

Data logging of body temperatures provides precise information on phenology of reproductive events in a free-living arctic hibernator

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Received: 29 March 2011 / Revised: 23 May 2011 / Accepted: 30 May 2011 / Published online: 21 June 2011
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Abstract Precise measures of phenology are critical to understanding how animals organize their annual cycles and how individuals and populations respond to climate-induced changes in physical and ecological stressors. We show that patterns of core body temperature (T_b) can be used to precisely determine the timing of key seasonal events including hibernation, mating and parturition, and immergence and emergence from the hibernacula in free-living arctic ground squirrels (*Urocitellus parryii*). Using temperature loggers that recorded T_b every 20 min for up to 18 months, we monitored core T_b from three females that subsequently gave birth in captivity and from 66 female and 57 male ground squirrels free-living in the northern foothills of the Brooks Range Alaska. In addition, dates of emergence from hibernation were visually confirmed for four free-living male squirrels. Average T_b in captive females decreased by

0.5–1.0°C during gestation and abruptly increased by 1–1.5°C on the day of parturition. In free-living females, similar shifts in T_b were observed in 78% ($n = 9$) of yearlings and 94% ($n = 31$) of adults; females without the shift are assumed not to have given birth. Three of four ground squirrels for which dates of emergence from hibernation were visually confirmed did not exhibit obvious diurnal rhythms in T_b until they first emerged onto the surface when T_b patterns became diurnal. In free-living males undergoing reproductive maturation, this pre-emergence euthermic interval averaged 20.4 days ($n = 56$). T_b -loggers represent a cost-effective and logistically feasible method to precisely investigate the phenology of reproduction and hibernation in ground squirrels.

Keywords Arctic ground squirrels · Biological rhythms · Emergence · Heterothermy · Hibernation · Life-history stage · Parturition · Phenological changes

Communicated by G. Heldmaier.

Electronic supplementary material The online version of this article (doi:10.1007/s00360-011-0593-z) contains supplementary material, which is available to authorized users.

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Introduction

Determining the flexibility of timing of annually recurring life cycle events such as migration, hibernation, and reproduction is fundamental to investigating how changes in ecological stressors (e.g., climate trends, food availability, predation, inclement weather) may affect physiological and behavioral components of fitness in natural populations. Observational studies conducted in the field, for example, have associated climate warming in recent decades with an advancement in the timing of seasonal reproduction and related behaviors in mammals and birds (Inouye et al. 2000; Root et al. 2003; Post and Forchhammer 2008; Møller et al. 2010; Ozgul et al. 2010). Obtaining precise measures of phenological patterns can be difficult, however, in free-living animals since visibility is

often limited by vegetation, topography, or nocturnal habits of study animals (Gillingham and Bunnell 1985). It can also be difficult or impossible to observe events without disturbing animals, particularly for those that spend time sequestered in burrows. Indirect approaches for estimating the timing of annual events such as the date of parturition include inferences from change in female external morphology (McAdam and Boutin 2003), back dating from the growth curve of offspring (Franken and Hik 2004), or by trapping and holding pregnant females in captivity and recording when they give birth (O'Donoghue and Krebs 1992). These methods provide only estimates of timing or require significant disturbance.

Timing of hibernation and associated use of hibernacula are also difficult to determine with high accuracy. Hibernation is a seasonal interval when an endotherm significantly decreases its activity and periodically or continuously exhibits depressed metabolism and body temperature (T_b) while typically remaining sequestered within its hibernacula (Boyer and Barnes 1999; Tøien et al. 2011). In small- and medium-sized mammals, hibernation in winter includes a regulated period of heterothermy characterized by multiday torpor bouts interrupted by regular spontaneous arousal intervals when T_b returns to euthermic levels for less than 24 h (Geiser 2004). During torpor, T_b decreases to near ambient temperature (T_a) over a wide range of T_a ; if a drop in T_a causes T_b to decrease below a minimum T_b set-point, T_b is defended through thermogenesis (Buck and Barnes 2000). Hibernation can also be accompanied by prolonged periods when animals remain below ground in a euthermic state, in fall prior to heterothermy or in spring after sustained euthermia has resumed but prior to first emergence from the hibernaculum (Barnes et al. 1986; Michener 1993). Although the timing of the hibernation season can be inferred based on the last day in the fall and the first day in the spring that an animal was trapped or seen, estimates made in this manner are likely to be imprecise (Cranford 1978; McLean and Towns 1981; Michener 1992; Buck and Barnes 1999a; Inouye et al. 2000). Furthermore, trapping cannot provide information on the timing of an animal's post-immersion or pre-emergence euthermic intervals.

