

MINI-SERIES

Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming

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circannual clock; hibernation; phenology; photoperiodism; Sciuridae; squirrel; seasonality; torpor.

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Abstract

Mammalian hibernation is characterized by prolonged dormancy consisting of pronounced depression of metabolism and body temperature. Though hibernation occurs in at least seven mammalian orders and several families of the order Rodentia, the ecology and physiology of hibernation in rodents has been most extensively studied in the family Sciuridae, particularly in the so-called ground squirrels, that is, the tribe Marmotini. Early studies of these rodents demonstrated the important role of an endogenous circannual clock in the persistence of annual timing and phasing of key seasonal events, including weight gain, hibernation and reproduction. Here, we review the causes and consequences of intraspecific variation in the timing of hibernation and reproduction in these sciurids and examine the physiological mechanisms that contribute to phenotypic plasticity in seasonal timing. Although the duration, annual phasing and predictability of seasonal change in environmental conditions likely promoted the evolution of endogeneity, precision and brevity of breeding seasons in the annual cycles of sciurids, substantial intraspecific variation in hibernation and reproductive phenology exists along latitudinal and altitudinal clines, as well as among locally varying environmental micro-conditions. We suggest that much of this variation is a function of plasticity in the physiological mechanisms controlling annual cycles. While studies of captive animals have been instrumental in establishing the role of an endogenous rhythm, a greater emphasis on experimental field manipulations is needed to better understand the function, causes and consequences of phenological shifts in wild populations. Ultimately, the capacity of hibernators to adjust their timing in response to changing environmental conditions, either through phenotypic plasticity or microevolution, will be an important determinant of the resilience of sciurid species to changing climate.

Introduction

Seasonality of environmental conditions is one of the most important forces shaping the evolution of annual rhythms of behavior and physiology (Baker, 1938; Boyce, 1979; Gwinner, 1986). For example, in environments where forage is predictably limited during one portion of the year, animals must organize their activity and energy budgets when food is available to balance the competing demands of reproduction and self-maintenance. A key component of self-maintenance includes accruing the resources needed to persevere during, or escape from (i.e. migrate away from), the predictable interval when food is limited. In resident species, decreasing

metabolic expenditure in anticipation of and during periods of food shortage, either through a reduction in activity levels (Humphries *et al.*, 2005) or through torpor, in which metabolism is reduced well-below basal levels (Geiser, 2004), plays an important role in surviving seasonally inhospitable environments. The most profound and sustained metabolic savings occurs via hibernation, which, in small to medium-sized mammals, consists of a regulated interval of profoundly reduced metabolism characterized by multiday torpor bouts interrupted by regular spontaneous arousal intervals when body temperature returns to euthermic levels for less than 24 h (Fig. 1; reviewed in Geiser & Ruf, 1995).

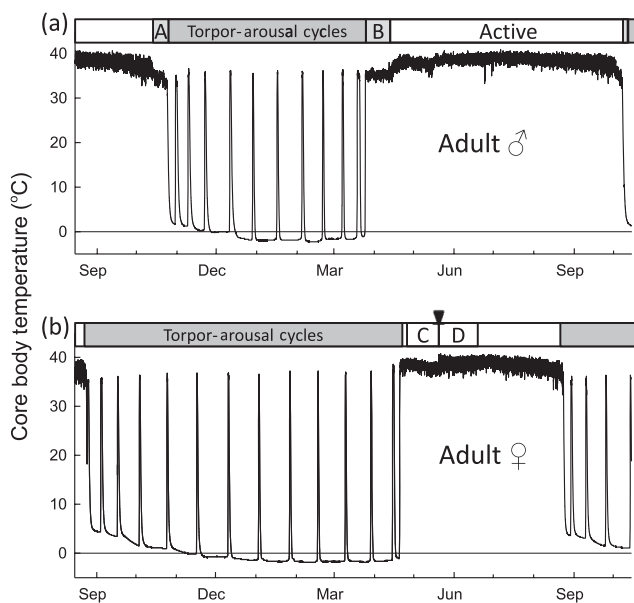


Figure 1 Core body temperature of a representative free-living (a) male and (b) female arctic ground squirrel (*Urocyon parryi*) living near Toolik Lake in northern Alaska. Changes in body temperature patterns indicate the timing of seasonally recurring life-cycle events (Sheriff *et al.*, 2011; Williams *et al.*, 2011). Adult males typically exhibit below-ground intervals of euthermia (light gray bars) that immediately precede (A) and follow (B) heterothermy, whereas these intervals of below-ground euthermia are typically very short (<3 days) or absent in females. Females become pregnant within a few days of emergence, gestate for ~28 days (C) and lactate for an additional ~35 days (D; Lacey, 1991). An abrupt shift in body temperature indicates timing of parturition (downward facing arrow).

