
The Influence of Environment, Sex, and Innate Timing Mechanisms on Body Temperature Patterns of Free-Ranging Black-Tailed Prairie Dogs (*Cynomys ludovicianus*)

Erin M. Lehmer*

Jonathan M. Bossenbroek

Beatrice Van Horne

Department of Biology, Colorado State University, Fort Collins, Colorado 80523

Accepted 9/23/02

ABSTRACT

Mechanisms that influence body temperature patterns in black-tailed prairie dogs are not well understood. Previous research on both free-ranging and laboratory populations of black-tailed prairie dogs (*Cynomys ludovicianus*) has suggested that reductions in ambient temperature and food and water deprivation are the primary factors that stimulate torpor in this species. In other species, however, torpor has been shown to be influenced by a multitude of factors, including innate circadian and circannual timing mechanisms, energy status, and reproductive behaviors. Our objective was to clarify the influence of weather, sex, and intrinsic timing mechanisms on the body temperature patterns of free-ranging black-tailed prairie dogs. We monitored body temperatures of eight adult (>1 yr) prairie dogs from November 1999 to June 2000. Prairie dogs showed distinct daily and seasonal body temperature patterns, which reflected changes in ambient temperatures that occurred during these periods. These patterns of daily and seasonal heterothermy suggest that body temperature patterns of black-tailed prairie dogs may be driven by an innate timing mechanism. All prairie dogs entered torpor intermittently throughout winter and spring. Torpor bouts appeared to be influenced by precipitation and reductions in ambient temperature. Our results also suggest that reproductive behaviors and circadian timing may influence torpor in this species.

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) display unusual overwinter body temperature patterns that are not well understood. Although these animals have entered torpor under laboratory conditions, it was long presumed that they remain active throughout winter in the natural environment (King 1955; Smith 1958; Tileston and Lechleitner 1966; Michener 1983a; Bakko et al. 1988; Harlow 1997). In a recent study, however, we demonstrated that free-ranging populations of black-tailed prairie dogs enter torpor intermittently during winter (Lehmer et al. 2001), demonstrating body temperature patterns intermediate to those of hibernators and nonhibernators. Both free-ranging and laboratory populations of prairie dogs enter torpor following reductions in ambient temperature (Hamilton and Pfeifer 1977; Harlow 1997; Lehmer et al. 2001). Under laboratory conditions, torpor is most common when prairie dogs are deprived of food and water for prolonged periods at these low temperatures (Harlow and Menkens 1986). In the natural environment, however, sudden food and water deprivation does not seem to be closely associated with torpor, since snowfall, which could prevent foraging, has not been associated with entrance into or arousal from torpor (Lehmer et al. 2001).

The underlying physiological mechanisms that drive torpor are complex; therefore, it seems unlikely that torpor in black-tailed prairie dogs is influenced solely by changes in ambient temperature or by fluctuations in food availability. In many mammalian species, daily and seasonal torpor are thought to be stimulated primarily by innate circadian and circannual timing mechanisms (Davis 1976; Körtner and Geiser 2000), but there is evidence that these forms of torpor can be influenced by a variety of external factors. For example, light cycles are thought to allow animals practicing daily torpor to entrain their body temperature patterns to promote activity during the most appropriate times of day (Geiser and Ruf 1995). Seasonal torpor can be influenced by certain aspects of an animal's natural history, including age and gender. Michener (1992) reported that female Richardson's ground squirrels (*Spermophilus richardsonii*) had longer torpor bouts, shorter intertorpor arousal periods, and longer hibernation seasons than did male squirrels. Similar patterns have been observed in free-ranging Columbian ground squirrels (*Spermophilus columbianus*; Young 1990). These sex-specific differences in torpor patterns are thought to

* Corresponding author; e-mail: emlehmer@lamar.colostate.edu.

result from the earlier onset of reproductive behaviors in male ground squirrels relative to female ground squirrels (Michener 1992). An animal's energetic status can also influence its torpor patterns. Torpor has been shown to occur more frequently in animals with limited access to food (Lovegrove et al. 2001a), and it is believed that a lower energetic status can make animals more sensitive to environmental cues (Körtner and Geiser 2000) and thus more likely to enter torpor.

Because there are few data on torpor in free-ranging black-tailed prairie dogs, mechanisms that stimulate the unusual body temperature patterns of this species in the natural environment are not well understood. Here we try to clarify the influence of environment, sex, and innate timing mechanisms on the initiation and duration of torpor in black-tailed prairie dogs. We also examine the potential for black-tailed prairie dogs to practice heterothermy and facultative estivation. To focus our analysis, we developed three hypotheses to evaluate the body temperature patterns of black-tailed prairie dogs: (1) immergence into torpor is associated with unfavorable changes in weather, such as reductions in ambient temperature, increased precipitation, and high wind speeds; (2) timing of torpor is more closely tied to weather and other ambient conditions than to an innate timing mechanism; and (3) male and female prairie dogs show different torpor patterns that coincide with sex-specific reproductive behaviors.

Material and Methods

Overwinter body temperature patterns were monitored in adult (>1 yr) black-tailed prairie dogs located on the Pawnee National Grassland in Weld County, Colorado, continuously from November 10, 1999, to June 15, 2000.

In the fall (November 1–10) of 1999, 10 prairie dogs (five males, five females) were livetrapped from two colonies separated by ca. 2 km. After capture, temperature-sensitive data loggers (Stow Away Tidbit, Onset Computer, Bourne, Mass.) were surgically implanted into the abdominal cavity of each prairie dog (Lehmer et al. 2001). Loggers were programmed to record body (abdominal) temperature (T_b) to the nearest 0.1°C in the temperature range of -20° to 50°C every 24 min throughout the study period. Loggers were calibrated in a stirred water bath of known temperature before implantation and after removal. Each animal was uniquely identified with a numbered tag in each ear (National Band and Tag, Newport, Ky.). Following recovery from anesthesia (ca. 4 h), prairie dogs were released to their original sites of capture.

Weather data, including minimum and maximum ambient temperature ($^\circ\text{C}$), precipitation (mm), wind speed (km/h), and soil temperature ($^\circ\text{C}$) were recorded daily from November 1999 to July 2000 by the Shortgrass Steppe Long-Term Ecological Research Station at a location <2 km from each prairie dog colony studied. Ambient temperature (T_a) and wind speed were measured 1.5 m above ground level. T_a measurements were

made in a Standard Weather Box (Belfort Instrument, Baltimore). Soil temperatures (T_s) were recorded at a depth of 186 cm.

