DISSERTATION

ECOLOGY AND PHYSIOLOGY OF FREE-RANGING BLACK-TAILED AND UTAH PRAIRIE DOGS

Submitted by

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In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY ERIN M. POWELL ENTITLED "ECOLOGY AND PHYSIOLOGY OF FREE-RANGING BLACK-TAILED AND UTAH PRAIRIE DOGS" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT

ECOLOGY AND PHYSIOLOGY OF FREE-RANGING BLACK-TAILED AND UTAH PRAIRIE DOGS

The ability of animals to enter torpor depends upon numerous physiological and environmental factors. Thus, torpor may be influenced by varying climatic conditions over a broad geographic range of a species. Because of their varied geographic distribution and distinct torpor patterns, prairie dogs present a model system for the study of torpor. Utah prairie dogs (*Cynomys parvidens*), which are believed to hibernate continuously during winter, can be contrasted with black-tailed prairie dogs (*Cynomys ludovicianus*), which enter torpor only during periods of environmental or physiological stress. The objective of my research was to evaluate differences in over-winter body temperature patterns used by these closely related species, and to examine the influence that diet quality and habitat conditions have on these patterns. I monitored body temperature for > 6 months in adult (>1 y) black-tailed and Utah prairie dogs from colonies located along elevational gradients in northern Colorado and southern Utah, and also examined their seasonal changes in body mass, lipid composition of stored fat, and diet and dietary nutrient quality.

My results indicate that body temperature patterns of both black-tailed and Utah prairie dogs differ across elevations, with lower elevation populations entering more shallow and infrequent torpor than prairie dogs at higher elevations. Body temperature patterns of black-tailed prairie dogs showed strong circadian rhythmicity, but torpor patterns of Utah prairie dogs did not display these same circadian patterns. I observed a single population of black-tailed prairie dogs with torpor patterns that strongly resembled those of free-ranging hibernators. This population experienced multiple and sequential bouts of torpor that increased in length and depth as winter progressed. Prairie dogs monitored from an adjacent colony remained euthermic for the majority of winter, and it appears that subtle differences in environment between these colonies may have been responsible for the distinct over-winter body temperature patterns observed in each colony.

My results also show that body masses of prairie dogs were variable across seasons and elevations, with prairie dogs from higher elevation sites generally having greater body mass in all seasons sampled. Seasonal changes in lipid composition of stored fat indicated that black-tailed prairie dogs do not have a clear pattern of essential fatty acid metabolism during winter, whereas Utah prairie dogs appeared to preferentially metabolize lipid in a manner that promotes deep and continuous torpor. Both black-tailed and Utah prairie dogs exercise strong dietary selection, and appear to prefer species higher in lipid and nitrogen content, relative to other plant species available on colonies. Vegetation on prairie dog colonies at higher elevations was generally higher in linoleic acid and nitrogen content than vegetation on colonies at lower elevations. Collectively, my results underscore the considerable variation in both physiological and environmental factors that exist within the ranges of black-tailed and Utah prairie dogs. Because torpor can result in significant energy savings, it is an essential component of the life history of prairie dogs that allows them to persist in habitats where food resources fluctuate seasonally and where environmental conditions are often unfavorable.

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INTRODUCTION

Prairie dogs (*Cynomys* spp.) once occupied a vast region of the western North American landscape. In the past century their populations have declined to a small fraction of their original numbers (Anderson et al. 1986; Marsh 1984). Utah prairie dogs (*C. parvidens*) are a federally listed Threatened species, black-tailed prairie dogs (*C. ludovicianus*) are candidates for listing under the Endangered Species Act, and white-tailed prairie dog (*C. leucurus*) populations are greatly reduced. Prairie dogs are considered by some to be keystone species of grassland ecosystems (Miller et al. 1994); therefore, the decline of these species will have negative effects on the biotic integrity of western grasslands at local and landscape levels (Antolin et al. 2002).

In recent years, federal and state management programs have attempted to restore sustainable prairie dog populations by restricting lethal control, artificially manipulating habitat, and by translocating encroaching colonies (Clark et al. 1989; McDonald 1993). The long-term success of these recovery programs is questionable, as viable prairie dog populations have not been restored (Utah Prairie Dog Recovery Implementation Team 1997). Recent reviews of these management efforts suggest that sub-optimal habitat may be the most important factor limiting the recovery of sustainable prairie dog populations (Utah Prairie Dog Recovery Implementation Team 1997). Unfortunately, little is known about the basic ecological physiology of these prairie dog species, making it difficult to formulate the optimal management strategy to restore suitable habitat for these populations.

Prairie dogs are capable of practicing either seasonal or non-seasonal torpor during periods of environmental or physiological stress. Torpor is defined as the regulated lowering of body temperature (T_b) to levels ranging from 4°C to 35°C below seasonal normal levels, maintenance of this low T_b for a period of time, and the subsequent return to seasonal normal T_b (Wang 1989). During seasonal torpor, typically referred to as hibernation or aestivation, animals become dormant for extended periods of time and undergo numerous and consecutive torpor bouts over the course of several weeks or months (Wang 1989). These patterns of torpor contrast with non-seasonal torpor, which is thought to be caused primarily by abrupt and unfavorable changes in environmental conditions and / or periods of low food and water availability (Harlow and Menkens 1986; Lehmer et al. 2001). Animals using non-seasonal torpor, including daily and facultative torpor, engage in both intermittent torpor and foraging to meet metabolic energy demands. It is generally believed that both Utah and white-tailed prairie dogs hibernate continuously during winter, when visual observations of field and laboratory populations suggest that these animals are dormant for extended periods (Harlow 1995; Harlow 1997; Harlow and Menkens 1986; Pizzimenti 1975). These patterns are in contrast to those observed in black-tailed prairie dogs, which enter torpor facultatively during winter when ambient temperatures rapidly decline (Lehmer et al. 2001; Lehmer et al. 2003). There is some evidence, however, that these patterns are not consistent throughout the ranges of these species (Tileston and Lechleitner 1966).

The reductions in body temperature associated with torpor result in considerable energy savings, as small mammals can save more than 20% of their daily energy expenditures by practicing daily torpor and nearly 90% of their annual energy expenditures by practicing seasonal torpor (Wang 1989). Therefore, torpor is an essential component of the life-history of prairie dogs, as it allows them to persist in habitats where food resources fluctuate seasonally and where environmental conditions are often unfavorable.

To maintain the low body temperatures associated with torpor, mammals rely heavily on endogenously stored polyunsaturated fatty acids (Geiser and Heldmaier 1995; Geiser and Kenagy 1987). Animals fed diets high in polyunsaturated fatty acids (PUFAs) have fewer arousals during seasonal torpor than their cohorts fed diets lower in PUFAs (Geiser et al. 1994). Arousal from torpor is energetically expensive and can often account for nearly 80% of the total energy that is expended during a typical season of torpor (Wang 1979). The storage of PUFAs in white adipose tissue (WAT) depots is also associated with lower metabolic rates during torpor (Geiser et al. 1994). Thus, dependence upon large amounts of stored PUFAs during torpor can convey considerable energy savings to the animal.

Dietary lipids play a critical role in torpor and animals must procure adequate lipid reserves prior to the onset of winter (Armitage et al. 1976; Florant et al. 1993; Ward and Armitage 1981). Foraging habits and diet become a valuable predictor of torpor patterns in hibernating rodents because many PUFAs can only be obtained in the diet (Downer 1985; Erasmus 1986). Dietary preferences differ among prairie dog populations (Hansen and Gold 1977; Hasenyager 1983; Lehmer and Van Horne 2001; Tileston and Lechleitner 1966). Consequently, the dietary lipid composition of white-tailed, black-tailed, and Utah prairie dog populations are also likely to differ, as the lipid composition of a plant is dependent on factors including the type of plant (i.e. forb, grass, etc) and its geographic location (Corn 1997; Hill and Florant 1999; Thompson et al. 1993). In general, plants in cooler environments produce greater amounts of unsaturated fatty acids than plants acclimated to warmer temperatures (Corn 1997). The levels of plant PUFAs are also reduced during periods of water stress (Monteiro de Paula et al. 1990; Monteiro de Paula et al. 1993). Therefore, prairie dogs in higher elevation environments are likely to ingest large amounts of PUFAs prior to winter, as these periods often coincide with decreasing temperatures and increasing precipitation (Corn 1997). A diet that is deficient in the essential PUFAs may prohibit prairie dogs in lower elevations from engaging in continuous torpor, while diets of higher elevation populations may provide PUFA levels that are optimal for hibernation. The substantial energy savings that hibernation provides during periods of low food and water availability should provide prairie dogs that hibernate with greater survival than those that are torpid intermittently during winter. Therefore, diet could indirectly affect the over-winter survival of free-ranging prairie dogs.

One way to test these hypotheses is to compare dietary nutrient content and torpor patterns between prairie dogs in differing environments. The geographic ranges of white-tailed, black-tailed, and Utah prairie dogs encompass environments that vary considerably in elevation, precipitation, temperature, and vegetation. It is therefore likely that torpor patterns will vary similarly within the ranges of these species. Some anecdotal evidence points to inconsistent torpor patterns across the geographic range of each prairie dog species, but these observations have never been validated. However, the physiological and ecological factors that influence these different over-winter strategies, and the impact that these strategies have on the survival and fitness of prairie dogs in their natural environments have not been reviewed.

The objective of this dissertation research was to evaluate differences in over-winter strategies used by black-tailed and Utah prairie dogs across elevational gradients in northern Colorado and southern Utah, and to determine how diet and dietary nutrient quality influence these patterns. We also measured differences in body mass and composition of stored energy of prairie dogs across elevations to assess how variation in habitat quality affects physical condition of prairie dogs. This research will increase our understanding of factors influencing the growth and persistence of prairie dog populations and will be used to make recommendations concerning future management policies.

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CHAPTER ONE

A RARE INCIDENT OF HIBERNATION IN FREE-RANGING BLACK-TAILED PRAIRIE DOGS

In the natural environment, hibernating sciurids generally remain dormant during winter and enter numerous deep torpor bouts from the time of first immergence in fall until emergence in spring. This is in contrast to free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*), which remain active throughout winter but periodically enter short and shallow bouts of torpor. Although previous studies suggest that weather and diet quality can trigger torpor in this species, the extent to which facultative torpor is influenced by external environmental conditions or by innate circadian timing is unknown. While investigating body temperature patterns of black-tailed prairie dogs from colonies across an elevational gradient in northern Colorado, we observed a single population (colony 22) al low elevation that displayed torpor patterns that strongly resemble those more commonly seen in hibernating species. This population experienced multiple bouts of torpor that increased in length and depth as winter progressed. Inter-torpor arousal periods were brief, with animals maintaining euthermic body temperatures for <24 h. Prairie dogs monitored from another colony (5W) in close proximity to colony 22 remained euthermic for the majority of winter

and entered shallow bouts of torpor at infrequent intervals. Local environmental conditions likely played a role in the deep torpor experienced by colony 22. Prior to winter, prairie dogs from colony 22 had lower body masses and concentrations of stored lipids in white adipose tissue than prairie dogs on colony 5W. The following spring prairie dogs on both colonies had similar body mass and white adipose tissue content. Nutrient analyses of plant species common in prairie dog diets revealed that plant species available to prairie dogs on colony 22 tended to have slightly lower levels of lipids, carbon, hydrogen, and nitrogen in all seasons than dietary plant species on colony 5W, although these differences were not statistically significant. Population genetic analyses of colonies 5W and 22, based on assignment and exclusion tests of microsatellite markers, revealed high genetic similarity between the colonies and implied that individuals regularly disperse between colonies. Differences in torpor patterns of black-tailed prairie dogs seem to result from subtle environmentally induced differences between separate populations. The results of our study call into question existing models that propose a clear delineation between homeothermy, facultative torpor, and hibernation.

INTRODUCTION

Mammalian herbivores face energetic challenges, as access to high quality food resources is seasonally variable. Thus, herbivorous mammals must balance costs of foraging on low quality diet items while maximizing the efficient use of stored energy. In several species, individuals can minimize energetic requirements and expenditures by allowing body temperature to fluctuate with ambient conditions (Davis 1976). Torpor is an extreme form of energy conservation used to compensate for severe environmental or physiological stress (Wang 1989).

Torpor has been defined as the regulated lowering of body temperature to levels ranging from 4° C to 35° C below seasonal euthermic normal levels, and has been described as occurring either seasonally or facultatively (Wang 1989). During seasonal torpor, animals experience numerous and sequential bouts of torpor during periods of excessively cold (hibernation) or hot weather (estivation; Davis 1976). Compared to animals in facultative torpor, animals practicing seasonal torpor will generally reach lower minimum body temperatures and maintain the low temperatures for longer periods of time as the season progresses (Wang 1989), while animals using facultative torpor animals enter bouts at infrequent and irregular intervals (Harlow and Menkens 1986; Lehmer et al. 2003; Lehmer et al. 2001; Wang 1989). Generally, bouts of facultative torpor are shorter with less extreme minimum temperatures than bouts that occur during seasonal torpor (Lehmer et al. 2003; Lehmer et al. 2001).

Different mechanisms may drive seasonal and facultative torpor. Seasonal torpor is thought to be a fixed trait controlled by factors that are generally independent of short-term changes in environmental conditions (Wang 1989). This dependence on circannual timing mechanisms has been illustrated by laboratory studies, which demonstrate that hibernators become dormant and aphagic during winter even when ambient temperatures are high and food is readily available (Barnes and Mrosovsky 1974; Harlow 1997). Furthermore, animals practicing seasonal torpor have relatively fixed and predictable patterns during each season, with little plasticity in torpor patterns across seasons and within same-sex animals of similar age (Davis 1976; Michener 1983; Michener 1992). Rigidity in these patterns suggests that the ability to practice seasonal torpor is a genetically fixed trait (Wang 1989).

In contrast, facultative torpor is greatly influenced by short-term changes in environment, as initiation of torpor has been correlated to reductions in ambient temperature and precipitation (Lehmer et al. 2003; Wang 1989). Facultative torpor is sporadic and difficult to predict because torpor bouts rarely occur simultaneously within a population at any given time, even among animals of the same sex and age. However, some evidence indicates that animals practicing facultative torpor also respond to innate timing mechanisms; torpor bout length and the timing of entrance into and emergence from torpor follow distinct circadian cycles (Lehmer et al. 2003). This raises the question of whether the ability to practice facultative torpor also has a genetic basis, similar to seasonal torpor. Alternatively, differences in torpor patterns among populations or among individuals within a single population would represent phenotypic variation induced by environmental differences rather than genetic differences.

Prairie dogs (*Cynomys* spp.) display both seasonal and facultative torpor. Members of subgenus *Leucocrossuromys*, which includes Utah (*C. L. parvidens*), white-tailed (*C. L. leucurus*), and Gunnison's (*C. L. gunnisoni*) prairie dogs, are believed to hibernate continuously during winter (Hoogland 1995; Lehmer *unpublished*). In contrast, members of subgenus *Cynomys*, including black-tailed (*C. C. ludovicianus*) and Mexican (*C. C. mexicanus*) prairie dogs, are thought to enter torpor facultatively during winter, spring, and summer (Harlow 1997; Lehmer et al. 2001; Lehmer et al. 2003). It is noteworthy that black-tailed prairie dogs are the only ground-dwelling sciurid species with a range that extends north of 40° latitude that does not hibernate continuously during winter (Bakko et al. 1988).

Previous studies have shown black-tailed prairie dogs maintain high body temperatures throughout most of the year, but enter torpor sporadically during winter and spring (Lehmer et al. 2003; Lehmer et al. 2001). Black-tailed prairie dogs appear to conserve additional energy by practicing seasonal heterothermy, in which average body temperature is highest during summer and declines to an annual low during winter (Bakko et al. 1988; Lehmer et al. 2003). Furthermore, black-tailed prairie dogs regularly engage in daily heterothermy, with animals subtly increasing body temperature during the day and reducing body temperature at night (Bakko et al. 1988; Lehmer et al. 2003).

While investigating body temperature patterns of black-tailed prairie dogs from several populations in northern Colorado, we encountered a single population displaying torpor patterns that strongly resemble those of free-ranging hibernators. Here we describe those patterns, as well as those of an adjacent population that entered shallow bouts of torpor at infrequent intervals during the same period of time (November 2001 to February 2002). In addition, we examine the potential for a genetic basis of population differences in torpor by examining variation in six microsatellite loci from these 2 focal colonies in addition to four nearby colonies on the Central Plains Experimental Range (Pawnee National Grassland, weld County, CO). Using multilocus genotypes, we determine whether population differentiation can explain differences in over-winter body temperature patterns between these colonies on the Central Plains Experimental Range.

METHODS

Body Temperature Patterns, Body Condition, and Diet Quality

Prairie dogs were monitored from two colonies (5W and 22) on the Central Plains Experimental Range (CPER), which is located on the Pawnee National Grassland in Weld County, CO. The study site (elev. 1650 m) is a semi-arid short-grass prairie with mean temperatures ranging from –5°C in January to 22°C in July (Stapp 1997). Colonies 5W and 22 are located within 10 km of each other (Figure 1) and share a similar vegetation structure. We determined vegetative cover of colonies seasonally (fall, spring, summer) by estimating plant cover at 20 random locations on each prairie dog colony using Daubenmire frames (0.5 x 0.25 m) as a sampling unit. In terms of relative abundance, these colonies are dominated by western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*).

In October 2001, we live-trapped five adult (> 1 year) black-tailed prairie dogs from colony 5W and 5 from colony 22 (total N = 10). All animals were captured from separate coteries; thus, it is unlikely that they interacted regularly during this study, shared burrow systems, or were genetically closely related to each other (Hoogland 1995). After capture, we surgically implanted temperature sensitive data loggers (Onset Computer Corp., Bourne, MA) into the abdominal cavity of each prairie dog (Lehmer et al. 2001). Data loggers were programmed to record body temperature (T_b) of animals in the range of –20° C to 50° C every 24 min throughout the study period. All loggers showed accurate calibration within 0.1°C before implantation and after removal (Lehmer et al. 2001; Lehmer et al. 2003). During surgery, we also collected small (<1g) white adipose tissue (WAT) biopsies from the omental fat pad of each animal (Lehmer and Van Horne 2001). Immediately after collection, WAT samples were stored at –20°C until further assays were run. Following recovery from surgery (<12 h), prairie dogs were released to their original sites of capture.

In January 2002, we live-trapped an additional five adult prairie dogs from each colony (5W and 22) and surgically obtained WAT biopsies. To minimize the number of surgical procedures performed on a single animal, these were initial captures without any known prior surgeries.

In June 2002, prairie dogs were recaptured from colonies 5W (N= two females, one male) and 22 (N = three females, two males). Immediately after capture, we surgically removed temperature loggers and obtained additional WAT biopsies. Following recovery from surgery, prairie dogs were released at the same burrow where they were originally captured. Data from the loggers were downloaded using Box Car Pro software (version 3.51, Onset Computer Corp., Bourne, MA).

We considered a prairie dog to be in torpor if it experienced a continuous reduction in T_b that at some point reached a level below 31°C, maintained T_b below 31°C, and subsequently re-warmed to T_b above 36°C. We established 31°C as the threshold T_b for torpor, as this is below the mean euthermic daily minimum T_b that has been previously reported for this species (Bakko et al. 1988; Lehmer et al. 2003). We determined cooling rates of prairie dogs during torpor by calculating the number of hours required to reduce T_b from euthermic levels (>36°C) to the minimum level reached during a torpor bout. We determined rewarming rates by calculating the number of hours required to increase T_b from the minimum level reached during the bout to a level above 36°C. The duration of inter-bout arousals were determined by calculating the number of hours that prairie dogs maintained T_b above 36°C between separate bouts of torpor.

We extracted fatty acids contained in WAT by soaking 10 mg of each sample in 10 ml of 2:1 hexane : isopropanol for 7 d (Hara and Radin 1978). Following extraction, free fatty acids were converted to methyl esters by adding 10 μl of MethPrep 2 (Alltech) to each sample and allowing reaction to proceed for 40 min. Eicosane (100 μg) was added to each sample as an internal standard. We identified individual fatty acids by comparison of retention times and mass spectra with those of authentic fatty acid methyl esters. Fatty acid methyl esters were quantified with gas-liquid chromatography (Hewlett-Packard 5890A) on a capillary column (Alltech Econocap Carbowax 30m x 0.32mm ID x 0.25μm) with detection by mass spectrometry (HP 5971) and corrected for their detector response differences.

During each season (fall, spring, and summer), we collected fecal samples (about five pellets) from each adult prairie dog captured on colonies 5W and 22. Seasonal species composition of individual prairie dog diets were quantified at the Composition Analysis Laboratory in Fort Collins, CO, using a microhistological technique based on fecal contents (Lehmer and Van Horne 2001; Sparks and Malechek 1968; Van Horne et al. 1998). To evaluate protein and lipid composition of the diet, we sampled specimens of plant species known to commonly occur in diets of prairie dogs on the Pawnee National Grassland (Lehmer and Van Horne 2001). Species collected were *Agropyron smithii, Artemisia frigida, Aristida purpurea, Buchloe dactyloides, Bouteloua gracilis, Carex* spp., *Gutierrezia sarothrae, Opuntia polyacantha*, and *Sphaeralcea coccinea*. We collected 20 individuals of each species at 10 m intervals along randomly placed transects through each colony. Immediately after collection, plants were stored at –20°C. We randomly combined parts (i.e.

stems, leaves, blades) collected from each plant to form three large samples from which a 20 mg subsample was used for extraction and quantification of protein and lipids. Plant protein content was assessed by drying each sample to a constant mass, igniting the sample in a closed chamber, and measuring the amount of nitrogen evolved (LECO Model FP-428, Leco Corp.). Fatty acids were extracted, transmethylated, and quantified from plant tissue using the technique described above for WAT.

All statistical analyses of T_b patterns were conducted on data recorded between 15 November 2001 to 15 February 2002. One-way analysis of variance was used to compare differences in general torpor patterns between prairie dogs on colonies 5W and 22 (SAS V.8; SAS Institute, Cary, NC). These tests included comparisons of the number and length of torpor bouts, as well as T_b prior to and following torpor, minimum T_b during torpor, time required to reach minimum T_b and return to euthermic T_b, and the duration of inter-bout arousals. One-way analysis of variance was used to compare differences in vegetative cover on colonies, diet composition of prairie dogs, and protein and lipid contents of plants common in prairie dog diets. One-way analysis of variance with repeated measures was used to compare differences in body mass and WAT lipid composition of prairie dogs. Unless otherwise stated, values describing differences in general torpor patterns, body mass, WAT lipid content, vegetative cover, diet, and diet quality are presented as mean ± SE and the maximum and minimum value for each variable. Differences in these variables were considered to be statistically significant if $P \leq 0.05$.

Genetic Tissue Sampling and Analyses

We trapped prairie dogs for genetic analyses between June and December 2000 and June to December 2001 at six and five colonies, respectively, on the CPER (Figure 1). Within each colony, we placed a transect along the length of the colony and clustered 30 live-traps at four locations along it, sampling two sites at the edge of the colony and two sites at the center of the colony. At each colony, we obtained tail tissue from approximately 16 adult males and 10 adult females, which were divided evenly between the four trapping clusters. We focused primarily on sampling male prairie dogs due to female philopatry within coteries and male-biased dispersal between coteries (Hoogland 1995). Sex-biased dispersal patterns result in females within coteries being more highly related than expected under conditions of random mating. Thus, by focusing our sampling on adult males we hoped to capture a more accurate picture of genetic diversity represented in a colony than would be possible from a sample weighted more heavily with females.

After capture, we weighed, sexed, ear tagged, and assessed the reproductive status of each prairie dog. We obtained a small sample of tail tissue from each prairie dog by removing the posterior caudal vertebra (1 cm). Prior to removal, the tail was thoroughly cleaned with antibacterial soap, a band tourniquet was applied, and lidocaine was administered as a local anesthetic. After removal of the tail, the wound was sealed with surgical glue and stainless steel staples.

In 2000, we obtained tissue samples from 141 individuals captured on six colonies, and in 2001 we obtained tissue samples from 124 individuals captured on five colonies. Immediately after collection, tissue samples were placed in a storage buffer (1X STE: 0.1 M NaCl, .05M Tris-HCl (pH 7.5), 0.001 M EDTA) and stored at -80°C until further analyses were performed. We isolated DNA from tail tissue using the CTAB (hexadecyltrimethylammonium bromide) procedure outlined by Black and DuTeau (1997). Extracted DNA was re-suspended and stored in TE (0.01 M Tris-HCl, 0.1 M EDTA (pH 8.0)). To assess genetic variation within colonies and differentiation between colonies, we amplified alleles at six microsatellite loci that have been used previously in black-tailed prairie dogs (Roach et al. 2001). We performed PCR amplification using M.J. Research PTC-100 thermocyclers in 25-μl volumes containing 30-90 ng DNA. The PCR protocols used followed Roach et al. (1999). Depending on fragment length, we electrophoresed PCR products at 45-55 watts for 2-7 hours in 8% denaturing polyacrylamide gels in 1X TBE buffer. We soaked each gel in 2L of 10% glacial acetic acid for 20 min to fix the DNA, and DNA was visualized by silver staining as described by Black and DuTeau (1997). Each sample was genotyped by comparing PCR product with sample standards, and a subset of individuals was sequenced to determine the exact repeat sequence and the length of each allele.

Statistical analyses of genetic data were performed using BIOSYS-2 (Swofford and Selander 1989), FSTAT version 2.9.3.2 (Goudet 1995) and GeneClass version 1.0.02 (Cornuet and Piry 2002; Cornuet et al. 1999). We used BIOSYS-2 to test for deviations from Hardy-Weinberg equilibrium within each colony at each locus using Levene's (1949) correction for small sample sizes and for calculating exact probabilities. Deviations were considered to be statistically significant if $P < 0.05$. Biosys-2 was also used to calculate genetic Nei's (1978) unbiased minimum distance and Cavalli-Sforza and Edwards (1967) chord distance matrices between each of the sampled colonies. FSTAT was used to calculate the Weir and Cockerham (1984) estimator of F_{st}, a measure of genetic differentiation, over all loci and colonies.

To determine the probability that an individual prairie dog originated from its colony of capture (source colony) based on its multilocus genotype, we used GeneClass to perform assignment and exclusion tests. Assignment tests use maximum likelihood to directly assign individuals to the population which maximizes the likelihood of their genotype. Individuals that are not assigned to their colony of capture, but instead are assigned to other colonies in the system, are inferred to be immigrants or direct descendents of immigrants (Cornuet et al. 1999). Exclusion tests use Bayesian methods to generate probabilities that an individual belongs to each population. Individuals can thus be excluded from none, any, or all colonies in the system, based on a designated rejection probability, which we set as the inverse of sample size. From exclusion tests we determined how many individuals were excluded from all of the sampled colonies and how many individuals were excluded from their source colony but not from other sampled colonies. All of these individuals were inferred to be immigrants or direct descendents of immigrants. Likewise, we determined the number of individuals that assigned only to their source colony and one other colony to get a sense of the level of gene flow that may take place between two individual colonies.

Weather Patterns

Weather data, including daily minimum and minimum ambient temperature (°C), precipitation (mm), and wind speed (km / h), were recorded daily throughout the study period by the Shortgrass Steppe Long-Term Ecological Research Station at a location within 5 km of each colony studied. Ambient temperature and wind speeds were measured 1.5 m above ground level.

