HOW DO WOODCHUCKS (*MARMOTA MONAX*) COPE WITH HARSH WINTER CONDITIONS?

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Woodchucks (*Marmota monax*) are a solitary species that, unlike other species of marmots, hibernate singly. The object of this study was to analyze how this species copes with harsh winter conditions in the field, in the northern part of its range. Woodchucks in the population studied have a pattern of hibernation similar to that of alpine marmots (*Marmota marmota*), they face comparable burrow temperatures, and their range of body temperatures is similar. However, woodchucks lose more weight than alpine marmots, both on a daily basis and throughout the period of hibernation. Woodchucks are less specialized than montane species of marmots, but their hibernacula provide better insulation than those employed by species residing in mountainous habitats.

Key words: *Marmota monax*, woodchuck, Sciuridae, hibernation, weight, body temperature, burrow temperature

The subtribe Marmotina in the family Sciuridae is represented by 14 species of marmots (Hafner, 1984). This subtribe spans the full range of social grades, from asocial species to those that live in harems (Armitage, 1981; Michener, 1983). Marmots typically live at high elevation or latitude and hibernate; most of them do so in extended family groups (Arnold, 1990*a*, 1990*b*, 1993). Arnold (1990*b*, 1993) and Arnold et al. (1991) have argued that group hibernation and social thermoregulation in highly social species are adaptations to cope with long and cold winters. They suggest that the evolution of sociality in these species is associated with this behavior.

Woodchucks (*Marmota monax*) are a solitary species that hibernate singly or, occasionally, in pairs (Hamilton, 1934). They are widely distributed in North America from Alaska and the Rocky Mountains to the eastern seaboard and primarily inhabit open woodlands, thickets, rocky slopes, fields, and clearings characterized by dry soils (Lee and Funderburg, 1982). Within this range, they face an array of climatic conditions in winter and are reported to remain active during winter in the most southern parts of their range (Anthony, 1962). In northern latitudes, where winters can be quite severe, this species apparently still hibernates singly, unlike other species of marmots.

The object of my study was to understand how *M. monax* copes with harsh winter conditions. This was done, in the field, by analyzing length of the hibernation period, the importance of loss of weight during hibernation, and body temperature compared to temperatures in the burrow and outside the burrow. Two questions were addressed. Do woodchucks face burrow conditions comparable to those of marmots living at high elevations? If so, how do they survive while hibernating singly rather than in a group as do other species of marmots.

MATERIALS AND METHODS

The study area was located in cultivated fields at Sainte-Luce, Québec (68°21'W; 48°32'N). For a detailed description of the area see Ferron and Ouellet (1989). Woodchucks were live-trapped in August 1991. Captured animals were weighed, gender was determined, and animals were tattooed on their belly for identification with a Ketchum's tattoo set. Radio-transmitters (model IMP-2 with temperature sensor, Lotek Engineering; 150.002–150.242 MHz) were surgically implanted in the abdominal cavity of 15 anesthetized woodchucks. Each transmitter was calibrated before use, with a precision of ±0.1°C. Woodchucks were released where they were captured. Body temperature of hibernating woodchucks was recorded for 11 animals (four males, seven females); signals from the four remaining animals were lost due to difficulties such as short range of the transmitters, excessive movements of woodchucks, or failure of transmitters. Data were recorded once a week from mid-August 1991 to early April 1992. Seven animals were recaptured shortly after emergence from hibernation and weighed again.

Temperature of burrows was measured, with a precision of ±0.1°C, using the technique described by Arnold (1993). A tube, with a diameter of 1 cm, was introduced into each hibernaculum (the burrow used for hibernation) before the woodchuck plugged it for the winter. To do so, one end of the tube was attached to the tail of the woodchuck with adhesive tape and the animal was released into its burrow. Woodchucks generally pulled 5-7 m of tube into the burrow. The tube was then pulled off of the marmot tail. As animals frequently moved from one burrow to another before hibernation, they were recaptured and several burrows in each home range fitted with tubing. When I determined which burrow was used for hibernation, I inserted a probe in it, through the tubing, and left it in place ($n = 9$). Temperature of the burrow was read with a portable thermometer plugged into a thermocouple wire. Ambient temperature also was recorded for each observation period.

According to Heldmaier et al. (1993), hibernating alpine marmots (*Marmota marmota*) have body temperatures of 5–12°C. Consequently, in the present study, I considered hibernation starting when body temperatures fell to <15°C, and ending when body temperature was >15°C and maintained as such. Values are presented as mean ± 1 *SD*.