Here we validate the use of small body temperature data loggers (T_b -loggers) implanted in the abdominal cavities of free-living arctic ground squirrels (*Urocitellus parryii*) to precisely measure their phenology of hibernation, use of heterothermy, and, in addition, parturition. As the northernmost hibernating small mammal in North America, arctic ground squirrels are exposed to profound seasonal changes in photoperiod, ambient temperatures, food availability, and the lowest known hibernacula temperatures (-24.3°C ; Buck and Barnes 1999b) and are likely to experience disproportionately large changes in climatic conditions associated with global warming (Serreze and Francis 2006). Using data

collected from captive and free-living animals, we show that T_b -loggers can be used to precisely determine when ground squirrels give birth, and from this the date of conception can be estimated. Although T_b -loggers have been used to monitor general patterns of heterothermy in a variety of free-living animals (Körtner and Geiser 1998; Boyer and Barnes 1999; Florant et al. 2000) including arctic ground squirrels (Buck et al. 2008), this is the first study to demonstrate their utility in precisely recording dates of below-ground euthermia and emergence and parturition.

Materials and methods

Study species

Arctic ground squirrels are the largest and most northern of the North American ground squirrels. During the 3–5 months they are active each year, they must reproduce, fatten, and cache food (males only) in preparation for spending 7–9 months hibernating alone (McLean and Towns 1981). In northern Alaska, mean body mass of females range from 600 to 1,000 g depending on season, whereas mean male body mass ranges from 740 to 1,000 g (Buck and Barnes 1999b). Immersion into hibernation takes place from August to mid-September with females immersing before males and adults immersing prior to juveniles (Buck et al. 2008; Sheriff et al. 2011). Mean soil temperatures during the heterothermic period (-8.9°C ; Buck and Barnes 1999b) are below minimum T_b (-2.9°C ; Barnes 1989) indicating squirrels must remain thermogenic during deep torpor. In May, when most females are pregnant and giving birth in the Toolik region, soil temperatures at hibernacula depth range from -11 to 1.5°C (Buck and Barnes unpublished data). Males terminate heterothermy 4–6 weeks earlier than females but remain below-ground for several weeks consuming a food cache as they undergo testicular growth and maturation (Barnes 1996). Females are not thought to cache food (Gillis et al. 2010) and emerge from their burrows shortly after terminating hibernation (Sheriff et al. 2011). Emergence from hibernation begins within the population in mid-April and lasts several weeks with reproductive males emerging before females and non-reproductive males emerging last (Buck et al. 2008). Females become pregnant shortly after emergence; gestation lasts approximately 28 days and pups do not appear on the surface until approximately 27 days later; weaning occurs when pups are approximately 5 weeks old (Lacey 1991).

Data collection

Between 1996 and 2009, we obtained annual records of body temperature at 20-min interval from 123 individual free-

living ground squirrels; some individuals were implanted more than once. We obtained T_b data during immergence events (i.e., the transition from the active season to heterothermy) from 65 females (112 events) and 52 males (68 events) and during emergence (i.e., the transition from hibernation to the active season) from 50 females (85 events) and 43 males (56 events). Arctic ground squirrels were captured using Tomahawk traps (models #103 & 104.5, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with carrot near the Toolik Field Station (68°38'N, 149°38'W) in the northern foothills of the Brooks Range, Alaska. Animals were implanted/explanted with abdominal T_b -loggers (modified TidBit Stowaway model TBICU32-05+44, package weight 14–15 g, Onset Computer Corporation) programmed to record T_b ($\pm 0.2^\circ\text{C}$) at 20-min interval for up to 18 months. For details of logger preparation and calibration and surgical procedures, see Long et al. (2007).