Hibernation is taxonomically and geographically widespread among mammals, occurring in the orders Monotremata, Diprotodontia, Erinaceomorpha, Carnivora, Chiroptera, Primates and Rodentia, and on all continents with the exception of Antarctica (Geiser, 2004). Among all these groups, hibernation has been most extensively studied within the squirrel family, Sciuridae, which includes hibernating ground squirrels, chipmunks, marmots and prairie dogs. The expression of torpor is highly variable among sciurid species, with some exhibiting only daily episodes, others exhibiting multiday torpor bouts as long as 24 days repeated over the course of a hibernation season (Geiser & Ruf, 1995) and others that do not express torpor at all (Kenagy, 1981a; Brigham & Geiser, 2012; Dausmann *et al.*, 2013). This review focuses on sciurids that hibernate, including ‘obligate’ hibernators, which predictably exhibit hibernation each year, and ‘facultative’ hibernators, which manifest the trait only under certain environmental conditions (Kenagy, 1981b; Humphries, Kramer & Thomas, 2003; Lehmer *et al.*, 2006).

The persistence and seasonal timing (‘phenology’) of hibernation events, including cycles of body mass and expression of torpor and reproductive readiness and their responses to changes in environmental conditions, have intrigued ecolo-

gists for decades (e.g. Shaw, 1925; Wade, 1950; Pengelley & Fisher, 1963; Mrosovsky, 1971; Michener, 1984). Interest in phenology has further increased recently as evidence accumulates that the timing of annually recurring life-cycle events, such as migration and hibernation, are changing in response to climate change (Inouye *et al.*, 2000; Parmesan & Yohe, 2003; Lane *et al.*, 2012). Phenological studies on vertebrates have focused on migratory species, particularly birds, because migrants are perceived as being more susceptible to climate change induced mismatches between linked trophic levels since they initiate their spring migration at far away wintering sites and perhaps are less able to make adjustments to local conditions at their breeding grounds (Visser & Both, 2005; Thackeray *et al.*, 2010). Although resident species, including hibernators, can potentially respond directly to local cues, it remains unclear whether they exhibit greater plasticity and/or resilience to environmental change than migrants. Intraspecific differences in timing between nearby populations of hibernating sciurids correspond with differences in altitude, aspect and snow cover that affect forage availability, which indicates plasticity and/or local adaptation (e.g. Shaw, 1925; Bronson, 1980; Murie & Harris, 1982; Sheriff *et al.*, 2011). However, interspecific variation in responsiveness to environmental conditions suggests species differ in their physiological capacity to alter timing or in the appropriateness of their response (Michener, 1977, 1984; Harlow & Menkens, 1986). Furthermore, while hibernating sciurids adjust the timing of annually recurring life-cycle events in response to climate, the magnitude and direction of changes in timing vary between locations and have differing demographic consequences (Ozgul *et al.*, 2010; Lane *et al.*, 2012).

Phenological plasticity in response to climate change can be driven by factors other than increasing temperature (e.g. Sheriff *et al.*, 2011; Lane *et al.*, 2012). However, our ability to predict how species might respond to rapid changes in their environment is hampered by insufficient knowledge regarding (1) the cues used to adjust timing, (2) the endogenous mechanisms that allow animals to keep time and (3) the inherent physiological capacity of hibernators to alter their annual cycle. Importantly, while phenological shifts in response to changes in environmental conditions over shorter time frames are generally thought to reflect physiological plasticity (Przybylo, Sheldon & Merilä, 2000; Clements *et al.*, 2010), persistent directional changes in environmental conditions should lead to changes in gene frequencies over time (i.e. microevolution) and both processes are likely important components of population resilience to climate change.

Here, we review the role of endogenous clocks, photo-periodic timing mechanisms and physiological plasticity in establishing the timing of seasonally recurring life-cycle events in hibernating sciurids. We then examine the intrinsic and environmental factors that drive intraspecific variation in the timing of seasonally recurring life-cycle events and explore the evolutionary and ecological drivers of variation in phenology within the family Sciuridae. We suggest that resilience of many populations of hibernators is likely tied to their capacity to alter phenology through clock-dependent and clock-independent physiological mechanisms. While we

contend that much of the phenotypic variation in timing between local populations is attributable to physiological plasticity, we caution that the role of genetic differences remains largely unexplored. Finally, we propose future avenues of research for phenological studies of hibernators and encourage more field experiments aimed at establishing the possible importance of genetic variance and physiological plasticity in contributing to within- and between-species variation in the timing of hibernation and reproduction in sciurids.

