2003

Seasonal Body Temperature Fluctuations and Energetic Strategies in Free-Ranging Eastern Woodchucks

Carmen M. Salsbury
Butler University, csalsbur@butler.edu

Recommended Citation

SEASONAL BODY TEMPERATURE FLUCTUATIONS AND ENERGETIC STRATEGIES IN FREE-RANGING EASTERN WOODCHUCKS (*MARMOTA MONAX*)

STAM. M. ZERVANOS* AND CARMEN M. SALSBURY

Department of Biology, Pennsylvania State University, P.O. Box 7009, Reading, PA 19610-6009, USA (SMZ)
Department of Biology, Albright College, P.O. Box 15234, Reading, PA 19612, USA (CMS)
Present address of CMS: Department of Biology, Butler University, 4600 Sunset Avenue, Indianapolis, IN 46208, USA

During a 2-year period, radiotelemetry was used to continuously monitor body temperature (T_b) of free-ranging woodchucks (*Marmota monax*) in southeastern Pennsylvania. Hibernation was preceded by daily T_b fluctuations ("test drops") of 2–4°C. During hibernation, woodchucks exhibited the characteristic pattern of torpor bouts. Time of arousals occurred randomly, but onset of torpor occurred predominantly between 1800 and 0000 h. Males had shorter hibernation periods (mean of 104.8 days) than did females (121.8 days). Males had shorter torpor bouts, but euthermic bouts were the same length as in females. Males also maintained higher T_b during torpor. Overall, the cost of hibernation was greater for males than for females: males spent 38% more energy than did females. The primary energetic expense for both sexes was the periodic maintenance of euthermy throughout hibernation, which accounted for 75.2% of the energy budget for males and 66.8% for females. Compared with the 1999–2000 hibernation seasons, woodchucks during the 1998–1999 season had longer euthermic bouts, fewer torpor bouts (11.8 compared with 13.1), and spent less time in torpor (68% compared with 75%). These differences conserved more energy during the 1999–2000 hibernation season and may have been the result of severe drought conditions during summer 1999. After emergence from hibernation, woodchucks generally maintained a constant state of euthermy throughout the active season, with T_b fluctuating daily by 1–2°C. However, during the summer drought of 1999, daily T_b fluctuated 8–17°C in 5 of 8 woodchucks, presumably to conserve energy and water.

Key words: body temperature, energetics, estivation, hibernation, *Marmota monax*, torpor, woodchucks

Hibernation is prominent among ground-dwelling squirrels of the family Sciuridae and is characterized by an extreme reduction in metabolic function and body temperature (T_b) that may extend over repeated bouts, each lasting several days (Lyman et al. 1982). Because of substantial energy savings from depressed metabolic function, hibernation is widely used as a mechanism to survive harsh conditions such as low ambient temperatures (T_a) and food scarcity.

The hibernation patterns of ground-dwelling squirrels have been studied extensively in the laboratory (French 1982; Geiser and Kenagy 1988; Harlow and Menkens 1986; Pivorun 1976). Fluctuations in T_b and arousal state have been documented for many species in captivity including species of *Marmota* (Armitage et al. 2000; French 1990; Heldmaier et al. 1993; Lyman 1958). Depletion of fat stores and changes in body mass throughout hibernation have also been examined (Armitage et al. 2000; Davis

* Correspondent: smzl@psu.edu

1967; Florant 1998; Snyder et al. 1961). Further, energy expenditure as estimated by O_2 consumption has been monitored in a large variety of species in the laboratory setting (Geiser 1988).

Field studies of hibernation have generally involved an assessment of immergence and emergence dates based on trapping information and field observations (Davis 1976; Ferron 1996; Michener 1977). Loss of body mass has been estimated for free-ranging hibernators by comparing body mass of animals captured late in the active season with body mass of animals shortly after emergence from hibernation (Arnold 1993; Barash 1989; Buck and Barnes 1999a, 1999b; Ferron 1996). The energetic cost of hibernation has been inferred from estimates of daily mass loss during hibernation. However, automated radiotelemetry monitoring of T_b of free-ranging hibernators (Zervanos and Salsbury 2001) may provide further insight into the patterns of hibernation in the field and may validate the relevance of the wealth of laboratory information on hibernation patterns that have been collected for a number of species.

The continual observation of T_b of hibernators may also afford investigators the opportunity to estimate energy expenditure of free-ranging hibernators. For example, one method for monitoring CO_2 production in animals in their natural environments is the use of doubly labeled water (Nagy 1989). The utility of this method for measuring the energetic costs of the different phases of hibernation—arousal, euthermy, and torpor—is limited because the resolution of this method is generally restricted to a period of several days and requires 2 blood samples from the focal animal. However, by monitoring T_b of free-ranging hibernators, energy expenditures in the field can be extrapolated from known relationships between metabolism and T_b generated under laboratory conditions. This technique has been used successfully to estimate energetic costs of hibernation for free-ranging Richardson's ground squirrels, *Spermophi-*

lus richardsonii (Wang 1972, 1973, 1978); however, surprisingly, few other field studies have been conducted that provide the detail necessary to estimate energy expenditure.

We monitored T_b of eastern woodchucks (*M. monax*) throughout hibernation and during the active season in an attempt to characterize and better understand T_b patterns under natural conditions. Additionally, we hoped to verify data generated from laboratory studies of hibernation patterns of woodchucks. Finally, we wanted to generate an estimate of energy expenditure for hibernation of free-ranging woodchucks by extrapolating laboratory data to field conditions.