From 1997 to 2008, we collected measurements of T_b across the entire reproductive season from 40 T_b -loggers implanted in 30 individual free-living female ground squirrels (we had two seasons of data for 10 squirrels). Data collection was initially focused on body temperature patterns during hibernation and therefore we lack T_b data during reproduction for some females when we attempted to retrieve loggers immediately following spring emergence. To validate that the upward shift in T_b observed during the breeding season in free-living females coincided with the day of parturition, three pregnant females were captured and transported to the University of Alaska Fairbanks where they were housed in metal laboratory cages (19 × 12.5 × 8.25"; Unifab Corp., Kalamazoo, MI, USA) within environmental chambers initially held at 18°C and 18 h light:6 h dark. These animals were also implanted with data loggers within 48 h of capture as above. Cages were provided with wood shavings and cotton for use as nest material. Squirrels were fed Mazuri Rodent Chow and given water ad libitum. After 2 weeks, we moved these females into an environmental chamber kept at 2°C which is within the range of soil temperatures measured during the parturition period at our study site. Cages were checked daily for the first appearance of pups.

We also validated the utility of T_b -loggers in determining the date of first emergence from hibernation of free-living males in natural burrows near Toolik Lake, Alaska. In four males that had been implanted the previous fall with T_b -loggers, we determined the date of their first appearance on the surface in spring by visually inspecting the hibernacula entrance sites daily and recording the day an opening appeared and tracks were observed on the snow (squirrels had to dig through snow to reach the surface). We then captured and identified the males using those burrows within 5 days of emergence and compared dates of emergence with T_b patterns obtained from the explanted loggers.

Data analysis

All modeling was performed using version 9.2 of the SAS software package (SAS Institute Inc., Cary, NC, USA). To empirically identify significant change points in time series of T_b , we applied linear regression models to mean daily T_b data that, for a hypothesized date of parturition, allow for different slopes (pre vs. post hypothesized date) and different intercepts (pre vs. post hypothesized date). For each squirrel, we used every date between 1 May and 30 June as a hypothesized parturition date (change point) and selected the most parsimonious model amongst all models using Akaike's Information Criterion (1973) adjusted for small sample bias (AIC_c). If the most parsimonious model (lowest AIC_c) is one with a single intercept and slope, then a change point is not detectable. For free-living females, we performed this analysis using mean daily T_b data from 1 May to 30 June for each year; dates when individuals were torpid or arousing from a torpor bout (i.e., $T_b < 30^\circ\text{C}$) were excluded from analyses. We also calculate Akaike weights (W_i), which gives an estimate of the probability that a model gives the most parsimonious fit to the data (Burnham and Anderson 2002). The sum of W_i values across all models adds to one.

Based on visual examination of logger data collected from males, T_b did not exhibit a diel rhythm until days-weeks following the return to euthermia. To empirically identify significant change points in time series of T_b for the four males for which we had visually estimated emergence dates, we applied non-linear regression models in SAS that allowed for different mean T_b (different intercepts) pre versus post putative emergence and for a circadian pattern post-emergence (a model consisting of cosine curves with a known period of 24 h). For each squirrel, we used every day during the first 5 weeks of euthermia as a hypothesized date of emergence (change point) and selected amongst models using AIC and AIC weights. Day 35 of euthermia was selected as the final possible date of emergence because visual examination of T_b data indicated all free-living males exhibited obvious diel rhythms within the first 5 weeks. We also used Clocklab software (Actimetrics, Evanston, IL, USA) to test for the presence and periodicity of significant T_b rhythms prior to and following emergence using Lomb-Scargle periodogram analysis (Ruf 1999). Means are reported \pm SD.

