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35 Overwinter body temperature patterns in free-living Arctic Squirrels (*Spermophilus parryii*)

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Abstract

We measured overwinter body temperature (T_b) of 89 free-living Arctic Ground Squirrels (*Spermophilus parryii*) on the North Slope of Alaska over ten consecutive years to test for effects of age, sex and year on patterns of T_b change. We were unable to detect year effects on any of the parameters tested suggestive of similarity of cues that modulate circannual timing of heterothermy or a relative inflexibility in circannual timing by this species. Timing of initiation and termination of heterothermy differed by age and sex and resulted in significant differences in duration of the heterothermic season. The phenology of initiation and termination of heterothermy reflected published immergence and emergence chronologies, respectively. Differing durations of the heterothermic season were primarily driven by plasticity in date of initiation of heterothermy rather than in its termination. Once heterothermic, age and sex of animals did not significantly influence either minimum T_b of torpor, or average duration of periods of torpor or bouts of arousal, or percentage of time aroused or torpid. This suggests that once animals are heterothermic they maximise energy savings of heterothermy equally.

Introduction

Mammalian hibernation is a behavioural and physiological adaptation that seasonally confers significantly reduced rates of energy expenditure (for review see Lyman *et al.* 1982). Because most mammalian hibernators are typically sequestered for weeks to months at a time, what we know of regulation of body temperature (T_b) during hibernation and the phenology of hibernation comes primarily from either studies of captive animals or is inferred from above-ground activity patterns of free-living animals. Field studies of free-living animals are generally limited to those of animals during their active season because animals are inaccessible during hibernation, and captive studies fail to mimic all of the cues (social, biotic and abiotic) that free-

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living animals may integrate to establish timing of their annual cycle. Patterns of hibernation of captive animals may also be influenced by the stressors associated with captivity, and thus patterns of T_b across the annual cycle of hibernators often differ between captive and free-living animals (Geiser *et al.* 2000).

The Arctic Ground Squirrel (*Spermophilus parryii*) is the farthest north hibernator in North America. From captive studies we know that this species exhibits the most extreme hibernation phenotype including the ability to reduce T_b to as low as -2.9°C (Barnes 1989), the longest bouts of torpor, and metabolic rates that decrease to as low as 2% of basal (Buck & Barnes 2000). From field studies we know that Arctic Ground Squirrels are exposed to the most severe overwinter hibernacula temperatures described for any hibernator with substantial requirements for thermogenesis that continue during most of the hibernation season (Barnes & Buck 2000; Bieber & Ruff 2004; Buck & Barnes 1999a,b). In this contribution, we evaluate age- and sex-specific patterns of T_b change across the hibernation season and differences in phenologies of termination and initiation of heterothermy. Data are from ten consecutive years of research on a natural population of Arctic Ground Squirrels inhabiting the North Slope of Alaska near the farthest north extent of the species range.

Methods

Study area

This study was conducted with free-living Arctic Ground Squirrels near the Toolik Field Station (TFS) approximately 300 km north of the Arctic Circle in the northern foothills of the Brooks Range, Alaska, USA. Data are presented from fall 1997 to spring 2007.

Animal handling

Marked animals were live-trapped during their active season using Tomahawk traps baited with carrot, and handled at an adjacent TFS laboratory where they were assessed for age from previous trap records, sex, and, in spring, for reproductive status as breeding (males with descended testes, females with evidence of lactation) or non-breeding (males with undescended testes, females in moult). Once per year captured animals were abdominally implanted with temperature-sensitive data loggers (TidBit Stowaway, Onset Computer Corporation) programmed to record T_b ($\pm 0.2^\circ\text{C}$) at 20-min intervals for up to 18 months. Loggers were coated in Elvax (DuPont), calibrated prior to implantation, and had a mass of approximately 14.1 g (Long *et al.* 2007). Loggers were not recalibrated following explant; prior tests indicated no drift in calibration over the hibernation season (F. Kohl unpubl. data). Animals were anaesthetised for surgery using isoflurane and allowed 12 hr to recover before being released at the capture site. We considered animals 'juvenile' if they had not yet completed a hibernation season and 'adult' if they had completed ≥ 1 season of hibernation.