Clocks, photoperiod and seasonal timing

Manifestations of an endogenous circannual clock

In some relatively long-lived organisms, an endogenous, circannual clock determines the persistence and sequence of seasonal life-cycle events and the temporal window during which physiologically linked events, such as weight gain, hibernation, migration, reproduction and molt occur. The critical role of a circannual clock in regulating endogenous rhythms of morphology, physiology and behavior was first demonstrated in hibernators over 50 years ago when Pengelley & Fisher (1963) observed an ~11-month rhythm of food consumption, body mass and hibernation that continued throughout life in captive golden-mantled ground squirrels (*Callospermophilus lateralis*) maintained in constant temperature and photoperiod conditions. Endogenous, circannual clocks permit animals to persist in their cycles of hibernation, body mass and reproduction even during phases of the annual cycle when external time cues are absent. Although much of the early work emphasized the importance of predictable seasonal conditions in promoting the evolution of a robust circannual rhythm, it was also evident that, similar to circadian rhythms, the circannual rhythm must be entrained by external cues for individuals to maintain synchrony with the environment (Heller & Poulson, 1970; Armitage & Shulenberg, 1972; Kenagy, 1980, 1981*b*; Ward & Armitage, 1981).

From circadian clocks to the seasonal organization of physiology and behavior

In the past 30 years, our understanding of circadian physiology has been transformed as the interacting molecular feedback loops that make up the circadian clock have been identified and the mechanisms through which light entrains the clock have been established (reviewed in Golombek & Rosenstein, 2010). Further, the discovery that the mammalian circadian system is hierarchical, with a master clock within the hypothalamic suprachiasmatic nuclei (SCN) responsible for synchronizing peripheral oscillators within cells and tissues throughout the body, has been instrumental in increasing our understanding of how photic and nonphotic cues affect circadian physiology, entrainment and function (Buhr, Seung-Hee

& Takahashi, 2010; Dibner, Schibler & Albrecht, 2010). Similar to the master circadian clock, the circannual clock generates an endogenous rhythm entrained by environmental cues (Zeitgeber), a process that enhances the fitness of organisms by improving their ability to adjust physiology and behavior in anticipation of predictable change in seasonal conditions. However, the location, molecular structure and biochemical function of the circannual clock remain unknown, and reports on the intrinsic mechanisms of circannual pacemakers remain highly speculative (Wikelski *et al.*, 2008; Hazlerigg & Lincoln, 2011). Regardless of its molecular underpinnings, the expression of the circannual clock is apparently little affected by the pronounced seasonal depression in body temperature, metabolism, gene transcription and translation that accompany deep torpor in ground squirrels.

Light–dark (LD) cycles and changing photoperiod are the dominant Zeitgeber for circadian and circannual rhythms, with the coarse timing of seasonal events determined by an entrainment of circannual rhythmicity by photoperiod (Bradshaw & Holzapfel, 2007). The importance of light in entraining circadian rhythms led to early speculation that the circannual clock depends on daylength indirectly through the circadian clock, and that entrained, circannual rhythms might emerge as a super-harmonic of circadian rhythms through ‘frequency demultiplication’ (i.e. counting of 365 days; Gwinner, 1986). This hypothesis failed to find support because circannual rhythms are independent of artificial LD cycles set to non-24-hour periods (Gwinner, 1973; Carmichael & Zucker, 1986; Wikelski *et al.*, 2008). Recent findings of changes in expression profiles of circadian clock genes under different photoperiods, however, suggests the circadian clock not only acts as a pacemaker, but is capable of measuring day length (e.g. Sumová *et al.*, 2003; Tournier *et al.*, 2003). Thus, circadian clocks *may* play a role in entraining circannual clocks, although it is clearly not occurring via frequency demultiplication.

Though the molecular makeup of the circannual clock remains unknown, our understanding of seasonality has advanced markedly in the past decade by the finding that annual changes in photoperiod can entrain neuroendocrine pathways that drive seasonal metabolic and reproductive cycles in vertebrates (reviewed in Ikegami & Yoshimura, 2012). In some long-lived species, annual rhythms of hormone production rely on a circadian-based, melatonin-dependent timer within the pars tuberalis (part of the anterior lobe of the pituitary gland), which activates or inhibits the reproductive axis (Lincoln *et al.*, 2006; Hazlerigg & Loudon, 2008; Dardente, 2012). In these species, annual changes in physiology are driven by an alteration between photostimulation in spring followed by photorefractoriness (spontaneous reversion in physiology to that of the previous photoperiodic state). In sheep that exhibit circannual rhythms, it is hypothesized that the refractory state might result from a disassociation between the melatonin-dependent timer within the pars tuberalis and a circannual timing mechanism (Lincoln *et al.*, 2005).