In the summer (June 15–25) of 2000, eight prairie dogs (five males, three females) were recaptured. One of these females (F1) had been implanted with a temperature logger in November 1998, and thus her T_b was recorded for approximately 19 consecutive months. Immediately after capture, temperature loggers were surgically removed, and prairie dogs were released to their original sites of capture. Data from the loggers were downloaded using Box Car Pro software (version 3.51, Onset Computer, Bourne, Mass.) A prairie dog was considered to be in torpor if it experienced a continuous reduction in T_b that, at some point, reached a level below the mean seasonal low reported for this species (31°C ; Bakko et al. 1988). Because 31°C is below the mean daily minimum T_b that we observed in prairie dogs at any time during winter or spring, this criterion ensured that torpor bouts were distinguished from daily and seasonal fluctuations in T_b that prairie dogs regularly experienced. Thus, we have defined a torpor bout as the reduction in T_b below seasonal euthermic normal levels (36°C ; Bakko et al. 1988; Lehmer et al. 2001), the maintenance of a minimum T_b less than 31°C , and the subsequent increase in T_b above 36°C . The duration of a torpor bout was measured in hours from the time in which T_b decreased below 36°C until the time at which T_b approximated pretorpid levels ($>36^\circ\text{C}$). We determined cooling rates during torpor by calculating the average number of hours required to reduce T_b from euthermic levels ($<36^\circ\text{C}$) to the minimum level reached during the torpor bout. Rates of rewarming were determined by calculating the average number of hours required to raise T_b from the minimum level reached during a torpor bout to a level above 36°C .

All statistical analyses were conducted on data recorded between November 10, 1999, and June 15, 2000, since all animals were implanted with loggers during this period. One-way ANOVA was used to compare subtle daily and seasonal differences in T_b during periods in which prairie dogs were not in torpor (i.e., daily and seasonal heterothermy; SAS V.8, SAS Institute, Cary, N.C.). We also used one-way ANOVA to compare differences in general torpor patterns between male and female prairie dogs and between seasons. These tests included comparisons of the number and length of torpor bouts, differences in minimum T_b , and time required to reach minimum T_b and return to euthermic T_b . We evaluated differences in dates of first and final torpor bouts between male and female prairie dogs by comparing Julian dates of first immergence and final emergence from torpor for each animal (ANOVA). One-way ANOVA was also used to compare weather patterns (minimum and maximum T_a , precipitation, and wind speed) between winter and spring during periods when animals were in torpor. Unless otherwise stated, values describing differences in these general torpor and weather patterns are presented as mean \pm SE and the maximum and minimum value for each

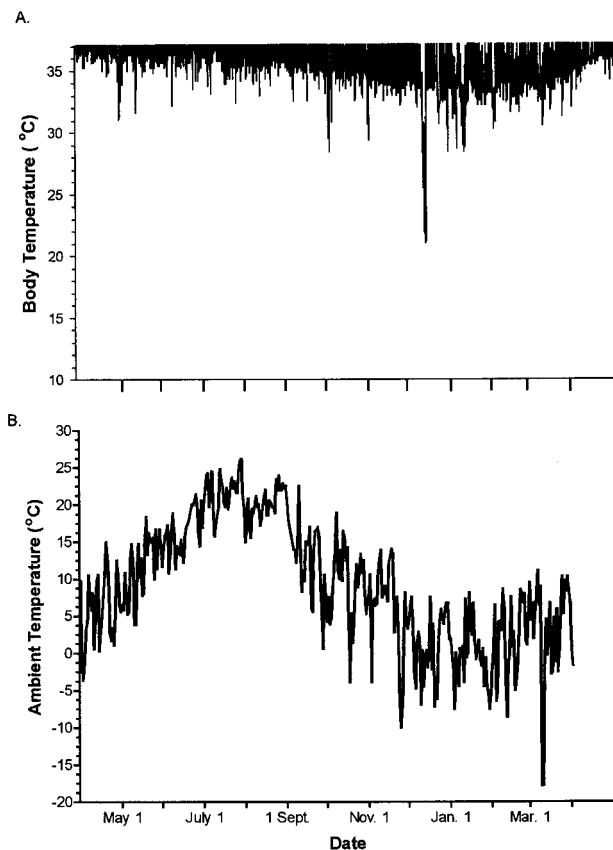


Figure 1. Relationship between seasonal fluctuations in body temperature and ambient temperature in a free-ranging black-tailed prairie dog (*Cynomys ludovicianus*) monitored at the Central Plains Experimental Range (Weld County, Colo.). A, Daily minimum body temperature of a single adult female recorded continuously from April 1, 1999, to April 1, 2000. B, Daily mean air temperature recorded 1.5 m above ground level at a location within 2 km of the prairie dog colony studied.

variable. Differences in these variables were considered to be significant if $P < 0.05$. Spearman correlations were used to determine relationships between minimum T_b of prairie dogs during torpor, bout length, and T_s . We used cross correlations to further evaluate relationships between mean daily minimum T_b of prairie dogs and individual weather variables (minimum T_a , maximum T_a , precipitation, and wind speed; Minitab V. 13.31, Minitab, State College, Pa.). We treated these variables as time series data and checked for lags in correlation from -10 to $+10$ d. Separate cross correlations were made between each weather variable and daily average minimum T_b of prairie dogs. Unless otherwise stated, values describing these cross correlations are represented by the correlation coefficient with its associated time lag.

Results

General Body Temperature Patterns

Excluding torpor bouts, T_b of prairie dogs was highly variable across seasons. Daily mean ($P < 0.01$) and minimum ($P = 0.04$) T_b of prairie dogs varied monthly and generally decreased to an annual low from November 10 to January 15 and then increased from January 15 to June 15. Changes in T_b were reflected by changes in T_a , which also decreased from November 10 to January 15 and increased from January 15 to June 15. Patterns of seasonal heterothermy are especially apparent when examining a full year of T_b and T_a data in a representative animal, F1 (Fig. 1). Excluding periods in which animals were torpid, prairie dogs also displayed a daily T_b cycle throughout the year, with mean diurnal T_b always significantly higher than mean nocturnal T_b ($P < 0.01$). Mean diurnal T_b 's were highest during May (40.2°C) and lowest during December (36.4°C). Likewise, mean nocturnal T_b 's were also highest during May (36.8°C) and lowest during December (31.7°C). The greatest amplitude of mean T_b on a single day was 6.8°C , which occurred during December.

All prairie dogs entered torpor sporadically from November 10 to April 1, with the first torpor bout beginning November 11 and last bout beginning on March 29. From February 1 to February 9, no animals entered torpor. Therefore, for the purposes of this study, we have used this period to arbitrarily delineate winter and spring seasons. Torpor was more common during winter (November 10–February 1) than during spring (February 2–April 1; $P < 0.01$; Fig. 2). General body temperature patterns of torpor bouts during winter and spring—including number of bouts, bout lengths, minimum T_b , time spent at

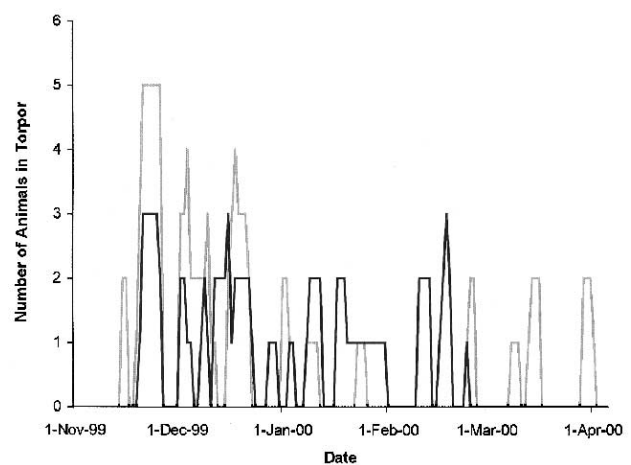


Figure 2. Number of male (gray lines) and female (black lines) black-tailed prairie dogs (*Cynomys ludovicianus*) in torpor daily from November 10, 1999, to April 1, 2000. Eight (five male, three female) adult (>1 yr) prairie dogs were monitored at the Central Plains Experimental Range (Weld County, Colo.).