Results

Visual examination of T_b data revealed shifts in T_b that appeared to coincide with annually recurring life-cycle events (Fig. 1). Female arctic ground squirrels that gave birth in captivity exhibited an abrupt increase in T_b ranging

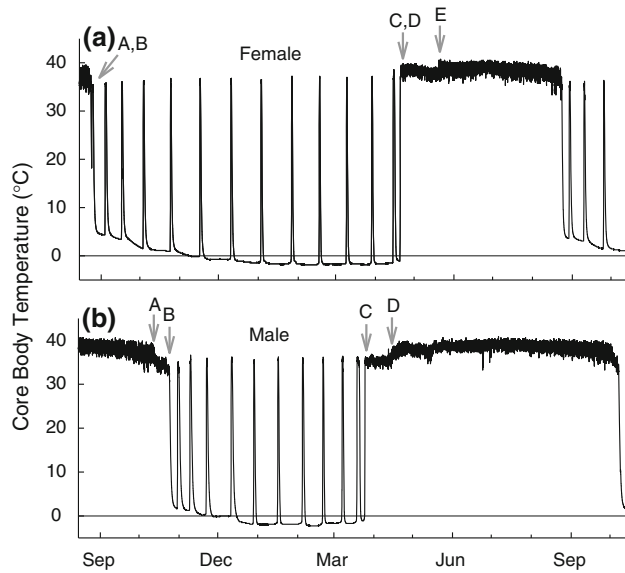


Fig. 1 Core body temperature (T_b) of a representative free-living **a** female and **b** male arctic ground squirrel living near Toolik Lake in northern Alaska. Time courses of T_b can potentially provide information on the timing of annually recurring life cycle events including *A* entrance into the hibernacula, *B*, *C* the start and end of seasonal heterothermy, *D* first emergence from the burrow in spring, and *E* parturition

from 1.0 to 1.5°C that occurred on the day of parturition as demonstrated by the appearance of pups in the cage (Fig. 2a). For these three females, the most parsimonious model (i.e., lowest AIC_c) had a change-point (different intercept and slope pre vs. post change point) in mean daily T_b that coincided with the date of parturition. A summary of the AIC_c weight support for the top three models for each captive female can be found in supplementary Table S1. We were able to make a visual and subjective identification of a similar abrupt increase in mean daily T_b during the reproductive season in 29 of 31 free-living adult females (94%) and 7 of 9 free-living yearling females (78%) for which we had T_b data throughout the reproductive season. In each of the 36 cases, the most parsimonious model had a change-point that coincided with an abrupt change in T_b which we had independently visually identified from plots of raw T_b data. For 34 of the 36 cases, the most parsimonious model had an AIC_c $W_i \geq 0.95$. In one of the two remaining cases, the top two models ($W_i = 0.65$ and 0.31, respectively) both agreed on the data of parturition and differed only on whether there was (top model) or was not a change in slope following parturition. In the final case, there was uncertainty as to whether parturition occurred on May 25 ($W_i = 0.53$) or May 26 ($W_i = 0.45$). The mean R^2 for the most parsimonious model of each free-living female was 0.88 (range 0.76–0.97). All free-living females exhibited a downward trend in T_b during gestation prior to an abrupt increase in T_b on the presumed

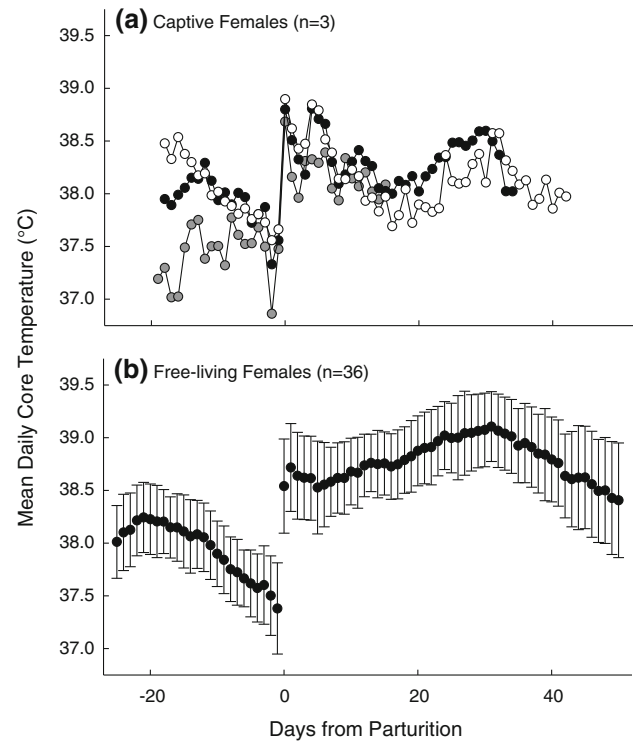


Fig. 2 Daily mean core body temperature (T_b) of **a** three female arctic ground squirrels that gave birth in captivity, and of **b** 36 free-living females (mean \pm SD) that exhibited a similar abrupt rise in T_b that we presumed to be indicative of parturition. The date of parturition in free-living females was empirically determined using an information-theoretic approach to model selection. The empirically determined change-point matched our subjective estimates based on visual examination of plots of daily mean T_b