Although changes in photoperiod activate the reproductive axis of many mammals, it is notable that hibernating sciurids

naturally remain sequestered for months within a constant dark environment in their hibernacula immediately prior to the onset of reproduction (e.g. Körtner & Geiser, 2000; Williams, Barnes & Buck, 2012a; Williams *et al.*, 2012b). Given the lack of exposure to photoperiodic cues, it seems likely that both spontaneous termination of torpor-arousal cycles and activation of the hypothalamus-pituitary-gonadal (HPG) axis promoting reproductive maturation in sciurids must predominantly rely on the circannual clock, although fine tuning of breeding is also likely influenced by nonphotic environmental cues (Michener, 1984). Interestingly, even in ground squirrel species that do not hibernate, the recrudescence and regression of the testes fails to exhibit a photoperiodic response and is instead driven by an endogenous circannual rhythm (Kenagy & Bartholomew, 1979; Kenagy, 1981a). This is not necessarily the case for hibernators from other groups; European hamsters (*Cricetus cricetus*), for example, exhibit a robust photoperiodic response (Hanon *et al.*, 2010). Further, while states of hibernation and reproduction do not overlap in sciurids, other hibernators including some bats and marsupials exhibit deep prolonged torpor during pregnancy (Willis, Brigham & Geiser, 2006; Morrow & Nicol, 2009).

In most hibernators, entrance into the hibernaculum occurs during seasons of decreasing day length, which could theoretically entrain the circannual clock during this time frame. Although early laboratory studies using static daylengths suggested that photoperiod was a weak entraining agent (Pengelley & Fisher, 1963; Pengelley *et al.*, 1976), more recent evidence comparing static and naturally changing photoperiods and intact and SCN-ablated ground squirrels indicates that changing day length acts to entrain circannual rhythms (Lee & Zucker, 1991). Understanding circadian or circannual entrainment of free-living ground squirrels is further complicated by their semi-fossorial lifestyles that place them underground during dawn and dusk (Hut, van Oort & Daan, 1999). Collectively, it is apparent that in sciurids, both the termination of torpor-arousal cycles and activation of the HPG axis are strongly influenced by the circannual clock. Observed plasticity of spring timing indicates that both clock-dependent (e.g. entrainment) and clock-independent mechanisms work in concert to fine-tune seasonal timing and may function through an endogenously driven seasonal shift in responsiveness to environmental cues.

Intraspecific variation in phenology

Annual timing of hibernation and reproduction differs between sex and age cohorts and reflects differences in autumnal and vernal (spring) behaviors and requirements for reproductive maturation of males and females. The degree of difference in timing between sexes, however, varies among species, with greater synchrony in those marmots that hibernate in family groups, relative to solitarily hibernating ground squirrels. Differences in timing between the sexes have also been observed in chipmunks (Kawamichi, 1996), which often fuel metabolism during hibernation primarily

using hoarded food supplies rather than stored fat, with the result that variation among individuals in their expression of torpor depends on quality and composition of the food cache (French, 2000; Munro, Thomas & Humphries, 2005).

Sex effects in ground squirrels

In ground squirrels, adult males typically precede females in both ending torpor-arousal cycles and emerging to the surface in spring (Michener, 1983), and it is hypothesized that it is the endocrine initiation of gonadal maturation that triggers the earlier termination of torpor in sexually maturing males (Barnes, 1996). In golden-mantled ground squirrels, testosterone levels are elevated during the first half of arousal episodes prior to the last arousal, and levels of follicle-stimulating hormone increase during the final days of the last torpor bout (Barnes *et al.*, 1988). Further, Lee *et al.* (1990) demonstrated that elevating plasma testosterone in gonadectomized ground squirrels inhibits hibernation, and Dark, Miller & Zucker (1996) showed that gonadectomy in males following the last arousal can lead to the resumption of torpor-arousal cycles for several weeks. Measurement and biopsy of testes of captive golden-mantled ground squirrels showed that little testicular growth and no advancement of spermatogenic phase occurs during torpor-arousal cycles and 1 month of sustained euthermia after the end of torpor is required for motile spermatozoa to appear in the epididymides (Barnes *et al.*, 1986; Barnes, Licht & Zucker, 1987). Low body temperature during torpor inhibits sexual maturation, as male ground squirrels forced to prematurely terminate torpor by exposure to warm ambient temperatures become sexually mature earlier (Barnes & York, 1990). Thus, early termination of torpor-arousal cycles by males allows sufficient time for gonadal growth and development. Though this pattern of reproductive development is consistent in males across species, the rate at which it occurs appears to be species-specific, occurring in as little as 12–21 days in Richardson's (*Urocitellus richardsonii*) and arctic ground squirrels (*U. parryii*) and taking as long as 2 months in California ground squirrels (*Otospermophilus beecheyi*; Holekamp & Talamantes, 1991; Michener, 1992; Barnes & Ritter, 1993).