RESULTS

Body Temperature Patterns, Body Condition, and Diet Quality

From 15 November 2001 to 15 February 2002, prairie dogs on colonies 5W and 22 had remarkably different T_b patterns. All animals from colony 5W, (2 females, 1 male) maintained high euthermic T_b throughout winter, but entered shallow bouts of torpor intermittently (Figure 2A). In contrast, all prairie dogs on colony 22 (3 females, 2 males) experienced numerous, sequential bouts of torpor (Figure 2B). As winter progressed, these torpor bouts reached lower minimum T_b that persisted for longer periods of time. Prairie dogs from colony 22 had lower T_b during torpor and spent more time in torpor than did prairie dogs from colony 5W (Table 1). Likewise, prairie dogs on colony 22 required more time to cool to minimum $\mathrm{T_b}$ during torpor, but the time required to re-warm to euthermic T_b did not differ between animals on colonies 5W and 22 (Table 1). Prairie dogs on colony 22 also spent more time at minimum T_b during torpor, had longer bouts, and had shorter inter-bout arousal periods than prairie dogs on colony 5W (Table 1).

Body mass of prairie dogs was highest during the fall, declined to an annual low during winter (P <0.01), and remained unchanged through early summer (P = 0.66; Figure 3). Body mass of prairie dogs on colony 5W was higher than that of prairie dogs on colony 22 during fall (F = 8.23, P = 0.021), but body masses of animals on these colonies were not different during either winter (F = 0.01, P= 0.920) or summer (F = 0.75, P = 0.75).

Diet composition of prairie dogs on colonies 5W and 22 did not differ in any season (F = 2.68, P = 0.932), and more than 90% of the mean diet consisted of 8 plant species during fall, spring, and summer (Figure 4). In all seasons, three grass species (*Agropyron* *smithii, Bouteloua gracilis, Carex* spp.) comprised between 31% and 80% of prairie dogs' diets. *Sporobolus cryptandrus* comprised a large portion of prairie dog diets during fall (22.2% ± 12.8) and spring (51.6% ± 10.4), but was absent in summer diets. In addition to these major diet items, *Artemisia frigida* was consumed in large amounts during fall (11.6% of diet ± 3.1), and prairie dogs consumed both *Opuntia polyacantha* (4.3% of diet ± 2.8) and *Oryzopsis hymenoides* (2.6% of diet ± 1.2) during spring. *Sphaeralcea coccinea* comprised a large portion (18.2% ± 7.0) of the summer diet.

Prairie dogs on colonies 22 and 5W had similar WAT depots during all seasons (Figure 5), as indicated by similar concentrations of hexadecenoic acid (16:0; $F = 1.03$, $P = 0.31$), 9-octadecenoic acid (18:1, $F = 3.56$, $P = 0.07$), octadecadiaenoic acid (18:2; $F = 0.19$, $P = 0.66$), and octadecatrienoic acid (α18:3; $F = 0.04$, $P = 0.85$) in stored lipids. However, the concentration of octadecenoic acid stored in WAT was different between prairie dogs on colonies 5W and 22 (18:0; $F = 4.23$, $P < 0.01$). Although differences in WAT lipid content generally were not significant, prairie dogs on colony 22 tended to have slightly lower concentrations of most lipid classes during October sampling, including the essential fatty acids, 18:2 and α 18:3, (Figure 5A) than prairie dogs on colony 5W (Figure 5B). By January, however, prairie dogs on colony 22 tended to have greater stores of most types of lipids in WAT depots, including 18:2 and α 18:3, than prairie dogs on colony 5W, and these patterns persisted until our June sampling period.

Nutrient concentration of plants common in prairie dog diets did not differ between colonies 22 and 5W in any season. Although levels of carbon, hydrogen, and nitrogen (Table 2) in vegetation collected from colony 22 were consistently lower than levels of these nutrients in plants collected from colony 5W, these differences were not significant when averaged across seasons ($P > 0.05$; one-way ANOVA). Likewise, concentrations of lipids in plant species common in prairie dog diets (Table 3) were also slightly lower on colony 22 than on colony 5W, but these differences were not significant for any lipid class during any season ($P > 0.05$; one-way ANOVA).

Genetic Analyses

We observed no departures from Hardy-Weinberg equilibrium in the six microsatellite markers sampled within each of the six colonies on the CPER. Therefore, there is no evidence of null alleles segregating for any loci, and the assumption of Hardy-Weinberg equilibrium for calculating genetic distances is adequately supported. Populations were genetically differentiated: estimates of F_{st} were 0.133 in 2000 (95% CI 0.106, 0.162) and 0.098 in 2001(95% CI 0.072, 0.122) implying moderate genetic differentiation between colonies on the CPER. Regardless, assignment tests revealed a significant amount of dispersal between all colonies, and in particular between colony 5W and 22. In 2000 and 2001 respectively, 19.15% and 23.39% of all individuals could not be assigned to their colony of capture, and these unassigned individuals are inferred to be immigrants or direct descendants of immigrants (Cornuet et al. 1999). Of the individuals that could not be assigned to their colony of capture, three of six in colony 5W were assigned to colony 22, and four of eight in colony 22 were assigned to colony 5W in 2000. In 2001, two of 12 in colony 5W were assigned to colony 22, and two of three in colony 22 were assigned to colony 5W.

Exclusion tests also demonstrated significant dispersal within the CPER. With rejection probabilities of 1/141 (0.0071) in 2000 and 1/124 (0.0081) in 2001, we found that 7.8% and 7.26%, respectively, of all individuals were excluded from either their colony of capture or all other colonies sampled; these individuals were inferred to have immigrated from outside our study area (Cornuet et al. 1999). In 2000 and 2001, 17.02% and 13.7% of individuals could not be excluded from both their source colony and one other colony. For colony 5W, five of five such individuals in 2000, and two of four such individuals in 2001 could not be excluded from 5W and 22. For colony 22, 3 such individuals in 2000, and 1 individual in 2001 could not be excluded from both 5W and 22, demonstrating high genetic similarity of 5W and 22.

Genetic distances showed that of the six colonies on the CPER, 5W and 22 were the most similar (Table 4). Evidence of moderate genetic differentiation between these colonies is seen in values of Nei's (1978) unbiased minimum genetic distance that range from 0.078-0.404, and values of 0.226-0.427 for Cavalli-Sforza and Edwards (1967) chord distance. Pairwise comparisons of all colonies on the CPER show that colonies 5W and 22 have either the smallest or next to smallest genetic distances in both 2000 and 2001 using both of these distance measures (Table 4).

Weather Patterns

Because the weather station operated by the Shortgrass Steppe Long-Term Ecological Research Program was located between colonies 22 and 5W, we were not able to measure differences in ambient temperature, precipitation, or wind speed between these colonies continuously throughout this study. These colonies are located within 10 km of each other and are at similar elevations, so it is not likely that these colonies differed considerably in general weather patterns. Rain gauges installed and maintained on colonies 22 and 5W showed that these colonies differed significantly ($P < 0.01$) in the amount of precipitation they received between 9 April to 9 November in 2000, 2001, and 2002. These gauges revealed that colony 22 received less precipitation in the form of rain than colony 5W in 2000 (128.5 mm vs. 202.4 mm), 2001(232.7 mm vs. 285.2 mm), and 2002 (70.6 mm vs. 128.8 mm).

DISCUSSION

Body temperature (T_b) patterns of prairie dogs on colonies 5W and 22 were remarkably different from 15 November 2001 to 15 February 2002. Animals on colony 5W maintained high euthermic T_b throughout most of winter, but entered short and shallow bouts of torpor intermittently. These latter patterns are similar to the T_b patterns we previously observed in other black-tailed prairie dogs on the Pawnee National Grassland (Lehmer et al. 2001; Lehmer et al. 2003), as well as at numerous other sites in northern Colorado (Lehmer *unpublished*). On colony 22, prairie dogs entered consecutive bouts of deep torpor during winter. As winter progressed, these torpor bouts reached lower minimum T_b that were maintained for longer periods of time, which is similar to torpor patterns of free ranging hibernators (Michener 1992; Young 1990). These differences in over-winter T_b patterns are noteworthy because colonies 5W and 22 are located within 10 km of each other on the CPER. Despite differences in minimum T_b reached during torpor, prairie dogs on colony 5W and 22 did not differ in rewarming times, which indicates that black-tailed prairie dogs are capable of re-warming rapidly even from extremely low T_b, and that rates of re-warming are somewhat independent of minimum T_b reached during torpor.

For most of the year, prairie dogs on colonies 5W and 22 had similar body masses, concentrations of stored lipid, and concentrations of carbon, hydrogen, nitrogen, and lipid available in dietary plant species. Prior to winter prairie dogs on colony 22 had significantly lower body masses and less stored energy in the form of WAT lipid. Nonetheless, rain gauge data showed that colony 22 received less precipitation during the summers of 2000, 2001, and 2002. Collectively, these results suggest that, prior to winter, prairie dogs on colony 22 experienced greater physiological stress than prairie dogs on colony 5W. Slight deficiencies in body mass, stored energy, and dietary nutrients would generally have a negligible effect on the over-winter T_b patterns of black-tailed prairie dogs, but underlying stress levels of prairie dogs were unusually high during our study. Between 1997 and 2003, northern Colorado, including the CPER, experienced one of the most severe droughts in recorded history (Colorado Climate Center 2003). Extreme and prolonged drought could amplify slight deficiencies in diet quality or stored lipid, decrease body mass, and cause prairie dogs on colony 22 to hibernate during winter. Likewise, drought could amplify effects of small differences in precipitation that we detected between colonies 5W and 22 during the growing seasons of the 2 years preceding our study. Other researchers working in drought-affected areas of Colorado have observed black-tailed prairie dogs becoming dormant for prolonged periods during both summer and winter (P. Young, personal communication).

Genetic analyses do not support the idea that differences in over-winter T_b patterns between prairie dogs on colonies 5W and 22 resulted from genetic differences between populations. We did not measure loci specifically associated with T_b patterns, and it is unlikely that genetic patterns measured by these highly variable loci were correlated with those of adaptive loci (Hedrick 1999). Regardless, we cannot completely exclude the possibility that T_b differences between colonies 5W and 22 are caused by genetic differences between the colonies. However, of all populations sampled, 5W and 22 were the most closely related as estimated from microsatellite multi-locus genotypes and we detected a high level of gene flow between colonies 5W and 22. This level of genetic mixing between the two colonies supports the idea of phenotypic plasticity in torpor in black-tailed prairie dogs.

Other recent research also indicates that a continuum of hibernation patterns exists in small mammals (Lovegrove et al. 2001). It is evident that groups of mammals exhibit rigid patterns of either hibernation or homeothermy, but that some species fall between these two extremes. Our results suggest that differences in T_b patterns between individuals of a particular species may result from phenotypic plasticity of a broadly heterothermic genotype. In this system, differences in phenotypic expression of this genotype appeared to be triggered by subtle environmental and physiological cues. Clearly, our results call into question existing models that propose a clear delineation between homeothermy, facultative or daily torpor, and hibernation (Geiser and Ruf 1995).

Black-tailed prairie dogs have exceptionally plastic T_b patterns, as they practice both daily and seasonal heterothermy, and can enter torpor facultatively during winter, spring, and summer (Lehmer et al. 2001; Lehmer et al. 2003; Harlow 1997). T_b patterns of this species vary considerably between animals in a single population and among separate populations across their geographic range (Lehmer et al. 2001; Lehmer et al. 2003; Lehmer unpublished). These variations reflect the highly variable climate that characterizes the Great Plains inhabited by black-tailed prairie dogs. This is unlike habitats occupied by most sciurid hibernators, which generally have consistent and predictable weather patterns during winter. Predictably cold winters are thought to have played an important role in the evolution of hibernation in ancestral mammals inhabiting extreme northern latitudes (Davis 1976; Geiser 1998), and the ability to hibernate is thought to have been lost as populations expanded southward (Davis 1976). The fossil record indicates that ancestral prairie dogs (*Cynomys* spp.) occupied northern latitudes and this is where hibernating species in subgenus *Leucocrossuromys* are thought to have originated (Goodwin 1995). The two species in subgenus *Cynomys* are thought to have evolved as prairie dog populations expanded southward (Goodwin 1995). Examination of over-winter T_b patterns among prairie dog species offers some support for the theory that hibernation evolved at northern latitudes in response to unfavorable climate, as Gunnison's, white-tailed, and Utah prairie dogs (*Leucocrossuromys*) are believed to hibernate during winter, whereas black-tailed and Mexican prairie dogs (*Cynomys*) are believed to have lost this ability. Results of our study provide clear evidence that black-tailed prairie dogs are capable of hibernating in the natural environment during winter, but may only use this strategy under extreme conditions, like prolonged drought. T_b patterns of free-ranging black-tailed prairie dogs are rarely studied, therefore it is also possible that these animals hibernate frequently, but this behavior has been previously undetected.

Although critical for energy conservation, hibernation is also an important adaptation for water conservation (Bintz 1984). Hibernation can virtually eliminate water loss through urine and feces (Bakko 1977), and considerably reduces evaporative water loss by lowering respiratory rates and the relative humidity of exhaled air (Bintz 1984). Foraging on dry vegetation can potentially satisfy energetic requirements of hibernators during winter, but metabolic water requirements of digestion and assimilation results in animals continually losing weight while consuming food resources with low water content (Hudson 1964; Reidesel et al. 1964). Most sciurid hibernators store large amounts of fat in WAT depots prior to winter, but these energy stores generally cannot provide sufficient energy to survive winter at euthermic T_b (Bintz 1984). Furthermore, catabolism of stored lipids results in a net loss of water at even moderate rates of evaporative water loss (Baudinette 1972). Therefore, when vegetation is excessively dry and fat is the primary source of energy, it is unlikely that animals will be able to achieve a positive water or energy balance at euthermic T_b. By reducing both evaporative water loss and energy requirements, hibernation makes it possible for animals to survive winter by relying primarily on stored lipid.

Inability to maintain appropriate water balance has been cited as an important stimulus for hibernation in several ground dwelling sciurids, as increased ambient temperatures, coupled with low relative humidity and dry vegetation often coincide with the end of the active season (Linsdale 1946; MacMillen 1965). Laboratory studies have shown that torpor can be induced by prolonged water deprivation (Davis 1967), and this has also been demonstrated in laboratory populations of black-tailed prairie dogs (Bakko 1977; Harlow 1995; Harlow and Menkens 1986). Although some laboratory studies have suggested that food deprivation, rather than dehydration, was the primary environmental stimulus for torpor (Davis 1967), these studies do not accurately reflect natural environmental conditions, where food is the primary source of water (Bintz 1984). Black-tailed prairie dogs depend heavily on succulent green plant material during spring, summer, and fall (Fagerstone et al. 1981; Kelso 1939), and drier material, including seeds and invertebrates constitute a small portion of the diet at all times of the year. During drought conditions, availability of moisture-rich vegetation is severely limited, thus diets of prairie dogs can be water limited. Black-tailed prairie dogs have a remarkable tolerance for water deprivation, as this species has higher maximum urine osmolarity, renal medullary thickness, and can survive longer without water than closely related white-tailed prairie dogs (Bakko 1977; Hamilton and Pfeiffer 1977; Harlow 1997; Stephens and Fevold 1993). The ability to endure prolonged water deprivation has been offered as an explanation for the absence of hibernation in black-tailed prairie dogs by some researchers (Bakko 1977; Harlow 1997). Indeed, all available evidence indicates that black-tailed prairie dogs do not hibernate during winter throughout most of their geographic range (Hoogland 1995). Therefore, it is unlikely that low ambient temperatures alone can induce hibernation in black-tailed prairie dogs. Our results suggest that low ambient temperatures coupled with dry, and low quality vegetation can stimulate hibernation in this species.

It is likely that prairie dogs on colony 22 conserved considerable energy by engaging in deep and prolonged torpor during winter, leading to increases in body mass and levels of stored lipid during this period. Prior to winter, prairie dogs on colony 22 had lower body masses and concentrations of WAT lipids than animals on 5W, but by spring prairie dogs on colony 22 had achieved similar body masses and greater levels of stored lipids than prairie dogs on colony 5W. These energy savings could be critical for over-winter survival and reproductive success, especially during severe drought. Animals practicing seasonal torpor can potentially conserve more than 85% of their annual energetic expenditures, and animals can conserve more than 30% of their daily energetic expenditures through daily torpor (Wang 1989). These energy savings underscore the adaptive nature of the T_b patterns we have observed in black-tailed prairie dogs.

The body temperature patterns we have reported may provide important clues about evolution of hibernation and facultative torpor in prairie dogs, as well as in other species. Although hibernation patterns are believed to be driven primarily by innate timing mechanisms (Wang 1989), our study demonstrates that environment can also play a large role in triggering continuous deep torpor. The results of this study may also provide answers to broader ecological questions about whether hibernators, including prairie dogs, can alter T_b patterns to reflect short-term changes in environment, or whether separate populations have adapted to long-term environmental conditions. Hibernation plays a critical role in over-winter survival and reproductive success of ground-dwelling sciurids. Because populations of all prairie dog species are greatly reduced, increasing our understanding of life-history dynamics of these species will undoubtedly help researchers and wildlife managers promote and maintain sustainable populations.

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Table 1. Comparison of general torpor patterns of adult (>1year) black-tailed prairie dogs monitored on two colonies (5W and 22) on the Central Plains Experimental Range (Weld County, CO). Comparisons were made on body temperatures recorded from 15 November 2001 to 15 February 2002, using one-way analysis of variance. Values represent means for individual animals on each colony (5W n=3; 22 n=5).

	Colony 5W				Colony 22				
	$\bar{x}$	S.E.	Min.	Max.	$\bar{x}$	S.E.	Min.	Max.	P Value
Total Number of Bouts	14	6.0	8	20	21	1.6	18	27	0.46
Minimum T_b (°C)	29.7	0.4	22.3	31.7	18.7	1.0	8.2	31.4	<0.01
Total Time Spent in Torpor (h)	431.0	151.0	280.0	582.0	1993.0	50.0	1880.4	2177.4	0.03
Cooling Time (h)	10.9	2.2	2.0	44.4	94.5	8.0	6.6	202.4	<0.01
Rewarming Time (h)	13.5	1.8	3.8	32.8	16.9	2.5	1.2	100.4	0.27
Time at Minimum T_b (h)	5.5	0.9	0.8	13.6	47.9	5.7	3.2	151.6	<0.01
Bout Length (h)	28.3	2.9	20.8	76.0	125.4	10.0	9.2	255.6	<0.01
Inter-Bout Arousal Length (h)	203.4	65.5	20.4	1128.8	33.0	5.6	0.4	205.6	0.02

Table 2. Comparison of seasonal changes in mean carbon, hydrogen, and nitrogen content of plant species common in diets of black-tailed prairie dogs (*C. ludovicianus*) at the Central Plains Experimental Range (Pawnee National Grassland, Weld County, CO). Values of carbon, hydrogen, and nitrogen are expressed as a percentage of total dry mass. Comparisons were made between vegetation collected on two colonies (22 and 5W) separated by <10km. Levels of these nutrients did not differ between colonies 22 and 5W in any season ($P > 0.05$; One-way ANOVA).

	Nutrient											
	Carbon				**Hydrogen**				**Nitrogen**			
	22		**5W**		**22**		**5W**		**22**		**5W**	
	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**
Oct. 2001	42.54	3.4	45.12	2.7	6.22	0.5	6.35	0.3	1.48	0.6	1.76	0.5
Jan. 2002	43.02	3.1	45.35	3.5	6.29	0.5	7.01	0.6	1.28	0.5	1.51	0.4
Jun. 2002	41.55	4.3	44.43	2.3	6.06	0.7	6.56	0.4	1.42	0.6	1.67	0.4

Table 3. Comparison of seasonal changes in mean lipid content of plant species common in diets of black-tailed prairie dogs (*C. ludovicianus*) at the Central Plains Experimental Range (Weld County, CO). Values are expressed as concentration of lipids (mg/ml) in plant tissue. Comparisons were made between vegetation collected on two colonies (22 and 5W) separated by <10km. Levels of these nutrients did not differ between colonies 22 and 5W in any season ($P >$ 0.05; One-way ANOVA).

	October 2001				**January 2002**				**June 2002**			
	22		**5W**		**22**		**5W**		**22**		**5W**	
	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**
16:0	0.99	0.4	0.23	0.4	0.81	0.3	0.86	0.4	0.34	0.2	0.31	0.2
18:0	0.68	0.3	0.72	0.6	0.67	0.2	0.72	0.3	0.24	0.1	0.27	0.1
18:1	0.40	0.3	0.52	0.3	0.81	0.7	0.86	0.5	0.11	0.1	0.15	0.1
18:2	0.52	0.5	0.55	0.4	0.28	0.3	0.32	0.4	0.09	0.1	0.12	0.2
18:3	0.89	0.6	0.95	0.5	0.25	0.2	0.29	0.1	0.57	0.5	0.72	0.3

Table 4. Nei's (1978) unbiased minimum genetic distance and Cavalli-Sforza and Edwards (1967) chord distance matrices for black-tailed prairie dogs (*C. ludovicianus*) on the Central Plains Experimental Range (Weld County, CO) in 2000 and 2001. Colonies 5W and 22 have the smallest or next to smallest genetic distance of all pairwise comparisons using either method, indicating a high degree of relatedness between these colonies, relative to other colonies sampled.

Nei's (1978) unbiased minimum genetic distance							**Cavalli-Sforza & Edwards chord distance**						
2000													
Pop	**5W**	**29**	**30**	**22**	**35**	**27**	**Pop**	**5W**	**29**	**30**	**22**	**35**	**27**
5W	****						5W	****					
29	0.195	****					29	0.354	****				
30	0.217	0.059	****				30	0.331	0.265	****			
22	0.08	0.118	0.078	****			22	0.25	0.317	0.297	****		
35	0.157	0.404	0.382	0.156	****		35	0.295	0.426	0.427	0.293	****	
27	0.206	0.262	0.175	0.142	0.205	****	27	0.355	0.383	0.348	0.322	0.343	****
2001													
Pop	**5W**	**29**	**22**	**35**	**27**		**Pop**	**5W**	**29**	**22**	**35**	**27**	
5W	****						**5W**	****					
29	0.077	****					**29**	0.305	****				
22	0.05	0.082	****				**22**	0.26	0.299	****			
35	0.081	0.178	0.145	****			**35**	0.226	0.319	0.321	****		
27	0.121	0.209	0.215	0.186	****		**27**	0.324	0.349	0.361	0.309	****	

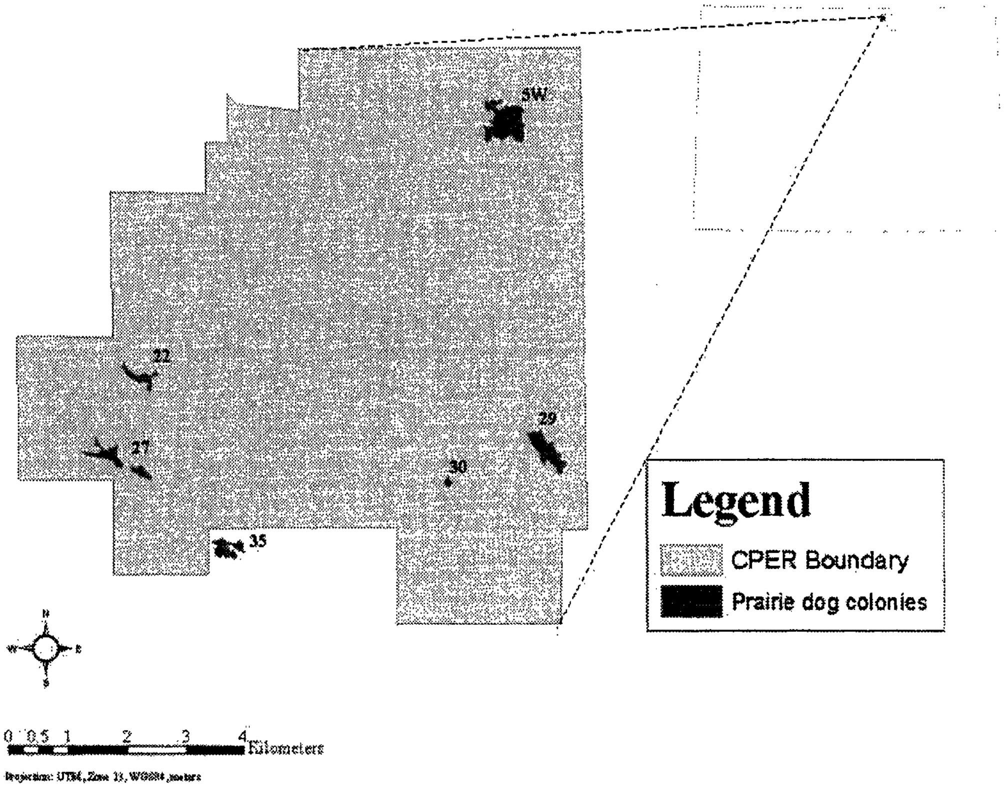

Figure 1. Black-tailed prairie dog (*C. ludovicianus*) colonies on the Central Plains Experimental Range in Weld County, CO. Map represents sizes and position of colonies in June 2000.

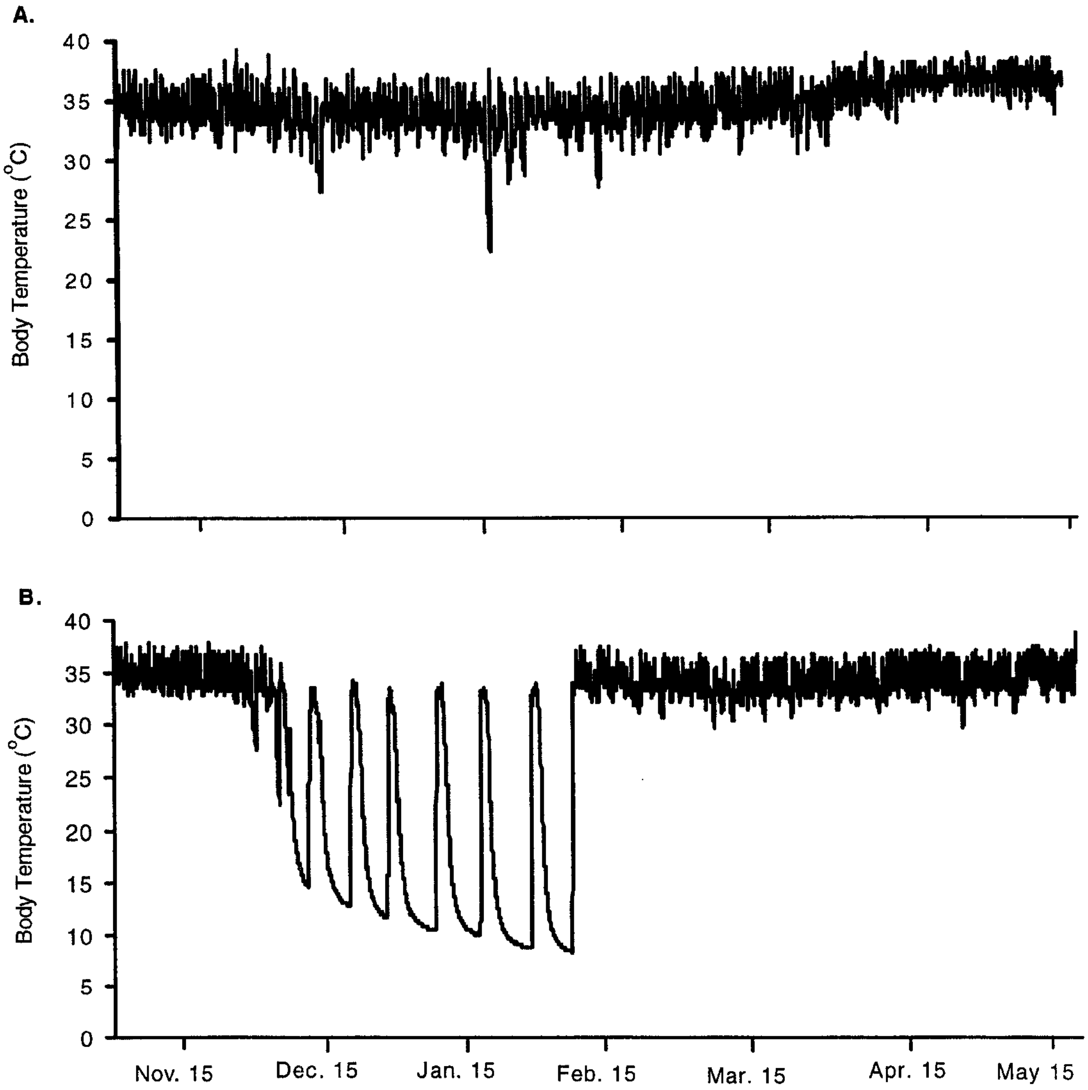

Figure 2. Body temperature patterns of representative (i.e. displayed mean values for most torpor patterns reported) adult (> 1 yr) female black-tailed prairie dogs (*C. ludovicianus*). "A" illustrates the body temperature of a prairie dog monitored on colony 5W from 15 November 2001 to 15 May 2002, and "B" shows the body temperature of a prairie dog monitored on an adjacent colony (22) during this period. All animals were monitored at the Central Plains Experimental Range in Weld County, CO.