Table 1: Comparison of general torpor patterns between winter (November 10, 1999, to February 1, 2000) and spring (February 2 to April 1, 2000)

	Winter				Spring				P Value
	\bar{X}	SE	Minimum	Maximum	\bar{X}	SE	Minimum	Maximum	
Number of bouts	5.4	3.2	1	12	1.5	1.5	0	4	<.01
Bout length (h)	72.5	41.9	14.0	187.5	49.3	18.9	24.2	73.6	<.01
Minimum T_b ($^{\circ}\text{C}$)	27.3	5.1	10.1	30.9	30.4	.6	28.8	30.9	<.01
Time to reach minimum T_b (h)	39.0	25.6	5.2	129.9	32.8	10.4	14.8	55.0	.11
Time at minimum T_b (h)	4.0	2.5	2.7	10	4.9	5.1	.8	7.8	.28
Time to rewarm to euthermic T_b (h)	25.2	25.5	1.0	98.2	13.0	12.1	1.2	36.0	.01

Note. Body temperature (T_b) patterns were monitored in eight adult (>1 yr) black-tailed prairie dogs (*Cynomys ludovicianus*) at the Central Plains Experimental Range (Weld County, Colo.). Differences in torpor patterns between winter and spring were evaluated with one-way ANOVAs.

minimum T_b , and rates of cooling and rewarming—are presented in Table 1. Minimum T_b of prairie dogs during torpor was strongly correlated to bout length ($r = -0.62$; Fig. 3). In contrast, T_s was not strongly correlated to either torpor bout duration ($r = 0.18$; Fig. 4A) or minimum T_b reached during torpor ($r = 0.06$; Fig. 4B).

Torpor bouts of prairie dogs showed a pronounced circadian cycle. In 85% of the torpor bouts we observed ($n = 58$), immergence occurred between 11 A.M. and 4 P.M. (Fig. 5). Likewise, in 79% of the torpor bouts we observed, emergence took place between 11 A.M. and 3 P.M. (Fig. 5). There was no difference between the circadian timing of immergence ($P = 0.56$) or emergence ($P = 0.47$) from torpor between male and female prairie dogs. With the exception of one torpor bout, all bouts were within ± 6.5 h of a 24-h interval (Fig. 6). The single bout that did not follow this pattern was 14 h in length.

Influence of Weather on Torpor Patterns

Changes in weather and declines in T_b were strongly cross correlated, and reductions in T_b were primarily affected by weather in the previous 24-h period (Figs. 7, 8). During winter, average minimum T_b of prairie dogs was most strongly cross correlated to maximum T_a ($r = 0.48$) and minimum T_a ($r = 0.44$) at time lags of 1 d (Fig. 7). These cross correlations decayed below $r = 0.05$ by day 3. There was also a strong cross correlation between precipitation and minimum T_b in winter ($r = -0.76$) that occurred at -1 d, suggesting that reductions in T_b were not directly caused by precipitation but that precipitation often coincided with low T_b . There was no clear relationship between wind speed and reductions in T_b during winter, since the strongest cross correlation between these variables ($r = -0.25$) occurred at a time lag of -5 d. During spring, average minimum T_b of prairie dogs was strongly cross correlated to maximum T_a ($r = 0.75$) as well as minimum T_a ($r = 0.55$) at time lags of 1 d (Fig. 8). These cross correlations decayed below $r = 0.05$ by day 4. Precipitation and wind speed

did not appear to have a large effect on minimum T_b during spring, since the strongest cross correlations between these variables were $r = 0.18$ (time lag = 2 d) and $r = 0.34$ (time lag = 3 d), respectively.

Weather triggers associated with the immergence into torpor were not different between winter (November 10–February 1) and spring (February 2–April 1). Torpor bouts that occurred during winter were associated with reductions in maximum and minimum $T_a < 6^{\circ}\text{C}$ in the 24 h before the onset of a torpor bout, whereas during spring, torpor bouts were associated with reductions in maximum and minimum $T_a < 9^{\circ}\text{C}$ in the 24 h before the onset of the bout. During periods in which animals were torpid, minimum T_a (winter $\bar{X} = -6.7^{\circ}\text{C}$, spring $\bar{X} = -5.7^{\circ}\text{C}$; $P = 0.11$), maximum T_a (winter $\bar{X} = 8.1^{\circ}\text{C}$, spring $\bar{X} = 5.5^{\circ}\text{C}$; $P = 0.15$), precipitation (winter $\bar{X} = 0.2$ mm, spring $\bar{X} = 0.9$ mm; $P = 0.07$), and wind speed (winter $\bar{X} = 68$ km/h, spring $\bar{X} = 84.6$ km/h; $P = 0.24$) did not differ between winter and spring. However, it is noteworthy that, during

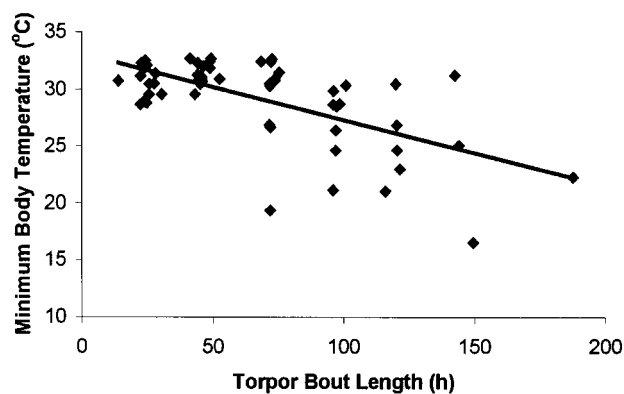


Figure 3. Correlation between torpor bout lengths and minimum body temperatures reached during torpor. Torpor patterns were monitored in eight adult (>1 yr) black-tailed prairie dogs (*Cynomys ludovicianus*) at the Central Plains Experimental Range (Weld County, Colo.).