In total, we recovered data from 89 logger deployments: 33 from adult females, 11 from juvenile females, 38 from adult males and 7 from juvenile males. Body temperatures encompassing a complete hibernation season were available from 81 animals (27 adult females, 11 juvenile females, 36 adult males and 7 juvenile males). The eight remaining body temperature time-

series were incomplete due to logger malfunction or filling of logger memory. Incomplete time-series were used only in the analyses for which data were available (e.g. first day $T_b < 30^\circ\text{C}$ but not average torpor bout duration). Six loggers were found on the tundra and showed signs of predation (marginal chewing) – T_b records in these indicated these animals survived the hibernation season and died during the subsequent active season. All procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee and work was conducted under appropriate state permits.

Response variables

We assessed three response variables associated with hibernation phenology and 18 from within the heterothermic period including variables from 'mid-winter' torpor bouts and arousal episodes (Table 1). Bouts of torpor and episodes of arousal refer to uninterrupted periods of time spent torpid ($T_b < 30^\circ\text{C}$) or aroused ($T_b \geq 30^\circ\text{C}$) during the heterothermic season, respectively. Mid-winter torpor bouts are those following and preceding the first and last two multi-day torpor bouts, respectively. Mid-winter periods of arousal are those following and preceding the first and last two periods of arousal, respectively. This approach effectively removes anomalously short initial and concluding hibernation period torpor bouts and the anomalously long penultimate period of arousal.

Statistical analyses

In a preliminary analysis, we assessed the contribution of year and the interactions year*age and year*sex to all of our variables (Table 1) using three-way ANOVA and ordinary least squares (OLS) regression models. Prior to fitting the regression models, age and sex groups were pooled into cohorts (juvenile males, juvenile females, adult males, adult females). P-values from these tests indicated the effect of year (three-way ANOVAs) and the slopes of the regression lines may have been exactly equal to zero with > 0.05 probability (not statistically significant). Based on this result, we dropped year from the analyses presented in this contribution and instead focused on the effects of age and sex and their interaction, using two-way ANOVA models fitted independently to each variable. Significant interactions were decomposed using the Holm-Sidak method for pair-wise comparisons. We also fitted the number of torpor bouts and the number of days spent torpid to the duration of the heterothermic season using OLS regression. All analyses were performed using Sigma Stat version 3.01 (Systat Software, Inc.). Results are presented as means \pm standard error. With a few exceptions, we review only statistically significant results below; these results and non-significant results are summarised in Table 1. Significant pair-wise comparisons reported below were statistically significant at the 0.05 level.

Results

Phenology

Timing of initiation of the heterothermic season in late summer or early fall depended on sex and, among females, age (Table 1). Females entered heterothermy before males, and adult females

Table 1. A summary of the response variables considered in this contribution. Also provided are the statistical analyses used to assess each variable, results of statistical significance from these tests and the identity of the figure summarising results when available.