date of parturition (i.e., the change-point identified by visual examination and confirmed using AIC_c; Fig. 2b). This downward trend in T_b also occurred in two of the three captive females. During the last 20 days of gestation, mean daily T_b decreased from 38.2 to 37.4°C ($n = 36$). Following the abrupt increase in T_b of $1.2 \pm 0.3^\circ\text{C}$, the mean daily T_b of females increased steadily to a peak at 30 days post-parturition before decreasing by approximately 0.5°C over the next 20 days. We were not able to confirm that these females gave birth, as we avoided trapping during late gestation and early lactation to minimize disturbance. An abrupt increase in mean daily T_b was not observed in males.

When we calculated the dates females became pregnant by subtracting a mean gestation length of 25 days (Lacey 1991) from the date of parturition, we found that conception always occurred after heterothermy ended. On average, the estimated date of conception was 5.1 ± 2.7 days (range 0–14) after females first developed a diurnal T_b pattern indicative of when they began above ground activity. In the four cases where we did not visually identify an abrupt increase in T_b , a change-point was still identified based on

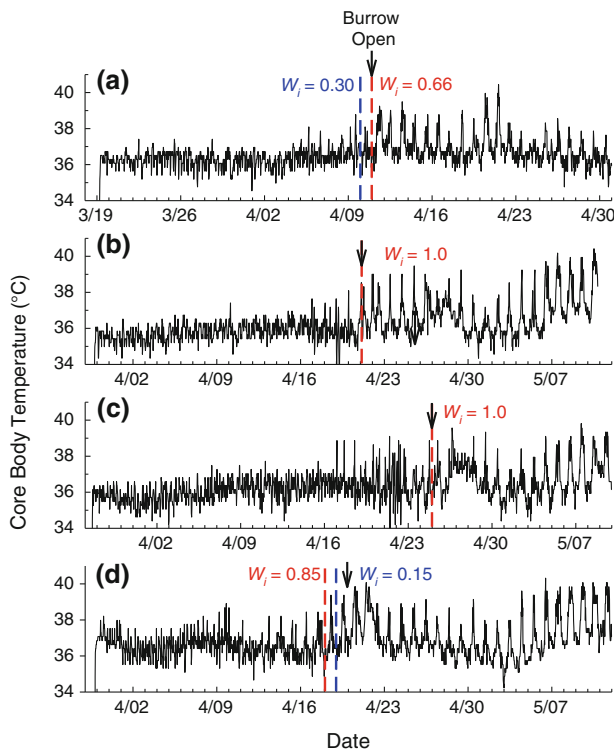


Fig. 3 Core body temperature (T_b) of four free-living male arctic ground squirrels during the first 6 weeks of euthermia following the final torpor bout of the hibernation season. Downward facing arrows indicate the first day the entrances to the hibernacula were confirmed to have been completely dug open (through the snow). T_b patterns changed rapidly to a pronounced diurnal rhythm after the entrance to the hibernacula was first observed to be open. Red and blue dashed lines indicate the date of emergence (transition to a sinusoidal temperature rhythm with a periodicity of 24 h) based on the two most parsimonious models. Model weights (W_i) provide an estimate of the probability that the model provides the most parsimonious fit to the data

the most parsimonious model. However, an abrupt increase in T_b was not associated with these change-points and there was greater uncertainty in model selection (Table S2). One of these atypical change-points occurred within 13 days of ending hibernation and therefore could not have been associated with birth. Thus, the date of parturition is defined by the occurrence of a change-point which has to be associated with an abrupt increase in T_b .