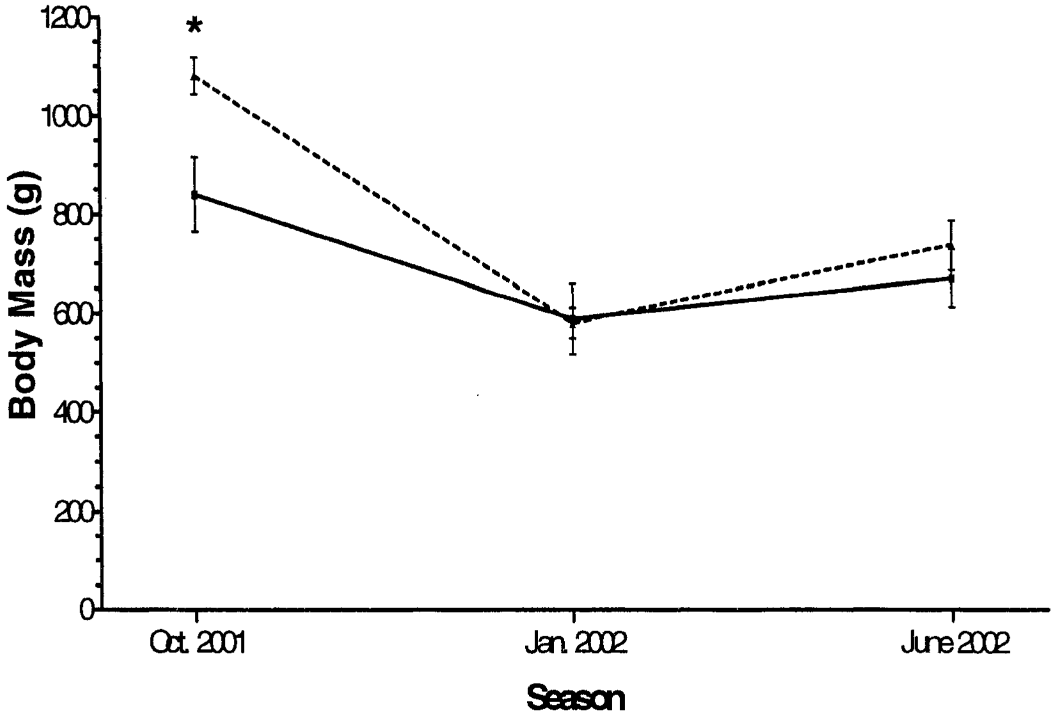

Figure 3. Comparison of seasonal changes in body mass of adult (> 1 yr) black-tailed prairie dogs (*C. ludovicianus*) monitored on two colonies at the Central Plains Experimental Range (Weld County, CO). Solid line illustrates body mass of prairie dogs from colony 22, and dashed line illustrates body mass of prairie dogs on colony 5W. * indicates seasons in which differences in body mass were significant ($P < 0.05$).

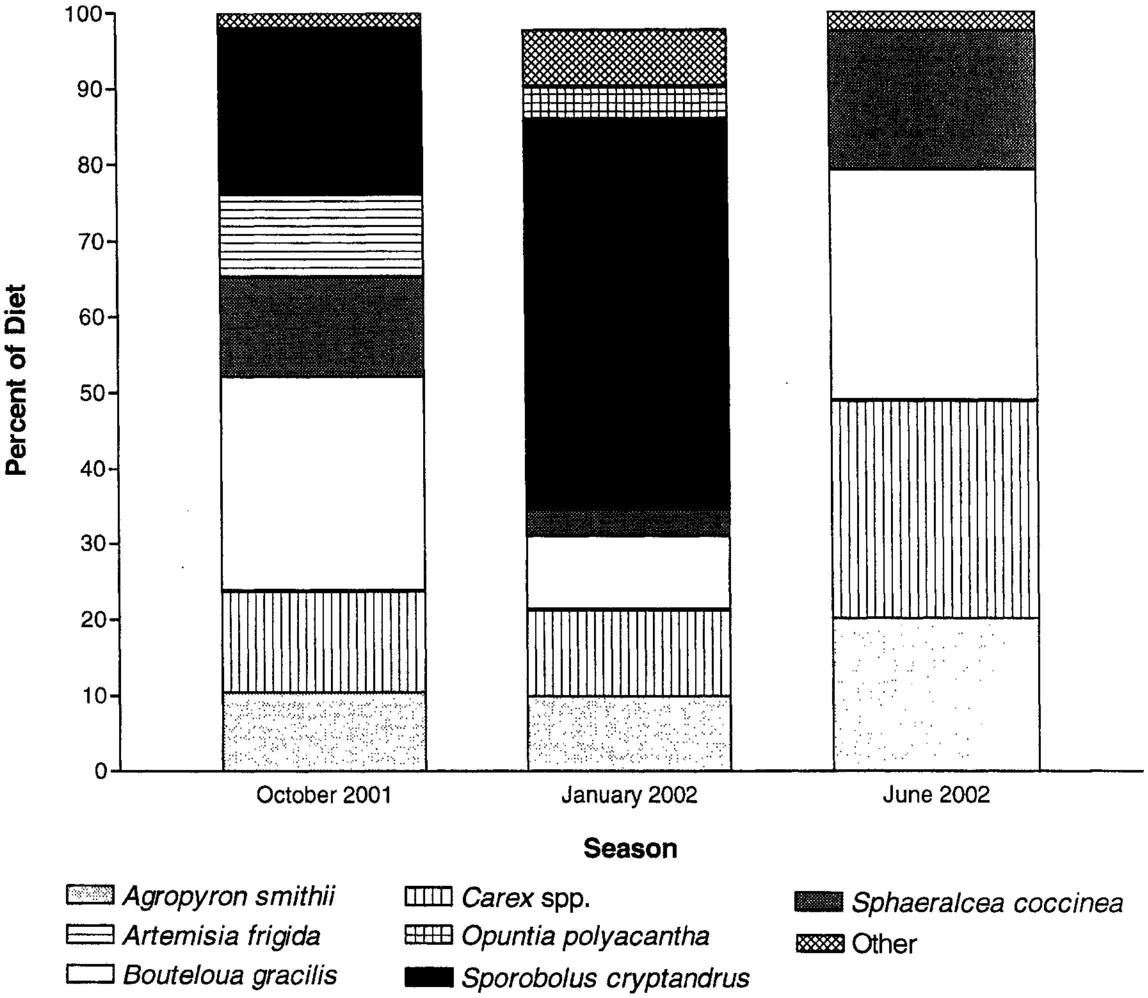

Figure 4. Seasonal changes in diet composition of adult black-tailed prairie dogs (*C. ludovicianus*) monitored on two colonies at the Central Plains Experimental Range (Weld County, CO). Diet was determined by identifying plant fragments contained in fecal samples and values represent mean frequency of each plant in the diet (n = 10 prairie dogs per season).

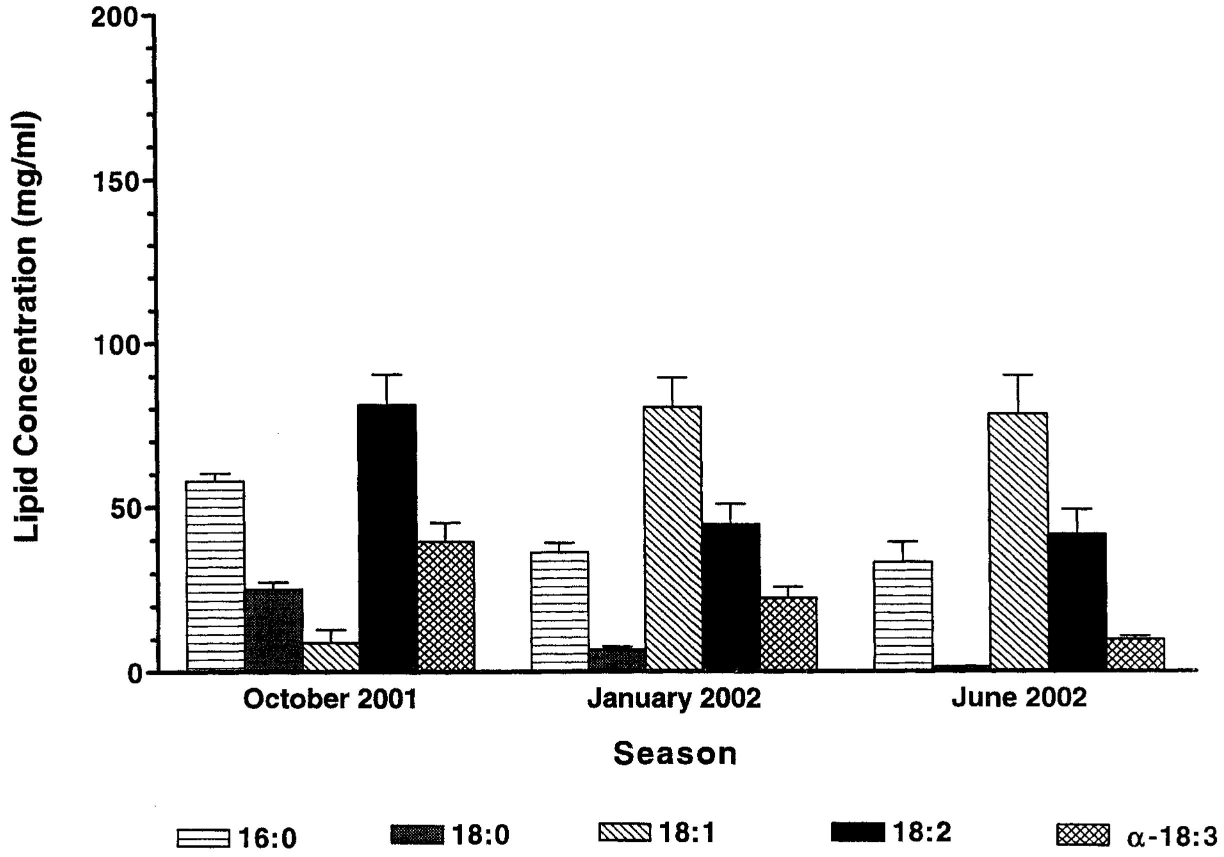

Figure 5. Comparison of lipids contained in white adipose tissue (WAT) depots between black-tailed prairie dogs (*C. ludovicianus*) monitored on two colonies at the Central Plains Experimental Range (Weld County, CO). "A" shows composition of stored lipids among prairie dogs on colony 22 and "B" shows lipid composition of animals on colony 5W. * indicates seasons in which differences in concentration of a particular lipid were significant between colonies 5W and 22 ($P < 0.05$).

CHAPTER TWO

VARIATION IN TORPOR PATTERNS OF FREE-RANGING BLACK-TAILED AND UTAH PRAIRIE DOGS ACROSS ELEVATIONAL GRADIENTS

The ability of animals to enter torpor depends on numerous physiological and environmental factors, and species with broad geographic ranges that span habitats with varying climatic conditions should display torpor patterns that reflect this variation. The varied ranges and distinct torpor patterns of prairie dogs (*Cynomys* spp.) make them model systems for the study of torpor. Torpor patterns of Utah prairie dogs (*C. parvidens*), which are believed to hibernate continuously during winter, contrast to those of black-tailed prairie dogs (*C. ludovicianus*), which enter torpor during periods of environmental or physiological stress. We compared over-winter body temperature (T_b) patterns for more than six months in adult (>1 y) black-tailed prairie dogs in northern Colorado and Utah prairie dogs from colonies located along elevational gradients. In general, black-tailed prairie dogs entered torpor facultatively during winter, whereas Utah prairie dogs hibernated continuously for extended periods. Both black-tailed and Utah prairie dogs displayed significant differences in T_b patterns across elevations, with lower elevation populations entering more shallow and infrequent torpor than prairie dogs at higher elevations. Minimum T_b reached during torpor was correlated with bout length in both species, and these correlations were strongest at higher elevations. T_b patterns of black-tailed prairie dogs showed strong circadian rhythmicity, as most prairie dogs entered into and aroused from torpor between 11 am and 5 pm and bout lengths increased in increments of approximately 24 h. Torpor patterns of Utah prairie dogs did not display the same circadian patterns, as these animals entered into and aroused from torpor during all times of the day and bout lengths did not approximate 24 h intervals. Collectively, our observations indicate that environmentally induced variation in torpor patterns results from limitations imposed by environmental factors and habitat quality, rather than from fixed physiological differences between separate populations. Furthermore, differences in circadian patterns of torpor between black-tailed and Utah prairie dogs indicate that underlying mechanisms that stimulate and control torpor patterns may differ between these two species.

INTRODUCTION

The importance of torpor in the life histories of ground-dwelling sciurids cannot be overstated. The energetic savings associated with torpor allow animals to survive prolonged periods when thermoregulation is costly during excessively cold, wet, hot or dry conditions (Davis 1976). Energy savings are also critical for surviving periods when the nutritional quality of available forage is at an annual low. The energy conserved during these sub-optimal periods can be used later to further increase an animal's potential fitness through reproduction (Davis 1976; Michener 1992). Despite the importance of torpor in the annual cycles of ground-dwelling sciurids, the influence of environmental and geographic variation on this behavior in free-ranging animals is not well understood.

The closely related black-tailed (*Cynomys ludovicianus*) and Utah (*C. parvidens*) prairie dogs display different body temperature patterns during winter. Several studies have demonstrated that under laboratory conditions black-tailed prairie dogs can enter torpor when deprived of food or water (Hamilton and Pfeifer 1977; Harlow and Menkens 1986; Thomas and Reidesel 1975), but it was presumed that these animals remain active throughout winter in the field (Bakko 1977; Bakko et al. 1988; King 1955; Smith 1958). Previously, we demonstrated that free-ranging black-tailed prairie dogs enter torpor intermittently during winter, using an intermediate strategy between those of hibernators and non-hibernators (Lehmer et al. 2001). Further, we found that black-tailed prairie dogs conserve energy by foraging and practicing heterothermy throughout winter, and then enter torpor during physiological or environmental stress (Lehmer et al. 2003). Some evidence indicates that black-tailed prairie dogs estivate facultatively during hot and dry periods (Lehmer et al. 2003).

In contrast, visual observations of Utah prairie dogs have led to the conclusion that this species hibernates during winter (Hoogland 1995; Pizzimenti 1975). We are not aware, however, of any study documenting body temperature patterns of either free-ranging or captive Utah prairie dogs. Anecdotal evidence indicates that Utah prairie dogs estivate when water stressed and that low elevation populations only enter torpor facultatively during winter, as they have been observed above ground on mild winter days (Collier and Spillet 1975). Thus, torpor patterns of Utah prairie dogs may vary throughout their geographic range and may be influenced by external environmental conditions. This contrasts with the prevailing view that Utah prairie dogs are true hibernators, which are not generally affected by changes in above-ground environmental conditions between immergence in the fall and emergence in spring (Davis 1976).

The ability to enter torpor depends on both environmental and physiological factors; thus, the geographic range of a species can indirectly influence its over-winter strategy. The geographic ranges of black-tailed and Utah prairie dogs encompass environments that vary considerably in elevation, precipitation, temperature, and vegetation. For example, within a 300 km radius in southern Utah, populations of Utah prairie dogs occur at elevations ranging from 1500 m to 3300 m. The range of black-tailed prairie dogs spans western Great Plains between southern Canada and northern Mexico. Within a 350 km radius in northern Colorado black tails are found at elevations ranging from 1200 m to 2500 m. Although observational evidence suggests that torpor patterns of prairie dogs vary throughout their ranges, these patterns have not been linked to physiological and ecological factors that may influence these different over-winter strategies.

The objective of this research was to increase our understanding of the over-winter body temperature patterns of free-ranging black-tailed and Utah prairie dogs across elevational gradients in northern Colorado and southern Utah. We predicted that at higher elevations prairie dogs would reach lower minimum body temperatures that would be maintained for longer periods than at lower elevations. At lower elevations, bouts would be of shorter duration and minimum body temperature would be higher. At comparable elevations, we hypothesized that Utah prairie dogs would have longer bouts with lower minimum body temperatures than black-tailed prairie dogs. Variation in torpor patterns across the elevational gradient would provide evidence that environmentally induced variation in torpor patterns results from limitations imposed by environmental factors and habitat quality, rather than by fixed physiological differences between populations. A lack of within-species variation would suggest that the ability to enter torpor is caused by innate physiological constraints, with the environment playing a role in cueing the beginning and end of torpor bouts but not affecting the depth or length of torpor bouts.

METHODS

Study Sites

We selected six black-tailed prairie dog colonies and six plots on three Utah prairie dog colonies at low, mid, and high elevations (Table 1). To facilitate within and across site comparisons and for replication, we attempted to monitor prairie dogs from two colonies or experimental plots at each elevation that were within10 km of each other. To minimize sources of large-scale geographic variation for each species, all colonies we studied occurred within a 300 km radius.

Torpor Patterns

We attempted to monitor body temperature (T_b) patterns for at least six months in five animals at 12 colonies or experimental plots. In June 2001, we live-trapped 10 adult (> 1 year) Utah prairie dogs at each elevation and surgically implanted temperature sensitive data loggers (Stow Away ™ TidbiT, Onset Computer Corp., Bourne, MA) into animals' abdominal cavities (Lehmer et al. 2001). After recovering from surgery (about four h), prairie dogs were released to their original sites of capture. This procedure was duplicated for black-tailed prairie dogs in October 2001. Due to difficulty in trapping black-tailed prairie dogs at our original mid-elevation site, we replaced this colony with another black-tailed prairie dog colony in December 2001, and commenced T_b measurements in prairie dogs at this mid-elevation site in December 2001. Implanted loggers were programmed to record T_b to the nearest 0.1°C every 24 minutes.

In June 2002, we attempted to recapture all implanted animals ($n = 60$) but were successful in recapturing and surgically removing temperature loggers from 16 black-tailed prairie dogs (five high elevation, three mid elevation, and eight low elevation) and 11 implanted Utah prairie dogs (seven high elevation, two mid elevation, two low elevation). We recovered two more temperature loggers at our low elevation site from deceased Utah prairie dogs. These loggers provided T_b readings until February 2002 so we were able to include these data in our analyses of torpor patterns. Animals were released to sites of original capture after recovery from surgery to remove loggers. T_b data were downloaded from loggers using Box Car Pro software (version 3.6, Onset Computer Corp., Bourne, MA). Calibration of loggers was verified before implantation and after removal (Lehmer et al. 2001; Lehmer et al. 2003); most loggers showed accurate calibration within 0.1°C. For loggers that were not appropriately calibrated ($n = 4$), calculations of T_b patterns were based on absolute differences between recorded values, which yielded results that did not differ from measurements obtained from non-drifting loggers within the same study population ($F = 1.79$, $P = 0.56$).

We considered a prairie dog to be in torpor if it experienced a continuous reduction in T_b that reached a level below 31°C at some point, maintained a T_b below 31°C, and subsequently re-warmed to a T_b above 36°C. We established 31°C as the threshold T_b for torpor because this is below the mean euthermic daily minimum T_b previously reported for prairie dogs in their natural environments (Bakko et al. 1988; Lehmer et al. 2003). We determined cooling rates of prairie dogs during torpor by calculating the number of hours required to reduce T_b from euthermic levels (>36°C) to the minimum level reached during a torpor bout, and re-warming rates by calculating the number of hours required to increase T_b from the minimum level reached during the bout to a level above 36°C. The duration of inter-bout arousals were determined by calculating the number of hours that prairie dogs maintained $\mathrm{T_b}$ above 36°C between separate bouts of torpor.

Black-tailed prairie dogs from one colony at our low elevation site displayed unusual T_b patterns (Chapter 1: Lehmer et al. *submitted*), so we omitted these data from analyses in this report. The description of torpor patterns reported here for our low elevation population of black-tailed prairie dogs reflect T_b patterns of a single colony (n = 3 prairie dogs). The unusual T_b patterns we observed in the other colony at this elevation resembled true hibernation and were likely a response to severe drought at the site during 2002 (Chapter 1: Lehmer et al. *submitted*).

Statistical Analyses

All statistical analyses of torpor patterns of Utah prairie dogs were of data recorded between 15 September 2001 and 15 April 2002. Although two temperature loggers at our low elevation site were recovered from animals that died in late winter, we included the complete set of T_b data for these animals in our study. Analyses of torpor patterns of black-tailed prairie dogs at low and high elevation sites were of data recorded between 15 September 2001 and 15 April 2002. However, analyses of T_b data for our mid elevation site were conducted only on T_b measurements recorded between 15 December 2001 and 15 April 2002. Although the period in which loggers recorded T_b differed between elevations, all cross-site comparisons for black-tailed prairie dogs were conducted on complete sets of $\mathrm{T_b}$

data, and therefore represent the most conservative estimates of differences between populations at different elevations.

General linear models were used to compare differences in general torpor patterns of prairie dogs across elevations (SAS V.8, SAS Institute, Cary, NC). These tests included comparisons of the average number and length of torpor bouts, differences in minimum T_b, time spent at minimum T_b, elapsed time between bouts, time required to reach minimum T_b and return to euthermy, and total amount of time spent in torpor. Spearman correlations were used to determine relationships between minimum T_b of prairie dogs during torpor and bout length. We evaluated differences in mean dates of first and final torpor bouts of across elevations by comparing Julian dates of first immergence and final emergence from torpor for each animal (ANOVA), with all animals weighted equally regardless of their total number of bouts. Unless otherwise stated, values describing differences in these general torpor patterns are presented as the mean ± standard error per animal for each variable. Differences were considered to be significant if $P \leq 0.05$. Spearman correlations were used to determine relationships between minimum T_b of prairie dogs during torpor and bout length.

RESULTS

Both black-tailed and Utah prairie dogs displayed significant differences in T_b patterns between elevations, with lower elevation populations entering more shallow and infrequent torpor than prairie dogs at higher elevations (Figures 1 and 2). During torpor, black-tailed prairie dogs displayed differences between elevations (Table 2), with prairie dogs at higher elevations reaching lower minimum T_b, requiring more time to reach minimum

T_b, and maintaining these low T_b for longer periods than prairie dogs at lower elevations. Conversely, prairie dogs at higher elevations had longer bouts, greater total changes in T_b, and shorter inter-bout arousal periods than prairie dogs at lower elevations. Although the total number of torpor bouts was similar among black-tailed prairie dog populations, the prairie dogs at higher elevation colonies spent a greater amount of time in torpor than prairie dogs at lower elevation colonies. Dates of first torpor bouts varied between elevations, but dates of final bouts were similar among black-tailed prairie dog populations.

Elevation also influenced torpor in Utah prairie dogs (Table 3), with prairie dogs at higher elevations reaching lower minimum T_b, requiring more time to reach minimum T_b and maintaining minimum T_b for longer periods than prairie dogs at lower elevation colonies. Re-warming times did not differ between elevations in this species. Utah prairie dogs at higher elevations also had longer bouts and greater changes in T_b during torpor than prairie dogs from lower elevation colonies, but elapsed time between bouts did not differ across elevations. Like black-tailed prairie dogs, Utah prairie dog populations experienced similar numbers of torpor bouts across elevations; but prairie dogs at higher elevations spent a greater amount of time in torpor than prairie dogs at lower elevation colonies. Utah prairie dog populations also differed in average dates of immergence into and emergence from hibernation between populations, with prairie dogs at higher elevation colonies commencing hibernation earlier in fall and terminating hibernation later in spring than prairie dogs at lower elevation colonies.

Minimum T_b reached during torpor was correlated with bout length in both black-tailed and Utah prairie dogs (Figures 3 and 4). Among black-tailed prairie dogs, these correlations were strongest at higher elevation colonies and weakest at lower elevations. Utah prairie dogs showed strong correlations between these variables at all elevations.

Body temperature patterns of black-tailed prairie dogs showed strong circadian rhythmicity. Timing of immergence into torpor and emergence from all torpor bouts occurred between 10 AM and 7 PM. More specifically, at high elevation colonies, 88.8% of immergence and 92.2% of emergence from torpor took place between 11am and 5pm (Figure 5A). At mid elevations, 90.5% of immergence into and 95.2% of emergence from torpor took place between 11am and 5pm (Figure 5B), and at low elevations, 85.7% of immergence and 100% of emergence occurred during this period (Figure 5C). The 24-h rhythmicity in immergences and emergences resulted in bout lengths clustered around 24 h intervals and multiples thereof. At high elevations, 83.8% of all bouts fell within three h of a 24 h interval (Figure 6A). We detected similar patterns in mid and low elevation populations of black-tailed prairie dogs, with 90.5% and 85.7%, respectively, of bouts occurring within three h of a 24 h interval (Figure 6B and C).

Timing of immergence into and emergence from torpor among Utah prairie dogs did not display a clear pattern, with prairie dogs entering into and arousing from bouts at all times of the day. At high elevations, only 38.7% of immergence and 27.7% of emergence occurred between 11am and 5 pm (Figure 7A). At mid elevations, 34.3% of immergence and 32.8% of emergence took place between 11 am and 5pm (Figure 7B), and at low elevations, 31.1% of immergence and 32.8% of emergence took place during this period (Figure 7C). Bout lengths of Utah prairie dogs were not clustered around 24 h intervals or multiples of 24 h intervals. At high elevations, 23.5% of bouts fell within three h of a 24 h interval (Figure

8A). Likewise, at mid and low elevations, 25.7% and 37%, respectively, of all torpor bouts occurred within three h of a 24 h interval (Figure 8B and C).

All black-tailed prairie dogs entered torpor sporadically during winter. The onset of torpor occurred earliest among prairie dogs at high elevation colonies, but prairie dogs at low elevation colonies continued to enter torpor later into spring than prairie dogs at mid and high elevation colonies (Figure 9). Torpor occurred more frequently at higher elevations, with at least one prairie dog in torpor on 77.0% of days between the mean dates of the first and final bouts (November 16 to March 18) at high elevation colonies. Between the mean dates of the first and final bouts, at least one prairie dog was in torpor on 61.2% of days at mid elevation colonies (19 December to 14 March), and on 39.5% of days at low elevation colonies (20 November to 20 March).