	Statistical Significance, p value†			Figure	Statistical Analysis
	age	sex	age*sex‡		
Phenology					
Date of initiation of heterothermy	0.010	< 0.001	0.008	1a	2-way ANOVA
Date of termination of heterothermy	< 0.001	< 0.001	< 0.001	1b	2-way ANOVA
Duration of the heterothermic season	0.004	< 0.001	< 0.001	2b	2-way ANOVA
Torpor					
Percentage of the period spent torpid	0.665	0.083	0.559	3b	2-way ANOVA
Number of days spent torpid	0.007	< 0.001	< 0.001		2-way ANOVA
Number of torpor periods	0.157	< 0.001	0.002		2-way ANOVA
Number of multi-day torpor periods	0.070	< 0.001	< 0.001		2-way ANOVA
Number of single day torpor periods	0.475	0.809	0.475		2-way ANOVA
Average duration of torpor periods	0.603	0.512	0.833	3c	2-way ANOVA
Average duration of torpor periods not exceeding one day	0.052	0.829	0.024		2-way ANOVA
Average duration of mid-winter torpor periods	0.703	0.876	0.187		2-way ANOVA
Duration of their first multi-day torpor period	0.823	0.317	0.383		2-way ANOVA
Initiation date of first multi-day torpor period	0.034	< 0.001	0.004		2-way ANOVA
Initiation date of last multi-day torpor period	0.001	< 0.001	< 0.001		2-way ANOVA
Arousal					
Number of arousal bouts	0.114	< 0.001	0.001		2-way ANOVA
Average duration of arousal bouts	0.847	0.073	0.706		2-way ANOVA
Average duration of mid-winter arousal bouts	0.838	< 0.001	0.303		2-way ANOVA
Duration of penultimate arousal bouts	0.021	0.426	0.039		2-way ANOVA
Body Temperature					
Minimum T_b attained during the heterothermic season	0.142	0.838	0.562	3a	2-way ANOVA
Regressions¶					
	$b_1 \pm SE$	p value†	r^2		
Number of torpor bouts against duration of the heterothermic season (days)	0.07 ± 0.005	< 0.001	0.70	2b	OLS Regression§
Number of days spent torpid against duration of the heterothermic season (days)	0.96 ± 0.016	< 0.001	0.98		OLS Regression

† The probability that the true size of the effect was exactly zero; or in the case of the slope (b_1) of the regression line, the probability that the true slope of the line was exactly zero.

‡ Significant interactions were decomposed using the Holm-Sidak method for pair-wise comparisons and are reported in the results.

§ Ordinary Least Square (OLS) Regression.

¶ b_1 = an estimate of the slope of the regression line.

entered heterothermy 9 days, on average, prior to juvenile females (Figure 1a). Adult and juvenile males did not differ regarding when heterothermy began (Figure 1a, Table 1). Sex and, among males, age effects were both significantly correlated with when heterothermy ended (Table 1). Males ended before females and adult males ended heterothermy on average 6 weeks before juvenile males (Figure 1b). Differences in dates of initiation and termination of heterothermy resulted in significant differences in the duration of the heterothermic season between ages ($p = 0.004$) and sexes ($p < 0.001$), with a significant age*sex interaction ($p < 0.001$). Adult males had the shortest heterothermic season (averaging 172 days) followed by juvenile males and females (213 and 227 days, respectively) and adult females (245 days); juvenile males and females did not significantly differ in duration of heterothermy (Figure 2a).

Patterns of T_b within the heterothermic season

The date animals began their first multi-day torpor bout differed between age ($p = 0.034$) and sex ($p < 0.001$), with a significant age*sex interaction ($p = 0.004$): adults preceded juveniles, and females preceded males. Adult females initiated multi-day torpor bouts about 18 days before juvenile females; adult males and juvenile males did not differ significantly. The number of torpor bouts differed by age and sex, and there was a significant age*sex interaction (Table 1, Figure 2b). Adult females had the greatest number of torpor periods (16.2 ± 0.45) followed by juvenile females (15.1 ± 0.70) and males (14.6 ± 0.89). Adult males had the fewest number

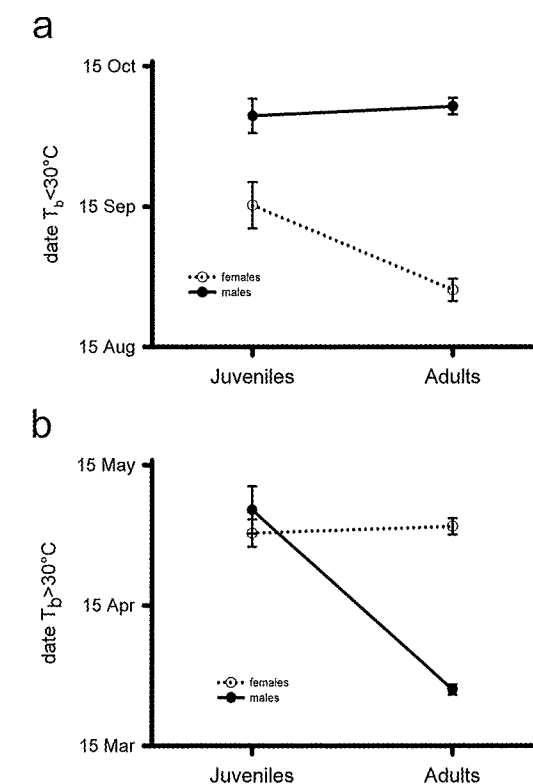


Figure 1.