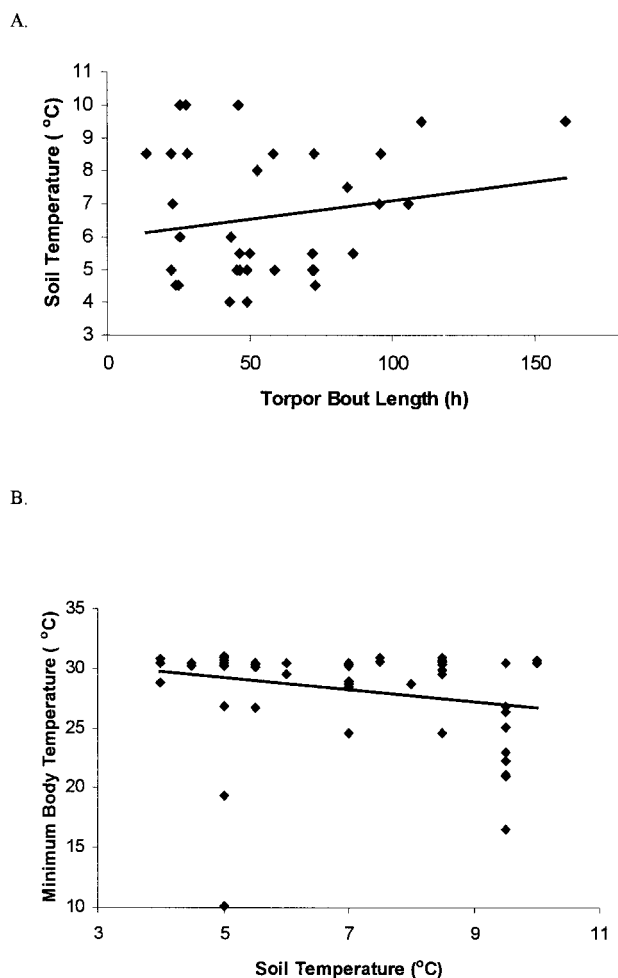


Figure 4. Relationship between soil temperature and torpor patterns of adult ($n = 8$) black-tailed prairie dogs (*Cynomys ludovicianus*). A, Correlation of torpor bout length and soil temperatures. B, Correlation of minimum body temperatures during torpor and soil temperatures. Soil temperatures were measured 186 cm below ground level.

winter, 7.4% of the days prairie dogs spent in torpor had precipitation in the form of rain or snow, whereas during spring, 54.5% of the days spent in torpor had rain or snow.

Gender Differences in Torpor Patterns

Comparisons of torpor patterns between male and female prairie dogs are presented in Tables 2 and 3. Male and female prairie dogs did not differ in their number of torpor bouts, minimum T_b reached during torpor, bout lengths, time spent at minimum T_b , or time required to rewarm to euthermic T_b . However, male prairie dogs required more time to reach minimum T_b during torpor than females. Male prairie dogs began to enter torpor earlier in the winter than females and continued to enter torpor later into the spring than female prairie dogs (Fig. 2); however,

the total number of hours spent torpid did not differ between males and females (Table 2). Neither male nor female prairie dogs entered torpor during the period between February 1 and February 9, a period that may coincide with copulation. Masses of male prairie dogs were greater than female prairie dogs both in the fall (male $\bar{X} = 1,126$ g; female $\bar{X} = 879$ g; $P = 0.02$) and in the spring (male $\bar{X} = 1,030$ g; female $\bar{X} = 780$ g; $P = 0.01$).

Evidence of Facultative Estivation

During the summer of 1999 (May 1–September 30), prairie dog F1 experienced six episodes in which her T_b dropped below the mean seasonal low reported for this species (37°C; Bakko et al. 1988) for more than 15 h. Cyclical T_b patterns during these episodes strongly resembled torpor patterns we recorded in prairie dogs during winter and spring, since F1 experienced a reduction in T_b below seasonal euthermic norms, maintained a low T_b for a period of time, and subsequently increased T_b to levels that approximated seasonal euthermic norms. Thus, although the mean minimum T_b of these bouts (31.4°C) was above our criterion for torpor during winter and spring (31°C), we will refer to these episodes as torpor bouts. Minimum T_b during these summer torpor bouts averaged 31.4°C (± 1.5), with 3.4 h (± 1.8) spent at the minimum T_b . F1 required 24.33 h (± 17.9) to reach minimum T_b and 27.8 h (± 33.0) to rewarm to euthermic levels. Minimum T_b during torpor and bout length were strongly correlated ($r = -0.79$). In contrast, correlations between T_s and minimum T_b during torpor ($r = -0.09$) as well as between T_s and torpor bout length ($r = -0.03$) were not strong. During all summer torpor bouts, T_b began to decline between 1 P.M. and 6 P.M., and rewarming occurred between 11 A.M. and 5 P.M. From May 1 to September 1, all torpor bouts were less than 24 h in length; however, bouts averaged 122.1 h in length before May 1 and after September 1. Average minimum T_b of F1 during torpor was cross correlated to maximum T_a ($r = 0.40$) and minimum T_a ($r = 0.27$) at time lags of 1 d. Precipitation was also cross correlated to minimum T_b ($r = -0.35$); however, these cross correlations did not show a time lag effect (time lag = 0 d). Wind did not appear to have a large influence on summer torpor, since the strongest cross correlation between wind speed and minimum T_b was $r = 0.15$, which occurred at a time lag of -4 d. Torpor bouts during this summer period were generally associated with increases in $T_a > 10^\circ\text{C}$ and > 1.5 mm rainfall within a 24-h period. It is possible that F1 entered torpor in response to physiological stress rather than to environmental cues; however, we did not find evidence to suggest that the physical condition of F1 was exceptionally poor relative to other female prairie dogs in our study. F1 was an adult female who was at least 24 mo old at the time of final capture (May 2000). At the time of original capture (November 1998), F1 weighed 855 g, and the average mass of other female prairie dogs we captured at this time was

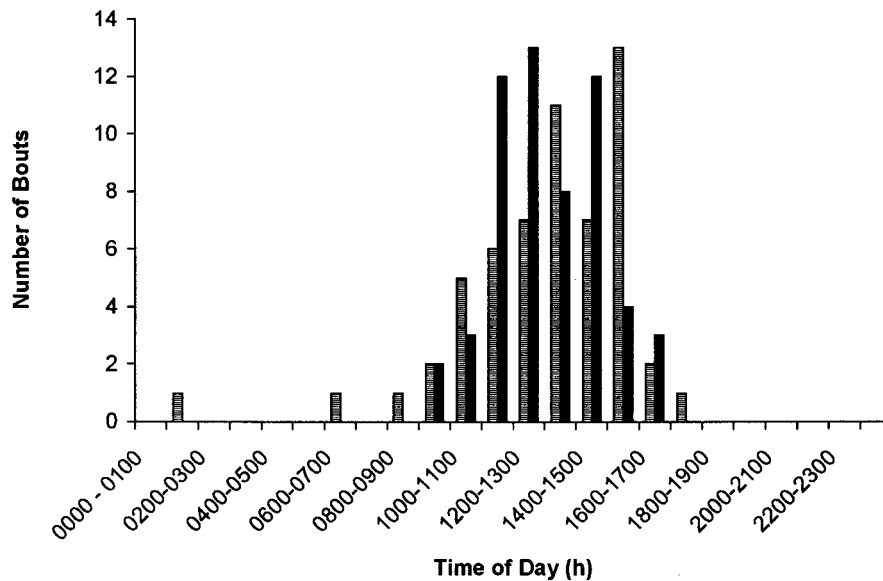


Figure 5. Circadian timing of immergence into torpor (*striped bars*) and emergence from torpor (*solid bars*). Torpor patterns were monitored in eight (five male, three female) adult (>1 yr) black-tailed prairie dogs at the Central Plains Experimental Range (Weld County, Colo.) from November 1999 to June 2000.