Torpor patterns were more consistent among Utah prairie dogs (Figure 10). At least one animal was in torpor on 100% of days between the mean dates of the first and final bouts at high elevation colonies (27 September to 17 March), 97.2% of days at mid elevation colonies (1 October to 24 February), and on 89.3% of days at low elevation colonies (18 October to 16 February). It is noteworthy that Utah prairie dogs at low elevation colonies appeared to break the torpor cycle after January 1, 2002, with animals immerging into and emerging from torpor at irregular intervals from January 1, 2002 to February 16, 2002.

DISCUSSION

Our results show that black-tailed prairie dogs entered torpor facultatively during winter, while Utah prairie dogs hibernated for longer uninterrupted periods. Black-tailed prairie dogs at all elevations maintained high euthermic body temperatures for most of winter, but entered torpor intermittently. Across elevations, Utah prairie dogs entered deep bouts of torpor for a prolonged period during winter, but at low elevations torpor was intermittent at both the beginning and end of the hibernation season. Despite differences between species in these general torpor patterns, we also found considerable within species variation in body temperature patterns across elevations. At higher elevations, black-tailed prairie dogs entered torpor more frequently, reached lower minimum body temperatures, and maintained these minimum temperatures for longer periods than prairie dogs at lower elevations. Like black-tailed prairie dogs, higher elevation populations of Utah prairie dogs spent a greater portion of winter in torpor, reached lower minimum body temperatures, and remained at minimum body temperatures for longer periods during torpor than prairie dogs at lower elevations.

Both black-tailed and Utah prairie dogs are capable of practicing a wide range of torpor patterns, and the extent of variation in body temperatures that we detected between prairie dog populations within a relatively small geographic area underscores the plasticity inherent in the heterothermic strategies of hibernation and facultative torpor. Variation in torpor patterns among prairie dogs results primarily from environmental factors and habitat quality, rather than from fixed physiological differences between separate populations. In addition to affecting the depth and length of torpor bouts, environmental conditions also seemed to affect the overall length of the hibernation season among Utah prairie dogs, and influenced the occurrence of intermittent bouts in black-tailed prairie dogs.

Body temperature patterns of other ground-dwelling sciurids are also influenced by environmental and habitat conditions. In Columbian and Richardson's ground squirrels, the duration of the hibernation season, as well as the depth and length of individual torpor bouts are closely related to both ambient air and soil temperatures present in burrow chambers (Michener 1992; Young 1990). In black-tailed prairie dogs, sudden and extreme reductions in above-ground air temperatures are strongly correlated to immergence (Lehmer et al. 2001, Lehmer et al. 2003). Quality and availability of above-ground forage can also influence body temperature patterns, and in many species, the onset of hibernation coincides with times when the quality and availability of plant material is at an annual low (Davis 1976). In species practicing facultative torpor, immergence is strongly correlated to precipitation, which could preclude foraging (Lehmer et al. 2001), and torpor occurs most frequently during periods when the quality of available forage is at an annual low (Lehmer et al. 2001 and Lehmer and Van Horne 2001). Nutrient composition of forage available during active periods can also have a large influence on body temperature patterns of hibernators. The storage of large amounts of the essential lipid, linoleic acid, allows animals to reach and maintain low minimum body temperatures during torpor (Geiser et al. 1994), whereas excess storage of linolenic acid can interfere with natural torpor patterns (Frank and Storey 1995; Hill and Florant 2000).

Considering the range of environmental conditions present along the elevational gradients of our study areas, prairie dog populations experienced considerable differences in ambient air and soil temperatures, precipitation, and forage quality and availability during winter. The lower body temperatures and more frequent torpor bouts we observed in higher elevation populations of prairie dogs correspond to differences in environment and habitat conditions across elevations. Although environmental conditions influence torpor patterns of prairie dogs, it is difficult to rule out the possibility that cross-elevation differences in body temperature patterns we observed were also influenced by long-term adaptation of individual populations to local environmental conditions.

Black-tailed prairie dogs appeared to adhere strongly to a 24 h circadian system, but Utah prairie dogs did not follow this pattern. These differences in circadian patterns indicate that underlying mechanisms that stimulate and control torpor may differ between these species. Geiser and Ruf (1995) suggest that, because of their short bouts (<12 h) and inter-bout foraging episodes, animals that practice daily torpor are able to regularly entrain to natural light cycles. In contrast, hibernators may not follow a 24 h circadian cycle during torpor because the long bouts and tendency to remain in hibernacula between bouts prevent them from entraining on natural light during winter (Geiser and Ruf 1995). Black-tailed prairie dogs display over-winter body temperature patterns intermediate to those of hibernators and daily heterotherms. Most of their bouts exceeded 12 h, but they regularly engaged in above ground activities during inter-bout arousals. This species adheres to a daily circadian cycle, possibly because intermittent torpor bouts and above-ground foraging between bouts cues circadian timing during multi-day torpor. However, the length of individual torpor bouts can be influenced by a multitude of environmental factors, making it difficult to rule out the possibility that differences in circadian timing of torpor between black-tailed and Utah prairie dogs result from the influence of external environmental factors. Further investigation of these possibilities might provide clues about the evolution of hibernation, daily torpor, and homeothermy among ground-dwelling sciurids.

Differences in torpor patterns across elevations undoubtedly translated into differences in metabolic energy expenditures between separate black-tailed and Utah prairie dog populations. The most costly phases of torpor are re-warming and inter-bout arousal periods, but sciurids can conserve more than 80% of total metabolic energy needed for euthermy per month by practicing deep and continuous torpor (Wang 1979). At higher elevations, both black-tailed and Utah prairie dogs had longer torpor bouts and shorter inter-bout arousal periods, and thus fewer re-warming episodes, than prairie dogs at lower elevations. Furthermore, the length of time that high elevation populations of black-tailed prairie dogs were in torpor exceeded that of prairie dogs at mid-elevation colonies by more than 16 days and that of prairie dogs at low elevations by more than 24 days. Similarly, high elevation populations of Utah prairie dogs were in torpor for 31 days longer than prairie dogs at mid-elevation colonies and about 70 days longer than prairie dogs at low elevations.

These patterns suggest that energetic costs during winter are considerably greater for prairie dogs at lower elevations, but it is difficult to translate exactly how much energy use varied among prairie dogs at different elevations. High elevation populations may have conserved energy by practicing deeper and more frequent torpor. During inter bout arousals, however, these animals had to maintain euthermic body temperatures in presumably lower ambient temperatures than those experienced by prairie dogs at lower elevations. This increased thermal gradient has been shown to substantially increase over-winter energetic expenditures for Columbian ground squirrels at high elevations compared to lower elevation populations (Young 1988). In addition, because black-tailed prairie dogs continue to forage throughout winter, lower elevation populations may have more opportunity to increase energy inputs during winter than prairie dogs at higher elevations. Nevertheless, calculations of energetic expenditures and savings for prairie dogs at each elevation are beyond the scope of this study, and the potential for differences in over-winter energetic expenditures among separate prairie dog populations is difficult to estimate.

In recent years, a number of studies have questioned whether a clear distinction can be made between hibernators and non-hibernators (Lehmer et al. 2001; Lehmer et al. *submitted*; Lovegrove et al. 2001). Facultative torpor is an adaptive physiological behavior, yet hibernation patterns are thought to be somewhat rigid within each species (Davis 1976). Our study, however, demonstrates plasticity inherent in both of these over-winter behaviors and underscores the extent that environmental conditions can affect body temperature patterns. The climate of the inter-mountain west is highly variable, thus the ability of animals to manipulate its body temperature patterns in response to short-term changes in environmental conditions would be highly adaptive. The advantage of such an adaptive phenotype is reflected by the widespread historic distributions of these species throughout the Great Plains and Great Basin of the Western United States (Goodwin 1995). In the future, this adaptability may prove to be essential in the recovery and long-term sustainability of these species, which are both at risk of extinction. Because of the importance of over-winter body temperature patterns to survival and reproductive success of ground dwelling sciurids, increasing our understanding of body temperature patterns of black-tailed and Utah prairie dogs in their natural environments will help biologist develop comprehensive management and recovery plans that incorporate this important aspect of their life histories.

ACKNOWLEDGEMENTS

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Table 1. Overview of colony elevations, locations, and sampling dates for investigation of over-winter body temperature patterns of free-ranging adult (>1 y) black-tailed (*C. ludovicianus*) and Utah (*C. parvidens*) prairie dogs. Each species was sampled across an elevational gradient in northern Colorado (*C. ludovicianus*) and southern Utah (*C. parvidens*). We monitored two black-tailed colonies at each elevation and two experimental plots on a single Utah prairie dog colony at each elevation.

Site	**Elevation**	**County**	**Site Name**	**Sampling Dates**
		Black-Tailed Prairie Dogs		
Low Elevation	1650 m	Weld	Central Plains Experimental Range	October 2001* June 2002
Mid Elevation	1880 m	Boulder	Rabbit Mountain	
High Elevation	2185 m	Boulder	Heil Valley Ranch	
		Utah Prairie Dogs		
Low Elevation	1575 m	Iron	Horse Hollow	June 2001 June 2002
Mid Elevation	2350 m	Garfield	Tom Best Spring	
High Elevation	3000 m	Wayne	The Tanks	

*Temperature loggers were not implanted into black-tailed prairie dogs at mid elevation colonies until December 2002, as these sites replaced a previous study population.

Table 2. Comparison of general torpor patterns of adult (> 1 year) black-tailed prairie dogs (*C. ludovicianus*) across an elevational gradient in northern Colorado from 15 September 2001 to 15 April 2002. Sample sizes differed between elevations (n= 5 high elevation; 3 mid elevation; 3 low elevation). Differences in torpor patterns between elevations were evaluated with one-way analyses of variance.

	High Elevation		**Mid Elevation**		**Low Elevation**		***P* Value**
	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	
Date of First Torpor Bout	16 November		19 December		20 November		0.031
Date of Last Torpor Bout	18 March		14 March		20 March		0.077
Time to Reach Minimum T_b (h)	29.2	1.8	25.9	4.7	13.1	2.0	< 0.001
Minimum $\mathrm{T_b}$ During Torpor (°C)	27.4	0.3	29.1	0.5	29.8	0.4	< 0.001
Time at Minimum T_b (h)	8.3	0.6	7.9	0.8	5.3	0.7	0.054
Time to Rewarm to Euthermic T_b (h)	10.1	1.2	16.5	2.7	14.5	1.4	0.032
Total Change in T_b (°C)	8.2	0.3	6.3	0.4	6.3	0.4	0.003
Total Bout Length (h)	43.7	2.3	46.0	5.5	30.8	2.5	0.022
Time Between Bouts (h)	85.2	9.2	128.9	33.1	211.1	53.8	0.001
Total Time Spent in Torpor (h)	1005.3	64.9	615.6	32.1	430.9	26.4	0.001
Total Number of Bouts	23.2	4.0	7.0	2.7	14.0	6.0	0.066

Table 3. Comparison of general torpor patterns of adult (> 1 year) Utah prairie dogs (*C. parvidens*) across an elevational gradient in southern Utah from 15 September 2001 to 15 April 2002. Sample sizes differed between elevations (n= 7 high elevation; 2 mid elevation; 4 low elevation). Differences in torpor patterns between elevations were evaluated with one-way analyses of variance.

	High Elevation		**Mid Elevation**		**Low Elevation**		***P* Value**
	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	
Date of First Torpor Bout	27 September		1 October		18 October		0.041
Date of Last Torpor Bout	17 March		24 February		16 February		0.035
Time to Reach Minimum T_b (h)	193.1	8.6	161.3	15.7	122.9	9.5	< 0.001
Minimum T_b During Torpor (°C)	9.7	0.7	10.5	1.1	15.4	0.9	< 0.001
Time at Minimum T_b (h)	156.8	7.9	126.5	12.5	125.4	9.5	0.023
Time to Rewarm to Euthermic T_b (h)	4.2	0.3	4.2	0.6	5.6	1.4	0.342
Total Change in T_b (°C)	24.5	0.7	24.2	1.0	18.9	0.8	< 0.001
Total Bout Length (h)	252.0	12.7	202.2	17.3	175.7	11.1	< 0.001
Time Between Bouts (h)	9.6	0.9	22.1	14.2	17.8	4.3	0.167
Total Time Spent in Torpor (h)	4284.5	54.6	3538.8	48.7	2591.3	35.4	<0.001
Total Number of Bouts	17.0	0.8	17.5	3.5	15.3	1.9	0.608

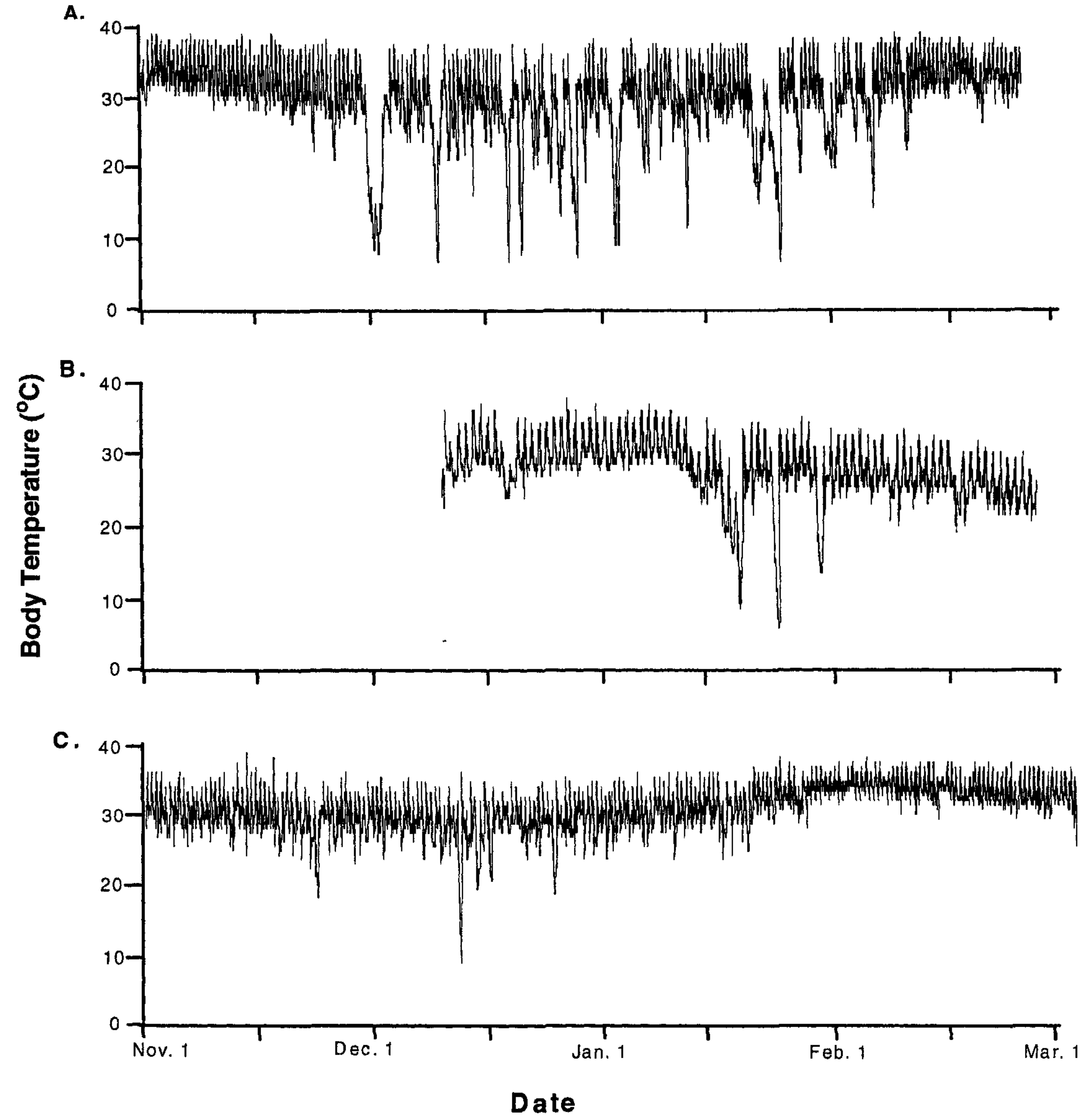

Figure 1. Comparison of body temperature patterns of representative (i.e. displayed mean values for most torpor patterns reported) black-tailed prairie dogs (*C. ludovicianus*) from high (A), mid (B), and low (C) elevation colonies in northern Colorado from November 2001 to March 2002. Body temperature measurements for prairie dogs at mid elevation colonies are only available from 15 December 2001 to 1 March 2002, as this site replaced a previous study population.

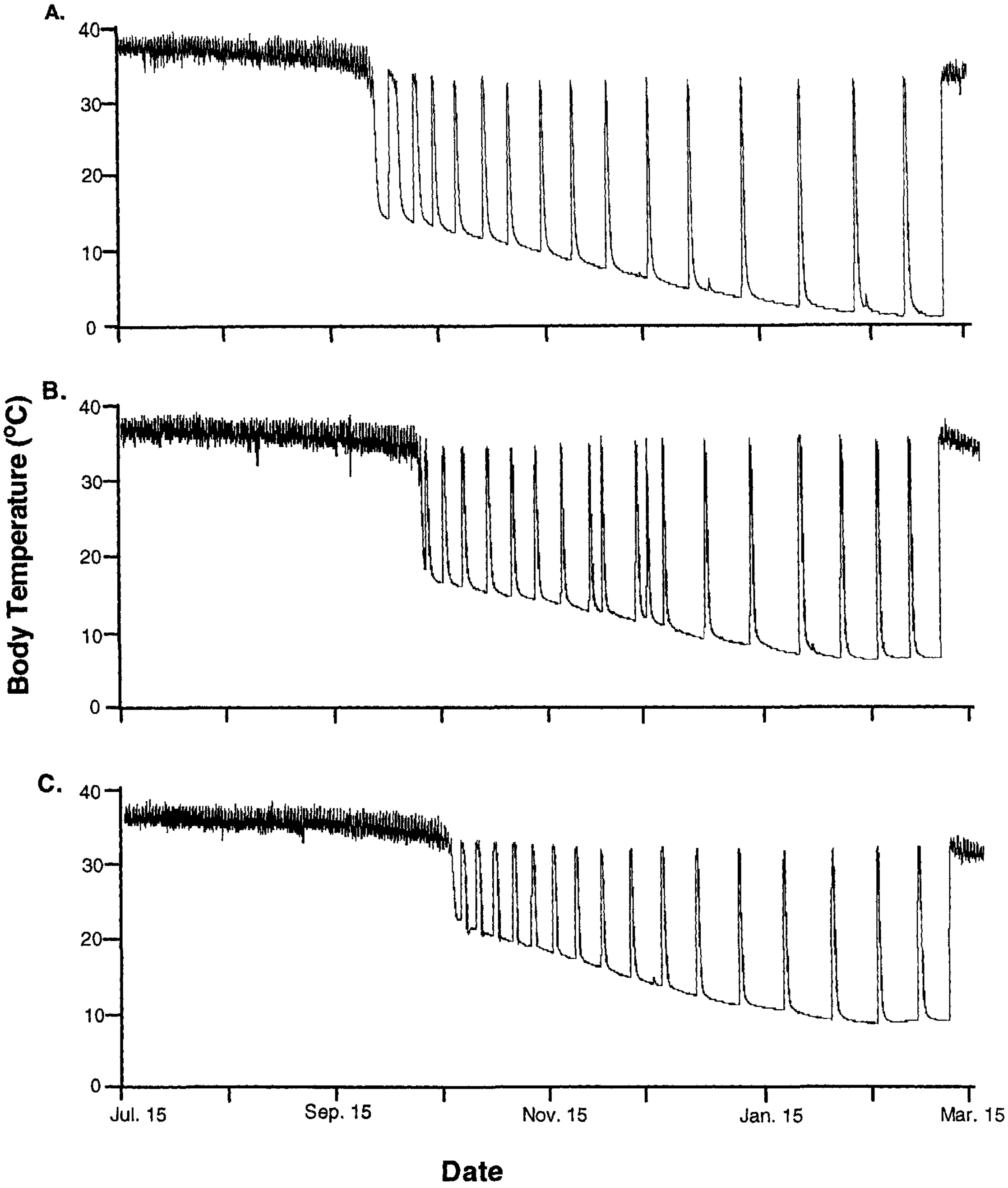

Figure 2. Comparison of body temperature patterns of representative (i.e. displayed mean values for most torpor patterns reported) Utah prairie dogs (*C. parvidens*) from high (A), mid (B), and low (C) elevation colonies in southern Utah. Body temperature patterns were measured continuously from 15 July 2001 to 15 March 2002.

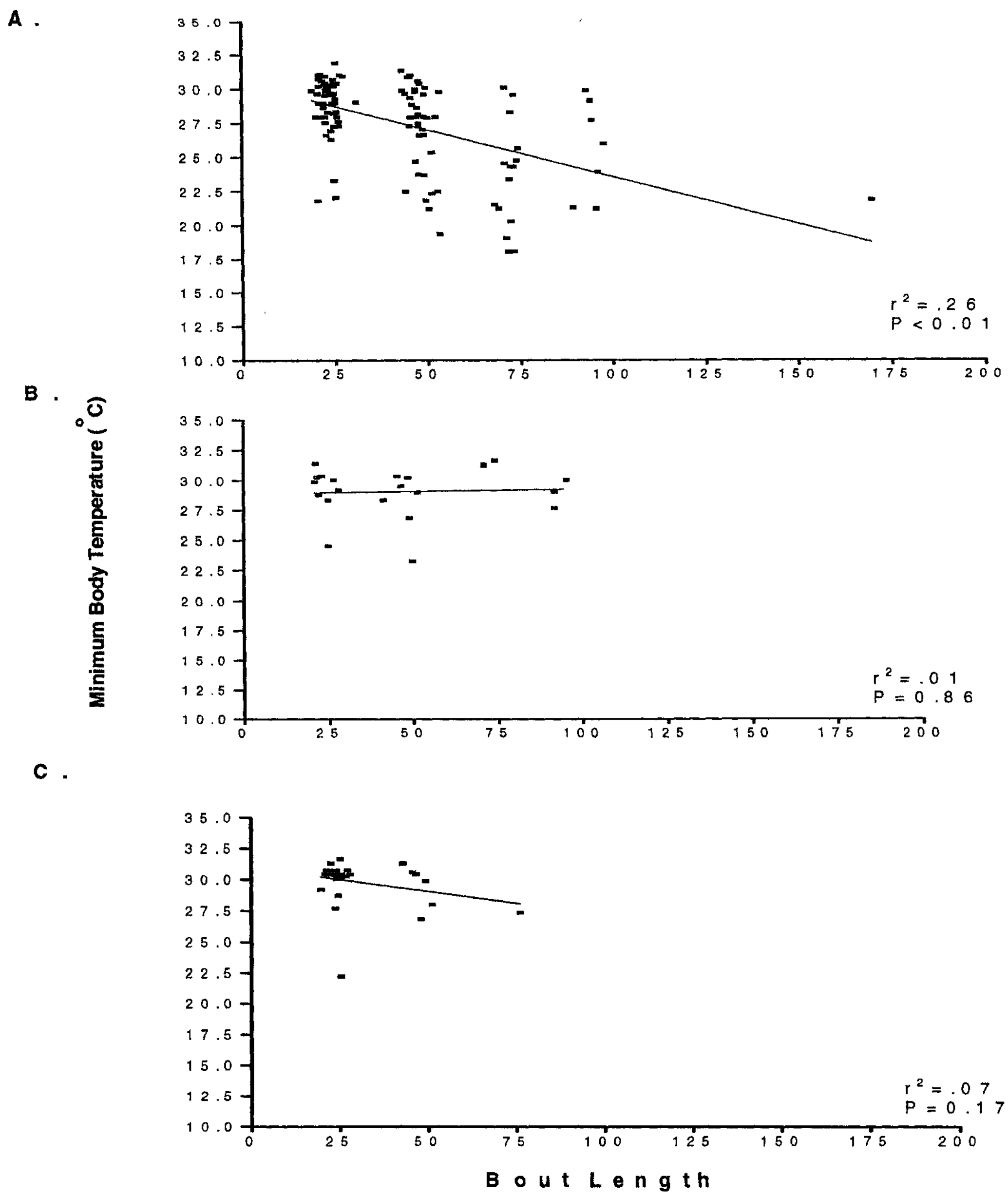

Figure 3. Correlation between torpor bout lengths and minimum body temperatures reached during torpor in adult (> 1 year) black-tailed prairie dogs (*C.ynomys ludovicianus*). Torpor patterns were monitored in black tailed prairie dogs at high (A), mid (B), and low (C) elevation colonies in northern Colorado. Prairie dogs at high and low elevation sites were monitored continuously from September 2001 to June 2002, and from 15 December 2001 to June 2002 at the mid elevation site.

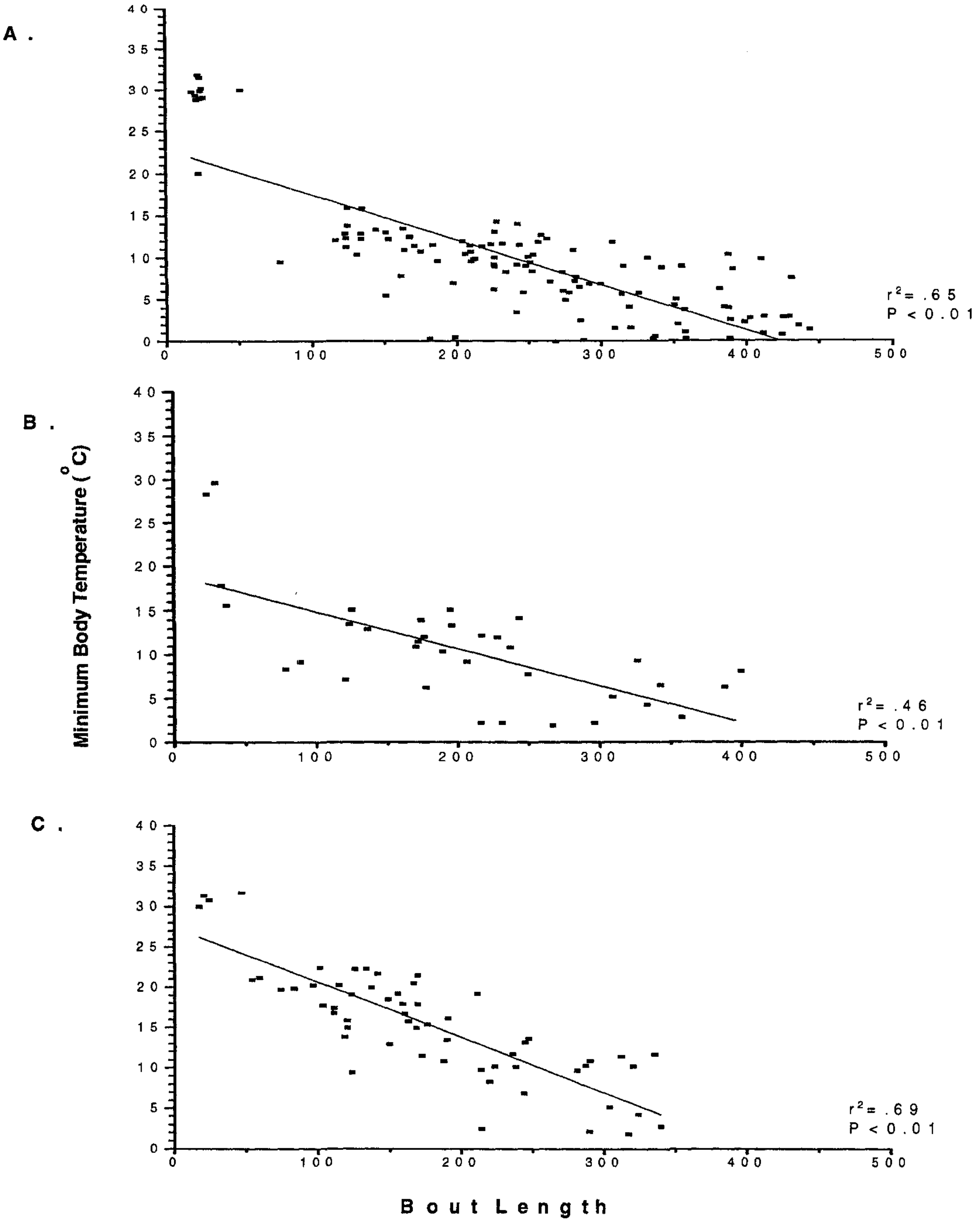

Figure 4. Correlation between torpor bout lengths and minimum body temperatures reached during torpor in adult (>1 year) Utah prairie dogs (*C. parvidens*) at high (A), mid (B), and low (C) elevation colonies in southern Utah. Prairie dogs were monitored continuously from June 2001 to June 2002.