To offset the energetic costs of euthermia and reproductive maturation experienced by males while they are sequestered below ground, in some species (e.g. Richardson's, arctic and California ground squirrels), males consume a food cache, which they accumulated during the previous active season (Holekamp & Nunes, 1989; Michener, 1992; Gillis *et al.*, 2005; Zazula, Mathewes & Harestad, 2006). This strategy has the advantages of reducing predation risk in early spring, reducing reliance on stored fat and increasing body mass prior to emergence and reproduction; indeed, body masses of adult male arctic ground squirrels when first trapped in spring do not differ from body masses attained immediately prior to hibernation in fall (Buck & Barnes, 1999a). In contrast, adult male Richardson's ground squirrels emerge at a lower body mass in spring compared with their pre-immigrant fall body mass, though a surplus of food in the cache following

emergence is associated with a reduction in the amount of mass lost throughout hibernation (Michener, 1992). In California ground squirrels, which hibernate from May or June until October or November, caching by adult males occurs immediately prior to commencing hibernation during the early summer (Holekamp & Nunes, 1989). In other species, males are reported not to cache (reviewed in Michener, 1984), or the tendency to cache varies across their geographical range. Shaw (1925) documented caching behavior by male Columbian ground squirrels (*U. columbianus*) in Washington state, whereas Young (1990*a,b*) found that male Columbian ground squirrels in Alberta, further north, exhibit a short (~3–12 days) pre-emergent euthermic interval, yet do not cache food. Given that most studies have inferred phenologies from trapping animals on the surface after emergence or by measuring body temperature using telemetry or loggers, information on how much time individuals spend below ground in a euthermic state prior to emergence is generally lacking.

Similar to vernal timing, chronology of autumnal immergence into the hibernaculum and initiation of torpor in ground squirrels differs by sex; whether males or females initiate hibernation first varies across species (Michener, 1984). The ecological and evolutionary drivers for sex differences in chronology of immergence are unclear; however, monthly survival is often higher during hibernation compared with the active season presumably because inactivity minimizes predation (Turbill *et al.*, 2011; Bieber *et al.*, 2012). Thus, earlier entry into hibernation by males might occur because their reproductive season ends earlier and they gain a survival advantage by fattening and hibernating earlier. The function of later initiation of hibernation by males in some species remains unclear, although we speculate that the much later (~28–42 days; Sheriff *et al.*, 2011) immergence of adult male arctic ground squirrels is dictated by their need to accumulate and defend a large food cache that is subsequently consumed during the spring pre-emergent euthermic interval (Buck & Barnes, 2003; Gillis *et al.*, 2005). This hypothesis does not appear to be supported by the chronology of immergence in other species. For example, adult male European ground squirrels (*Spermophilus citellus*) immerge slightly later than females in fall, yet are not known to cache (Millesi *et al.*, 1999), and adult male Richardson's ground squirrels cache food yet immerge earlier than females (Michener, 1992).

Using both implanted body temperature loggers and light loggers affixed to collars, we recently demonstrated directly that adult male arctic ground squirrels also exhibit a post-immergent euthermic interval in autumn, prior to initiating torpor, though the function and/or cause of this euthermic interval is not known (Sheriff *et al.*, 2011; Williams *et al.*, 2011, 2012*b*). Because the surface entrances to hibernacula of arctic ground squirrel are not blocked, and because the hibernacula contains a food cache, it is possible that delayed torpor following immergence is an act of vigilance in defense of the accumulated cache. Indeed, aggression among male arctic ground squirrels is high in autumn and is associated with territorial defense (Buck & Barnes, 2003).

Age effects in ground squirrels

Consistent with the hypothesized role of the HPG axis in triggering earlier termination of torpor in spring by males, termination of torpor-arousal cycles and vernal emergence is later for males that fail to undergo reproductive development than for both males and females that do become reproductively mature (Knopf & Balph, 1977; Morton & Sherman, 1978; Smith & Johnson, 1985; Millesi *et al.*, 1999; Healy *et al.*, 2012). However, in species where males become reproductively mature following their first winter of hibernation, juvenile males emerge at the same time as adult males (Michener, 1983, 1984).