MATERIALS AND METHODS

Trapping and field observations.—The study was conducted from 29 August 1998 to 19 September 2000 on the Peiffer Farm of the Pennsylvania State University's Berks Campus located in southeastern Pennsylvania (40°22′N, 75°22′W). About 35 ha of the 44-ha farm were planted with corn (maize) each summer. Three woodlots (mixed hardwoods), encompassing an area of approximately 4 ha, are contained within the farm boundaries. The remainder of the farm consists of open fields in various stages of succession, experimental study plots, and farm and maintenance buildings. An estimated population of 46 woodchucks (*M. monax*) inhabits the farm, primarily along the ecotones of the woodlots and fields.

Woodchucks were trapped 5 days/week from emergence in March until immergence in October of each year. Trapped animals were sexed, weighed, tagged, and then released. Times of emergence during the hibernation period were determined by placing straw in all the entrances of inhabited burrows. The entrances were examined 3 times/week, and any disturbance of the straw was assumed to be an emergence.

Radiotelemetry system.—Radiotelemetry was used to monitor hourly T_b of free-ranging adult woodchucks (Zervanos and Salsbury 2001). At any given time during the study, 6–14 woodchucks were simultaneously monitored using surgically implanted intraperitoneal temperature transmitters (model IMP/300/L, Telonics, Mesa,

Arizona). Temperature transmitters (model MOD-205, Telonics) were also placed 2–3 m into 4 woodchuck burrows to monitor burrow temperatures. To determine the placement of the transmitters in the burrows, a 6-m graduated string (marked at 1-m intervals) was tied to the transmitter that was then taped to the tail of a captured woodchuck. The animal was released at the entrance of its burrow, and when it stopped moving, the distance entered was measured and the string was pulled to release the transmitter. Another transmitter was placed in an outdoor weather station to monitor T_a. All transmitters provided a 0.2°C resolution through the entire period of data collection. Telemetry data were automatically recorded with a data acquisition system (Zervanos and Salsbury 2001). In addition, each animal was manually tracked and located on a weekly basis with portable telemetry equipment.

Weather data (T_a, wind velocity and direction, humidity, and rainfall) were also collected automatically each hour the year round by an outdoor weather station and were stored in a computer file.

Data analysis.—We examined torpor, arousal, and euthermic bouts for each individual throughout hibernation. We defined euthermy as $T_b >$ 30°C and torpor as $T_b <$ 30°C. We defined deep torpor as the period of low stable $T_b <$ 20°C. We defined hibernation season as starting with the 1st deep torpor in autumn and ending with the last arousal in spring and active season as the rest of the year. During the hibernation season, time of day for each arousal was measured as the point at which the T_b started to rise above the T_b of stable deep torpor, and beginning of decline into torpor was measured as the point at which T_b began to decline below stable euthermic T_b. We used these data to test randomness of starting time for both arousal from and decline into torpor. We divided the day into four 6-h periods of observations starting at midnight (0000 h). A chi-square analysis was performed assuming an expected equal distribution of starting times within each 6-h time period.

We calculated arousal and cooling rates (°C/ min and °C min^{-1} kg^{-1}) for each torpor arousal sequence for which we had interpretable, continuous data, and values were averaged for each animal. Arousal rate was calculated from time in hours for T_b to rise from stable deep torpor to 30°C, and cooling rate was calculated from

time in hours for T_b to fall from 30°C to a stable deep torpor temperature. Because the absolute decline of T_b was not the same for all individuals, we also calculated mean cooling rate from 30°C to 20°C for each individual. We examined relationships of arousal and cooling rates to burrow temperatures by calculating Spearman correlation coefficients. Arousal and cooling rates, as well as total time to arouse and cool, were compared between sexes using Student's t-tests.

The hibernation season of each animal for which we collected interpretable data was divided into 3 phases of equal duration—early, mid, and late. Mean T_b during torpor, mean T_b during euthermy, mean torpor length (h), and mean euthermy length (h) were calculated for each animal during each phase. These 4 variables were analyzed in separate repeated-measures 3-way analyses of variance (ANOVA), where sex, year, and hibernation phase (repeated measure nested within sex) were designated as main effects in a general linear model. Significance was assigned based on a probability of $\alpha < 0.05$. Hibernation phase, when not involved in significant interactions, was examined in post hoc tests using the Tukey–Kramer multiple comparisons method. All repeated-measures ANOVA and post hoc tests were performed using Minitab statistical software (Release 13 for Windows, Minitab Incorporated, State College, Pennsylvania).

Body mass data were averaged by month for each sex. We compared mean monthly body mass between sexes by using Student's t-statistics. Because animals did not emerge from their burrows, it was not possible to weigh them during hibernation; therefore, we estimated rate of daily mass loss through hibernation by subtracting posthibernation body mass from prehibernation body mass and dividing by length of hibernation. Because animals were difficult to trap just before and after hibernation, daily mass loss estimates were based on mean body masses collected for the population in October and March and mean length of hibernation for each sex. We also calculated mass-specific daily mass loss (mg g [immergence mass]$^{-1}$ day^{-1}) during hibernation for each sex.

RESULTS

Seasonal climate conditions.—Mean burrow temperatures ranged from summer highs of 20.3°C to winter lows of 6.3°C. These seasonal changes were gradual and

reflect the relative protection of burrows from seasonal extremes. Mean burrow temperature during June–August was higher in 1999 (16.9 *SE* ± 0.4°C) than in 2000 (15.3 ± 0.2°C: $t = 1.94$, $d.f. = 172$, $P < 0.05$). Mean burrow temperatures during the hibernation season in 1998–1999 (7.3 ± 0.2°C) and 1999–2000 (7. 7 ± 0.2°C) were not different ($t = 1.13$, $d.f. = 196$, $P > 0.10$). Daily burrow temperature fluctuated about 1.8°C during both summers and about 1.0°C daily during both hibernation seasons.