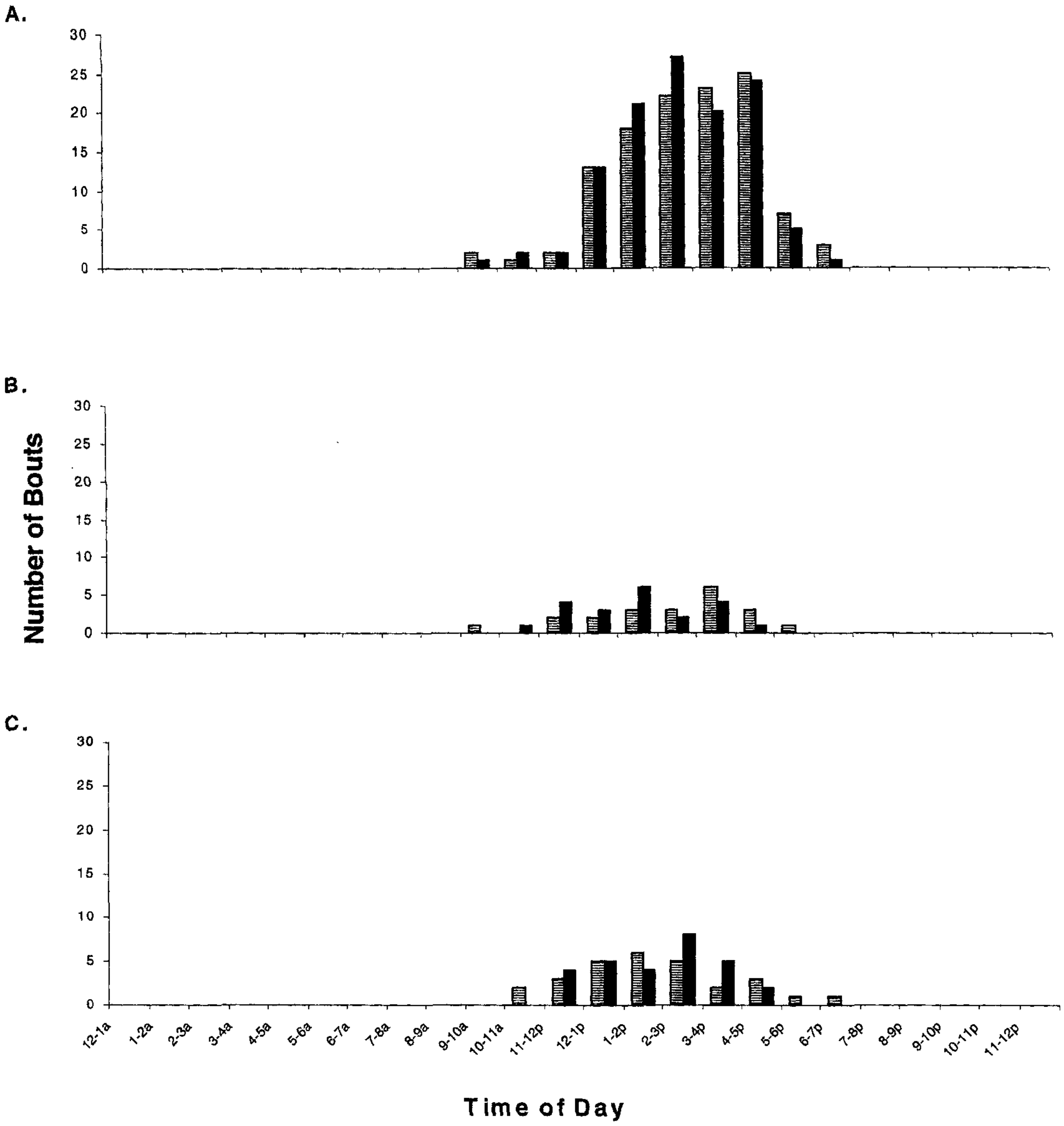

Figure 5. Circadian timing of immergence into torpor (striped bars) and emergence (solid bars) from torpor in adult (>1 year) black-tailed prairie dogs (*C. ludovicianus*). Prairie dogs were monitored at high (A), mid (B), and low (C) elevation colonies in northern Colorado. Prairie dogs at high and low elevation colonies were monitored continuously from September 2001 to June 2002, and from 15 December 2001 to June 2002 at the mid elevation colony.

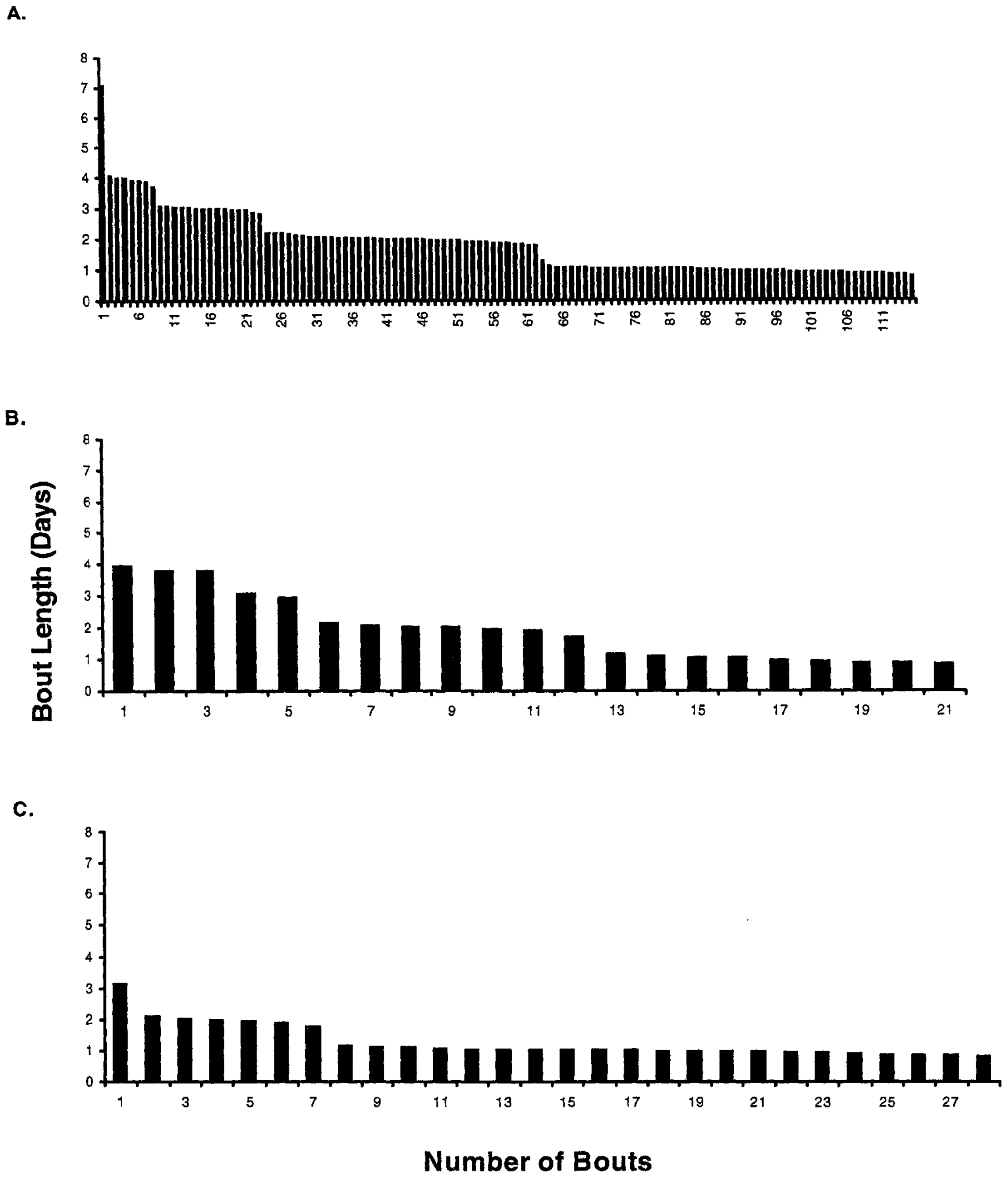

Figure 6. Rank order of torpor bout lengths of black-tailed prairie dogs (*C. ludovicianus*). Body temperature patterns were monitored in adult (>1 year) prairie dogs at high (A), mid (B), and low (C) elevation colonies in northern Colorado. Prairie dogs at high and low elevation sites were monitored continuously from September 2001 to June 2002, and from 15 December 2001 to June 2002 at the mid elevation site.

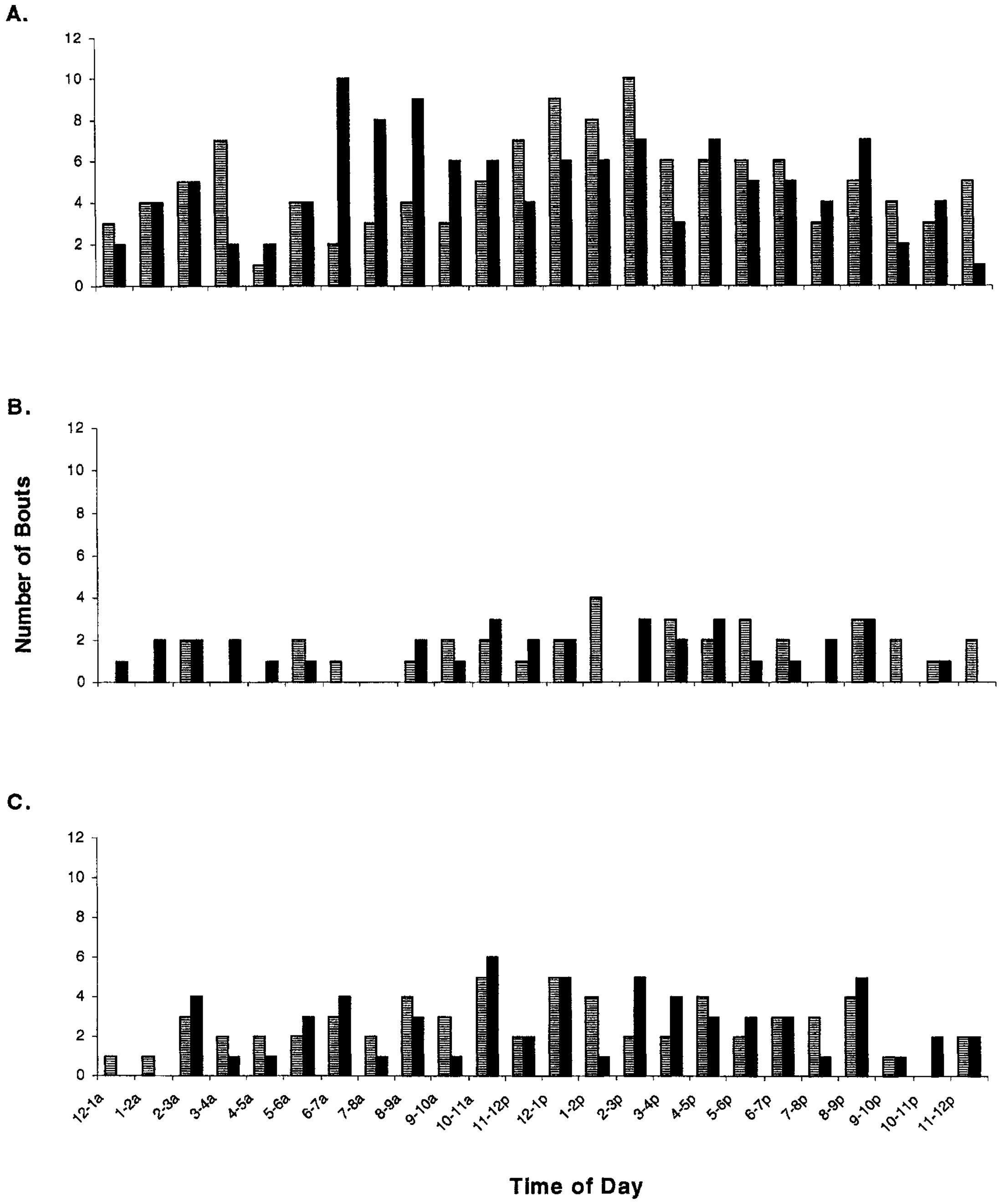

Figure 7. Circadian timing of immergence into torpor (striped bars) and emergence (solid bars) from torpor in adult (>1 year) Utah prairie dogs (*C. parvidens*). Prairie dogs ere monitored at high (A), mid (B), and low (C) elevation colonies in southern Utah. Prairie dogs were monitored continuously from June 2001 to June 2002.

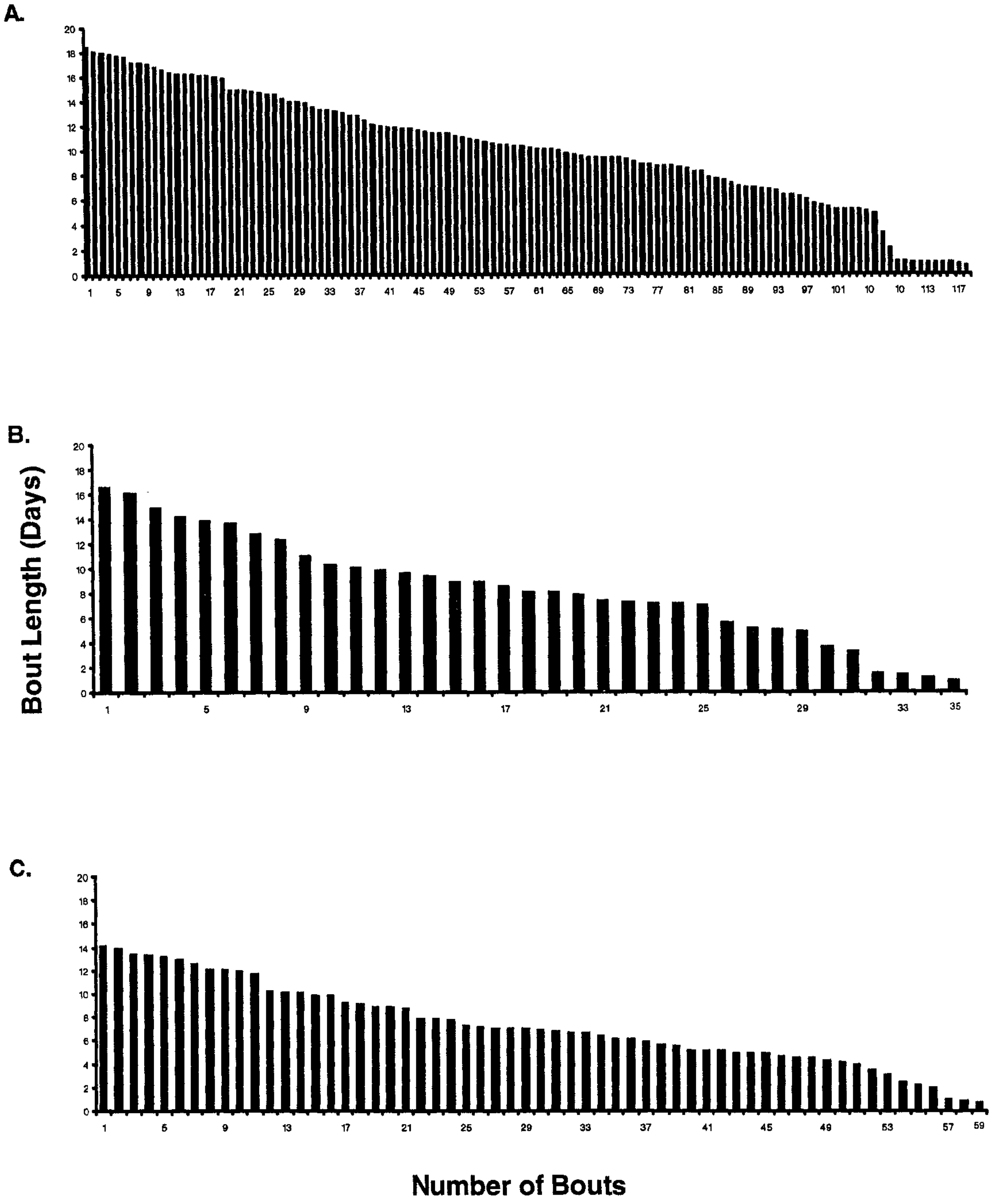

Figure 8. Rank order of torpor bout lengths of Utah prairie dogs (*C. parvidens*). Body temperature patterns were monitored in adult (>1 year) prairie dogs at high (A), mid (B), and low (C) elevation colonies in southern Utah. Prairie dogs were monitored continuously from June 2001 to June 2002.

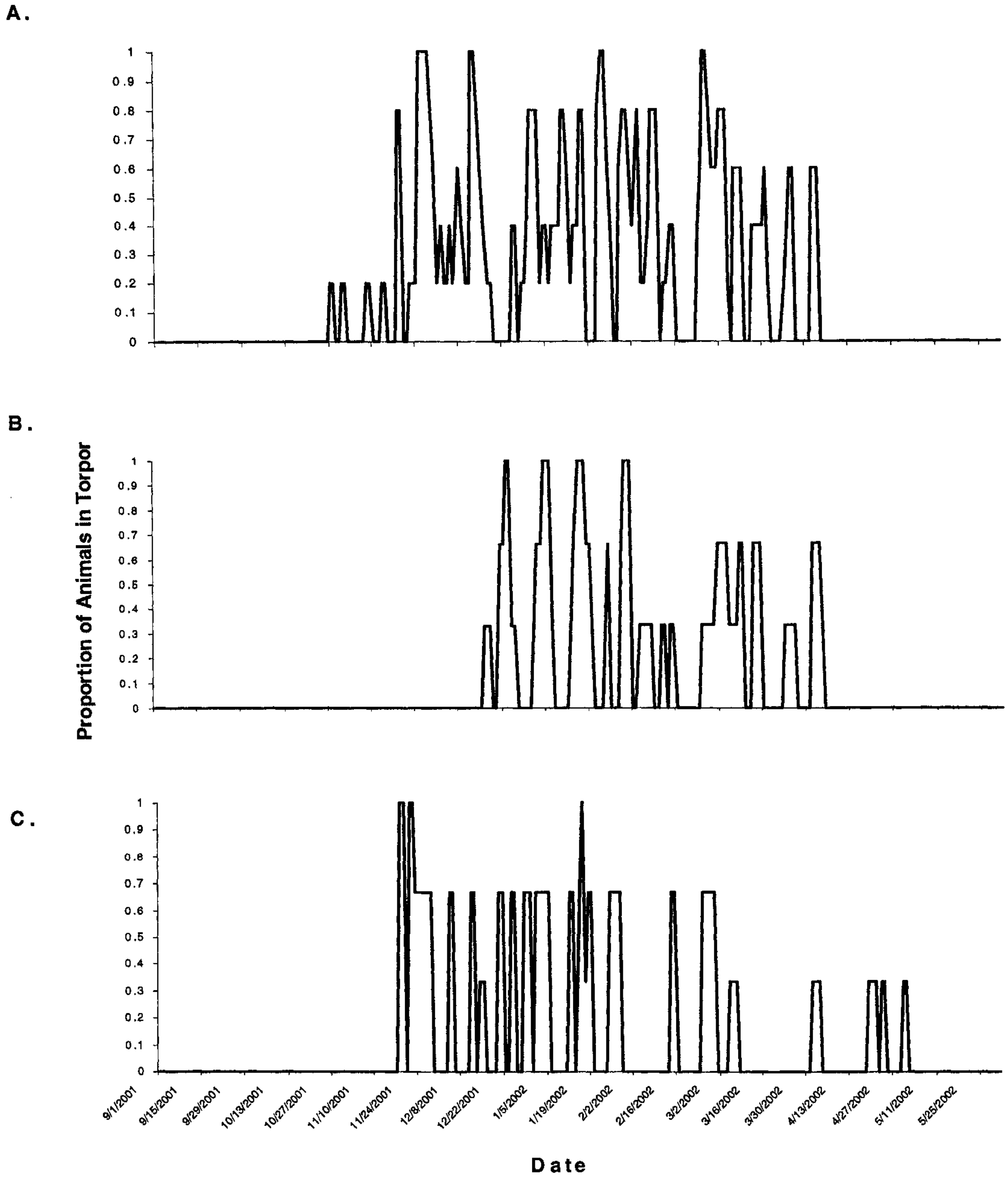

Figure 9. Proportion of black-tailed prairie dogs (*C. ludovicianus*) in torpor daily from September 2001 to June 2002. Prairie dogs were monitored at high (A), mid (B), and low (C) elevation colonies in northern Colorado. Body temperature measurements for prairie dogs at mid elevation colonies are only available from 15 December 2001 to 1 June 2002, as this site replaced a previous study population.

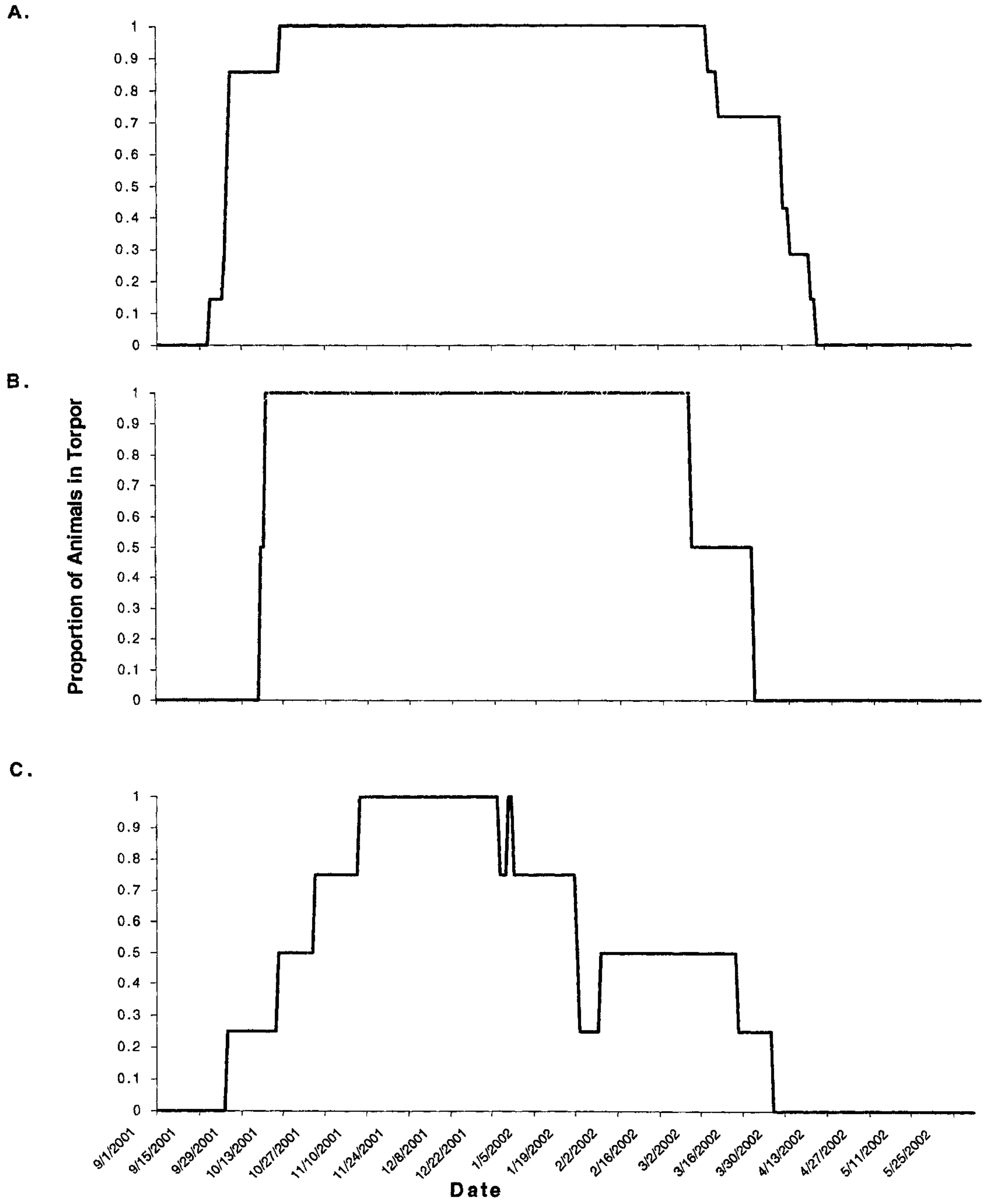

Figure 10. Proportion of Utah prairie dogs (*C. parvidens*) in torpor daily from September 2001 to June 2002 Prairie dogs were monitored at high (A), mid (B), and low (C) elevation colonies in southern Utah.

CHAPTER THREE

ECOLOGICAL AND PHYSIOLOGICAL INDICATORS OF HABITAT SUITABILITY FOR FREE-RANGING BLACK-TAILED AND UTAH PRAIRIE DOGS

Geographic ranges of black-tailed (*Cynomys ludovicianus*) and Utah (*Cynomys parvidens*) prairie dogs encompass environments that vary both spatially and temporally. It is thus likely that considerable differences in habitat quality exist within the ranges of these two species. The objective of this study was to increase our understanding of the relationship between physical condition of prairie dogs and their diets, as influenced by elevation gradients in northern Colorado and southern Utah. Our results show that body masses of prairie dogs were highly variable across seasons and elevations, with higher elevation populations generally having higher body masses in all seasons sampled. Seasonal changes in white adipose tissue composition indicate that black-tailed prairie dogs do not have a clear pattern of linoleic and linolenic acid metabolism during winter. Utah prairie dogs, however, appeared to store linoleic acid in white adipose tissue and preferentially catabolized linolenic acid during winter. Both black-tailed and Utah prairie dogs exercised strong dietary selection in all seasons sampled, and appeared to prefer species higher in linoleic and linolenic acid concentration, as well as total lipid and nitrogen contents. Prairie dog colonies at higher elevations generally had vegetation containing higher levels of linoleic acid and nitrogen, whereas colonies at lower elevations had vegetation containing higher levels of linolenic acid. Our results suggest that black-tailed prairie dogs may be able to achieve high over-winter survival and reproductive success in a variety of habitats, whereas Utah prairie dogs may fare best at higher elevations.