Dates of initiation (a) and termination (b) of the season of heterothermy in a free-living Arctic Ground Squirrel population near Toolik Lake, Alaska (1997–2007). A 2-Factor ANOVA revealed significant interactions between age and sex for the date of initiation of heterothermy ($p = 0.008$) and for date of termination of heterothermy ($p < 0.001$); see text and Table 1 for more details.

of torpid bouts (11.6 ± 0.39) over the heterothermic season. The number of days spent torpid was a significant function of age ($p = 0.007$), sex ($p < 0.001$), and the age*sex interaction ($p < 0.001$); this variable was also significantly correlated with the duration of heterothermy ($p < 0.001$, $r^2 = 0.70$, Table 1). Adult females maintained $T_b < 30^\circ\text{C}$ for an average of 230 ± 2.8 days, followed by juvenile females, 215 ± 4.3 days, juvenile males, 199 ± 5.4 days, and adult males, 161 ± 2.4 days (Figure 2b). The percentage of the heterothermic season spent torpid did not significantly differ among cohorts (Table 1) and averaged $94.1 \pm 0.31\%$ (Figure 3b). Thirty-six of the 84 winter records of T_b included torpor bouts that were < 24 hours in duration. Among these, there was no evidence of an age or sex propensity to undergo single day torpor bouts (Table 1). There was, however, a significant age*sex interaction in the average duration of a single day torpor bout (Table 1) – juvenile females displayed longer bouts (0.69 ± 0.09 days) than adult females (0.34 ± 0.07 days). The penultimate arousal and the average duration of mid-winter arousal ($T_b > 30^\circ\text{C}$) differed significantly by sex (Table 1) – males exhibited slightly longer mid-winter arousal bouts than females (19.0 hr vs 15.6 hr, respectively) and juvenile males displayed significantly longer penultimate arousals than all other cohorts (Figure 4). No juvenile males ($n = 7$) were reproductively mature after emergence (end of heterothermic period) in spring, whereas all adult males ($n = 38$), adult females ($n = 27$) and juvenile females ($n = 11$) were reproductive after emergence.

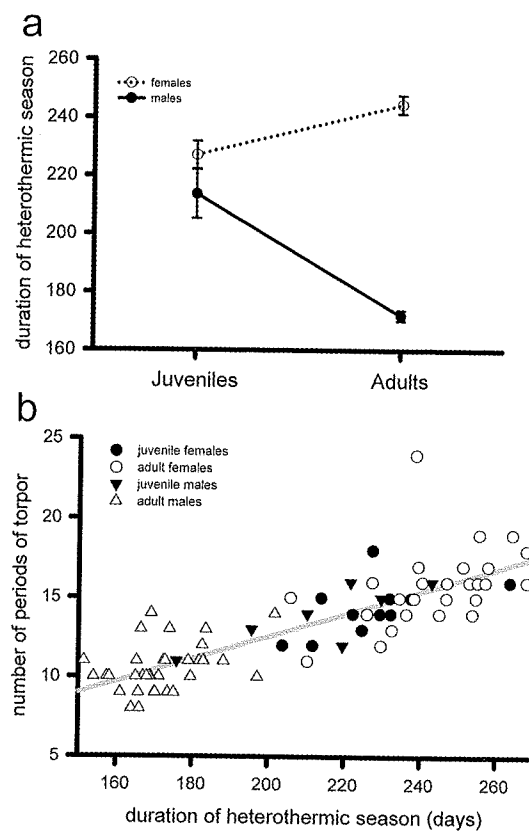


Figure 2.