863 g (± 36 g). At the time of final capture, F1 did not appear to have lactated recently, which suggests that she probably did not reproduce during the previous spring. We do not have body mass data for F1 from November 1998 to May 2000; thus, we cannot speculate about her condition during the summer of 1999 when she entered torpor. At the time of final capture (May 2000), F1 weighed 763 g, and the average mass of other nonreproductive female prairie dogs we captured at this time was 792 g (± 23 g); the mass of reproductive females at this time was 727 g (± 31 g). F1 did not show any obvious signs of injury, disease, or dehydration at the time of first or final capture.

Discussion

Body temperature patterns of black-tailed prairie dogs appear to be influenced by an innate rhythm. Prairie dogs in this study demonstrated distinct seasonal changes in T_b that are characteristic of heterothermy, since T_b decreased continuously from fall to winter and increased from spring to summer. Prairie dogs also had distinct daily T_b patterns, in which T_b was reduced at night and increased during the day. Bakko et al. (1988) reported similar T_b patterns in free-ranging black-tailed prairie dogs, since the average T_b of animals they observed varied by up to 2.8°C daily and 5.8°C across seasons. It is possible that these patterns of heterothermy are the result of animals responding to short-term changes in their environments, since changes in T_b reflected changes in T_a during these periods.

However, uniformity in these T_b patterns among animals in our study at all times of the year suggest that T_b patterns are influenced, at least in part, by an innate daily and seasonal timing mechanism that is perhaps linked to a circadian or circannual rhythm. Distinct circadian timing of immergence into and emergence from torpor as well as the distinct 24-h intervals of bout duration that prairie dogs in this study experienced offer further evidence that T_b patterns of this species are highly dependent on an innate timing mechanism. Black-tailed prairie dogs have been shown to have distinct seasonal

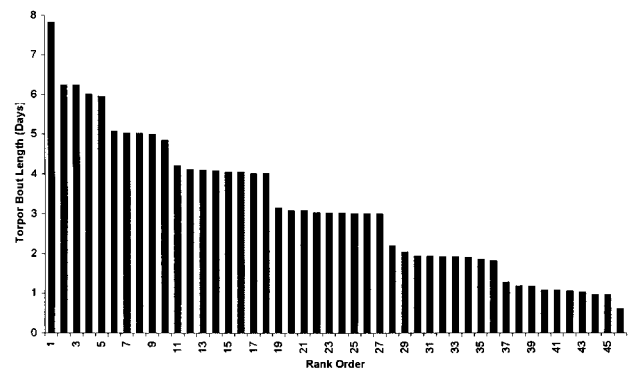


Figure 6. Rank order of torpor bout lengths of black-tailed prairie dogs (*Cynomys ludovicianus*). Body temperature patterns were monitored in eight adult (>1 yr) prairie dogs at the Central Plains Experimental Range (Weld County, Colo.) from November 1999 to June 2000.

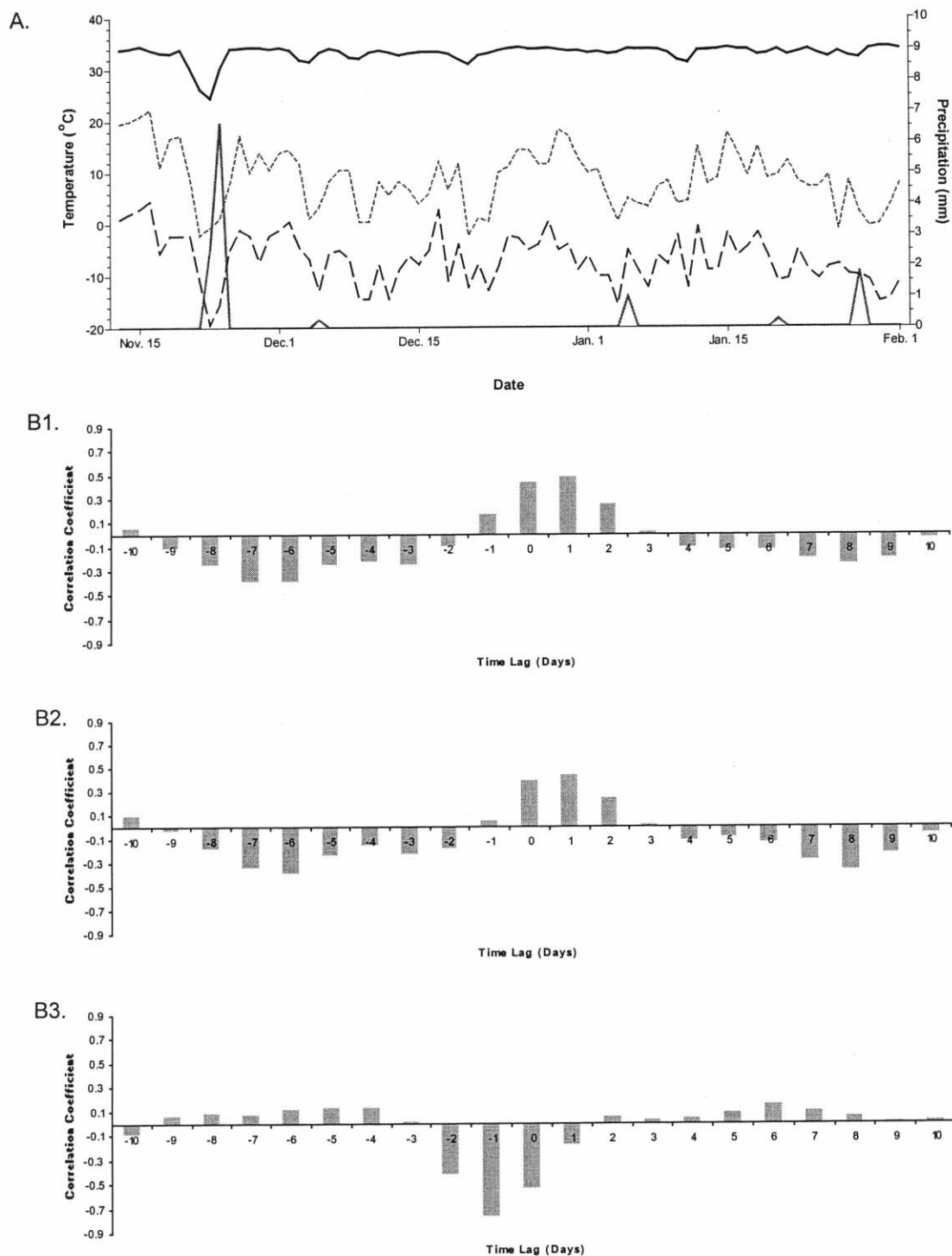


Figure 7. Relationship between weather variables and body temperature patterns of eight adult black-tailed prairie dogs (*Cynomys ludovicianus*) measured daily in winter (November 10, 1999, to February 1, 2000) at the Central Plains Experimental Range (Weld County, Colo.). A, Time series plot of mean daily minimum body temperature (*top line*), daily maximum air temperature (*second line*), daily minimum air temperature (*third line*), and precipitation (*bottom line*). B, Correlation coefficients for time series cross correlations of mean daily minimum body temperature of prairie dogs and daily maximum ambient air temperature (B1), daily minimum ambient air temperature (B2), and precipitation (B3) at time lags of -10 d to +10 d.