INTRODUCTION

The over-winter strategies of facultative torpor and hibernation used by black-tailed (*Cynomys ludovicianus*) and Utah (*C. parvidens*) prairie dogs require a unique set of adaptations to survive periods of low food and water availability and cold temperatures. Animals that practice facultative torpor forage throughout winter even if the nutritional quality of their diet is lower than in other seasons. When available forage cannot meet metabolic energy demands, these animals must rely on internally stored nutrients. Likewise, most hibernators become aphagic prior to winter and must rely on internal energy stores until emergence in spring. Therefore, the abundance of nutrients during spring, summer, and fall play a large role in the over-winter success of prairie dogs. However, little is known about variations in the nutrient qualities of the diets within and among black-tailed and Utah prairie dogs, making it difficult to predict how nutrition affects over-winter behaviors and subsequent life-history patterns.

Mammals rely heavily on endogenously stored lipid during torpor, both as a primary source of energy (Florant et al. 1993; Willis 1982) and to maintain the low body temperatures associated with torpor (Geiser and Heldmaier 1995; Geiser and Kenagy 1987). Polyunsaturated fatty acids (PUFAs) have a profound effect on torpor, as animals fed diets high in linoleic acid have fewer arousals during seasonal torpor than those fed diets lower in this PUFA (Geiser et al. 1994). Arousal from torpor can account for nearly 80% of the total energy expended during a typical season of torpor (Wang 1979). The storage of linoleic acid in white adipose tissue (WAT) is also associated with lower metabolic rates and minimum body temperatures during torpor (Geiser et al. 1994). Thus, storage of large amounts of linoleic acid during winter can convey considerable energy savings to the animal. In contrast, storage of linolenic acid, also an essential PUFA, can be energetically costly to hibernators. Hibernators that increase the amount of linolenic acid in their WAT during winter are much less likely to hibernate than their counterparts with low levels of linolenic acid (Frank and Storey 1995; Hill and Florant 2000). Differences in lipid deposition and use between black-tailed prairie dogs and hibernating sciurids may partially explain the differences in torpor patterns between these groups of animals.

Dietary protein is essential for growth, reproduction, and development in mammalian species, and the seasonal abundance of dietary protein also plays an important role in hibernation. During summer, hibernators, like Utah prairie dogs, must procure and store adequate protein for the rest of the year. During winter, hibernators undergo periods of fasting when protein is conserved (Karmann et al. 1994) and lipid is the primary source of energy (Florant et al. 1993), then rely on stored protein during reproduction in spring. Therefore, both the availability of dietary protein and the ability to conserve it play a role in the fitness of hibernators. In contrast, black-tailed prairie dogs practice facultative torpor and rely more heavily on protein for energy in times of metabolic stress, saving lipid stores for energy during reproduction (Harlow 1995; Harlow and Braun 1995). Differences in protein metabolism between hibernators and animals that practice facultative torpor could result from seasonal and habitat-specific differences in the availability of dietary protein. In general, plants that occur at higher elevations have greater protein concentrations than their low elevation counterparts (McDonald et al. 1995). Parallels in seasonal changes in dietary protein content and torpor patterns would provide useful insight into the presumably different over-winter strategies of hibernation and facultative torpor used by Utah and black-tailed prairie dogs. However, the extent to which dietary protein varies within and across the geographic ranges of these species is unknown.

The nutrient composition of plants depends upon the type of plant (i.e. forb, grass, etc.) and its geographic location (Corn 1997; Hill and Florant 1999; Thompson et al. 1993). Consequently, diet and nutrition are also likely to differ between black-tailed and Utah prairie dog populations along elevation gradients, which could result in differences in over-winter survival and reproductive success. Comparisons of dietary nutrient content between prairie dogs in differing environments are lacking. Given that ongoing recovery and management of prairie dogs frequently includes translocation and revegetation, understanding the dietary nutrient requirements and how imbalances in these nutrients affect physiology and ecology of prairie dogs could influence the success of recovery efforts. The objective of this study was to determine the diet and dietary nutrient content of free-ranging black-tailed and Utah prairie dogs across elevation gradients in northern Colorado and southern Utah. We also measured differences in body mass and composition of stored energy of prairie dogs across elevations to assess how habitat variation affects physical condition of these species.

METHODS

Study Sites and Animals

We monitored six black-tailed prairie dog colonies and two plots on each of three Utah prairie dog colonies at low, mid, and high elevations (Table 1). To facilitate within and across site comparisons and for replication, we attempted to monitor prairie dogs from two colonies or experimental plots at each elevation that were within10 km of each other. To minimize various sources of large-scale geographic variation for each species, all colonies we studied occurred within a 300 km radius of each other.

We conducted sampling in seasons most relevant to the annual cycle of prairie dogs. We sampled Utah prairie dog populations in June 2001, September 2001, and June 2002. High and low elevation populations of black-tailed prairie dogs were sampled in October 2001, January 2002, and June 2002. Because of difficulty in trapping black-tailed prairie dogs at our original mid-elevation site, we replaced this colony with another black-tailed prairie dog colony in January 2002. Thus, we do not have measurements for the mid-elevation site in Fall 2001.

Body Mass and White Adipose Tissue Composition

In each sampling season, we live-trapped adult (>1 year) black-tailed and Utah prairie dogs. Sample sizes, sex ratios, and recapture rates varied from season to season, and therefore seasons were treated independently (Table 2). After capture, animals were anesthetized and their sex and reproductive status was determined. Under sterile conditions, we surgically removed a small (<50mg) WAT tissue sample from the omental fat pad of each animal (Lehmer and Van Horne 2001). Immediately after collection, WAT samples were placed in sealed containers and were stored at –20°C for further assays. After recovering from surgery (about 4 h), prairie dogs were released to their original sites of capture.

To extract lipids, we soaked 10 mg of each WAT sample in 10 ml of 2:1 hexane: isopropanol in sealed glass vials for 7 d (Hara and Radin 1978). Following extraction, free fatty acids were converted to methyl esters by adding 10 μl of MethPrep 2 (Alltech) to each sample and allowing reaction to proceed for 40 min. Eicosane (100 μg) was added to each sample as an internal standard. We identified individual fatty acids by comparison of retention times and mass spectra with those of authentic fatty acids. Fatty acid methyl esters were quantified with gas-liquid chromatography (Hewlett-Packard 5890A) on a capillary column (Alltech Econocap Carbowax 30m x 0.32mm ID x 0.25μm) with detection by mass spectrometry (HP 5971). We quantified and corrected for detector response differences among fatty acid methyl esters.

Diet Content and Forage Selectivity

In each sampling season, we collected fecal samples (< 5 pellets) from each prairie dog trapped. Seasonal composition of individual prairie dog diets were determined at the Composition Analysis Laboratory in Fort Collins, CO, using a microhistological technique that identified plant fragments contained in scat (Sparks and Malechek 1968). The validity of this technique in correctly determining diet composition of small mammals has been verified previously (Van Horne et al. 1998). Plant species that were unidentifiable or that individually composed less than 5% of the total diet were grouped into a separate category, identified as "other". Distinguishing blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*) in diet analyses for black-tailed prairie dogs is difficult, so these species were combined in assessment of diet composition and estimates of forage selectivity and diet quality.

We determined seasonal abundance of plant species on each prairie dog colony by estimating vegetative cover at 20 random locations using Daubenmire frames (.25 m x .5 m) as sampling units. To establish a selection index for common dietary items, we used Savage's (1931) forage ratio, which considers abundance of a species in the diet relative to its abundance in the environment. A ratio >1 indicated that a plant species was consumed in greater proportion than its abundance on prairie dog colonies (Fagerstone and Williams 1982; Van Horne et al. 1998), suggesting that the item was preferred forage. Avoided species were those with lower consumption than abundance on colonies, and values of 0.00 indicate species completely avoided by prairie dogs (Fagerstone and Williams 1982; Van Horne et al. 1998).

Dietary Nutrient Content

To evaluate protein and lipid composition of the diet, we sampled plant species thought to occur in diets of prairie dogs on each colony. Because we could not predict diets at each site and in each season, we were unable to collect all dietary species and in some cases collected some species that did not occur in the diet at any time. We collected 20 individuals of each species at 10-m intervals along randomly placed transects through each colony. Immediately after collection, plants were stored at –20°C. We combined all collected plants to form three pooled samples for each species. Small (20 mg) subsamples were removed from each pooled sample for extraction and quantification of protein and lipids. Plant protein content of each species was assessed by drying each subsample to a constant mass at 55°C, igniting the sample in a closed chamber, and measuring the amount of nitrogen evolved (LECO Model FP-428, Leco Corp.). Fatty acids were extracted, transmethylated, and quantified from plant tissue using the technique described above for WAT.

We calculated mean linoleic acid (18:2) concentration, linolenic acid concentration (18:3), total lipid concentration (sum of hexadecenoic (16:0), octacecenoic (18:0), 9-octadecenoic (18:1), linoleic and linolenic acids) and nitrogen content for all plant species collected in each season. We determined mean nutritional content of preferred and avoided species by averaging quantities of these nutrients in individual species that were collected. To estimate seasonal changes in overall nutrient content of plants common on prairie dog colonies, we multiplied values of nutrients in individual species collected by their relative abundances on the colonies.

Statistical Analyses

To assess differences in estimated diet of prairie dogs across seasons and elevations, we used multivariate ANOVA of percent relative frequency for the most common plant species detected in fecal samples. General linear models with factors including season, elevation, and season by elevation interactions were used to compare differences in protein and lipid contents of plants common in prairie dog diets (SAS V.8; SAS Institute, Cary, NC). In instances where interactions were not significant, these models were reduced to include only main effects. In these models, both season and elevation were treated as continuous factors. For analyses of body mass and white adipose tissue lipid content, our initial and final sampling seasons for each species (i.e. Summer 2001 and Summer 2002; Fall 2001 and Spring 2002) contained a portion of recaptured animals. However, the number of recaptured animals was generally small and was variable across study sites and species. Thus, we treated estimates of body mass and white adipose tissue lipid composition in each season as independent measurements, with adjustments for unbalanced samples. To ensure that differences detected in white adipose tissue and body mass were not artificially inflated by inherent autocorrelation, general linear models with factors including season, elevation, animal, and associated interaction terms were used to compare differences in these variables. "Animal" was not significant in these comparisons, and was eliminated from the model. We measured all post-hoc pairwise differences of interest using least-squares means comparisons with Tukey-Kramer adjustments for multiple comparisons. Unless otherwise stated, values describing body mass, white adipose tissue lipid content, and dietary nutrient content are presented as mean ± SE of each variable. Differences in these variables were considered to be statistically significant if $P \leq 0.05$. Sample sizes and sex ratios for assessments of body mass, white adipose tissue lipid content, and diet composition varied among seasons and sites (Table 2).

RESULTS

Body Mass and White Adipose Tissue Composition

Body masses of black-tailed prairie dogs varied across seasons ($P < 0.01$) but there was a significant season x elevation interaction ($P < 0.01$; Figure 1). Additional post-hoc comparisons revealed that masses of black-tailed prairie dogs at low elevations declined ($P < 0.01$) from fall to winter, but was unchanged from winter to spring ($P = 0.66$). At high elevations, black-tailed prairie dogs maintained a constant mass from fall to winter ($P = 0.98$) and from winter to spring ($P = 0.35$). Mass of black-tailed prairie dogs at mid elevations was also unchanged from winter to spring ($P = 0.99$). Body masses of Utah prairie dogs were variable across elevations ($P = 0.02$) and seasons ($P < 0.01$) and there was a significant elevation x season interaction ($P = 0.03$; Figure 2). Post-hoc comparisons of pairwise differences showed that masses of Utah prairie dogs at low elevations were relatively constant from summer to fall ($P = 0.98$) and over winter ($P = 0.99$). At mid elevation colonies, masses of Utah prairie dogs were unchanged from summer to fall ($P = 0.68$) and over winter ($P = 0.37$). At high elevations, body masses of Utah prairie dogs increased from summer to fall ($P = 0.02$) and decreased over winter ($P < 0.01$). Across elevations, mean body masses of black-tailed prairie dogs did not differ from that of Utah prairie dogs in either fall 2001 ($P = 0.16$), or June (Spring /Summer) 2002 ($P = 0.09$).

Concentrations of linoleic acid in white adipose tissue depots of black-tailed prairie dogs (Figure 3A) varied across elevation ($P < 0.01$) but did not vary across seasons ($P = 0.09$). In contrast, concentrations of linolenic acid (Figure 3B) in white adipose tissue of black-tailed prairie dogs did not vary across elevations ($P = 0.92$), but differed across seasons ($P < 0.01$). The season x elevation interaction was not significant for either lipid. Levels of both linoleic and linolenic acid in white adipose tissue depots of Utah prairie dogs differed across seasons ($P < 0.01$) and elevations ($P < 0.01$), and there were significant season x elevation interactions ($P = 0.02$ and $P < 0.01$, respectively). Across elevations, concentrations of linoleic acid were unchanged from summer to fall in Utah prairie dogs at low ($P = 0.82$) and high ($P = 0.45$) elevation colonies, but increased among prairie dogs at mid elevation colonies ($P < 0.01$; Figure 4A). Linoleic acid levels decreased over the following winter in low elevation populations ($P = 0.04$) and remained unchanged in Utah prairie dogs at mid ($P = 0.83$) and high elevations ($P = 0.98$; Figure 4A). In contrast, linolenic acid concentrations increased from summer to fall in Utah prairie dogs at mid elevations ($P < 0.01$). However, levels of these lipids remained unchanged among Utah prairie dogs at low ($P = 0.69$) and high elevation colonies during this period ($P = 0.50$). Although levels of linolenic acid remained unchanged over winter in low elevation populations ($P = 0.99$), they decreased significantly in prairie dogs at mid and high elevation colonies ($P < 0.01$; Figure 4B). Across elevations, concentrations of linoleic acid in white adipose tissue depots did not differ between black-tailed and Utah prairie dogs in fall 2001 ($P = 0.23$) or June (Spring /Summer) 2002 ($P = 0.45$).

Black-tailed prairie dogs had significantly higher linolenic acid concentrations than Utah prairie dogs during fall 2001 ($P < 0.01$), but by June (Spring /Summer) 2002, linolenic acid concentrations did not differ between the two species ($P = 0.39$).

Diet Content and Forage Selectivity

Diets of black-tailed prairie dogs varied seasonally and were comprised of several plant types (i.e. forbs, grasses, sedges, shrubs; Figure 5). Across elevations, wheatgrass (*Agropyron* spp.) comprised 10% to 65% of black-tailed prairie dog diets in each season. At low elevations, buffalograss (*Buchloe dacytloides*) and blue grama (*Bouteloua gracilis*) together comprised a large portion (10% to 30%) of black-tailed prairie dog diets, as did sedges (*Carex* spp.), which comprised between 11-29% of the diet in each season (Figure 5A). Diets of black-tailed prairie dogs at mid elevation colonies were abundant in fringed sage (*Artemisia frigida*), which comprised between 10-17% of the diet in each season (Figure 5B). During winter, prickly-pear cactus (*Opuntia polyacantha*) comprised a large portion (35%) of the diet at mid elevation colonies. At high elevations, black-tailed prairie dogs consumed large amounts of buffalograss and blue grama (13% to 32%) and cheatgrass (*Bromus tectorum*; 2% to 21%) in each season (Figure 5C). Diets of Utah prairie dogs were also seasonally variable and differed across elevations (Figure 6). At low elevations (Figure 6A), diets in each season consisted primarily of scarlet globemallow (*Sphaeralcea coccinea*; 9% to 53%), needle and thread grass (*Stipa comata*; 19% to 51%), and rice grass (*Oryzopsis hymenoides;* 7% to 22%). At mid elevation colonies, Utah prairie dogs consumed large amounts of scarlet globemallow (2% to 39%), winterfat (*Eurotia* spp.; 5% to 60%), and cheatgrass (18% to 82%) in each season (Figure 6B). Diets of Utah prairie dogs on high elevation colonies were comprised primarily of sedges (47% to 66%) and cheat grass (6% to 12%) in each season (Figure 6C).

Vegetative cover on black-tailed and Utah prairie dog colonies varied considerably across elevations (Tables 3 and 4). Black-tailed prairie dog colonies at low elevations contained large amounts of blue grama and buffalograss in all seasons sampled (52% to 66%). Mid elevation colonies had abundant cheatgrass and hairy golden aster (*Heterotheca villosa*) during winter, comprising 28% and 26% of the total vegetative cover, respectively. During summer, black-tailed prairie dog colonies at mid elevations were dominated by fringed sage (16%) and wheatgrass (36%). Cover of black-tailed prairie dog colonies at high elevations was dominated by cheatgrass and bindweed (*Convolvulus arvensis*), which comprised between 18% to 55% and 15% to 21%, respectively, of the total vegetation on the colonies in all seasons. Vegetation on Utah prairie dog colonies at low elevations consisted primarily of broom snakeweed (*Gutierrezia sarothrae*) and red threeawn (*Aristida purpurea*), which comprised between 32% to 45% and 2% to 22% , respectively, of the total cover in each season. Utah prairie dog colonies at mid elevations were dominated by wheatgrass (30% to 41%) and black sagebrush (*Artemisia nova;* 15% to 24%) in all seasons. High elevation Utah prairie dog colonies were comprised primarily of black sage (26% to 38%), sedges (12% to 22%), blue grama (6% to 27%) and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*; 10% to 29%).

Forage selection indices (Table 5) indicate that black-tailed prairie dogs select plant species nonrandomly relative to their abundance on colonies in all seasons. At all elevations and in each season, black-tailed prairie dogs preferentially foraged on wheatgrass (*Agropyron* spp.) and sand dropseed (*Sporobolus cyrptandrus*). In each season, black-tailed prairie dogs at low and mid elevations also preferred scarlet globemallow. At mid and high elevations, prairie dogs selectively foraged on blue grama and buffalograss in each season. Like black-tailed prairie dogs, Utah prairie dogs forage selectively in each season (Table 6). At low elevations, prairie dogs foraged almost exclusively on wheatgrasses, rice grass, scarlet globemallow, needle-and-threadgrass, and blue grama in each season. Utah prairie dogs on mid-elevation colonies strongly preferred cheat grass, sedges, and winterfat in each season. At high elevations, Utah prairie dogs preferentially foraged on wheatgrasses, cheatgrass, scarlet globemallow, and sedges in each season.

Dietary Nutrient Content

Although differences were generally not statistically significant, plant species preferred by black-tailed prairie dogs generally had higher levels of linoleic and linolenic acids, total lipids, and nitrogen than plant species avoided when foraging (Table 7). Plant species preferred by Utah prairie dogs were generally higher in linolenic acid, total lipid and nitrogen content and lower in linoleic acid concentration than were plants they avoided, although these differences were not statistically significant (Table 8). It is noteworthy that plant species preferred by Utah prairie dogs were generally higher in linoleic acids ($P = 0.04$) and total lipids ($P = 0.05$) than were plants preferred by black-tailed prairie dogs; however, linolenic acid and nitrogen content of preferred diet items did not differ between the two prairie dog species ($P = 0.17$ and $P = 0.14$, respectively).

Mean linoleic acid concentrations (Figure 7A) of plants on black-tailed prairie dog colonies differed across elevations ($P = 0.01$) and seasons ($P < 0.01$), and there was a significant elevation x season interaction ($P < 0.01$). Linoleic acid concentration was generally higher in plants at higher elevation black-tailed prairie dog colonies than in plants on low elevation colonies. Levels of linolenic acid found in plants common on black-tailed prairie dog colonies (Figure 7B) also varied across elevations ($P < 0.01$) and seasons ($P < 0.01$), and the interaction of elevation x season was significant ($P < 0.01$) for this nutrient, as well. Concentrations of linolenic acid were generally lower in plants on low and mid elevation colonies than in plants on high elevation colonies, although these differences were not statistically significant. Mean nitrogen concentration of plants on black-tailed prairie dog colonies also differed across elevations ($P = 0.03$) and seasons ($P = 0.01$), and there was a significant elevation x season interaction ($P = 0.02$). Nitrogen concentration was generally higher in plants at higher elevations (Figure 7C). Concentrations of linoleic and linolenic acid in plants common on Utah prairie dog colonies varied across elevations ($P < 0.05$) and seasons ($P < 0.05$), and elevation x season interactions were significant ($P < 0.05$) for both of these nutrients. Although not statistically significant, mean concentrations of linoleic acid in plants generally increased with elevation (Figure 8A), whereas mean concentrations of linolenic acid generally decreased with elevation (Figure 8B). Mean nitrogen concentration of plants common on Utah prairie dog colonies differed across elevations ($P = 0.03$) and seasons ($P = 0.01$) and there was an elevation x season interaction ($P < 0.01$). Although not statistically significant, mean nitrogen concentration of plants common on Utah prairie dog colonies generally increased with elevation (Figure 8C). Across elevations, plants common on Utah prairie dog colonies were generally higher in linoleic acid concentration than plants on black-tailed prairie dog colonies in fall 2001 (*P* = 0.03) and summer 2002 (*P* = 0.04). Linolenic acid concentration of plants did not differ between black-tailed and Utah prairie dog colonies in fall 2001 (*P* = 0.17); however, in June (Spring / Summer) 2002 levels of these lipids were higher in plants on black-tailed prairie dog colonies (*P* = 0.04). There were no differences in nitrogen concentration between plants common on black-tailed and Utah prairie dog colonies in either fall 2001 (*P* = 0.18) or June (Spring / Summer) 2002 (*P* = 0.21).

DISCUSSION

Body Mass and White Adipose Tissue Composition

It is noteworthy that black-tailed prairie dogs at mid and high elevations experienced little change in body mass during winter, as these populations presumably experienced the lowest ambient temperatures and the greatest precipitation during this period. In contrast, black-tailed prairie dogs at low elevations had large fluctuations in body mass across seasons, despite presumably higher temperatures and lower amounts of precipitation. In a concurrent study, we found that black-tailed prairie dogs at these same high elevation colonies enter torpor more frequently and reach lower body temperatures than prairie dogs at these same low elevation colonies (Chapter 1; Lehmer et al. *submitted A*). Together, these results indicate that practicing more frequent and deep torpor may have provided energy savings to prairie dogs at high elevation colonies, allowing them to minimize reductions in body mass during winter. Such over-winter energetic savings may have provided a mechanism for black-tailed prairie dogs to expand their range to include these high elevation areas.

Similar to black-tailed prairie dogs, Utah prairie dogs at higher elevation colonies had greater body masses than prairie dogs at low elevation colonies prior to winter. However Utah prairie dogs at low elevation colonies experienced the least fluctuation in body mass across seasons. These minimal changes in body mass could be the result of the extended active season of prairie dogs at low elevations (Lehmer et al. *submitted A*), allowing them to continue to forage later into fall and begin foraging earlier in spring than prairie dogs at mid and high elevation colonies. High body mass is a primary predictor of over-winter survival and reproductive success in black-tailed prairie dogs (Hoogland 1995). Thus, prairie dogs at higher elevations may have an advantage despite a shorter active season, especially if this species is capable of practicing deep and continuous torpor during periods of environmental and physiological stress. Although prairie dogs at low elevations are able to forage later into fall and earlier in spring, the nutritional quality of forage available during these periods is reduced. Our results suggests that remaining active during these periods may result in a net energetic loss for Utah prairie dogs at low elevations, which is reflected by their lower body masses in all seasons.

White adipose tissue deposition and use by black-tailed prairie dogs displayed considerable variation, indicating that this species may not have a consistent or predictable pattern for metabolism of essential fatty acids during winter. Furthermore, comparisons between concentrations of essential fatty acids contained in white adipose tissue and concentrations of these lipids in plants available to black-tailed prairie dogs on colonies does not show any clear patterns of preferential storage or metabolism of these lipids at any elevation or in any season. The absence of consistent patterns of essential fatty acid metabolism may result from black-tailed prairie dogs continuing to forage throughout winter (Harlow 1997; Hoogland 1995; Thompson et al. 1993), which would allow them to alter their white adipose tissue lipid composition continuously in response to environmentally imposed demands or physiological need. However, it is also possible that this variable lipid metabolism is a product of the unusual over-winter body temperature patterns common to this species. Although hibernators maintain relatively uniform torpor patterns throughout winter (Davis 1976; Michener 1992; Young 1990) and consequently possess rather specific requirements for lipid deposition prior to winter (Florant et al. 1993; Frank 1991), black-tailed prairie dogs display highly variable over-winter body temperature patterns, including daily and seasonal heterothermy and facultative torpor (Bakko et al. 1988; Lehmer et al. 2003; Lehmer et al. 2001). Thus, it is possible that such highly variable body temperature patterns require or are associated with similarly flexible patterns of white adipose tissue lipid deposition and use. However, further evaluation of this possibility is beyond the scope of the present study.

Unlike black-tailed prairie dogs, Utah prairie dogs showed distinct patterns of linoleic acid storage in white adipose tissue lipid both prior to and during winter. In general, our results suggest that, over winter, Utah prairie dogs at mid and high elevation colonies may store linoleic acid in white adipose tissue and preferentially metabolize linolenic acid, whereas at low elevations Utah prairie dogs may metabolize linoleic acid and store linolenic acid. It is possible that physiological differences between separate Utah prairie dog populations are responsible for these distinct differences in essential fatty acid metabolism over winter. It is also possible, however, that variation in environmental conditions within the range of this species result in temporal differences in availability of these essential fatty acids. Patterns of lipid availability in plants common on Utah prairie dog colonies support the latter hypothesis, as the concentration of linoleic acid in vegetative cover was generally highest on mid and high elevation colonies, and concentration of linolenic acid was highest on low elevation colonies. Ecological consequences for Utah prairie dogs are the same in either case, because the concentrations of these lipids in white adipose tissue depots have a substantial influence on torpor patterns during winter. Indeed, in a separate study, we determined that Utah prairie dogs on these low elevation colonies spent significantly fewer hours in torpor and had higher minimum body temperatures than prairie dogs on these mid and high elevation colonies (Chapter 2; Lehmer et al. *submitted A*).

The patterns we observed support predictions posed by several laboratory studies of hibernating sciurids, in which the preferential storage of linoleic acid during winter promotes low body temperatures and longer torpor bouts (Geiser et al. 1994; Geiser and Kenagy 1993), while the storage of linolenic acid can interfere with deep and prolonged torpor (Frank and Storey 1995; Hill and Florant 2000). Although field studies such as ours are associated with numerous sources of uncontrolled variation, our results provide the first assessment of patterns of lipid deposition and use across the geographic range of a free-ranging hibernator.

Diet Content and Forage Selectivity

High elevation populations of both black-tailed and Utah prairie dogs displayed the greatest dietary diversity. However, Utah prairie dogs at all elevations preferred fewer dietary items than did black-tailed prairie dogs. Utah prairie dogs showed strong dietary preference for grasses, and preference for forbs and sedges was limited in all seasons. Although Utah prairie dog colonies are dominated by shrubs, shrubs were either absent or constituted a small portion of the total diet in all seasons and at all elevations. Previous studies have also shown that Utah prairie dogs avoid consumption of shrubs (Hasenyager 1983). In contrast, black-tailed prairie dogs demonstrated strong dietary preference for certain species of grasses, forbs, sedges, and shrubs. Although differences in dietary in preferences between black-tailed prairie dogs may result from variations in the ability of each species to digest certain plants (Fagerstone and Williams 1982), differences in dietary preference may also reflect differing nutritional requirements of prairie dogs prior to and during winter. Hibernators must consume a rather specific diet during the summer active season in preparation for winter (Florant 1990; Frank 1991), and it is possible that nutrients essential for prolonged winter dormancy are most abundant in grasses. Our results indicate that, relative to other plant species common on Utah prairie dog colonies, wheatgrass, cheatgrass, and blue grama were abundant in linoleic, linolenic, and total fatty acids in all seasons. Black-tailed prairie dogs continue to forage throughout winter. Thus consumption of a broad diet may provide nutrients, such as water and protein, that are essential for over-winter survival and that promote reproductive success in spring. Likewise, black-tailed prairie dogs have plastic over-winter behaviors (Bakko et al. 1988; Lehmer et al. 2003; Lehmer et al. 2001), and this flexibility may allow them to cope with a more diverse diet prior to and during winter.