Except for 2 periods, seasonal ambient conditions were similar throughout the study. The 1st exception was for December–February 1999–2000, when mean T_a was significantly lower (0.8°C) than for the same period in 1998–1999 (2.9°C). For the 2nd exception, June–August 1999, rainfall was at a record low (10.3 cm) compared with the same 3-month period in 2000 (30.1 cm), vegetation was dry and unproductive, and freestanding water was only available during limited rainfalls or from a creek along the eastern boarder of the study area. Activities around the farm buildings also offered some drinking water. However, only 3 of the study animals were within 45 m of any of these water sources; the rest were at least 250 m away from a permanent water source. The drought ended in September when 20.8 cm of rain fell over a 26-day period.

Seasonal T_b patterns.—Hibernation typically started with daily fluctuations of T_b ("test drops"—Pivorun 1976) several days before the 1st torpor bout (Fig. 1a). These fluctuations ranged between 2°C and 4°C, with a steady decline in the euthermic range. The majority (85%) of the daily high T_bs were reached between 1400 and 1700 h. The majority (85%) of daily low T_bs were reached between 0400 and 0600 h. This general pattern was observed for all animals during both autumn seasons. A significant number (69%) of declines into the 1st torpor bout occurred between 1800 and 0600 h ($\chi^2 = 3.85$, $d.f. = 1$, $P < 0.05$).
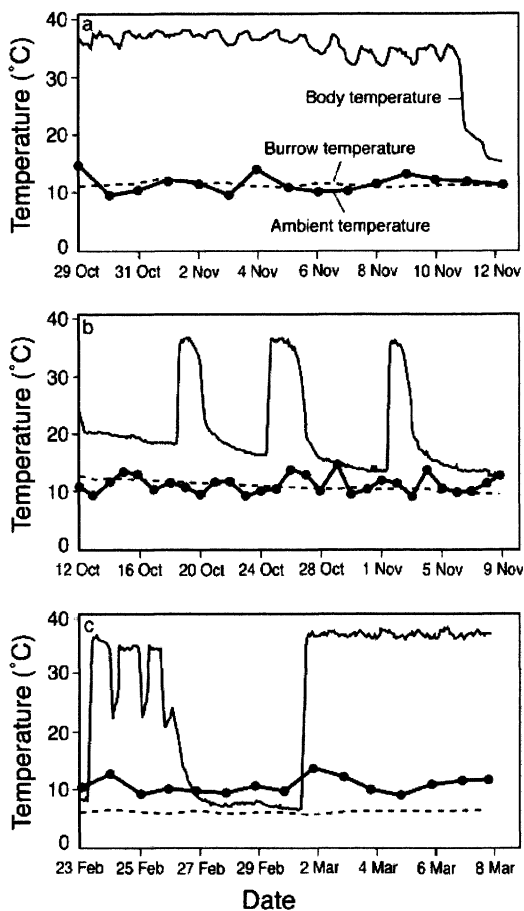

FIG. 1.—a) Body temperature fluctuations of female *Marmota monax* (number 1) before initial torpor bout of 1999–2000 hibernation season. b) Torpor bouts of female *M. monax* (number 2) at beginning of the 1999–2000 hibernation season. c) Body temperature fluctuations of female *M. monax* (number 3) before last arousal of 1999–2000 hibernation season. Burrow (averaged from 4 burrow locations) and ambient temperatures are also presented.

During hibernation, woodchucks exhibited the characteristic pattern of torpor bouts (Fig. 1b). During each successive bout, deep torpor T_b declined with declining burrow temperature, reaching winter lows of 6.5–8.4°C during 1998–1999 and 6.8–8.8°C during 1999–2000. Animals aroused randomly throughout the day with no discernable pattern. However, time of entry into torpor was not randomly distributed;

41% occurred between 1800 and 0000 h (χ^2 = 8.66, *d.f.* = 3, *P* < 0.05).

Final emergence from hibernation was usually preceded by a relatively long euthermic period of 3–4 days in 15 of 18 animals observed. The 3 exceptions exhibited shorter euthermic periods of 1–2 days. Nine of the 15 animals with long euthermic periods were characterized by daily fluctuations in T_b (Fig. 1c). The brief but significant declines reached a low T_b (23–28°C) between 2100 and 0300 h. A significant number (67%) of arousals from the final torpor bout occurred during the day (χ^2 = 5.44, *d.f.* = 1, *P* < 0.02).