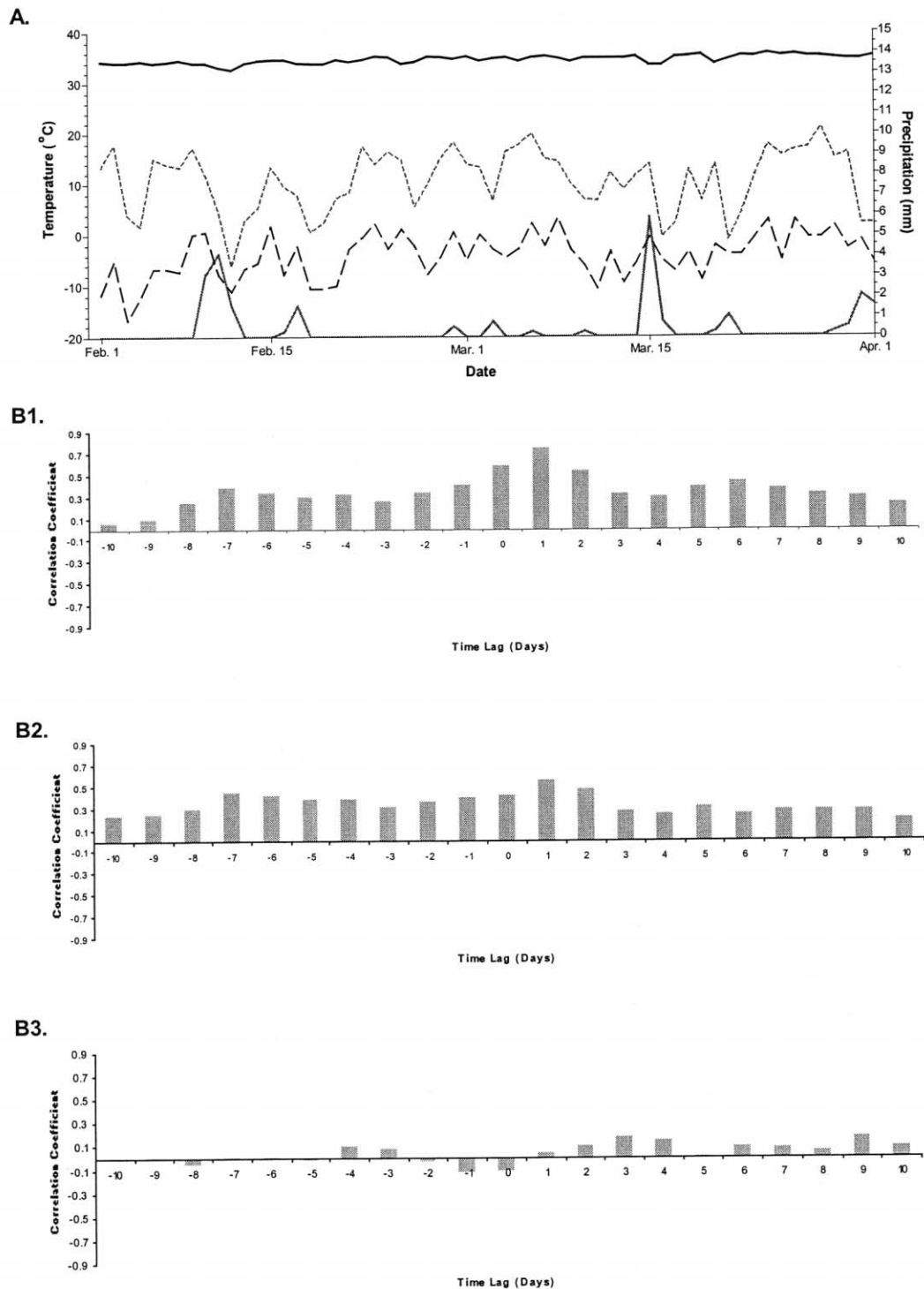


Figure 8. Relationship between weather variables and body temperature patterns of eight adult black-tailed prairie dogs (*Cynomys ludovicianus*) measured daily in spring (February 2, 2000, to April 1, 2000) at the Central Plains Experimental Range (Weld County, Colo.). A, Time series plot of mean daily minimum body temperature (*top line*), daily maximum air temperature (*second line*), daily minimum air temperature (*third line*), and precipitation (*bottom line*). B, Correlation coefficients for time series cross correlations of mean daily minimum body temperature of prairie dogs and daily maximum ambient air temperature (*B1*), daily minimum ambient air temperature (*B2*), and precipitation (*B3*) at time lags of -10 d to $+10$ d.

Table 2: Comparison of torpor bouts of adult (>1 yr) male ($n = 5$) and female ($n = 3$) black-tailed prairie dogs (*Cynomys ludovicianus*)

	Females	Males	<i>P</i> Value
Total time spent in torpor (h)	172.1	195.6	.12
Date of first torpor bout	November 21	November 11	.05
Date of last torpor bout	February 24	March 29	.03

Note. Prairie dogs were monitored from November 1999 to June 2000 at the Central Plains Experimental Range (Weld County, Colo.). One-way ANOVA was used to compare differences in general torpor patterns between male and female prairie dogs.

fluctuations in body mass that are independent of food consumption (Harlow 1997), and patterns such as these can be indicative of an endogenous circannual rhythm (Mrosovsky and Faust 1985).

Our results indicate that torpor in black-tailed prairie dogs is influenced by weather; however, it is unlikely that weather is the only stimulus for torpor in this species. Immersion into torpor during winter and spring was most closely associated with reductions in T_a in the 24-h period before the onset of a bout. However, the changes in T_a that occurred during these periods were relatively small, and there were periods when T_a was reduced to an even greater extent in which no animals entered torpor. Furthermore, torpor was not synchronized in all animals, which suggests that weather may trigger torpor only in some animals or that weather acts concomitantly with other factors to stimulate torpor. The female prairie dog, F1, displayed evidence of facultative estivation, since she engaged in torpor intermittently during summer. These torpor bouts appeared to be influenced by weather, primarily by increasing T_a . It is possible that rainfall may also influence facultative estivation in this system, since most summer torpor bouts coincided with precipitation. It is noteworthy, however, that precipitation during this summer period was minimal. Daily precipitation during summer averaged 0.18 mm/d, and the greatest accumulation of precipitation on a single day was 2.15 mm. Thus, there were few days during this summer period that could be characterized as “cool and rainy.” At our study site, brief afternoon thundershowers are typical when daily T_a 's are exceedingly high (Central Plains Experimental Range, unpublished data). Therefore, F1 may be responding to typical summer weather systems of high T_a , which, coincidentally, often include rainfall. Although estivation has been reported anecdotally in black-tailed prairie dogs (D. Biggins, personal communication), other published studies have not observed estivation in free-ranging black-tailed prairie dogs (Bakko et al. 1988).