RESULTS

From mid-July to mid-August, when woodchucks were still regularly active above ground, the maximal body temperature recorded for each, within their respective burrow, averaged 38.7°C (range, 34.5–42.0°C). Hibernation began between 18 September and 16 November (mean date ± 1 *SD*, 13 October ± 18.5 days; median, 15 October; $n = 11$). The earliest emergence from hibernation was 15 March and the latest 1 April (25 March ± 7.5 days; median, 25 March; $n = 10$). Hibernation lasted 167 days ± 18.7 days (median, 162 days; $n = 10$; Table 1). Only one animal, a male, died during hibernation.

Loss of weight during hibernation was recorded for seven animals (two males, five females) that were captured shortly before entry into and shortly after emergence from hibernation (Table 1). The two males lost 47% of their weight (mean = 1.6 kg),

TABLE 1.—*Weight loss during hibernation and length of hibernation in free-living* Marmota monax. *Daily loss of mass is based on pre-hibernation mass (in g). Length of hibernation is based on the period when body temperature was <15°C.*

Animal and sex	Pre-hibernation weight (kg)	Weight lost[a] (%)	Daily loss of mass (mg day^{-1} g^{-1})	Length of hibernation (days)
Males				
1	3.60			172
2	3.65	48	2.74	175
4	3.45			144
9	3.37	45		
Mean (males)	3.52	47		164
Females				
3	3.00	40	1.97	186
5	2.66	30	1.77	172
6	3.30	33	1.97	169
7[b]	3.23	40	2.48	166
8[b]				134
10	2.61	42	2.17	196
11				152
Mean (females)	2.96	37	2.07	168
Mean (all animals)	3.12	40	2.18	167

[a] Calculated for animals recaptured shortly after emergence from hibernation.

[b] Marmot #7 hibernated with marmot #8.

TABLE 2.—*Average body temperature, burrow temperature, and above-ground temperature recorded October 1991–March 1992 for 11 woodchucks (four males, seven females).*

Month	Body temperature $\bar{X} \pm SD$	Burrow temperature $\bar{X} \pm SD$	Above-ground temperature $\bar{X} \pm SD$
October	17.5 ± 1.3	6.9 ± 2.4	7.3 ± 3.6
November	12.4 ± 3.3	2.8 ± 0.8	4.6 ± 2.6
December	11.6 ± 6.3	2.2 ± 0.2	−11.9 ± 6.0
January	6.6 ± 0.5	1.9 ± 0.3	−15.6 ± 9.6
February	8.2 ± 1.4	2.0 ± 0.3	−12.5 ± 2.5
March	16.5 ± 4.2	2.3 ± 0.3	−0.8 ± 4.4

whereas the five females lost 37% of their weight (mean = 1.1 kg). Because of the small samples, sexes were not compared statistically. However, relative loss of weight in males was higher than for females, and might be related to spermatogenesis, which occurs during hibernation (Davis, 1976). Female 7, which hibernated with female 8 (as determined by trapping data and visual observation), had loss of weight similar to that of other females. Loss of weight during hibernation also can be expressed in terms of daily, mass-specific loss of weight (mg g^{-1} day^{-1}; g = body mass on entry into hibernation; Arnold, 1993; Table 1). The average daily loss in mass-specific weight for six woodchucks (one male, five females) was 2.18 mg.

Mean body temperature, burrow temperature, and above-ground temperature recorded for all animals (n = 11) in the field between October 1991 and March 1992 were lowest in January (Table 2). The lowest body temperature recorded for each animal was 4.2 ± 1.5°C (range, 2.0–7.0°C) while the lowest burrow temperature was 0.7 ± 0.5°C (range, 0.1–1.3°C). More than one-half (53%) of the lowest body temperatures were recorded in January, while 47% of the lowest burrow temperatures were observed in the second one-half of December. As data were recorded once each week, the duration of these lowest body and burrow temperatures was not documented. The lowest recorded ambient temperature was −26.2°C, in January.

As I did not continuously record body temperature in the field, I could not document arousal episodes during hibernation. However, body temperatures of ca. 30°C were recorded occasionally, particularly in mid-December, which indicates that arousal bouts occur in the field, as Davis (1967) reported for captive woodchucks.

DISCUSSION

Maximum body temperature of 38.7°C (range, 34.5–42.0°C) recorded in the field on active woodchucks during the present study is similar to that of other species of marmots. Arnold (1988) reported a maximum body temperature of 40°C and mean daily body temperature of 37.7 and 37.9°C, for two active females of *M. marmota*. Mean body temperature for laboratory animals ranged from 35.1 to 36.9°C (Armitage et al., 1990) for *Marmota flaviventris*. In a study of free-ranging *M. flaviventris*, Melcher et al. (1990) reported that highs in daytime body temperature average 39.8°C and body temperature of active animals rarely exceeds 40°C.

