsylvania State University/Berks Research Grant, to C.R.M. by grants from the National Science Foundation and the University of Southern Maine, and to G.L.F. by a private Lipid Foundation grant. This article is dedicated to the loving memory of Dr. Jerry A. Waldvogel.

Literature Cited

- Anthony M. 1962. Activity and behavior of the woodchuck in southern Illinois. Occas Pap C C Adams Cent Ecol Stud 6: 1–25.
- Armitage K.B., B.C. Woods, and C.M. Salsbury. 2000. Energetics of hibernation in woodchucks (*Marmota monax*). Pp. 73–

- 80 in G. Heldmaier and M. Klingenspor, eds. *Life in the Cold: Eleventh International Symposium*. Springer, Berlin.
- Barnes B.M. and C.L. Buck. 2000. Hibernation in the extreme: burrow and body temperatures, metabolism, and limits to torpor bout length in arctic ground squirrels. Pp. 65–72 in G. Heldmaier and M. Klingenspor, eds. *Life in the Cold: Eleventh International Symposium*. Springer, Berlin.
- Boyer B.B. and B.M. Barnes. 1999. Molecular and metabolic aspects of mammalian hibernation. *BioScience* 49:713–724.
- Buck C.L. and B.M. Barnes. 1999. Temperatures of hibernacula and changes in body composition of arctic ground squirrels over winter. *J Mammal* 80:1264–1276.
- . 2000. Effects of ambient temperature on metabolic rate, respiratory quotient, and torpor in an arctic hibernator. *Am J Physiol* 279:R255–R262.
- Carey H.V., M.T. Andrews, and S.L. Martin. 2003. Mammalian hibernation: cellular and molecular responses to depressed metabolism and low temperature. *Physiol Rev* 83:1153–1181.
- Davis D.E. 1967. The role of environmental factors in hibernation of woodchucks (*Marmota monax*). *Ecology* 48:683–689.
- . 1976. Hibernation and circannual rhythms of food consumption in marmots and ground squirrels. *Q Rev Biol* 51:477–514.
- Dunbar M.B. and T.E. Tomasi. 2006. Arousal patterns, metabolism rate, and an energy budget of eastern red bats (*Lasiurus borealis*) in winter. *J Mammal* 87:1096–1102.
- Fenn A.M., S.M. Zervanos, and G.L. Florant. 2009. Energetic relationships between field and laboratory woodchucks (*Marmota monax*) along a latitudinal gradient. *Ethol Ecol Evol* 21 (forthcoming).
- Ferron J. 1996. How do woodchucks (*Marmota monax*) cope with harsh winter conditions? *J Mammal* 77:412–416.
- Fowler P.A. and P.A. Racey. 1990. Daily and seasonal cycles of body temperatures and aspects of heterothermy in the hedgehog *Erinaceus europaeus*. *J Comp Physiol B* 160:299–307.
- French A.R. 1982. Effects of temperature on the duration of arousal episodes during hibernation. *J Appl Physiol* 52:216–220.
- Geiser F. 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol* 66: 239–274.
- Geiser F. and G.J. Kenagy. 1988. Torpor duration in relation to temperature and metabolism in hibernating ground squirrels. *Physiol Zool* 61:442–449.
- Grizzell R.A. 1955. A study of the southern woodchuck, *Marmota monax monax*. *Am Midl Nat* 53:257–293.
- Heldmaier G., S. Ortmann, and R. Elvert. 2004. Natural hypometabolism during hibernation and daily torpor in mammals. *Respir Physiol Neurobiol* 141:317–329.
- Heller H.C. and N.F. Ruby. 2004. Sleep and circadian rhythms in mammalian hibernators. *Annu Rev Physiol* 66:275–289.
- Humphries M.M., D.W. Thomas, and D.L. Kramer. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiol Biochem Zool* 76:165–179.
- Lee D.S. and J.B. Funderburg. 1982. Marmots. Pp. 176–191 in J.A. Chapman and G.A. Feldhamer, eds. *Wild Mammals of North America*. Johns Hopkins University Press, Baltimore.
- Lehmer E.M., L.T. Savage, M.F. Antolin, and D.E. Biggins. 2006. Extreme plasticity in thermoregulatory behaviors of free-ranging black-tailed prairie dogs. *Physiol Biochem Zool* 79: 454–467.
- Lyman C.P., J.S. Willis, A. Malan, and L.C.H. Wang. 1982. *Hibernation and Torpor in Mammals and Birds*. Academic Press, New York.
- McNab B.K. 2002. *The Physiological Ecology of Vertebrates*. Cornell University Press, Ithaca, NY.
- Nevo E. and E. Amir. 1964. Geographic variation in reproduction and hibernation patterns of the forest dormouse. *J Mammal* 45:69–87.
- Pivorun E.B. 1977. Hibernation of a southern subspecies of *Tamias striatus*: thermoregulatory patterns. *Am Midl Nat* 98: 495–499.
- Van Vuren D. 1989. Effects of intraperitoneal transmitter implants on yellow-bellied marmots. *J Wildl Manag* 53:320–323.
- Wang L.C.H. 1989. Ecological, physiological and biochemical aspects of torpor in mammals and birds. Pp. 361–401 in J. Balthazart, ed. *Advances in Comparative Environmental Physiology*. Springer, Berlin.
- Waßmer T. and F. Wollnik 1997. Timing of torpor bouts during hibernation in European hamsters (*Cricetus cricetus* L.). *J Comp Physiol B* 167:270–279.
- Zervanos S.M. 2003. Timing of hibernation immergence and emergence in woodchucks (*Marmota monax*). Pp. 157–164 in R. Ramousse, D. Allaine, and M. LeBerre, eds. *Adaptive Strategies and Diversity in Marmots*. Proceedings of the Fourth International Conference on the Genus *Marmota*, Montreux, Switzerland. International Network on Marmots ([http://www.cons-dev.org/marm/MARM/EMARM/ framarm/framarm.html](http://www.cons-dev.org/marm/MARM/EMARM/framarm/framarm.html)).
- Zervanos S.M. and C.M. Salsbury. 2003. Seasonal body temperature fluctuations and energetic strategies in free-ranging eastern woodchucks (*Marmota monax*). *J Mammal* 84:299–310.
- Zervanos S.M., C.M. Salsbury, and J.K. Brown. 2009. Maintenance of biological rhythms during hibernation in eastern woodchucks (*Marmota monax*). *J Comp Physiol B* 179:411–418.