Duration of the heterothermic season in days (a) and its effect on number of torpor bouts exhibited by age and sex classes (b) of free-living Arctic Ground Squirrels near Toolik Lake, Alaska (1997–2007). There was a significant interaction between age and sex in the duration of the heterothermic season ($p < 0.001$; 2-Factor ANOVA; a). The number of bouts of torpor was positively related to the duration of the heterothermic season ($p < 0.001$, $R^2 = 0.70$; b); see text and Table 1 for more details.

Discussion

Our results from ten consecutive hibernation seasons describe age and sex effects on timing of both initiation and termination of heterothermy as well as patterns of T_b modulation during the heterothermic season of free-living Arctic Ground Squirrels. Significant age, sex and age*sex interactions were primarily confined to annual timing of the beginning or end of heterothermy and, by extension, on the duration of heterothermy. Once animals were in the heterothermic season, there were few significant differences in body temperature change and patterns of torpor or arousal. Interestingly, we found no significant differences or trends across years in either timing of heterothermy (initiation, termination or duration) or patterns of body temperature (e.g. T_b minimum, duration of arousal or length of torpor, number or frequency of arousal bouts) for the population or for specific age and sex cohorts. Below, we relate differences in patterns of body temperature regulation to the natural history of the various age and sex cohorts.

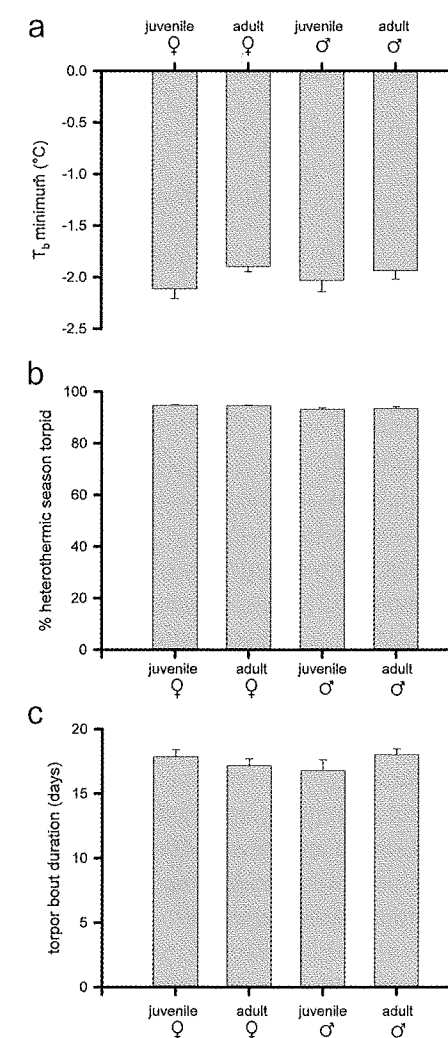


Figure 3.

Minimum T_b (a), percentage of the heterothermic season spent torpid (b) and average duration of torpor bouts (c) for age and sex classes of hibernating Arctic Ground Squirrels monitored near Toolik Lake, Alaska. No significant age or sex effects were detected by a 2-Factor ANOVA (Table 1).

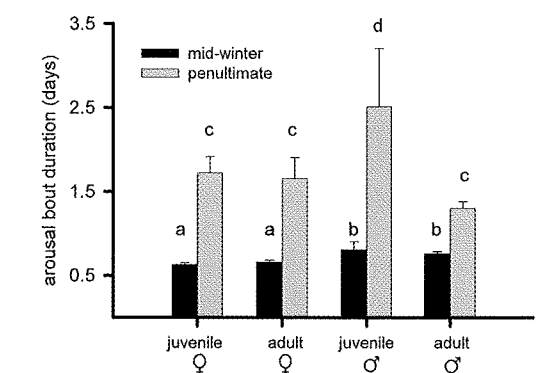


Figure 4.

Age and sex effects on average mid-winter and penultimate arousal duration ($T_b > 30^\circ\text{C}$) of free-living Arctic Ground Squirrels near Toolik Lake, Alaska. Letters above the error bars denote significant differences in duration between bout types (mid-winter vs penultimate; c, d), age and sex classes (a, b) as indicated by 2-Factor ANOVA (Table 1).