After emergence, most animals maintained a constant state of euthermy throughout the active season with T_b fluctuating daily by 1–2°C. Excluding animals with daily T_b fluctuations >2°C, April 2000 mean daily T_b was significantly lower (37.1°C) than in July 2000 (37.6°C; *t* = 2.93, *d.f.* = 60, *P* < 0.01). However, some adults of both sexes exhibited daily T_b fluctuations in excess of 10°C. Between 10 March 1999 and 6 May 1999, 3 of 8 animals had daily T_b fluctuations of 10–14°C. Between 2 April 2000 and 4 June 2000, 2 of 10 animals had daily T_b fluctuations of about 10°C. We were unable to find environmental correlates to these fluctuations. However, during summer of 1999, daily T_b fluctuated 8–17°C in 5 of 8 woodchucks (Fig. 2a). These fluctuations occurred between 2 August and 17 September and were associated with severe drought and high temperature conditions during this period. One of the 5 animals died during this period. Starting in mid-August, significant rain (>1 cm in 24 h) fell, and 2 animals returned to stable euthermia within 2 days, whereas 2 animals continued to fluctuate T_b by 6–12°C until mid-September. Of the 3 woodchucks with stable euthermia during August 1999, 2 lived in burrows within 40 m of the creek, and 1 inhabited a watered vegetable garden. During the same period in 2000, rainfall and T_as were normal, and
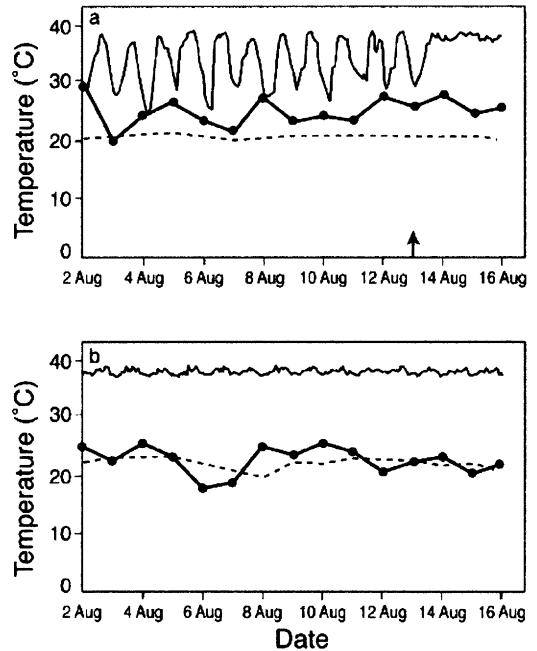

FIG. 2.—a) Body temperature fluctuations of female *Marmota monax* (number 4) during summer drought of 1999. Arrow indicates rainfall of 3.6 cm in a 28-h period. This was the 1st significant rainfall (>1 cm in 24 h) in 56 days. b) Body temperature fluctuations of female *M. monax* (number 5) during summer of 2000 without drought. Burrow (averaged from 4 burrow locations) and ambient temperatures are also presented. (Temperature labels as for Fig. 1a.)

none of the woodchucks exhibited daily T_b fluctuations >2°C (Fig. 2b).

Analysis of hibernation.—Male and female woodchucks living in our study area had similar body masses in March after hibernation and in October just before hibernation (Table 1). During the active season, males were significantly heavier than females only in June (2-tailed *t*-test: *t* = 3.18, *d.f.* = 25, *P* = 0.009). The population estimate of daily mass loss during hibernation was 2.11 mg g^{-1} day^{-1} for males and 1.78 mg g^{-1} day^{-1} for females.

Males had shorter hibernation periods (Table 1). Both males and females showed similar cooling rates, but length of the cooling phase was significantly shorter for males. Males and females did not differ in

TABLE 1.—Comparison of hibernating male and female woodchucks. Dates are reported in Julian calendar days. Asterisk denotes significant differences ($P \leq 0.05$, t-test).

	Females			Males			
	n	$\bar{X}$	SE	n	$\bar{X}$	SE	P
Body mass (kg)							
March	11	2.79	0.179	3	2.84	0.549	0.456
October	10	3.57	0.256	5	3.64	0.172	0.425
Date of 1st torpor	14	305.7	1.94	5	314.6	13.30	0.296
Date of last arousal	14	62.5	1.95	5	58.4	4.41	0.338
Number of torpor bouts	14	12.7	0.40	5	12.0	1.14	0.460
Length of hibernation (days)	14	121.8	1.83	5	104.8	8.82	0.010*
Arousal length (h)	9	4.3	0.23	3	4.3	0.67	0.944
Length of cooling phase (h)	9	66.3	3.70	3	52.1	3.20	0.023*
Arousal rate (°C/min)	9	0.100	0.0048	3	0.103	0.0110	0.851
Arousal rate (°C min^{-1} kg^{-1})	9	0.028	0.0027	8	0.031	0.0061	0.707
Cooling rate (°C/min)	9	0.0067	0.0003	3	0.0085	0.0015	0.371
Cooling rate between 30°C and 20°C (°C/min)	9	0.0241	0.0015	3	0.0247	0.0081	0.948

number of torpor bouts during hibernation, length of each arousal phase, or rate of arousal (Table 1). Neither cooling nor arousal rate was significantly correlated with burrow temperature ($r_s = -0.172$, $d.f. = 31$, $P > 0.05$ and $r_s = -0.280$, $d.f. = 40$, $P > 0.05$, respectively).

Repeated-measures ANOVA indicate that males engaged in significantly shorter torpor bouts throughout the hibernation period and maintained a higher T_b during torpor than did females (Table 2). There were no significant differences between sexes with regard to euthermy. Torpor length and

TABLE 2.—Effects of sex, year, and hibernation phase on hibernation characteristics of woodchucks. Means and SE are presented for the main effects. $P \leq 0.05$ was considered significant.

	Length of						T_b during					
	Torpor bouts (h)			Euthermy bouts (h)			Torpor (°C)			Euthermy (°C)		
	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE
Sex												
Male	5	144.5	12.6	5	66.5	5.9	5	11.3	0.7	5	35.4	0.9
Female	14	170.9	6.5	14	64.6	4.3	14	10.2	0.5	14	35.7	0.2
F		7.92			0.26			5.05			0.01	
P		0.007			0.614			0.030			0.923[a]	
Year												
1998–1999	9	166.8	8.0	9	76.5	6.0	9	10.5	0.6	9	35.6	0.3
1999–2000	10	161.5	8.9	10	54.8	2.7	10	10.5	0.6	10	35.7	0.5
F		0.09			8.80			0.00			0.64	
P		0.764[b]			0.005			0.973[c]			0.428[a]	
Hibernation phase												
Early	19	127.6	7.6	19	56.9	3.9	19	14.2	0.4	19	35.2	0.6
Mid	19	192.9	7.6	19	56.0	7.4	19	8.7	0.3	19	35.7	0.5
Late	19	171.4	9.8	19	63.5	5.9	19	8.6	0.5	19	36.0	0.3
F		10.07			3.96			43.56			0.64	
P		<0.001[b]			0.008			<0.001[c]			0.637	

[a] $F = 4.08$, $P = 0.049$ for significant interactions.
[b] $F = 3.05$, $P = 0.026$ for significant interactions.
[c] $F = 3.52$, $P = 0.014$ for significant interactions.