Dietary Nutrient Content

Plants had generally higher concentrations of linoleic and linolenic acids and nitrogen at higher elevations on both black-tailed and Utah prairie dog colonies. Furthermore, both black-tailed and Utah prairie dogs maintained greater body masses and practiced more deep and frequent torpor (Lehmer et al. *submitted A*) at higher elevations. Considered together, these factors suggest that higher elevation colonies provide both black-tailed and Utah prairie dogs with a higher quality diet than colonies at lower elevations. However, extreme drought during our study may have disproportionately influenced habitats at low elevations. Without further study, it is not possible to compare differences in nutritional quality of forage available on prairie dog colonies during an "average" year.

General Conclusions

Our results underscore the considerable variation in both physiological and environmental factors that exist within the ranges of black-tailed and Utah prairie dogs. These differences could translate into differences in life history (e.g. age at first reproduction, litter size, longevity) within each species.

Differences in ecological factors, including vegetative cover and diet quality, likely play roles in determining the geographic and elevation ranges of these species, and may have important implications for their persistence in the future. Both black-tailed and Utah prairie dogs evolved in grassland ecosystems (Collier and Spillett 1975; Goodwin 1995). Heavy grazing has substantially increased shrub cover across the range of Utah prairie dogs (Collier and Spillett 1975; Ellison 1960; Tueller and Blackburn 1974) and has also increased the abundance of exotic plants (i.e. cheatgrass and bindweed) on black-tailed prairie dog colonies in northern Colorado (M. Brennan and K. Manci, *pers. comm.*). Nonetheless, our results show that Utah prairie dogs retain a strong dietary preference for grasses, which are more abundant at higher elevations. Because higher elevation colonies are associated with higher body masses, more frequent and deep torpor (Lehmer et al. *submitted A*), and greater amounts of dietary lipids and nitrogen, these sites appear to provide high quality habitat and should be considered as relocation sites for future Utah prairie dog populations. This is in contrast to previous management reports, which suggested that low elevation sites provided the highest quality habitat for this species (Crocker-Bedford 1979). However, recommendations proposed by these previous reports were based solely on physical habitat characteristics (i.e. vegetation height and soil composition), rather than on physiological factors or life history dynamics of Utah prairie dogs.

Black-tailed prairie dogs at higher elevations had the highest body masses, most frequent and deep torpor (Lehmer et al. *submitted A*), and highest quality diet, despite an abundance of exotic plants at these sites. Consideration of these patterns, as well as the historically large and ecologically diverse range of black-tailed prairie dogs (Goodwin 1995), underscores the adaptability of this species to a variety of environmental conditions. The common interface of black-tailed prairie dog colonies with urban and agricultural development may necessitate that future management of this species is prioritized on the availability of land, rather than its ecological suitability. A large body of evidence suggests that black-tailed prairie dogs are highly adaptable to environmental conditions (Bakko 1977; Lehmer et al. *submitted B*; Pfeifer et al. 1979; Stephens and Fevold 1993; Thompson et al. 1993). Therefore, this species may be able to cope with sub-optimal habitat in the future.

Although our results provide important baseline ecological and physiological information, achieving a comprehensive understanding of how black-tailed and Utah prairie dogs are influenced by environment will require more study. The at-risk status of each of these species (Gober 2000; Utah Prairie Dog Recovery and Implementation Team 1997) should make answering these questions an even greater priority than it has been in the past.

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Table 1. Overview of colony elevations, locations and sampling dates for investigation of differences in diet, diet quality, and body condition of free-ranging adult (>1 y) black-tailed (*C. ludovicianus*) and Utah (*C. parvidens*) prairie dogs across an elevation gradient in northern Colorado and southern Utah. * Mid elevation black-tailed prairie dog colonies were not sampled until January 2002, as these sites replaced a previous study population.

Site	**Elevation**	**County**	**Site Name**	**Sampling Dates**
		Black-Tailed Prairie Dogs		
Low Elevation	1650 m	Weld	Central Plains Experimental Range	October 2001
Mid Elevation	1880 m	Boulder	Rabbit Mountain	January 2002*
High Elevation	2185 m	Boulder	Heil Valley Ranch	June 2002
		Utah Prairie Dogs		
Low Elevation	1575 m	Garfield	Horse Hollow	June 2001
Mid Elevation	2350 m	Iron	Tom Best Spring	September 2001
High Elevation	3000 m	Mineral	The Tanks	June 2002

Table 2. Sample sizes and sex ratios for seasonal assessments of body mass, white adipose tissue lipid content, and diet composition in free-ranging adult (> 1 y) black-tailed (*C. ludovicianus*) and Utah (*C. parvidens*) prairie dogs across elevational gradients in northern Colorado and southern Utah. Mid-elevation black-tailed prairie dog colonies were not sampled until January 2002, as these sites replaced a previous study population.

Season	***Low Elevation Colonies***	***Mid Elevation Colonies***	***High Elevation Colonies***
		Black-Tailed Prairie Dogs	
Fall 2001	5 females, 5 males	N / A	6 females, 4 males
Winter 2002	6 females, 4 males	6 females, 4 males	5 females, 5 males
Summer 2002	6 females, 4 males	5 females, 5 males	6 females, 4 males
		Utah Prairie Dogs	
Summer 2001	7 females, 3 males	7 females, 3 males	7 females, 3 males
Fall 2001	4 females, 2 males	4 females, 2 males	2 females, 4 males
Summer 2002	4 females, 1 male	4 females, 4 males	7 females, 2 males

Table 3. Summary of relative vegetative cover (%) on black-tailed prairie dog (*C. ludovicianus*) colonies along an elevation gradient in northern Colorado. Values represent mean percent cover of each species after excluding bare ground and litter material from plots. Estimates for mid-elevation colonies are not available for Fall 2001, as this site replaced a previous study area.

	Season					
Colony Location	**Fall 2001**		**Winter 2002**		**Spring 2002**	
	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**
Low Elevation						
Artemisia frigida	6.4	0.7	6.5	0.4	3.9	0.2
Carex spp.	13.1	0.8	13.6	0.6	8.1	0.5
Buchloe dactyloides / Bouteloua gracilis	51.9	2.3	52.1	3.5	65.7	3.2
Gutierrezia sarothrae	6.7	0.7	6.8	0.5	2.9	0.4
Agropyron smithii	8.8	1.2	9.0	0.9	0.0	0.1
Mid Elevation						
Artemisia frigida	N/A		16.2	1.2	15.8	0.7
Agropyron crisatum			16.6	0.6	36.0	0.4
Bromus tectorum			28.1	1.6	5.8	0.2
Aristida purpurea			9.0	0.4	7.0	1.2
Heterotheca villosa			25.5	1.3	4.8	0.3
High Elevation						
Artemisia frigida	16.9	0.8	4.8	0.5	7.6	0.5
Bromus tectorum	38.8	2.3	55.0	1.9	18.3	0.4
Buchloe dactyloides /Bouteloua gracilis	2.1	0.3	3.5	0.4	7.4	0.5
Convolvulus arvensis	14.7	0.7	15.6	0.2	20.6	0.8
Heterotheca villosa	6.1	0.5	15.0	0.9	10.9	0.9

Table 4. Summary of relative vegetative cover (%) on Utah prairie dog (*Cynomys parvidens*) colonies along an elevational gradient in southern Utah. Values represent mean percent cover of each species after excluding bare ground and litter material from plots.

	Season					
	Summer 2001		**Fall 2001**		**Summer 2002**	
Colony Location	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**	$\bar{x}$	**S.E.**
Low Elevation						
Aristida purpurea	7.1	0.6	22.4	1.5	19.7	0.9
Sphaeralcea coccinea	6.8	0.5	12.7	0.6	7.1	0.6
Chrysothamnus vicidiflorus	20.2	1.4	4.7	0.4	5.9	0.4
Bromus tectorum	10.9	0.5	12.8	0.4	2.3	0.3
Gutierrezia sarothorae	32.1	2.4	36.6	0.7	45.4	3.6
Mid Elevation						
Sphaeralcea coccinea	15.7	0.8	6.4	0.4	0.2	0.1
Chrysothamnus vicidiflorus	10.9	0.7	18.2	0.9	2.6	0.4
Agropyron crisatum	34.6	1.2	30.1	0.8	40.6	2.4
Artemisia nova	14.5	0.4	15.9	0.6	23.9	1.6
Chrysothamnus nauseosus	18.4	0.6	9.9	1.2	3.2	0.5
High Elevation						
Artemisia nova	37.7	0.9	26.1	0.5	32.8	1.9
Bouteloua gracilis	6.2	0.6	27.0	1.2	14.7	0.7
Chrysothamnus nauseosus	10.3	0.4	4.4	0.5	13.1	0.6
Chrysothamnus vicidiflorus	15.4	0.7	29.2	1.6	10.3	0.3
Carex spp.	22.0	1.5	12.4	0.6	16.4	0.8

Table 5. Seasonal mean dietary selection indices for adult (> 1 y) black-tailed prairie dogs (*Cynomys ludovicianus*) for species available on colonies located at varying elevations in northern Colorado. Estimates are not available for mid elevation colonies in Fall 2001, as this site replaced a previous study population. Where the plant was <0.1% of the vegetative cover, "high" items comprised >10% of the mean diet and "low" items comprised <10% of the mean diet. Although "high" and "low" indicate a generally high selection index, we have little confidence in the actual preference value because of the low proportionate cover of these species. Numeric values indicate relative degree of preference of prairie dogs for each plant species, with values of 1.0 representing species eaten in proportion to their abundance on the colony. Values of 0.00 indicate species most strongly avoided by prairie dogs, as these species were available on the colony but did not appear in the diet.

		Season		
Colony Location	**Plant Species**	**Fall 2001**	**Winter 2002**	**Spring 2002**
Low Elevation	*Agropyron smithii*	1.18	1.10	High
	Artemisia frigida	1.81	0.00	0.00
	Bouteloua gracilis / Buchloe dactyloides	0.55	0.18	0.46
	Carex spp.	1.03	0.84	3.59
	Opuntia polyacantha	0.00	1.21	0.00
	Sphaeralcea coccinea	4.40	Low	High
	Sporobolus cryptandrus	High	High	Low
	Gutierrezia sarothorae	0.00	0.00	0.00
	Aristida purpurea	0.00	0.00	0.00
	Astragalus spp.	0.00	Low	0.46
Mid Elevation	*Agropyron* spp.	N/A	1.22	1.83
	Artemisia frigida		1.08	0.61
	Bouteloua gracilis / Buchloe dactyloides		Low	High
	Bromus tectorum		0.18	Low
	Opuntia polyacantha		1.87	0.00
	Sphaeralcea coccinea		2.41	3.84
	Sporobolus cryptandrus		Low	Low
	Heterotheca villosa		0.00	0.00
	Convolvulus arvensis		0.00	0.00
	Aristida purpurea		0.00	0.00
High Elevation	*Agropyron* spp.	36.30	High	8.71
	Artemisia frigida	0.04	0.51	0.84
	Bouteloua gracilis / Buchloe dactyloides	6.45	3.77	4.32
	Bromus tectorum	0.20	0.38	0.12
	Carex spp.	0.14	2.51	Low
	Opuntia polyacantha	1.43	2.00	0.00
	Sphaeralcea coccinea	Low	1.21	0.69
	Sporobolus cryptandrus	Low	High	Low
	Astragalus spp.	0.00	0.00	0.00
	Convolvulus arvensis	0.00	0.00	0.00
	Aristida purpurea	0.00	0.00	0.00
	Heterotheca villosa	0.00	0.00	0.00

Table 6. Seasonal mean dietary preference of adult (> 1 y) Utah prairie dogs (*Cynomys parvidens*) for species available on colonies located at varying elevations in southern Utah. Where the plant was <0.1% of the vegetative cover, "high" items comprised >10% of the mean diet and "low" items comprised <10% of the mean diet. Although "high" and "low" indicate a generally high selection index, we have little confidence in the actual preference value because of the low proportionate cover of these species. Numeric values indicate relative degree of preference of prairie dogs for each plant species, with values of 1.0 representing plant species eaten in proportion to their abundance on the colony. Values of 0.00 indicate species most strongly avoided by prairie dogs, as these species were available on the colony but did not appear in the diet.

		Season		
Colony Location	**Plant Species**	**Summer 2001**	**Fall 2001**	**Summer 2002**
Low Elevation	*Agropyron smithii*	1.00	1.12	5.08
	Bouteloua gracilis	Low	Low	Low
	Bromus tectorum	0.13	0.75	0.00
	Oryzopsis hymenoides	High	Low	High
	Sphaeralcea coccinea	4.06	4.17	1.27
	Stipa comata	5.20	6.04	High
	Astragalus spp.	0.00	0.00	0.00
	Gutierrezia sarthothrae	0.00	0.00	0.00
	Chrysothamnus vicidiflorus	0.00	0.00	0.00
	Moss	0.00	0.00	0.00
	Leptodactylon pungens	0.00	0.00	0.00
	Aristida purpurea	0.00	0.00	0.00
Mid Elevation	*Agropyron spp.*	0.00	0.48	0.56
	Bouteloua gracilis	0.00	0.00	0.50
	Bromus tectorum	8.23	High	High
	Carex spp.	Low	Low	0.23
	Eurotia spp.	Low	Low	High
	Sphaeralcea coccinea	0.61	2.47	0.36
	Artemisia nova	0.00	0.00	0.00
	Artemisia frigida	0.00	0.00	0.00
	Chrysothamnus vicidiflorus	0.00	0.00	0.00
	Chrysothamnus nauseousus	0.00	0.00	0.00
	Moss	0.00	0.00	0.00
High Elevation	*Agropyron spp.*	3.30	Low	Low
	Astragalus spp.	0.33	Low	0.00
	Bouteloua gracilis	0.11	0.02	0.18
	Bromus tectorum	High	Low	Low
	Carex spp.	2.13	5.28	3.71
	Chrysothamnus nauseousus	0.71	0.50	0.08
	Sphaeralcea coccinea	Low	Low	Low
	Artemisia nova	0.00	0.00	0.00
	Artemisia frigida	0.00	0.00	0.00

Table 7. Comparison of seasonal nutrient concentrations (mg/ml) of plant species preferred (P) and avoided (A) by adult (> 1 y) black-tailed prairie dogs (*Cynomys ludovicianus*) on colonies in northern Colorado. Estimates for mid-elevation colonies are not available for Fall 2001, as this site replaced a previous study population. Preferred species are those that comprised a greater proportion of the diet than their abundance on colonies, and avoided species are those that comprised 0% of the diet when available on colonies. Values are expressed as the mean ± SE for all species preferred or avoided in a particular season. 18:2 = linoleic acid; α 18:3 = linolenic acid; Total Lipids = sum of hexadecenoic acid (16:0), octacecenoic acid (18:0), 9-octadecenoic acid (18:1), linoleic and linolenic acids. * indicates a significant difference ($P < 0.05$) in a particular nutrient between preferred and avoided species.

				Low Elevation Colonies				
	18:2		**α -18:3**		**Total Lipids**		**Nitrogen**	
	P	**A**	**P**	**A**	**P**	**A**	**P**	**A**
Fall 2001	0.80 (± 0.11)	0.68 (±0.04)	1.14 (± 0.31)	0.92 (± 0.32)	4.20 (± 1.3)	3.81 (± 1.20)	1.91 (± 0.09)	1.23 (± 0.07)
Winter 2002	0.51 (±0.04)	0.20 (±0.10)	0.33 (± 0.03)	0.13 (± 0.02)	3.43 (± 0.08)	2.36 (± 0.91)	1.31 (± 0.21)	1.21 (± 0.09)
Spring 2002	0.29 (±0.02)	0.14 (±0.05)	0.75 (± 0.05)	0.11 (± 0.01)	1.99 (± 0.09)	0.77 (± 0.06)	2.24 (± 0.68)	1.0 (± 0.07)
				Mid-Elevation Colonies				
	18:2		**α -18:3**		**Total Lipids**		**Nitrogen**	
	P	**A**	**P**	**A**	**P**	**A**	**P**	**A**
Fall 2001	N/A		N/A		N/A		N/A	
Winter 2002	0.88* (± 0.02)	0.13 (± 0.04)	0.73 * (± 0.06)	0.22 (± 0.02)	4.83 (± 0.87)	2.07 (± 0.08)	1.53 (± 0.06)	1.26 (± 0.11)
Spring 2002	0.61 (± 0.04)	1.48 (± 0.41)	2.47 (± 0.80)	3.02 (± 0.56)	4.36 (± 1.13)	4.95 (± 0.99)	1.96 (± 1.00)	2.13 (± 0.92)
				High Elevation Colonies				
	18:2		**α -18:3**		**Total Lipids**		**Nitrogen**	
	P	**A**	**P**	**A**	**P**	**A**	**P**	**A**
Fall 2001	1.37 (± 0.32)	0.72 (± 0.03)	3.24 (± 1.01)	2.93 (± 0.91)	6.71 (± 1.22)	6.49 (± 2.15)	2.47 (± 0.72)	2.40 (± 0.67)
Winter 2002	0.76 (± 0.06)	0.34 (± 0.01)	0.83 (± 0.07)	0.66 (± 0.04)	4.40 (± 0.78)	3.83 (± 0.41)	1.97 (± 0.12)	1.01 (± 0.09)
Spring 2002	0.65 (± 0.05)	0.31 (± 0.02)	1.94 (± 0.82)	1.31 (± 0.06)	3.90 (± 0.65)	2.38 (± 0.69)	2.20 (± 0.14)	1.92 (± 0.45)

Table 8. Comparison of seasonal nutrient concentrations (mg/ml) of plant species preferred (P) and avoided (A) by adult (> 1 y) Utah prairie dogs (*Cynomys parvidens*) on colonies in southern Utah. Preferred species are those that comprised a greater proportion of the diet than their abundance on colonies, and avoided species are those that comprised 0% of the diet when available on colonies. Values are expressed as the mean ± SE for all species preferred or avoided in a particular season. 18:2 = linoleic acid; α 18:3 = linolenic acid; Total Lipids = sum of hexadecenoic acid (16:0), octacecenoic acid (18:0), 9-octadecenoic acid (18:1), linoleic and linolenic acids. * indicates a significant difference (P <0.05) in a particular nutrient between preferred and avoided species.

Low Elevation Colonies

	18:2		α -18:3		Total Lipids		Nitrogen	
	P	**A**	**P**	**A**	**P**	**A**	**P**	**A**
Summer 2001	1.36 (± 0.07)	4.12 (± 0.13)	2.13 (± 0.92)	3.43 (± 1.32)	7.18 (± 2.17)	21.86 (±4.56)	1.72 (± 0.18)	1.94 (± 0.27)
Fall 2001	0.33 (± 0.02)	0.53 (± 0.06)	0.66 (± 0.04)	0.48 (± 0.05)	2.73 (± 0.78)	3.35 (± 0.65)	1.89 (± 0.56)	1.78 (± 0.23)
Summer 2002	0.54 (± 0.03)	0.26 (± 0.01)	1.37 (± 0.07)	0.29(± 0.02)	3.61 (± 1.01)	2.13 (± 0.43)	2.10 (± 0.76)	1.79 (± 0.43)

Mid-Elevation Colonies

	18:2		α -18:3		Total Lipids		Nitrogen	
	P	**A**	**P**	**A**	**P**	**A**	**P**	**A**
Summer 2001	2.67 (± 0.79)	6.54(± 2.13)	2.92 (± 0.09)	6.48(± 1.74.)	16.9(± 2.67)	15.56 (7 ±3.14)	1.80 (± 0.07)	1.84 (± 0.06)
Fall 2001	2.28 (± 1.03)	3.56(± 0.99)	2.33 (± 0.67)	3.77(± 1.56)	12.61 (± 5.56)	20.92 (±4.79)	1.61* (± 0.06)	0.89 (± 0.32)
Summer 2002	0.16 (± 0.02)	0.19(± 0.02)	0.02 (± 0.01)	0.22(± 0.04)	1.55 (± 0.08)	0.89 (± 0.07)	1.79* (± 0.04)	0.55 (± 0.07)

High Elevation Colonies

	18:2		α -18:3		Total Lipids		Nitrogen	
	P	**A**	**P**	**A**	**P**	**A**	**P**	**A**
Summer 2001	0.74 (± 0.05)	0.92 (± 0.06)	1.09 (± 0.07)	1.08 (± 0.32)	4.03 (± 1.31)	3.33 (± 1.07)	1.57 (± 0.09)	1.2 (± 0.11)
Fall 2001	1.45 (± 0.31)	1.09 (± 0.09)	3.79 (± 1.01)	0.49 (± 0.07)	8.37 (± 2.45)	3.19 (± 0.98)	1.42 (± 0.12)	1.55(± 0.06)
Summer 2002	1.46 (± 0.05)	2.38 (± 0.67)	3.31 (± 0.77)	3.11 (± 0.56)	8.11(± 3.01)	9.14 (± 2.79)	2.10 (± 0.08)	1.57 (± 0.34)

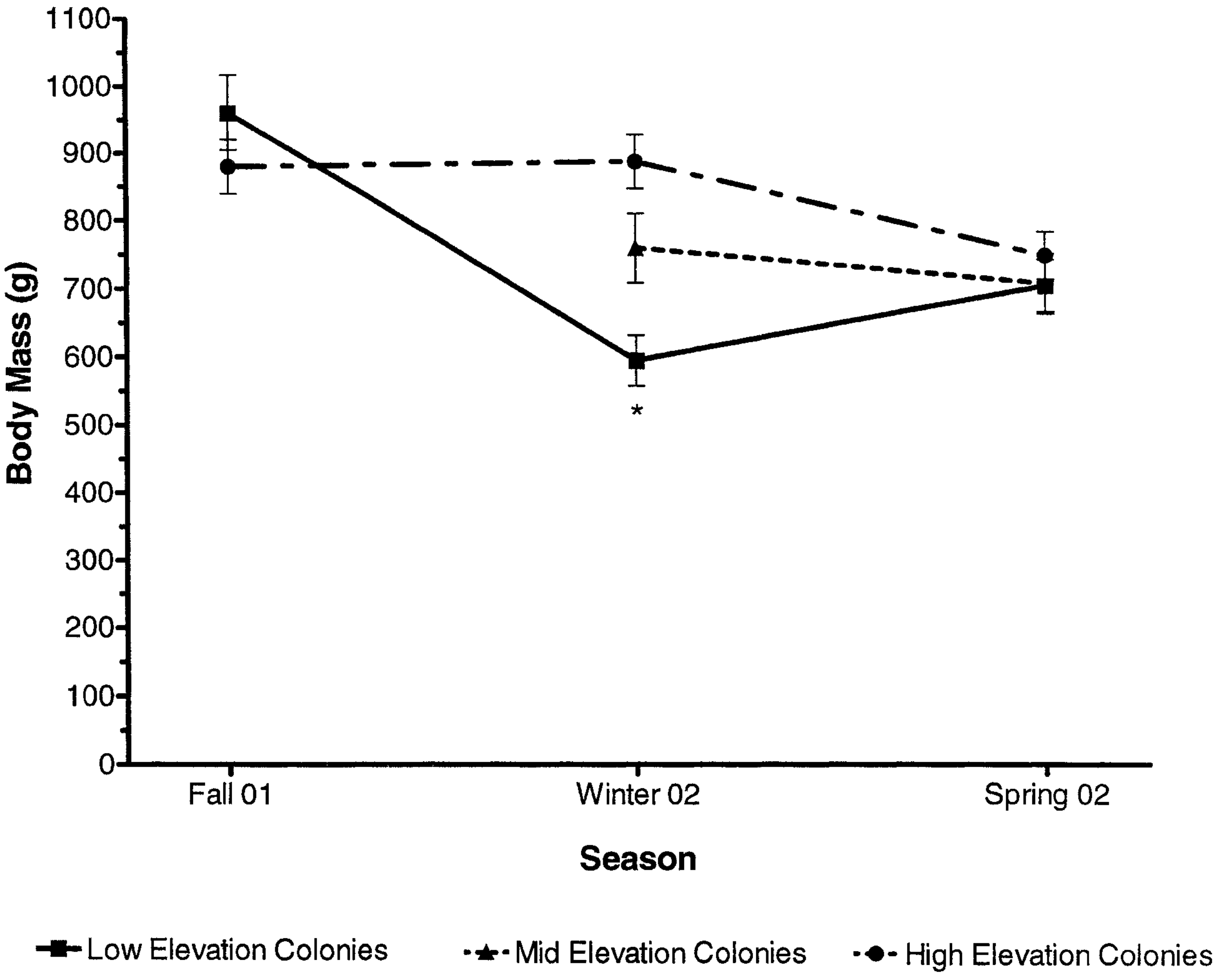

Figure 1. Seasonal changes in body mass of adult (> 1 y) black-tailed prairie dogs (*C. ludovicianus*). Prairie dogs were monitored on colonies located at low, mid, and high elevations in northern Colorado from October 2001 to June 2002. Body mass measurements for prairie dogs at mid elevation colonies are not available for Fall 2001, as this site replaced a previous study population. * indicates a significant change ($P \leq 0.05$) from the previous season among prairie dogs at a particular elevation.