All four free-living males for which we observed the date of emergence exhibited a change in T_b patterns that appeared to coincide with the date of emergence based on visual examination of T_b plots. For three of the males, our most parsimonious model for a transition to a 24-h rhythm coincided with the first day the burrow was observed to be open (Fig. 3a–c); the most parsimonious model for the fourth male indicated the transition occurred 2 days prior to our detecting an open burrow entrance (Fig. 3d). The

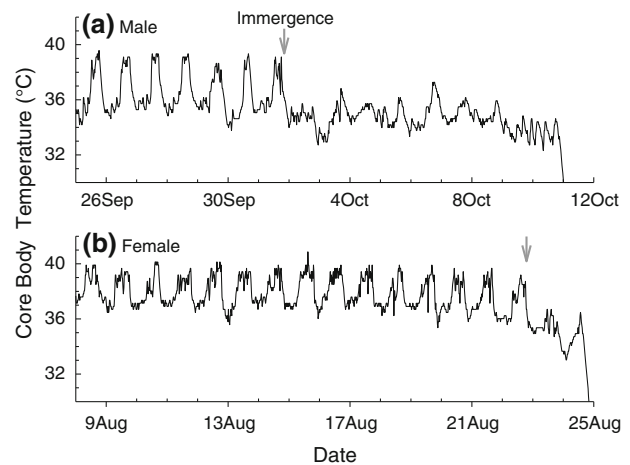


Fig. 4 Core body temperature (T_b) of **a** one representative male and **b** one representative female arctic ground squirrel during the 2 weeks preceding entry into the first torpor bout of the hibernation season. Downward-facing arrows indicate the time point at which the diurnal rhythm in T_b became dampened. We hypothesize that the date preceding the arrow is the last day the squirrel spent above ground

daily range in T_b during the first 10 days post-emergence was $3.3 \pm 0.2^\circ\text{C}$ and the peak-to-peak amplitude of the cosine wave was $1.6 \pm 0.2^\circ\text{C}$. Although there was no obvious pre-emergence diel rhythm in T_b for three of the four individuals, three of the four individuals exhibited significant ($P < 0.01$) rhythms with a periodicity of 25.7 h (male shown in Fig. 3a), 23.4 h (Fig. 3b), and 24.4 h (Fig. 3d) based on periodogram analysis of the entire euthermic period prior to discovery of an open burrow; the fourth individual (Fig. 3c) was arrhythmic (no significant ultradian or diel rhythms) prior to emergence. All individuals exhibited significant ($P < 0.01$) 24-h periodicity in T_b rhythms following emergence. The mean duration that free-living ground squirrels were euthermic prior to developing an obvious diel T_b pattern was 1.9 ± 2.7 days ($n = 85$) for adult females and 20.4 ± 8.1 days ($n = 56$) for adult males.

Although we lack observational data to confirm the last date that squirrels were active outside their burrows in fall prior to entering hibernation, we found that a large proportion of free-living males (43 of 68 hibernation entries in 52 individuals) and a small proportion of females (22 of 112 hibernation entries in 65 individuals) exhibited a substantially dampened diurnal rhythm for ≥ 3 days prior to their first torpor bout (Fig. 4). In the ten males that exhibited dampened rhythms for >10 days prior to entering torpor, the daily range of T_b decreased from $4.4 \pm 0.5^\circ\text{C}$ per day to $2.9 \pm 0.6^\circ\text{C}$ per day and mean T_b decreased from $36.9 \pm 0.6^\circ\text{C}$ per day to $35.4 \pm 0.6^\circ\text{C}$. Additionally, at least five males appeared to lose their diurnal rhythm in T_b prior to entering the heterothermic period.