T_b during torpor and euthermy did not vary significantly between the 2 hibernation seasons. Euthermy bouts were significantly longer during the 1998–1999 season than during the 1999–2000 season.

Length of torpor bout, length of euthermy bout, as well as T_b during torpor varied significantly across the 3 phases of hibernation (Table 2). Post hoc multiple comparisons of length of euthermy indicate that there is a trend toward longer euthermic bouts during the late phase of hibernation than during the early phase of hibernation, but the difference was not significant ($t = 2.88$, $P = 0.0628$). Interpretation of the variation in length of torpor bouts and T_b during torpor across the hibernation phases is difficult due to significant interactions between hibernation phase and year for both dependent variables. Post hoc examination of interactions suggests there is a trend, especially among females, toward shorter torpor bouts and higher T_b early in hibernation than in mid and late hibernation. These trends, however, were not consistent between sexes or across years.

Several other differences were observed between years. Average date of immergence was 7 November during 1998–1999 compared with 1 November during 1999–2000 ($t = 2.26$, *d.f.* $= 17$, $P < 0.05$). Average date of emergence was 6 March during 1998–1999 and 27 February for 1999–2000 ($t = 2.42$, *d.f.* $= 17$, $P < 0.05$). The average number of torpor bouts was significantly different, 11.8 for 1998–1999 compared with 13.1 for 1999–2000 ($t = 2.91$, *d.f.* $=17$, $P < 0.01$). Percentage of time spent in torpor was significantly less in 1998–1999 than in 1999–2000, 68% compared with 75% ($t = 2.98$, *d.f.* $= 17$, $P < 0.01$). However, average length of hibernation was not significantly different between hibernation seasons, 119 days for 1998–1999 compared with 115 days for 1999–2000 ($t = 1.19$, *d.f.* $= 17$, $P = 0.19$).

DISCUSSION

Active season strategies.—During the active season, woodchucks displayed a typical euthermic pattern of small daily T_b fluctuations (Fig. 2b). Hayes (1976) observed similar patterns in woodchucks from Arkansas. He also found, as we have, that mean daily T_b is significantly lower (by 0.5°C) in spring than in midsummer. Hayes concluded that higher T_b during summer reduced the thermal radiation gradient and facilitated passive heat loss. Lower T_b in spring would minimize heat loss and save thermoregulatory energy during colder spring days. Under environmental stress, woodchucks increased daily T_b fluctuations such that nightly T_b approached torpor levels. Spring T_b fluctuations occur during periods when food availability is low and energy cost for reproduction is high (Fall 1971; Snyder et al. 1961). Similar fluctuations in T_b were observed in August 1999 during a prolonged drought (Fig. 2a). This type of adaptive response has not, to our knowledge, previously been observed under field conditions in marmots (Davis 1976). However, Davis (1967, 1976) found that captive woodchucks can enter torpor at any time of the year, provided they are deprived of food and temperatures are low (6°C). He found that woodchucks kept at 20°C and deprived of food do not become torpid but become "lethargic" and lower T_b to 33°C. During the drought period in our study, woodchucks were rarely observed aboveground and, when they were, it was only during the cooler early morning or early evening hours. The lower T_b and restricted aboveground activity would conserve metabolic energy and reduce thermoregulatory water loss during periods of drought.

Dynamics of hibernation.—Test drops, similar to those in our study, have been observed during initial torpor in the eastern chipmunks (Pivorun 1976), alpine marmots (Arnold 1988), and woodchucks (Lyman 1958). Yet their function is unknown. Because these test drops precede only the 1st torpor bout, they may reflect the daily resetting of the hypothalamic thermostat and function to acclimate cellular functions to the onset of low T_b (Hammel 1967; Luecke

and South 1972). This concept is supported by observations made by Pivorun (1976) who found that the number of test drops for chipmunks increased with decreasing T_a. Thus, the lower the reset requirement, the more test drops that would be needed.

After the drought summer of 1999, woodchucks aroused more often but stayed euthermic less time per bout. As a result, length of hibernation remained the same between the 2 hibernating seasons, but percentage of time spent in torpor was higher for 1999–2000. The severe drought conditions during summer of 1999 could have influenced this pattern. Early immergence and emergence during the 1999–2000 season, together with higher percentage of time in torpor, would be consistent with the need to conserve more energy after a summer of low food resources. Early immergence may allow animals to conserve energy under poor forage conditions, whereas early emergence may allow animals to assess the environment sooner for potential resources. Mean daily maximum T_a between mid-February and mid-March was 6.5°C in 1999 compared with 13.5°C in 2000. However, it is not possible to assess whether environmental conditions, circannual rhythms, or nutrient needs were responsible for early emergence (Davis 1976, 1977; Pengelley 1967). Finally, percentage of time spent in torpor might be more important in total energy conservation than in the energy loss from more arousals (French 1992).