Phenology

Timing of initiation of heterothermy through direct measures of T_b confirms patterns of immergence and emergence described from trapping data for this population (Buck & Barnes 1999a). Adult females are the first to cease surface activity and then enter torpor in late August, followed by juvenile females in mid-September and juvenile and adult males in early October. Immergence of females coincides with when they attain maximum body mass and percentage body fat (Buck & Barnes 1999a). Juvenile females are delayed in fattening compared to adult females, likely because of the competing energetic demands of growth and dispersal. Their dates of immergence and first entry to torpor are 18 days later than in adult females, on average. Males, in contrast, attain peak mass and adiposity at approximately the same date as females yet remain active on the surface for nearly 40 days longer. We believe that males remain active later than females to acquire a cache of food. In August and September, male Arctic Ground Squirrels exhibit significant agonistic behaviours prior to immergence that is associated with caching and defence of hibernacula (Buck & Barnes 2003; Carl 1971; McLean & Towns 1981).

Timing of the termination of heterothermy also occurred in an age- and sex-specific sequence that did not differ from emergence phenologies derived for this population from trapping data (Buck & Barnes 1999a). Adult males returned to euthermia 38.4, 33.5, and 34.9 days, on average, before juvenile males, juvenile females and adult females, respectively. Adult males in this population first emerge above ground in spring between 12 and 20 April, yet they terminate heterothermy on an average date of 26 March. This difference in timing, combined with the observation that adult males emerge at body masses and compositions not significantly different from peak fall levels (Buck & Barnes 1999a), demonstrates a prolonged, pre-emergent, euthermic interval during which males feed from cached food while remaining at high body temperatures. The cache is essential fuel for the pre-emergent euthermic interval during which males undergo reproductive maturation (Barnes 1996; Barnes & Ritter 1993). Other cohorts emerge at significantly compromised body mass and condition as compared to immergence values, supporting the observation that only males cache in preparation for hibernation (Buck & Barnes 1999a,b; McLean & Towns 1981).

Interestingly, all seven juvenile males in our study failed to attain reproductive maturity following their first hibernation season and ended heterothermy on average 41 days later than adult males. From our studies of this population, we would have predicted that about 40% of juvenile males would have been reproductively mature (Buck & Barnes 1999a). It is possible that implantation of data loggers in the summer preceding their first hibernation season may have influenced their ability to acquire or defend a cache and thus translated to failed initiation of reproduction in the subsequent spring. All adult males, however, were reproductively mature in the spring. Records of T_b from some of the non-reproductive males indicate that they attempted to initiate a pre-emergent euthermic interval as evidenced by a multi-day arousal bout in early spring that was abandoned in favour of several more periods of torpor.

Not surprisingly, given age and sex effects on both initiation and termination of heterothermy, cohorts exhibited significant differences in duration of the heterothermic season. Variation in duration of the heterothermic season appears to be driven primarily by the date of immergence (SDs of date of initiation of heterothermy > SDs of date of termination of

heterothermy within each cohort). Given the truncated mating season in spring – lasting approximately three weeks (Buck & Barnes 1999a, 2003) – delayed emergence would likely result in missed reproductive opportunities. However, plasticity in the date of entering heterothermy provides opportunity for animals to maximise their body condition (fattening and juvenile growth) or reproductive potential (males accumulate and defend caches) as environmental conditions allow.

Patterns of T_b during the heterothermic season

Although age and sex cohorts exhibited heterothermic seasons of differing durations, the percentage of the season either aroused or torpid did not significantly differ by age or sex. We found no significant differences between cohorts in either minimum T_b of torpor or duration of multi-day torpor periods. Males exhibited slightly longer mid-winter bouts of arousal (~3 hr) than females. This difference in duration could be due to the influence of mass (males are heavier than females) on rates of cooling. However, the euthermic phase of arousals of adult and juvenile males did not significantly differ in duration even though adult males are larger than juvenile males. Interestingly, duration of the euthermic phase of penultimate arousals in females and adult males was approximately twice as long as that during preceding arousals, and longer still in juvenile males. Penultimate arousals have been shown to be prolonged in hibernating male Golden-mantled Ground Squirrels, when gonadotropin and androgen hormone levels become temporarily increased in their blood as part of reproductive activation (Barnes *et al.* 1988). It is not clear why juvenile Arctic Ground Squirrels that remain reproductively immature would extend the length of their arousals.