Effects of communal hibernation – marmots

In contrast to ground squirrels and chipmunks, most marmots (genus *Marmota*) are social hibernators in which adult males hibernate with one or more adult females, and mothers hibernate with their offspring (e.g. Arnold, 1988; Armitage, 1999; Blumstein *et al.*, 2004; Lee, Barnes & Buck, 2009). The composition and size of social groups varies across species (Armitage, 1999). All woodchucks and a subset of adult male yellow-bellied marmots hibernate solitarily (Blumstein *et al.*, 2004; Zervanos *et al.*, 2010), but none of the species are known to cache food (Woods & Armitage, 2003; G. L. Florant, pers. comm.). Using implanted temperature-sensitive data transmitters in free-living animals, Arnold (1988, 1993) demonstrated that, in alpine marmots (*Marmota marmota*), social hibernators exhibit synchronized bouts of torpor and arousal. However, despite this high level of coordination, differences in chronology among the sexes are still apparent as males terminate torpor-arousal cycles and emerge to the surface before females, though the size of this effect (a few days) is much smaller than in most ground squirrels. Similarly, male yellow-bellied marmots (*M. flaviventris*) emerge earlier than females, and juveniles emerge after adults (Blumstein *et al.*, 2004; Blumstein, 2009). However, whether marmots exhibit below-ground post-immergent or pre-emergent euthermic intervals is currently unknown. Interestingly, the composition of the social group appears to affect the timing of emergence, with males emerging about 2 days earlier with each additional male in the group (Blumstein, 2009). Overall, despite the relatively limited amount of data for social hibernators, it appears as though patterns of emergence are similar to those of solitary hibernating sciurids, though differences among sex and age classes are greatly reduced because of the high levels of coordination within groups. Published accounts of differences in chronology between sexes in solitary hibernating woodchucks are inconsistent. Based on lethal sampling, Snyder & Christian (1960) reported that males emerge 3–4 weeks earlier than females, and based on live-trapping data, Davis (1967) reported earlier spring emergence and later autumnal immergence in males. However, two more recent studies employing implanted temperature-sensitive radio-transmitters and temperature loggers failed to find significant differences in timing of entry or emergence, though sample sizes were small (Zervanos & Salsbury, 2003; Zervanos *et al.*, 2010). It is

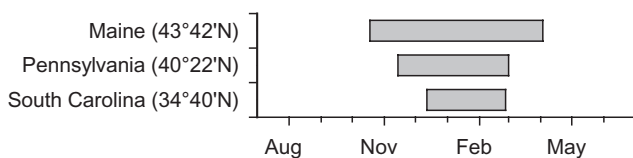


Figure 2 Latitudinal differences in timing and duration of heterothermy in free-living woodchucks at sites in Maine, Pennsylvania and South Carolina (data from Zervanos *et al.*, 2010).

unclear whether contrasting results are due to differences in methods or variation among sites or years.

Environmental effects on timing in obligate hibernators

Because our understanding of the mechanisms that generate and entrain circannual rhythms of physiology remains speculative, progress in understanding how hibernators perceive and integrate environmental cues to adjust their phenologies has been slow. Day length plays a major role in dictating the coarse timing of annually recurring life-cycle events in most mammals through the photoperiodic response and via entrainment of circannual clocks. However, the effects of nonphotoperiodic cues, such as precipitation, snow cover, food availability and temperature, are generally less pronounced and alter timing within a fairly narrow window. Given differences in timing between age and sex cohorts, it seems likely that the cues used to adjust timing, or the weighting of those cues, varies substantially within a species and perhaps by location.

Lability in dates of entry into and emergence from the hibernacula for a multitude of hibernating sciurids suggests either physiological plasticity in response to nonphotoperiodic environmental cues or genetic differences among individuals and populations (Michener, 1984). For example, the onset and termination of torpor-arousal cycles varies with latitude in woodchucks, with populations in Maine hibernating 2.2 times longer than populations in South Carolina (Fig. 2; Zervanos *et al.*, 2010). Differences in snow cover, aspect and altitude between nearby populations have also been associated with differences in the timing of spring emergence in several species of ground squirrels (Bronson, 1980; Murie & Harris, 1982; Sheriff *et al.*, 2011). One limitation of comparisons between sites, particularly over wide geographic ranges, is the potential for phenotypic differences to be influenced by genetic differences, rather than reflecting phenotypic plasticity. Time-series data, however, also indicate correlations between spring emergence and a variety of ambient conditions including snow cover and depth, as well as air and soil temperature that suggests flexibility in response to local conditions (Michener, 1979, 1984; Murie & Harris, 1982; Ozgul *et al.*, 2010; Lane *et al.*, 2012).