Reproductive behaviors may also influence the timing of torpor in free-ranging black-tailed prairie dogs. In this study, males began to enter torpor before females, and they continued to enter torpor much later into spring than females. This is in contrast to the patterns reported for hibernating sciurids, in which males are generally the first cohort to immerse in the fall and emerge in the spring (Michener 1983b, 1992; Young 1990). Such hibernation patterns are thought to be strongly influenced by sex-specific reproductive behaviors, since males emerge earlier in spring to prepare for mating but must rely heavily on cached food to meet energy demands, whereas females emerge for copulation later in spring at a time when the quality of forage has improved (Michener 1992). Female hibernators have been shown to have a limited propensity for torpor following mating in spring, and torpor and pregnancy or lactation do not occur simultaneously in many rodent hibernators (Geiser 1998; Körtner and Geiser 2000). Likewise, several studies have demonstrated that males with higher levels of testosterone have fewer and more shallow torpor bouts than males with lower testosterone levels (Hall and Goldman 1980; Steinlechner et al. 1986; Mzilikazi and Lovegrove 2002). In many hibernators, termination of seasonal torpor coincides with gonadal recrudescence (Jansky et al. 1981; Goldman et al. 1986), but in some species the onset of the hibernation season occurs before the regression of the testes or the cessation of reproductive activity (Jansky et al. 1981; Lyman et al. 1982; Geiser and Masters 1994). These findings have led to the general conclusion that elevated levels of testosterone do not inhibit torpor; rather, the production of testosterone and hibernation are separate processes that are affected individually by the pineal gland responding to changing photoperiods (Lyman et al. 1982; Goldman et al. 1986). Black-tailed prairie dogs at this latitude generally copulate in early February (Bakko et al. 1988), and young of the year first appear above ground in early May (Andelt and Beck 1998). In this study, both male and female prairie dogs remained euthermic for a 10-d period in early February, a period that may have coincided with copulation. Following this 10-d period, only one female entered a single bout of torpor, whereas four out of five male prairie dogs continued to enter torpor sporadically until late March. It is possible that females terminate torpor earlier in the spring during periods that generally coincide with gestation and lactation. After copulation and subsequent reductions in testosterone levels, male black-tailed prairie dogs may attempt to maximize energy consumption and conservation by continuing to enter torpor throughout spring until the quality of forage improves and T_a increases.

Minimum T_b 's of prairie dogs during torpor were considerably higher than those reported for hibernators and animals that practice daily torpor (Geiser and Ruf 1995); however, prairie dogs required more time to decrease their T_b to these lower levels and subsequently rewarm to euthermic T_b . Prairie dogs in this study required 34.4 h to reduce T_b below 31°C and 20.0

Table 3: Comparison of general torpor patterns of adult (>1 yr) male ($n = 5$) and female ($n = 3$) black-tailed prairie dogs (*Cynomys ludovicianus*)

	Females				Males				P Value
	\bar{X}	SE	Minimum	Maximum	\bar{X}	SE	Minimum	Maximum	
Number of bouts	10	3.6	7	14	5.6	1.8	3	8	.08
Bout length (h)	64.9	37.9	22.4	187.5	68.9	42.2	14.0	149.6	.33
Minimum T_b ($^{\circ}\text{C}$)	28.7	3.6	10.1	30.7	29.7	3.2	19.4	30.9	.15
Time to reach minimum T_b (h)	26.0	19.3	5.2	89.8	51.5	30.5	6.8	129.9	<.01
Time at minimum T_b (h)	4.5	2.3	2.7	7.8	3.4	2.2	.8	10.0	.07
Time to rewarm to euthermic T_b (h)	25.7	20.9	1.2	74.3	31.6	28.9	1.0	98.2	.22

Note. Prairie dogs were monitored continuously from November 1999 to June 2000 at the Central Plains Experimental Range (Weld County, Colo.). One-way ANOVA was used to compare differences in general torpor patterns between male and female prairie dogs.

h to rewarm T_b above 36°C . In contrast, Richardson's ground squirrels can reach minimum T_b below 10°C within 36 h and rewarm to euthermic T_b within 6 h (Wang 1979). Likewise, animals that practice daily torpor, such as elephant shrews (*Elephantulus* spp.), can rewarm from torpor to euthermic levels at rates ranging from 0.19° to $0.39^{\circ}\text{C}/\text{min}$ (Lovegrove et al. 2001b). Although prairie dogs have a relatively high body mass compared with Richardson's ground squirrels and elephant shrews, it is not likely that body mass is the primary factor preventing black-tailed prairie dogs from rapidly reducing body temperature and rewarming during torpor, since hibernating sciurids with higher body masses (i.e., *Cynomys leucurus*) have the ability to rapidly reduce and increase body temperature during torpor (Harlow 1997). The apparent limited ability of black-tailed prairie dogs to rapidly alter body temperature could be the result of physiological factors that inhibit their ability to practice shivering and nonshivering thermogenesis, which possibly result from differences in the composition of their brown adipose tissue and protein stores. Similar oxygen consumption patterns between laboratory populations of black-tailed and white-tailed prairie (*C. leucurus*) dogs following noradrenaline injection has led to the conclusion that black-tailed prairie dogs have a "nonshivering thermogenic response" that is similar to that of hibernators (Harlow 1997). However, in the natural environment, there may be factors that confound this thermogenesis and prevent black-tailed prairie dogs from rapidly altering T_b . Environmental factors, such as burrow temperatures, could also influence the ability of black-tailed prairie dogs to alter their T_b during torpor. Although T_s did not appear to have a large influence on torpor bout duration or on minimum T_b of prairie dogs during torpor, T_s has been shown to affect torpor bout duration and minimum T_b in some sciurid hibernators (Michener 1992). T_s 's that we report are higher than T_s 's reported at depths approximating hibernacula of free-ranging Richardson's ground squirrels (4° – 10°C vs. 1° – 4°C). A smaller T_s – T_b gradient could have a large effect on cooling rates,

minimum T_b , and rewarming rates of prairie dogs during torpor.