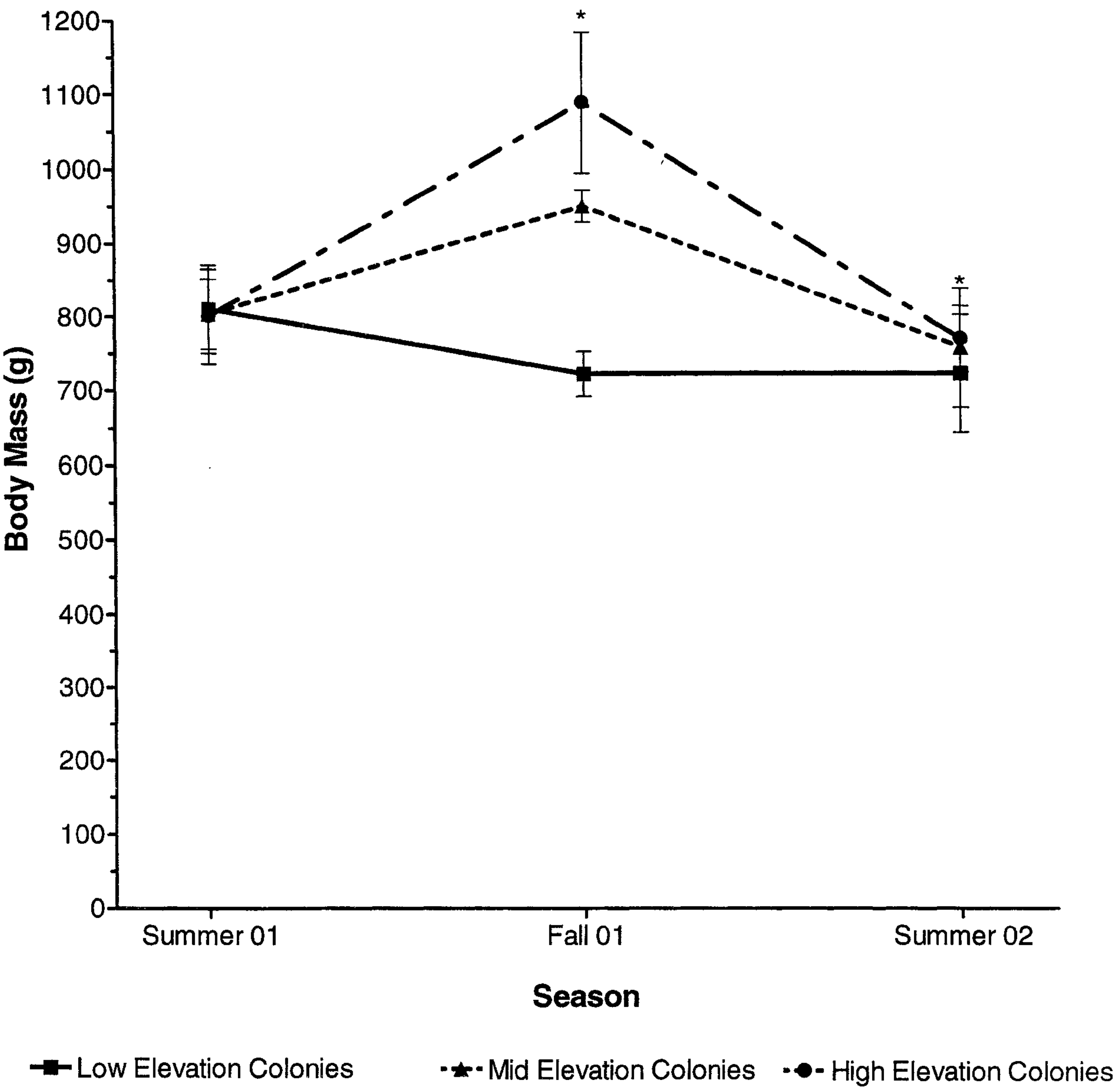

Figure 2. Seasonal changes in body mass of adult (> 1 y) Utah prairie dogs (*C. parvidens*). Prairie dogs were monitored on colonies located at low, mid, and high elevations in southern Utah from June 2001 to June 2002. * indicates a significant change ($P \leq 0.05$) from the previous season among prairie dogs at a particular elevation.

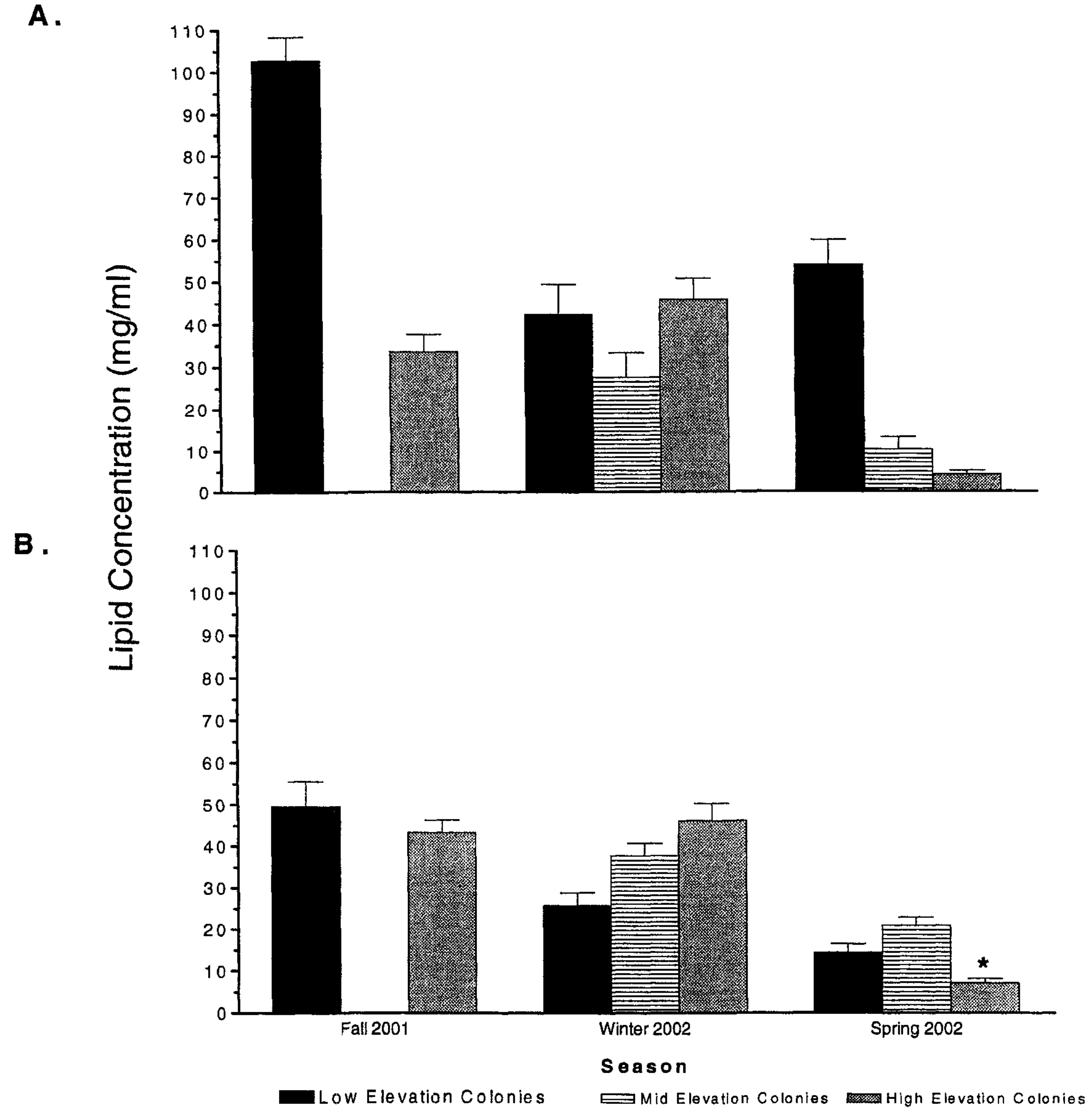

Figure 3. Comparison of white adipose tissue lipid composition of adult (> 1 y) black-tailed prairie dogs (*C. ludovicianus*) across elevations in northern Colorado. "A" illustrates seasonal changes in concentration of linoleic acid (18:2) and "B" illustrates seasonal changes in linolenic acid (α 18:3). White adipose lipid concentrations for prairie dogs at mid elevation colonies are not available for Fall 2001, as this site replaced a previous study population. * indicates a significant change ($P \leq 0.05$) from the previous season among prairie dogs at a particular elevation.

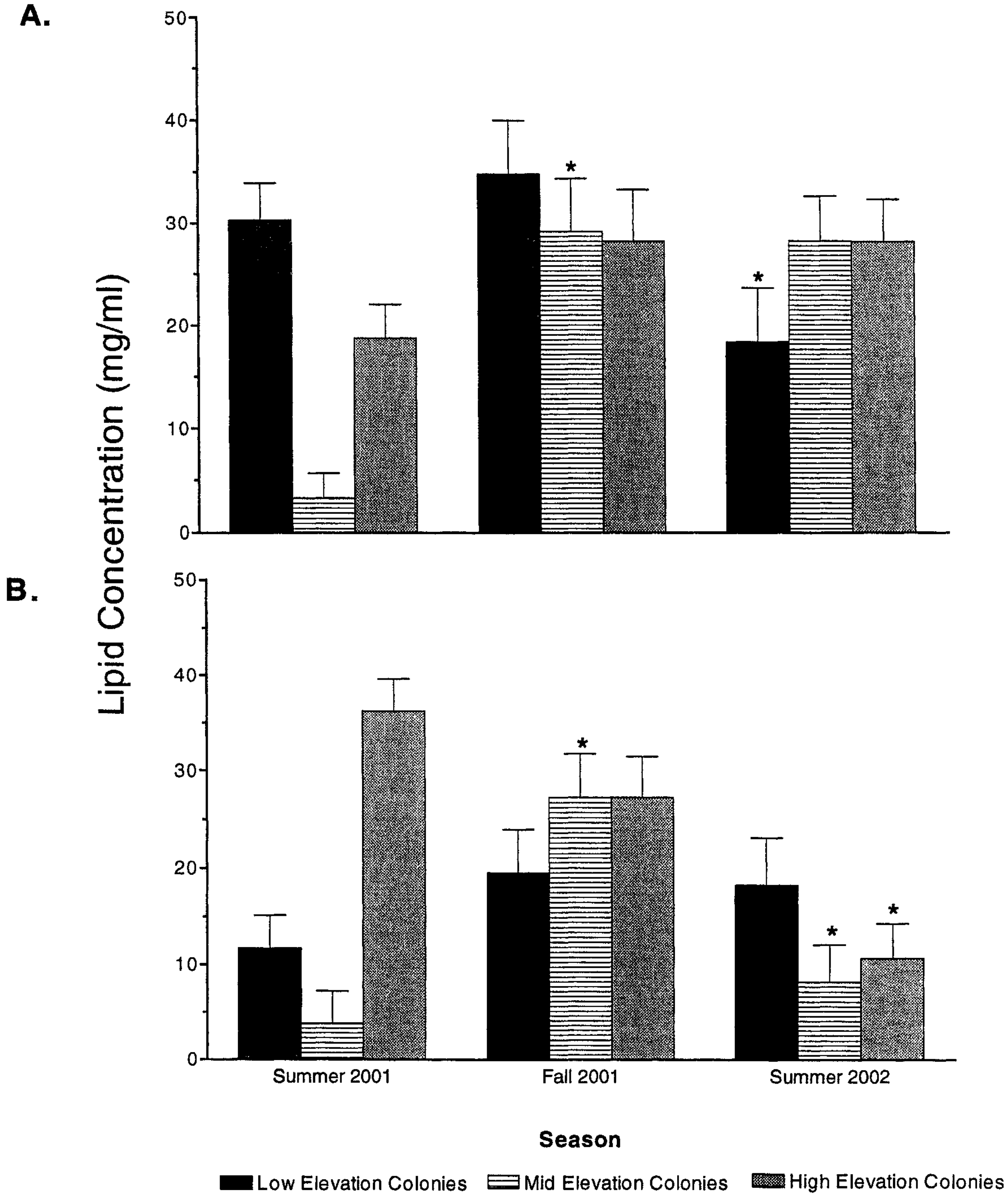

Figure 4. Comparison of white adipose tissue lipid composition of adult (>1 y) Utah prairie dogs (*C. parvidens*) across elevations in southern Utah. "A" illustrates seasonal changes in concentration of linoleic acid (18:2) and "B" illustrates seasonal changes in linolenic acid (α 18:3). * indicates a significant change ($P \leq 0.05$) from the previous season among prairie dogs at a particular elevation.

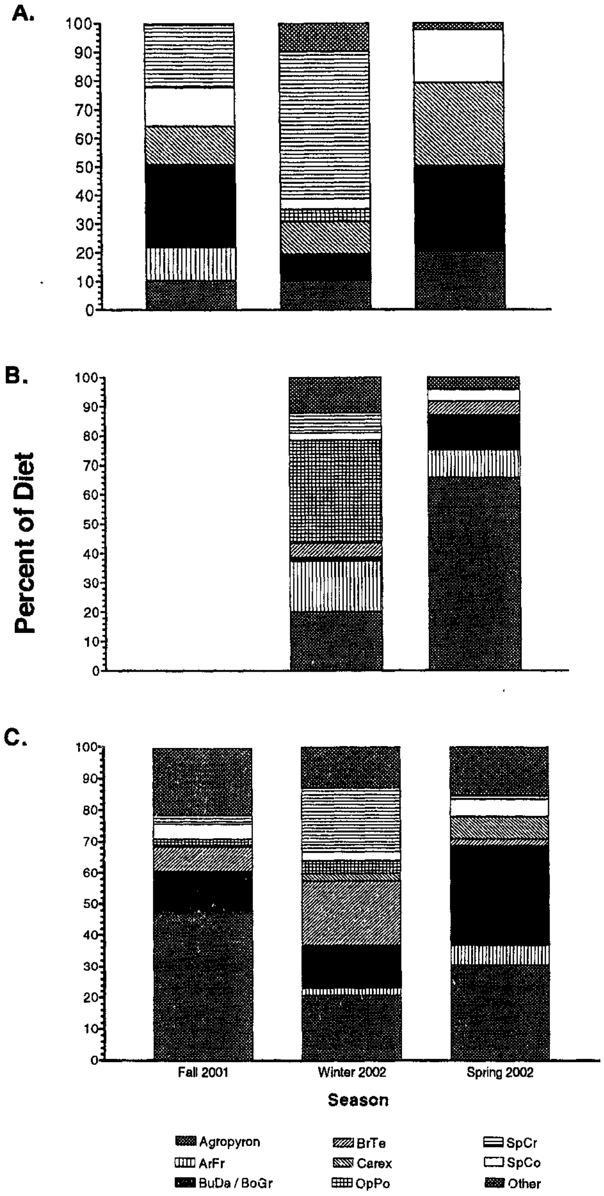

Figure 5. Seasonal changes in diet composition of adult (> 1 y) black-tailed prairie dogs (*C. ludovicianus*). Prairie dogs were sampled from colonies located at low (A), mid (B) and high (C) elevations in northern Colorado. Diet was determined by identification of plant fragments in fecal samples and values represent mean relative frequency. Estimates are not available for mid elevation colonies in Fall 2001, as this site replaced a previous study population. Agropyron = *Agropyron* spp.; ArFr = *Artemisia frigida*; BuDa/BoGr = *Buchloe dactyloides* and *Bouteloua gracilis*; BrTe = *Bromus tectorum*; Carex = *Carex* spp.; OpPo = *Opuntia polyacantha*; SpCr = *Sporobolus cryptandrus*; SpCo = *Sphaeralcea coccinea*.

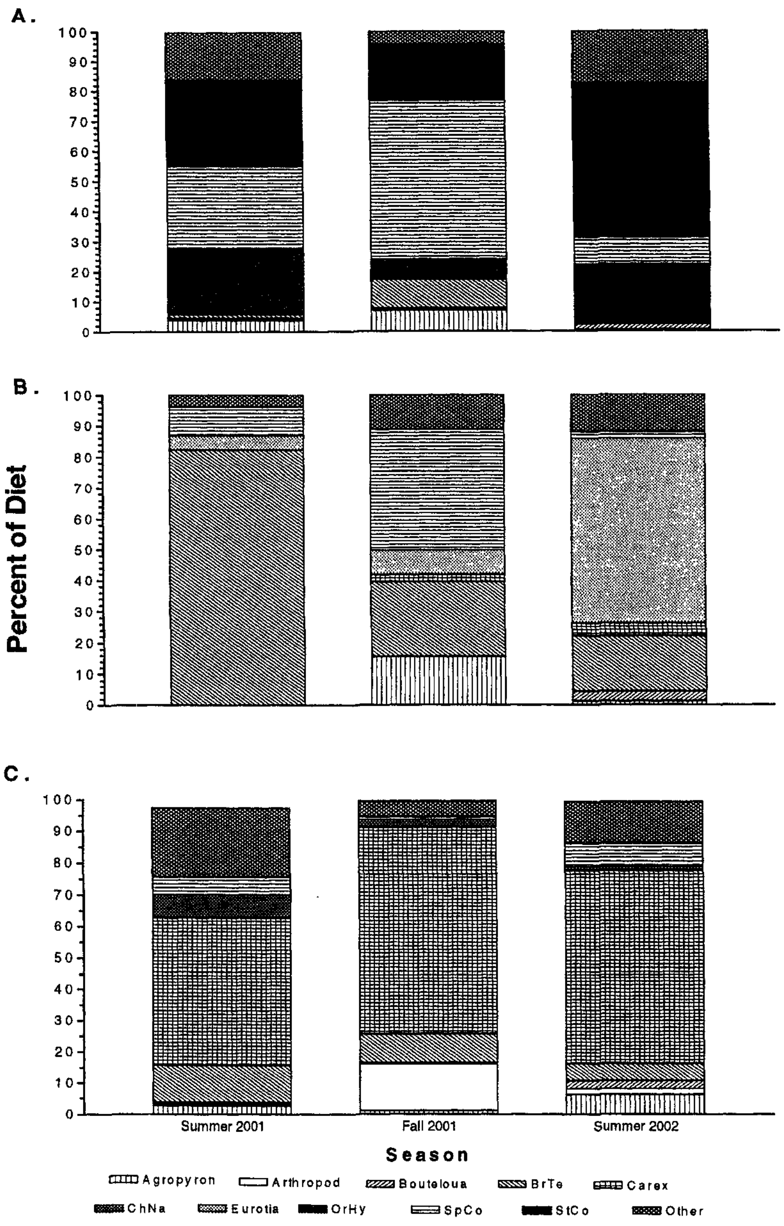

Figure 6. Seasonal changes in diet composition of adult (> 1 y) Utah prairie dogs (*C. parvidens*). Prairie dogs were sampled from colonies located at low (A), mid (B) and high (C) elevations in southern Utah. Diet was determined by identification of plant fragments in fecal samples and values represent mean relative frequency. Agropyron = *Agropyron* spp.; BoGr = *Bouteloua gracilis*; BrTe = *Bromus tectorum*; Carex = *Carex* spp.; ChNa = *Chrysothamnus nauseosus*; Eurotia = *Eurotia* spp.; OrHy = *Oryzopsis hymenoides*; SpCo = *Sphaeralcea coccinea*; StCo = *Stipa comata.*

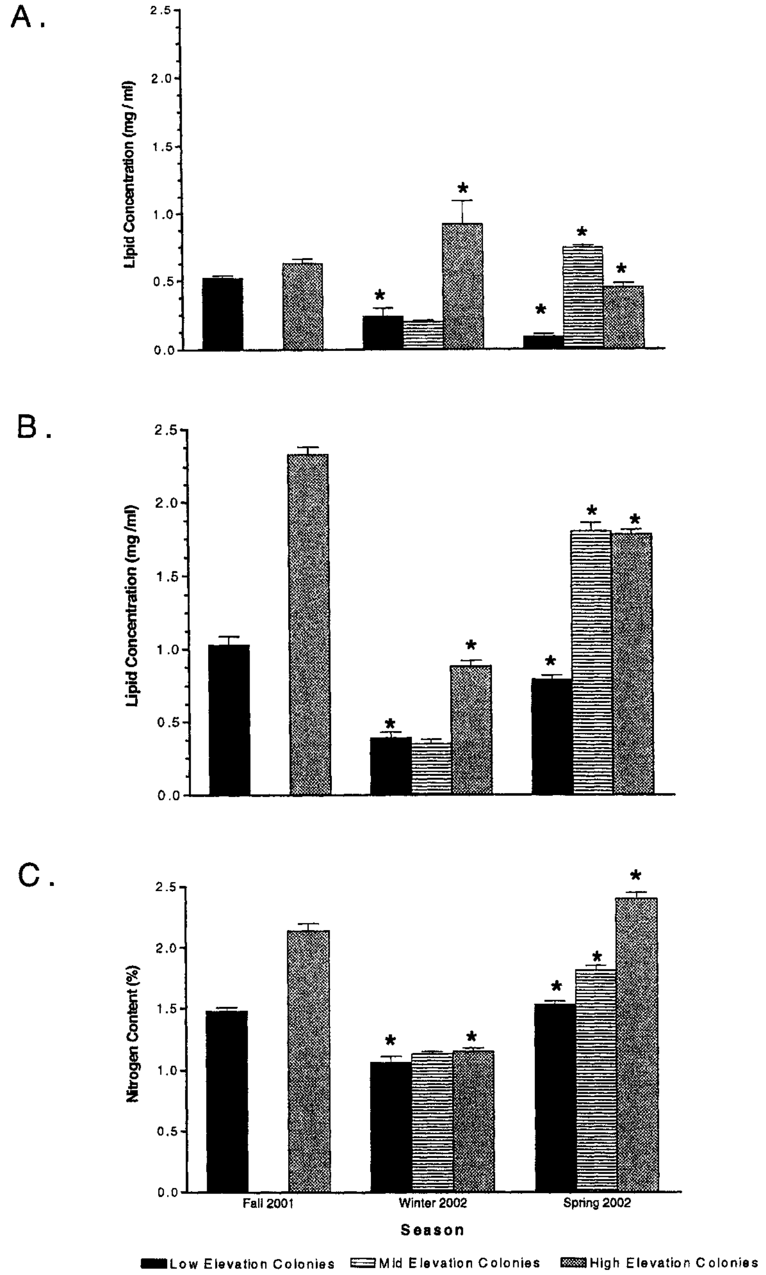

Figure 7. Seasonal changes in nutrient content of plants common on black-tailed prairie dog (*C. ludovicianus*) colonies located at high, mid, and low elevations in northern Colorado. Estimates for mid elevation colonies are not available in Fall 2001, as this site replaced a previous study area. Values represent mean value for all species, Weighed by their relative abundance on the colonies. "A" illustrates linoleic acid (18:2) concentration, "B" illustrates linolenic acid (α 18:3) concentration, and "C" illustrates nitrogen content of plants. * indicates a significant change ($P \leq 0.05$) from the previous season in mean abundance of a nutrient at a particular elevation.

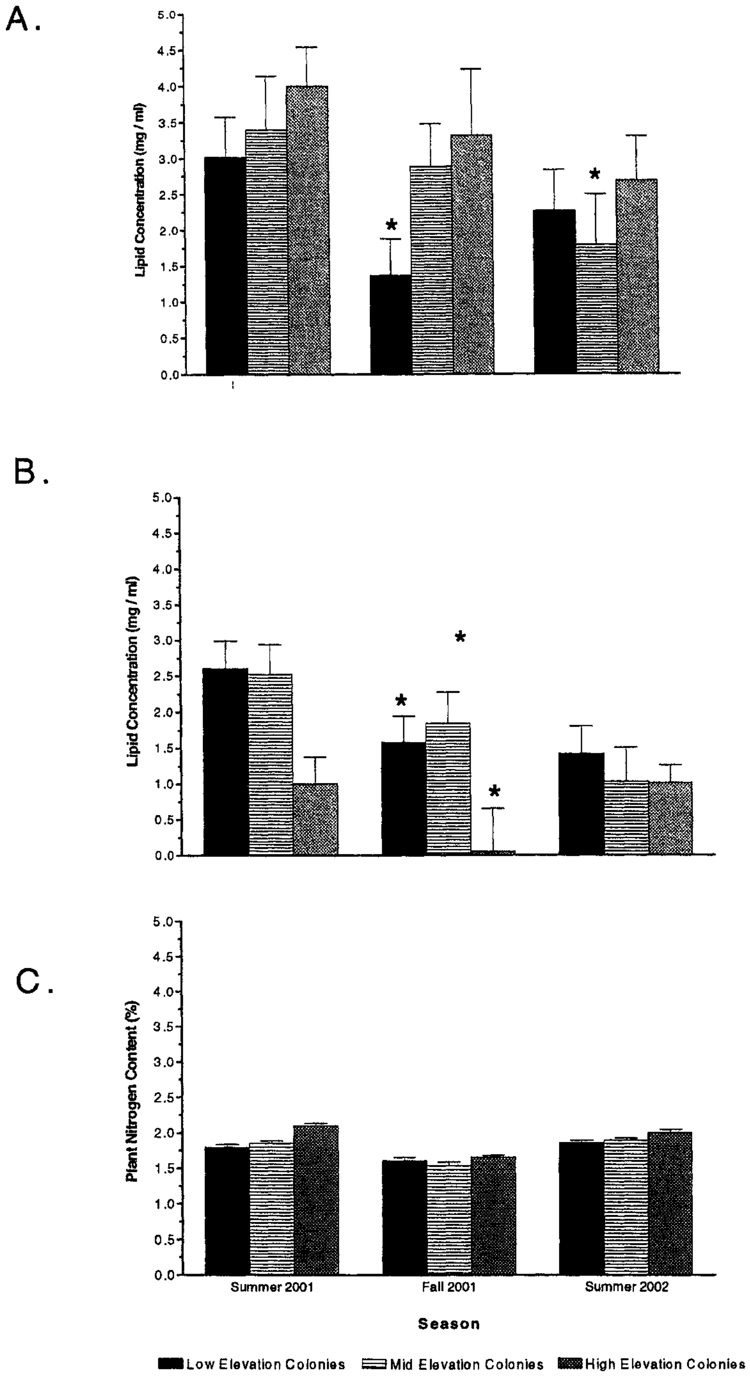

Figure 8. Seasonal changes in nutrient content of plants common on Utah prairie dog (*C. parvidens*) colonies located at high, mid, and low elevations in southern Utah. Values represent mean value for all species, Weighed by their relative abundance on the colonies. "A" illustrates linoleic acid (18:2) concentration, "B" illustrates linolenic acid (α 18:3) concentration, and "C" illustrates nitrogen content of plants. * indicates a significant change ($P \leq 0.05$) from the previous season in mean abundance of a nutrient at a particular elevation.

CONCLUSION

Black-tailed prairie dogs typically entered shallow bouts of torpor intermittently during winter, but some animals practiced deep and prolonged torpor when under extreme physiological stress. Utah prairie dogs hibernated continuously throughout winter across their geographic range. Despite these general patterns, prairie dogs displayed considerable within-species variation in over-winter body temperature patterns, as higher elevation populations of both black-tailed and Utah prairie dogs had lower body temperatures, longer torpor bouts, and spent a greater number of hours in torpor during winter than lower elevation populations. Timing of torpor in black-tailed prairie dogs adhered strongly to a 24 h circadian system, but torpor patterns of Utah prairie dogs did not follow this 24 h cycle. These differences in circadian patterns indicate that underlying mechanisms that stimulate and control torpor may differ between these species.

Body masses of prairie dogs were variable across seasons and elevations, with higher elevation populations generally having higher body masses in all seasons sampled. Seasonal changes in white adipose tissue composition indicate that black-tailed prairie dogs do not have a clear pattern of linoleic and linolenic acid metabolism during winter; however, Utah prairie dogs appeared to store linoleic acid in white adipose tissue depots and preferentially catabolized linolenic acid during winter. Both black-tailed and Utah prairie dogs exercised strong dietary selection in all seasons sampled, and appeared to prefer species higher in linoleic and linolenic acid concentration, as well as total lipid and nitrogen content. Prairie dog colonies at higher elevations generally had vegetation containing higher levels of linoleic acid and nitrogen, whereas colonies at lower elevations had vegetation containing higher levels of linolenic acid.

Our results suggest that environmentally induced variation in torpor patterns within and among prairie dog species results primarily from limitations imposed by environmental factors and habitat quality, rather than from fixed physiological differences between separate populations. Furthermore, the results of our study demonstrate the plasticity inherent in both hibernation and facultative torpor and underscore the influence that environmental conditions can have on body temperature patterns of both hibernators and animals that practice facultative torpor. The climate of the inter-mountain West is highly variable, therefore the ability of an animal to manipulate its body temperature patterns in response to short-term changes in environmental conditions would be highly adaptive. The advantage of such an adaptive phenotype is reflected by the widespread historic distributions of these species throughout the Great Plains and Great Basin of the Western United States (Goodwin 1995). In the future, this adaptability may prove to be essential in the recovery and long-term sustainability of these species, which are both at considerable risk of extinction.

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