Discussion

We found that patterns of core T_b recorded using abdominally implanted data loggers provides precise information on seasonal timing of reproduction in free-living female arctic ground squirrels and timing of heterothermy during hibernation and use of below-ground euthermia prior to and following heterothermy in free-living male and female ground squirrels. Female arctic ground squirrels exhibit pronounced shifts in core T_b patterns coincident with gestation and parturition (Fig. 2). Because the length of gestation is known in arctic ground squirrels (Lacey 1991), use of T_b -loggers also permitted an estimation of the date of conception. Furthermore, we show that T_b -loggers can be used to determine the date the heterothermic period begins and ends, the amount of time ground squirrels spend below ground in a euthermic state, and the date animals first emerge. For a detailed analysis of hibernation and reproductive phenologies in our study population based on the methodology described here, see Sheriff et al. (2011). Implanted and externally affixed T_b -transmitters and T_b -loggers have provided key insights into patterns of thermoregulation and metabolic demand under conditions of variable energy supply (reviewed in Geiser 2004). Use of these devices has also led to unexpected discoveries including freeze-resistance in arctic ground squirrels (Barnes 1989), the ability of penguins to depress abdominal temperatures by more than 10°C during foraging dives (Handrich et al. 1997), and the occurrence of hibernation in tropical primates (Dausmann et al. 2004). Although T_b -loggers are widely used in studies of metabolic ecology, they have additional potential for use in examining phenological events.

We found that T_b in female arctic ground squirrels decreased during gestation and then abruptly increased after giving birth; mean T_b of females remained high throughout lactation (Fig. 2). Although our sample size of captive females is low, we verified that free-living females exhibited a comparable shift in T_b pattern that did not occur in males. Calculated conception dates for these free-living squirrels occurred shortly after hibernation had ended supporting our contention that these temperature shifts were indeed reflective of parturition. However, conception dates calculated in this manner are only estimates and their accuracy will depend on variability in the length of gestation; Lacey (1991) reported a standard deviation of 0.8 days in gestation period based on field data from 42 females. Our empirical approach for calculating the date of parturition from T_b data in free-living females matched estimates based on visual identification of abrupt increases in daily T_b . However, care must be taken to scrutinize the pattern of change in mean daily T_b as atypical empirically

derived change-points were also identified in a few females that likely did not give birth.

The functional significance of a decreasing T_b during pregnancy that is adjusted upwards at parturition is not clear. Females will save energy during gestation by defending a lower T_b , especially in the cold environment of the natural burrow during spring. Soil temperatures at hibernacula depth range from -11.3 to 1.5°C in May when most females are pregnant and giving birth in the Toolik Lake region (Barnes and Buck unpub. data). However, at parturition ground squirrel neonates, which are born hairless and incapable of thermoregulation (Maxwell and Morton 1975), must be kept warm in the nest through active thermogenesis by their mother. Lactating female ground squirrels spend the majority of each day in association with their young in the burrow, typically emerging in morning and afternoon for foraging bouts that last 4–5 h each (Kenagy et al. 1990). The associated high level of metabolism as well as that required for synthesis of milk for lactation (Speakman and Król 2010) may lead to the higher maternal body temperatures that are defended after birth. Average T_b continuously increased prior to peaking at 39.0°C 30 days after parturition before decreasing over the next several weeks to 38.5°C . It is at about 30 days of age that juvenile arctic ground squirrels are weaned and begin foraging independently (Lacey 1991). The recorded pattern of maternal T_b may reflect the increase in metabolism that occurs throughout lactation that then decreases at weaning in ground squirrels (Kenagy et al. 1989).

Comparative data collected in livestock indicates that T_b exhibits significant, and in some cases predictable, shifts during reproductive events including parturition (Ewbank 1969; King et al. 1972; Lammoglia et al. 1997). Data from other small mammals show a similarity to our findings—mean T_b in rats (Fewell 1995) and dwarf-hamsters (Scribner and Wynne-Edwards 1994) increases on the date of parturition. Thus, we suggest that T_b -loggers could prove useful for elucidating the timing of birth in other species. Before undertaking such studies, however, investigators need to carefully consider the timing of implantation to ensure that capture, handling, and/or implantation does not adversely affect animals and that devices provide unbiased estimates of measured parameters (Dausmann 2005; Whidden et al. 2007). The exact pattern of change in T_b is also likely to differ amongst taxa. For example, the T_b of dwarf hamsters increases slightly during gestation, abruptly increases at parturition, and remains elevated during the first week of lactation before gradually returning to pre-parturition levels throughout weaning (Scribner and Wynne-Edwards 1994). In contrast, we found that T_b in free-living arctic ground squirrels decreased steadily during gestation, increased abruptly at parturition, and then increased steadily throughout lactation (Fig. 2b), similar to

what was observed in rats (Fewell 1995). Although a drop in T_b occurred around the time of weaning (~ 30 days post-parturition), T_b did not decrease to pre-parturition levels, in part because of the steady decrease observed during gestation.