Our inability to demonstrate a relationship between burrow temperatures and arousal rates is consistent with the findings of Wang and Hudson (1971) for eastern chipmunks. Lyman (1958) and Wang (1978) suggest that the mechanism controlling differential warming of body parts during arousal functions irrespective of T_a. However, temperature acclimation may also play a role. Squirrels kept at 15°C arouse more slowly than those kept at 5°C (French 1982). Similar relationships have been found for other mammals (Geiser and Bau-

dinette 1987; Zervanos and Henshaw 1970).

Cooling rates were not correlated with burrow temperatures for woodchucks in our study. Lyman (1958), Pivorun (1976), and Wang (1978) also found no relationships between cooling rates and ambient (burrow) temperatures. Pivorun (1976) observed that the cooling rate for a dead chipmunk is always significantly faster than that for the same animal alive and entering torpor. He attributed this to the existence of a control on cooling to prevent cellular damage from a too-rapid decline in T_b. Lyman (1958) attributed this phenomenon to vascular controls causing differential cooling of body core and periphery. If cooling is not passive, it would explain the lack of correlation between cooling rates and burrow temperatures.

Biological rhythms.—During the active season, high T_b during afternoon hours for woodchucks is consistent with diurnal activity patterns and is in agreement with fluctuations found for other ground squirrels (Michener 1992; Wang 1972). During hibernation, woodchucks arouse from torpor randomly but enter torpor primarily between 1800 and 2300 h. Canguilhem et al. (1994) found preferential times between 0000 and 0800 h for torpor entrance in the European hamster and a random pattern for arousal times. They speculate that randomness of arousal and rhythmicity of entrance into torpor indicate a resynchronization of the internal clock during arousal periods. They did not identify an entrainer (zeitgeber) for resynchronization. Because burrows are sealed during hibernation, photoperiod entrainment is not possible (Davis 1976). Although the exact location of our temperature transmitters within the burrow system is unknown, the daily 1°C fluctuation in burrow temperature could have acted as an entrainer (Pittendrigh 1960; Zervanos 1969). During our study, both males and females were observed to 1st emerge from their burrows several weeks before their final arousal from hibernation. These

early forays occur in mid to late afternoon, and most animals initially stay within 2 m of the burrow entrance. They are unable to feed during this time due to snow cover and absence of edible vegetation. Thus, it is possible that early emergence behavior may be due, in part, to the need to resynchronize the hibernator's biological clock. The synchrony of final arousals from hibernation, the majority of which occur during daytime hours, indicates that a rhythmic pattern has been established by the end of hibernation. This supports the conclusion that some rhythmic behavior is maintained during hibernation (Canguilhem et al. 1994; Davis 1976) and may be further synchronized just before the end of hibernation.

Energetics of hibernation.—Knowing the hibernation patterns of free-ranging woodchucks provides a rare opportunity to verify data collected for this species under captive conditions. Also, by estimating energetic cost of hibernation in the field, it may be possible to ultimately gain insight into other aspects of woodchuck life histories such as overwinter mortality rates and variable reproductive success among individuals and seasons. Although we did not examine hibernation patterns of captive woodchucks in this study, woodchucks from the same study population were simultaneously examined in captivity by Armitage et al. (2000). These authors monitored hibernation state of individuals throughout hibernation and measured the oxygen consumption of hibernating woodchucks as they passed through periods of arousal, euthermy, and torpor at 6°C. Woodchucks hibernating in captivity displayed patterns of arousal and torpor similar to those of free-ranging hibernators. Captive animals entered torpor less frequently ($\bar{X} = 10.2 \pm 0.85$ bouts—K. B. Armitage, pers. comm.) throughout hibernation than did free-ranging hibernators ($\bar{X} = 12.4 \pm 0.41$ bouts; Student's *t*-test $P = 0.053$). The lower number of torpor bouts among captive animals may be due, in part, to the short hibernation period of some of the captive hibernators

($\bar{X} = 99.6 \pm 10.3$ days—K. B. Armitage, pers. comm.). Others have also found that hibernation periods are typically shorter for captives than for free-ranging animals (Heldmaier et al. 1993). Armitage et al. (2000) report a mean time spent in torpid of 52.9% for captive woodchucks on a monthly basis from November through March. This value is considerably less than estimates for free-ranging hibernators (males $\bar{X} = 68.9\%$ and females $\bar{X} = 72.8\%$); however, the estimate for captive animals is similar when the value is recalculated on an individual basis and periods of prehibernation euthermy are not included in the estimate ($\bar{X} = 69.3\%$—K. B. Armitage, pers. comm.). The decline in T_b to deep torpor after a euthermic period was much more rapid for animals in captivity ($\bar{X} = 33.4$ h—Armitage et al. 2000) than for animals in the field (overall for males and females: $\bar{X} = 63.3$ h). The difference in cooling rates may be explained by the fact that measurement of oxygen consumption in the laboratory involved an active flow of air over the hibernator (Armitage and Salsbury 1992) that may have increased convection and evaporative heat loss. Naturally hibernating woodchucks are known to use vegetation to plug the entrances of their burrow system (Grizzell 1955); this behavior would presumably minimize airflow and reduce passive heat loss.