Although correlations between timing and environmental variables are evident, there is uncertainty regarding what cue or cues function as proximate (mechanistic) drivers. Air tem-

perature is sometimes correlated with the timing of emergence (reviewed in Michener, 1984), but is unlikely to be an acute cue that triggers termination of torpor-arousal cycling because soil and snow overlaying or surrounding hibernacula serves as an insulative buffer that dampens the above-ground thermal signal even when there are considerable changes in air temperature (Buck & Barnes, 1999b). Snow cover and depth affects forage availability, yet it remains unclear how animals sequestered within hibernacula assess conditions at the surface. In addition to its insulative properties, snow reflects incident solar radiation, and thus later, snow melt generally leads to slower rates of soil warming (Coulson *et al.*, 1995; Ling & Zhang, 2003). However, whether a reduced rate of soil warming in spring effectively informs animals of surface conditions remains equivocal; some studies have found correlations between soil temperature and timing of emergence (Iverson & Turner, 1972; Michener, 1979), whereas others have not (Buck & Barnes, 1999b; Williams *et al.*, 2012c). Barnes & Ritter (1993) found that artificial warming of the soil surrounding hibernating arctic ground squirrels housed in outdoor enclosures resulted in earlier termination of torpor and emergence of males, but not females. However, the implications of this result are unclear given the termination of torpor in free-living males occurs prior to soil warming, whereas females end heterothermy and emerge coincident with soil warming (Buck & Barnes, 1999a; Sheriff *et al.*, 2011; Williams *et al.*, 2012c). Clearly, there is a need for more field manipulations designed to elucidate the patterns of phenotypic flexibility and their mechanisms and environmental cues.

Because adult males often remain below ground at euthermic body temperatures following the seasonal termination of torpor, earlier dates of emergence to the surface could reflect either an earlier end of torpor-arousal cycling or a shorter interval of pre-emergent euthermia, or both. For example, Sheriff *et al.* (2011) compared phenologies of two populations of arctic ground squirrels living at sites with different snow cover regimes and found that, although reproductive males ended torpor on the same date at both sites, males from the high snow cover site had longer pre-emergent euthermic intervals (25 vs. 16 days) and therefore emerged later (Fig. 3). In contrast, reproductive females and nonreproductive males spent little time below ground in a euthermic state prior to emergence (<3 days) at both sites, but terminated torpor-arousal cycles and emerged later at the high snow cover site (Fig. 3; Sheriff *et al.*, 2011). Most studies rely on trapping data to establish timing of emergence and therefore it is unclear whether adjusting the length of the pre-emergent euthermic interval explains most of the variation in timing of emergence by males in other species.

In general, precise timing of autumnal immergence is lacking for most species and how timing of entry into the hibernacula and initiation of torpor is influenced by environmental conditions is unknown. Ambient temperature and snow cover may be important determinants for the timing of autumnal immergence in cohorts that enter hibernacula late, such as young of the year. However, given the need for juveniles to grow prior to fattening, timing of immergence might be tied more closely to date of birth (Fig. 3). For earlier