We also found that the pre-emergence euthermic period in ground squirrels could be estimated based on T_b data alone (Fig. 3). When ground squirrels became euthermic in spring they initially lacked a clear diurnal rhythm in T_b . However, once they emerged from their burrows they rapidly developed a robust diurnal T_b pattern which remained apparent until hibernation resumed in the fall. One of the males exhibited obvious diurnal rhythms ~ 3 days prior to our observed date of emergence. It is possible that this individual was active above-ground earlier, but his emergence was not recorded because his hibernaculum was located some distance from where he was initially caught. It is also possible this individual developed diurnal rhythms while below-ground in response to photoperiodic cues if direct sunlight penetrated the snow into the burrow.

The pre-emergence euthermic period is critical to support testicular recrudescence, as spermatogenesis is not possible at T_b levels of torpid males (Barnes et al. 1986, 1987; Fietz et al. 2004). Consistent with this requirement, we found only males showed a euthermic period prior to emergence from the hibernacula. Trapping data indicate that male arctic ground squirrels emerge with enlarged testes descended into a pigmented scrotal sac, although androgen levels peak later, coincident with the emergence of receptive females (Buck and Barnes 2003). Because of the high metabolic costs associated with maintaining a prolonged euthermic T_b during hibernation (Karpovich et al. 2009), testicular recrudescence is an energetically expensive process in hibernators.

Examination of T_b of free-living ground squirrels also revealed an interesting dampening of diurnal rhythms prior to commencing the heterothermic period of hibernation in some animals, particularly males. Furthermore, a smaller proportion of males appeared to lose diurnal T_b rhythms prior to the first torpor bout. We suggest that this dampening of diurnal rhythms likely indicates the date of entry into hibernation, as elevated T_b during the day is known to correspond to above-ground activity (Long et al. 2007). A damped diurnal rhythm was also observed in European ground squirrels (*Spermophilus citellus*) held in outdoor enclosures after they became sequestered within their hibernacula (Hut et al. 2002). Furthermore, because animals likely are no longer exposed to photic cues after becoming sequestered in their hibernacula the disappearance of diurnal T_b rhythms in some individuals may indicate they are no longer returning to the surface each day. The functional significance of such a pre-hibernation

euthermic period remains unclear, although in males it may relate to the need to reorganize or guard food caches (females are not known to cache food). Consistent with this hypothesis, the below-ground euthermic period of hibernation that occurs prior to heterothermy is longer in males than in females (Sheriff et al. 2011).

Information on reproductive phenology is critical to estimating how populations will respond to long-term climate change. For example, changes in reproductive phenology could result in a trophic mismatch if offspring production no longer coincides with peak resource availability (Post and Forchhammer 2008). Our data indicate that T_b data can be used to precisely measure shifts in the timing of parturition. The appearance of such a clear shift in T_b during parturition in free-living ground squirrels suggests that T_b data might also be useful in determining which females successfully give birth in any given year. This information is likely to be important in understanding how environmental stressors influence population processes as physiological stress can impair reproduction in some small mammals (Charbonnel et al. 2008; Sheriff et al. 2009). For males, T_b -loggers can provide critical data on variation in the length of the pre-emergence euthermic period and on the proportion of yearlings that exhibit this trait, which is critical for testicular growth. This information will provide important insight into how environmental stressors influence an individual's fitness.

Acknowledgments We thank G.L. Florant, M. Richter, and four anonymous reviewers for their helpful comments on an earlier version of this manuscript. We also thank those who have assisted with the collection of field data including M. Richter, T. Lee, R. Fridinger, S. Karpovich, J. Jenkins, T. Martin, A. Fenn, and A. Wright. This study was supported by funding from the National Science Foundation to BMB (EF-0732763) and CLB (OPP-0732763) and awards from the US Army Medical Research and Materiel Command (#05178001) to BMB. All procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee and work was conducted under appropriate state permits.

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