We calculated metabolic costs of hibernation for each field-monitored animal using the following equation from French (1992): metabolic cost of hibernation = ([total hours of euthermy][ml O_2 g^{-1} h^{-1}][preimmergence body mass]) + ([total hours of torpor][ml O_2 g^{-1} h^{-1}][preimmergence body mass]) + ([total number of arousals][ml O_2/arousal]). The metabolic rates for woodchucks (euthermy = 0.141 ml O_2 g^{-1} h^{-1}, torpor = 0.014 ml O_2 g^{-1} h^{-1}, arousal = 0.229 ml O_2 g^{-1} h^{-1}) were obtained from Armitage et al. (2000). Metabolic cost (ml O_2) of each arousal phase was estimated for each individual by mul-

tiplying the mean arousal length (time in hours to increase T_b from deep torpor to 30°C) by the weight-specific cost per hour and the preimmergence mass. We assumed that the previously mentioned similarities in hibernation patterns of captive and field animals justified our extrapolation from laboratory to field setting. The metabolic costs for field hibernators are most likely overestimates because we were unable to weigh animals during hibernation in the field. Thus, mass lost during hibernation and any resultant decrease in total metabolism were not accounted for in the calculations. Also, faster cooling rates of woodchucks in captivity than in the field and the lower T_a in the laboratory study (6°C) than in the field (7–8°C) suggest that laboratory estimates may be higher than energetic costs incurred by animals under more insulated conditions in the field. Given that, one cannot correct for these factors; these metabolic cost estimates may be best used for relative comparisons among individuals rather than for absolute comparisons between studies.

Males spent 38% more energy for hibernation than did females (males $\bar{X} = 736.3$ liters of O_2 and females $\bar{X} = 531.9$ liters of O_2). Males also spent 56% more energy on a daily basis during hibernation than did females. The primary energetic expense for both sexes resulted from periodic euthermy throughout hibernation, which accounted for 75.2% of the energy budget for males and 66.8% for females. The greater energy expenditure by males for euthermy was the result of the greater proportion of time males spent euthermic in the field than did females. Why do males not use torpor to the same extent as females during hibernation? Unfortunately, our results do not provide the information necessary to address this question. It has been suggested for other species of ground squirrels, however, that euthermic T_b is necessary to support spermatogenesis (Barnes et al. 1986), which begins before hibernation ends (Christian et al. 1972). Male woodchucks also may benefit from maintaining euther-

my during late hibernation because it may allow them periodically to leave their burrows and assess climatic conditions for optimal timing of emergence. Male woodchucks in this study and others (Davis 1977; Grizzell 1955; Snyder and Christian 1960) have been observed aboveground for short periods in January and February. The earliest possible emergence from hibernation may be critical for males because reproductive success is dependent on their ability to establish territories, locate females, and complete spermatogenesis before females emerge. Thus, the higher cost of hibernation for males may result in substantial fitness payoffs as they emerge from hibernation physiologically ready to locate females and to mate. Females apparently adopt a more energy-conservative hibernation strategy consisting of longer torpor bouts and later spring emergence, preserving their energy stores for the energetic demands of reproduction.

The variation in strategies for hibernation practiced by males and females in this study emphasizes the need to examine more carefully the adaptational issues related to the synchrony of hibernation and the physiological mechanisms of torpor and arousal. Further, individual and yearly variations in T_b measurements indicate that hibernation patterns may vary with climatic conditions. Thus, application of the present T_b-monitoring technique to *M. monax* and other hibernating species in different habitats may help to further elucidate the relationships between climatic factors and hibernation patterns in the wild.

LITERATURE CITED

ARMITAGE, K. B., AND C. M. SALSBURY. 1992. Factors affecting oxygen consumption in wild-caught yellow-bellied marmots. Comparative Biochemistry and Physiology, A. Comparative Physiology 103:729–737.

ARMITAGE, K. B., B. C. WOODS, AND C. M. SALSBURY. 2000. Energetics of hibernation in woodchucks (*Marmota monax*). Pp. 73–80 in Life in the cold: Eleventh International Symposium (G. Heldmaier and M. Klingenspor, eds.). Springer-Verlag, Berlin, Germany.

ARNOLD, W. 1988. Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 158:151–156.

ARNOLD, W. 1993. Energetics of social hibernation. Pp. 65–80 in Life in the cold: ecological, physiological, and molecular mechanisms (C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.

BARASH, D. P. 1989. Marmots: social behavior and ecology. Stanford University Press, Stanford, California.

BARNES, B. M., M. KRETZMANN, P. LICHT, AND I. ZUCKER. 1986. The influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. Biology of Reproduction 35:1289–1297.

BUCK, C. L., AND B. M. BARNES. 1999a. Annual cycle of body condition and hibernation in free-living Arctic ground squirrels. Journal of Mammalogy 80:430–442.

BUCK, C. L., AND B. M. BARNES. 1999b. Temperatures of hibernacula and changes in body composition of arctic ground squirrels over winter. Journal of Mammalogy 80:1264–1276.

CANGUILHEM, B., ET AL. 1994. Search for rhythmicity during hibernation in the European hamster. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 163:690–698.

CHRISTIAN, J. J., E. STEINBERGER, AND T. D. MCKINNEY. 1972. Annual cycle of spermatogenesis and testis morphology in woodchucks. Journal of Mammalogy 53:708–716.

DAVIS, D. E. 1967. The role of environmental factors in hibernation of woodchucks (*Marmota monax*). Ecology 48:683–689.

DAVIS, D. E. 1976. Hibernation and circannual rhythms of food consumption in marmots and ground squirrels. Quarterly Review of Biology 51:477–514.

DAVIS, D. E. 1977. Role of ambient temperature in emergence of woodchucks (*Marmota monax*) from hibernation. American Midland Naturalist 97:224–229.

FALL, M. W. 1971. Seasonal variations in the food consumption of woodchucks (*Marmota monax*). Journal of Mammalogy 52:370–375.

FERRON, J. 1996. How do woodchucks (*Marmota monax*) cope with harsh winter conditions? Journal of Mammalogy 77:412–416.