Examination of the unusual torpor patterns of black-tailed prairie dogs may provide insight about the evolution of hibernation among sciurids. Although the evolution of hibernation is a subject of much contention, it is generally believed to be the ancestral condition among mammals that originated in northern climates (Davis 1976; Geiser 1998). Estivation is thought to have developed as species began to inhabit more southern latitudes (Davis 1976). Within the genus *Cynomys*, members of the subgenus *Leucocrossuromys* are thought to be most primitive and are believed to have evolved at extreme northern latitudes, whereas members of the subgenus *Cynomys* are thought to have evolved more recently as prairie dogs began expanding southward (Goodwin 1995). Members of *Cynomys Leucocrossuromys*, including white-tailed (*Cynomys Leucocrossuromys leucurus*), Gunnison's (*Cynomys Leucocrossuromys gunnisoni*), and Utah prairie dogs (*Cynomys Leucocrossuromys parvidens*), are thought to hibernate continuously during winter, whereas members of the subgenus *Cynomys*, including Mexican (*Cynomys Cynomys mexicanus*) and black-tailed prairie dogs, do not hibernate (Hoogland 1995). However, black-tailed prairie dogs are capable of entering torpor intermittently during both winter and summer but practice daily and seasonal heterothermy while continuing to forage throughout most of the year. There is a growing body of evidence to suggest that some species practice an intermediate strategy on the gradient between hibernation and daily torpor (Wilz and Heldmaier 2000; Lovegrove et al. 2001b). Likewise, black-tailed prairie dogs may represent an evolutionary step between seasonal torpor and normothermy.

In summary, body temperature patterns of black-tailed prairie dogs have a daily and seasonal rhythmicity that is indicative of an innate timing mechanism. However, T_b patterns in this species are also influenced by weather conditions, and there is evidence that torpor patterns may be influenced by reproduc-

tive behaviors. Our examination of torpor in this context reveals the complexity of this physiological strategy in the natural environment and underscores the need for further investigation of body temperature patterns in free-ranging animals.

Acknowledgments

This research was supported by a National Science Foundation Shortgrass Steppe Long-Term Ecological Research grant (DEB-9632852) to I. C. Burke and W. K. Lauenroth. Special thanks to E. Powell, L. Hartley, L. Savage, and M. Lindquist for help in the field. We also thank J. Zumbrunnen for statistical assistance. H. Wagner, R. Schooley, and two anonymous reviewers provided insightful comments on the manuscript.

Literature Cited

- Andelt W.F. and T.D.I. Beck. 1998. Effect of black-footed ferret odors on behavior and reproduction of prairie dogs. *Southwest Nat* 43:344–351.
- Bakko E.B., W.P. Porter, and B.A. Wunder. 1988. Body temperature patterns in black-tailed prairie dogs in the field. *Can J Zool* 66:1783–1789.
- Davis D.E. 1976. Hibernation and circannual rhythms of food consumption in marmots and ground squirrels. *Q Rev Biol* 51:477–514.
- Geiser F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. *Clin Exp Pharmacol Physiol* 25:736–740.
- Geiser F. and P. Masters. 1994. Torpor in relation to reproduction in the mulgara, *Dasyercus cristicauda* (Dasyuridae: Marsupialia). *J Therm Biol* 19:33–40.
- Geiser F. and T. Ruf. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol Zool* 68:935–966.
- Goldman B.D., J.M. Darrow, M.J. Duncan, and L. Yogeve. 1986. Photoperiod, reproductive hormones, and winter torpor in three hamster species. Pp. 341–351 in H.C. Heller, X.J. Musacchia, and L.C.H. Wang, eds. *Living in the Cold: Physiological and Biochemical Adaptations*. Elsevier, New York.
- Goodwin H.T. 1995. Pliocene-Pleistocene biogeographic history of prairie dogs, genus *Cynomys* (Sciuridae). *J Mammal* 76:100–122.
- Hall V. and B. Goldman. 1980. Effects of gonadal steroid hormones on hibernation in the Turkish hamster (*Mesocricetus brandti*). *J Comp Physiol* 135:107–114.
- Hamilton J.D. and E.W. Pfeifer. 1977. Effects of cold exposure and dehydration on renal function in black-tailed prairie dogs. *J Appl Physiol Respir Environ Exerc Physiol* 42:295–299.
- Harlow H.J. 1997. Winter body fat, food consumption, and nonshivering thermogenesis of representative spontaneous and facultative hibernators, the white-tailed prairie dog and black-tailed prairie dog. *J Therm Biol* 22:21–30.
- Harlow H.J. and G.E. Menkens. 1986. A comparison of hibernation in the black-tailed prairie dog, white-tailed prairie dog, and Wyoming ground squirrel. *Can J Zool* 64:793–796.
- Hoogland J.L. 1995. *The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal*. University of Chicago Press, Chicago.
- Jansky L., Z. Kahlerova, J. Nedoma, and J.F. Andrews. 1981. Hormonal control of hibernation in golden hamsters. Pp. 13–32 in X.J. Musacchia and L. Jansky, eds. *Survival in the Cold: Hibernation and Other Adaptations*. Elsevier, New York.
- King J.A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contrib Lab Vertebr Biol Univ Mich* 67:1–123.
- Körtner G. and F. Geiser. 2000. The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. *Chronobiol Int* 17:103–128.
- Lehmer E.M., B. Van Horne, B. Kulbartz, and G.L. Florant. 2001. Facultative torpor in free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). *J Mammal* 82:552–557.
- Lovegrove B.G., J. Raman, and M.R. Perrin. 2001a. Daily torpor in elephant shrews (Macroscelidea: *Elephantulus* spp.) in response to food deprivation. *J Comp Physiol B* 171:11–21.
- . 2001b. Heterothermy in elephant shrews, *Elephantulus* spp. (Macroscelidea): daily torpor or hibernation? *J Comp Physiol B* 171:1–10.
- 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. 1983a. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pp. 528–572 in J.F. Eisenberg and D.G. Kleiman, eds. *Recent Advances in the Study of Mammalian Behavior*. Special Publication, American Society of Mammalogists, Pittsburgh.
- . 1983b. Spring emergence schedules and vernal behavior of Richardson's ground squirrels: why do males emerge from hibernation before females? *Behav Ecol Sociobiol* 14:29–38.
- . 1992. Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. *Oecologia* 89:397–406.
- Mrosovsky N. and I.M. Faust. 1985. Cycles of body fat in hibernators. *J Obes* 9(suppl. 1):93–98.
- Mzilikazi N. and B. Lovegrove. 2002. Reproductive activity influences thermoregulation and torpor in pouched mice, *Saccostomus campestris*. *J Comp Physiol B* 172:7–16.
- Smith R.E. 1958. Natural history of the prairie dog in Kansas. *Univ Kans Mus Nat Hist Misc Publ* 16:1–17.
- Steinlechner S., H. Heldmaier, C. Weber, and T. Ruf. 1986. Role of photoperiod: pineal gland interaction in torpor control.

- Pp. 301–308 in H.C. Heller, X.J. Musacchia, and L.C.H. Wang, eds. *Living in the Cold: Physiological and Biochemical Adaptations*. Elsevier, New York.
- Tileston J.V. and R.R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. *Am Midl Nat* 75:292–316.
- Wang L.C.H. 1979. Time patterns and metabolic rates of natural torpor in Richardson's ground squirrel. *Can J Zool* 57: 149–155.
- Wilz M. and G. Heldmaier. 2000. Comparison of hibernation, estivation, and daily torpor in the edible dormouse, *Glis glis*. *J Comp Physiol B* 170:511–521.
- Young P.J. 1990. Hibernating patterns of free-ranging Columbian ground squirrels. *Oecologia* 83:504–511.