The average minimum T_b of torpor we recorded was -2.0°C – -0.9°C higher than the lowest published T_b from captive Arctic Ground Squirrels (Barnes 1989). Duration of a mid-winter period of torpor for free-living Arctic Ground Squirrels averaged 17.6 d. This is very close to the average duration – 15.1 days – from captive Arctic Ground Squirrels held at 0°C (Buck & Barnes 2000). However, given the relationship between torpor period duration and ambient temperature (T_a) in this species, we predicted much shorter periods of torpor. Captive Arctic Ground Squirrels shorten mid-winter bouts of torpor at decreasing T_a s below their T_b set-point (Buck & Barnes 2000). We know that the soils in which Arctic Ground Squirrels naturally hibernate are below their T_b set-point (mean = -8.9°C) throughout their heterothermic season (Buck & Barnes 1999b). The captive study predicted that animals in the field during mid-winter should exhibit periods of torpor of approximately 8 days.

Most studies of hibernation have been confined to studies of captive animals due to inaccessibility of free-living animals during hibernation. Because captive studies enable control of environmental conditions, precise measures of physiological parameters and easy access to animals, they have proven quite valuable for describing and understanding physiological mechanisms (for review see Geiser 2004; Lyman *et al.* 1982). Captive animal studies, however, are susceptible to behavioural responses to captivity, which are known to influence the expression (depth, duration) and timing of heterothermy (Geiser *et al.* 2000). Field studies of hibernators have been successful in inferring the duration of hibernation, but not heterothermy, from immergence and emergence dates collected during the active season. This has left them dependent on captive studies for insights on the depth and patterns of torpor.

Through long-term investigations of T_b of free-living populations of hibernators, hibernation biologists can assess the depth, duration and influences (age, sex, climate change) on hibernation phenotype in ways that are not possible with only captive or active season studies.

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36 Hypometabolism in primates: torpor and hibernation

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Abstract

Within the order Primates, reliable reports of hypometabolic states are only found in the family Cheirogaleidae of the Malagasy lemurs, which exhibit daily torpor, prolonged torpor, and hibernation under tropical, but nevertheless seasonal and energetically demanding conditions. There is an amazing physiological plasticity within the lemur group in regard to their thermoregulatory adaptations, not only between species of the same genera within one habitat, but also between populations of the same species, within populations, and even within the same individual. Apart from the Cheirogaleidae, only minor reductions in metabolic rate, presumably rather reflecting pronounced circadian cycles in body temperature, or partial heterothermy have so far been detected.

Primates – a very diverse group

The order Primates comprises a very diverse set of species. They are surprisingly variable in size (30 g to 200 kg) and in the kinds of habitats they inhabit (Lehman & Fleagle 2006b). Most extant primate species live in the tropics or subtropics of Africa, Asia, and South and Central America, although a few, most notably humans, also inhabit temperate regions. Including all the new lemur species that have been described during the last few years there are probably almost 350 species of living primates (Lehman & Fleagle 2006a). They are divided into two suborders, the “wet-nosed” Strepsirrhini (lemurs, lorises and pottos, and galagos), and the “dry-nosed” Haplorrhini (tarsiers, New World monkeys, Old World monkeys, gibbons, great apes, and humans).

Within the order Primates, daily and prolonged torpor has so far only been described for the Malagasy lemurs, and within these exclusively in the family Cheirogaleidae. This might not seem surprising, considering that torpor and hibernation are traditionally seen as an adaptation to cold and unproductive seasons, characteristics usually not associated with the habitats of primates. Many primate species do indeed live in habitats with little annual change in environmental conditions. Others, however, live in habitats characterised by pronounced seasonal fluctuations in climate or resource availability (Brockman & van Schaik 2005). Moreover, recent studies have shown that tropical climatic conditions are not necessarily an

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