FLORANT, G. L. 1998. Lipid metabolism in hibernators: the importance of essential fatty acids. American Zoologist 38:331–340.

FRENCH, A. R. 1982. Intraspecific differences in the pattern of hibernation in the ground squirrel *Spermophilus beldingi*. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 148:83–91.

FRENCH, A. R. 1990. Age-class differences in the pattern of hibernation in yellow-bellied marmots, *Marmota flaviventris*. Oecologia 82:93–96.

FRENCH, A. R. 1992. Mammalian dormancy. Pp. 105–121 in Mammalian energetics (T. E. Tomasi and T. H. Horton, eds.). Cornell University Press, Ithaca, New York.

GEISER, F. 1988. Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 158:25–37.

GEISER, F., AND R. V. BAUDINETTE. 1987. Seasonality of torpor and thermoregulation in three dasyurid marsupials. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 157:335–344.

GEISER, F., AND G. J. KENAGY. 1988. Torpor duration in relation to temperature and metabolism in hibernating ground squirrels. Physiological Zoology 61:442–449.

GRIZZELL, R. A. 1955. A study of the southern woodchuck, *Marmota monax monax*. American Midland Naturalist 53:257–293.

HAMMEL, H. T. 1967. Temperature regulation and hibernation. Pp. 86–96 in Mammalian hibernation III (K. C. Fisher, A. R. Dawe, C. P. Lyman, E. Schonbaum, and F. E. South, eds.). Oliver and Boyd, London, United Kingdom.

HARLOW, H. J., AND G. E. MENKENS, JR. 1986. A comparison of hibernation in the black-tailed prairie dog, white-tailed prairie dog, and Wyoming ground squirrel. Canadian Journal of Zoology 64:793–796.

HAYES, S. R. 1976. Daily activity and body temperature of the southern woodchuck, *Marmota monax monax*, in northwestern Arkansas. Journal of Mammalogy 57:291–299.

HELDMAIER, G., S. ORTMANN, AND G. KORTNER. 1993. Energy requirements of hibernating alpine marmots. Pp. 175–183 in Life in the cold: ecological, physiological, and molecular mechanisms (C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.

LUECKE, R. H., AND F. E. SOUTH. 1972. A possible model for thermoregulation during deep hibernation. Pp. 577–605 in Hibernation and hypothermia: perspectives and challenges (F. E. South, J. P. Hannon, J. R. Willis, E. T. Pengelley, and N. R. Alpert, eds.). American Elsevier Publishing Company, New York.

LYMAN, C. P. 1958. Oxygen consumption, body temperature and heart rate of woodchucks entering hibernation. American Journal of Physiology 194:83–91.

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.

MICHENER, G. R. 1977. Effect of climatic conditions on the annual activity and hibernation cycle of Richardson's ground squirrels and Columbian ground squirrels. Canadian Journal of Zoology 55:693–703.

MICHENER, G. R. 1992. Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. Oecologia 89:397–406.

NAGY, K. A. 1989. Doubly-labeled water studies of vertebrate physiological ecology. Pp. 270–287 in Stable isotopes in ecological research (P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, eds.). Springer-Verlag, New York.

PENGELLEY, E. T. 1967. The relation of external conditions to the onset and termination of hibernation and estivation. Pp.1–29 in Mammalian hibernation III (K. C. Fisher, A. R. Dawe, C. P. Lyman, E. Schonbaum, and F. E. South, eds.). Oliver and Boyd, London, United Kingdom.

PITTENDRIGH, C. S. 1960. Circadian rhythms and the circadian organization of living systems. Cold Spring Harbor Symposium on Quantitative Biology 25:159–184.

PIVORUN, E. B. 1976. A biotelemetry study of the thermoregulatory patterns of *Tamias striatus* and *Eutamias minimus* during hibernation. Comparative Biochemistry and Physiology, A. Comparative Physiology 53:265–271.

SNYDER, R. L., AND J. J. CHRISTIAN. 1960. Reproductive cycle and litter size of the woodchuck. Ecology 41:647–656.

SNYDER, R. L., D. E. DAVIS, AND J. J. CHRISTIAN. 1961. Seasonal changes in the weights of woodchucks. Journal of Mammalogy 42:297–312.

WANG, L. C. H. 1972. Circadian body temperature of Richardson's ground squirrel under field and laboratory conditions: a comparative radiotelemetric study. Comparative Biochemistry and Physiology, A. Comparative Physiology 43:503–510.

WANG, L. C. H. 1973. Radiotelemetric study of hibernation under natural and laboratory conditions. American Journal of Physiology 224:673–677.

WANG, L. C. H. 1978. Energetic and field aspects of mammalian torpor: the Richardson's ground squirrel. Pp. 109–145 in Strategies in the cold: natural torpidity and thermogenesis (L. C. H. Wang and J. W. Hudson, eds.). Academic Press, New York.

WANG, L. C. H., AND J. W. HUDSON. 1971. Temperature regulation in normothermic and hibernating eastern chipmunk, *Tamias striatus*. Comparative Biochemistry and Physiology, A. Comparative Physiology 38:59–90.

ZERVANOS, S. M. 1969. Effects of photoperiod on the daily activity of the Allegheny wood rat (*Neotoma floridana*). Mammalia 33:509–515.

ZERVANOS, S. M., AND R. E. HENSHAW. 1970. Graded effect of acclimation temperature on thermogenesis in winter-captured little brown bats. Pennsylvania Academy of Science 44:207–211.

ZERVANOS, S. M., AND C. M. SALSBURY. 2001. Telemetry system for the continuous monitoring of temperature, location and activity of free-ranging animals. Bulletin of the Ecological Society of America 82:189–191.