The lowest burrow temperature reached for *M. marmota* in hibernation was 0.2°C (Arnold, 1993), while it was 0.1°C for *M. monax* in the present study. Also, minimum body temperature recorded for *M. marmota* during torpor when burrow temperature was 0.2–4.0°C was 2.3–8.0°C (Arnold, 1993: figure 1). Direct comparison of these data with the present study is difficult as my data were recorded once per week, whereas Arnold (1993) recorded measurements every 10–15 min. However, the lowest body temperatures recorded for both species were ca. 4 ± 1.5°C.

The time spent hibernating by my population of *M. monax* was in the same range as for *M. marmota* and was shorter than for Asian species. Woodchucks spent an average of 167 days in hibernation in my study, compared to 170 days for adult *M. marmota* nold, 1993) and 200–250 days for different species of Asian marmots (*M. baibacina, M. bobac, M. camtschatica, M. caudata, M. menzbieri,* and *M. sibirica*—Arnold, 1993). The period of hibernation was calculated from data on body temperature in the present study; if data on time spent in the hibernaculum had been used, it would have slightly increased the length of hibernation reported for woodchucks. Time spent hibernating by my population of woodchucks also was longer than for more southern populations where emergence from hibernation can be as early as 29 January–13 February in Pennsylvania (Davis, 1976).

Consequently, I conclude that woodchucks in the population studied have a pattern of hibernation similar to that of *M. marmota* observed in the field by Arnold (1988, 1990*a*, 1990*b*, 1993), that they are facing comparable burrow temperatures, and that their response in terms of body temperature is similar. However, relative loss of weight is greater in *M. monax* (mean = 47% for males, 37% for females) than in *M. marmota* (mean = 34% for males, 31% for females, as calculated from table 2 in Arnold, 1993). The same tendency is observed for daily loss of mass-specific weight, which is greater for *M. monax* (mean = 2.74 mg for males, 2.07 mg for females) than for *M. marmota* (mean = 1.75 mg for males, 1.59 mg for females—Arnold, 1993). Thus, it appears that under comparable environmental conditions, the woodchuck is subject to greater loss of weight than the alpine marmot on a daily basis, as well as for the entire period of hibernation.

It may be argued that woodchucks are not as physiologically specialized for hibernation in harsh weather conditions as is *M. marmota*. Indeed, the alpine marmot typically lives at high elevation in the mountainous regions of Europe. It occurs between 1,400 and 2,700 m, but is found most often between 2,300 and 2,700 m (Perrin, 1993). Group hibernation evolved in this species to cope with harsh overwintering conditions (Arnold 1990*a*, 1990*b*, 1993). Conversely, woodchucks live in open, well-drained mesic fields, along hedgerows, adjacent to small woodlots, and near forest edges over a wide range in North America (Barash, 1989). They must cope with different climatic conditions in winter within their geographic range; they can even remain active during winter in the southern United States (Anthony, 1962).

The 40% loss of weight reported here for *M. monax* is similar to that reported for two high-elevation species of marmots, *M. caligata* and *M. olympus* (Barash, 1989). Arnold's studies (1990*a*, 1990*b*) were conducted at elevations between 1,100 and 1,500 m in the Berchtesgaden Alps of Germany, which are relatively low-elevation sites for this species. Total loss of weight or daily mass-specific loss of weight could thus be greater for *M. marmota* at higher elevation, but no data on this are available.

Finally, unlike species of marmots occupying high-elevation habitats, *M. monax* hibernates singly or, less often, in pairs (Hamilton, 1934; this study). The question then arises: how can woodchucks survive without group hibernation in the northern part of their range, where winter conditions are similar to those at high elevation and where social grouping is the rule to survive winter? In mountainous habitat, soil is generally much shallower than in habitats of woodchucks, and montane species may well dig shallower burrows because digging is considerably more difficult in their environment (Barash, 1989). Hibernacula of woodchucks may then provide better insulation than those in alpine and subalpine meadows. Indeed, our results suggest that burrow temperature is similar for *M. marmota* (Arnold, 1993) and *M. monax* (this study). If follows that a single woodchuck can afford to maintain temperatures in the hibernaculum within the same range as a group of alpine marmots. However, as discussed above, the process appears to be more costly in terms of total loss of weight and daily mass-specific loss of weight for our woodchucks than for alpine marmots from the Berchtesgaden Alps, but similar to that of *M. caligata* and *M. olympus,* two other high-elevation marmots that hibernate in groups. Another factor that might be considered to explain differences between species of marmots with regard to loss of weight over winter, is how long after emergence do marmots rely on use of their fat. Some Asian marmots apparently use their fat for several weeks after emergence (K. B. Armitage, pers. comm.). It is not known how long *M. marmota* uses body fat before it can forage, or how this compares with *M. monax.*

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