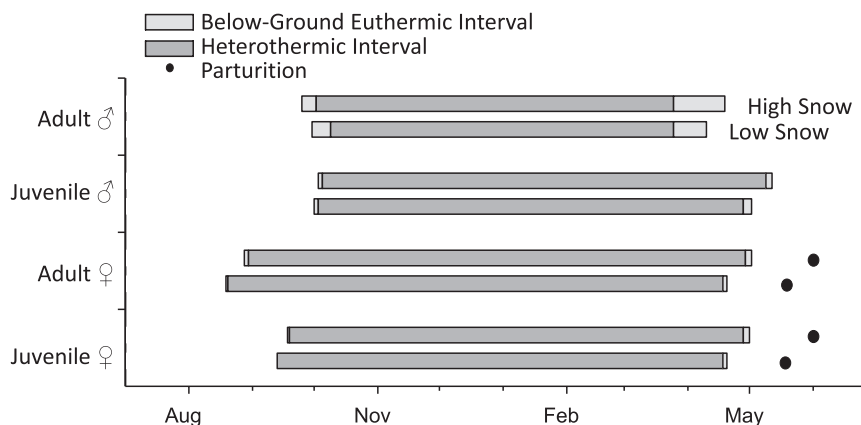


Figure 3 Differences in the timing of hibernation and reproduction within age and sex cohorts of arctic ground squirrels (*Urocitellus parryi*) from two nearby sites in northern Alaska that varied in snow cover (data from Sheriff *et al.*, 2011). Snow melt occurred 27 days earlier and snow cover began 17 days later at the low snow cover site (bottom bars for all groups). In adult males, there were no differences between sites in the date torpor-arousal cycling was terminated but emergence occurred ~9 days later at the high snow cover site. In contrast, all other groups terminated heterothermy and emerged later at the high snow cover site. As a consequence of later vernal emergence, females from the high snow cover site give birth and initiate hibernation later.

immerging cohorts, it is likely that timing is influenced by body condition, with timing of fattening controlled by a variety of inputs directed by an endogenous circannual clock (reviewed in Florant & Healy, 2012). However, there is evidence that, at least in some species, timing of immergence in females is dictated in part by the time required to replenish lipid stores following lactation. Neuhaus (2000) found that female Columbian ground squirrels that failed to wean a litter entered hibernation earlier in autumn and emerged earlier the following spring. Among females that successfully weaned a litter, early emergence in spring was associated with higher recruitment of offspring and earlier entry into hibernation during the subsequent autumn. Similarly, female arctic ground squirrels that give birth earlier will subsequently initiate hibernation earlier (Williams *et al.*, 2012c). Thus, carry-over effects, in which timing or processes in one season influence the success of an individual in the following season, can be important in hibernating species.

Environmental, sex and age effects in facultative hibernators

Expression and characteristics of hibernation are both extremely variable in chipmunks (French, 2000; Munro *et al.*, 2005; Landry-Cuerrier *et al.*, 2008) and black-tailed prairie dogs (*Cynomys ludovicianus*; Harlow & Menkens, 1986) compared with ground squirrels and marmots. Use of torpor by free-living black-tailed prairie dogs differs among sites; Bakko, Porter & Wunder (1988) reports an absence of torpor in black-tailed prairie dogs, whereas Lehmer *et al.* (2006) describe high plasticity in thermoregulatory behaviors ranging from sporadic use of daily torpor to ~2-month-long episodes of hibernation with average torpor bout lengths of 4 days. Captive studies indicate that black-tailed prairie dogs will

hibernate only when deprived of food (Harlow & Menkens, 1986). Hibernation in some chipmunk species is fueled predominantly using a food hoard rather than fat and, consequently, the amount of energy stored is not constrained by body size. In these species, the depth and duration of torpor bouts is affected by the quantity and quality (proximate composition and fatty acid composition) of the hoard (Geiser, McAllan & Kenagy, 1994; French, 2000; Humphries *et al.*, 2003; Munro *et al.*, 2005; Ruf & Arnold, 2008). Consequently, expression of torpor in free-living populations of eastern chipmunks (*Tamias striatus*), for example, relates to the local density of seed producing trees (Landry-Cuerrier *et al.*, 2008). Eastern chipmunks spend 9–11 months below ground when seeds or nuts are not available on the forest floor (Munro, Thomas & Humphries, 2008). Thus, food availability in the hoard and/or in the environment can greatly influence the expression, characteristics and phenology of hibernation in chipmunks. In captive yellow-pine chipmunks (*T. amoenus*), substantial fattening occurs prior to hibernation (i.e. a ~45% increase in body mass) and little food is consumed during hibernation (Geiser, Hiebert & Kenagy, 1990), which suggests that reliance on a food hoard during hibernation may not be universal among chipmunks. However, free-living yellow-pine chipmunks are known to accumulate extensive food caches in the winter nest (Broadbooks, 1958) and do not attain large stores of body fat (<7.4%), even immediately prior to hibernation (Kenagy & Barnes, 1988). Thus, it seems likely that free-living yellow-pine chipmunks are consuming hoarded food throughout hibernation.

Despite the high plasticity of hibernation in chipmunks, there is some evidence for sex and age effects on phenology; such data are not available for free-living black-tailed prairie dogs. Place *et al.* (2002) found that sexually mature male yellow-pine chipmunks emerge about 2 weeks before females,

followed shortly thereafter by nonbreeding males, a pattern similar to what is observed in most ground squirrels. Kawamichi (1996) observed that autumnal immergence in male Siberian chipmunks (*T. sibiricus*) was after females, but well before the onset of low temperatures during years of low food availability. In contrast, Humphries *et al.* (2002) found a synchronous cessation of above ground activity in eastern chipmunks coincident with a brief interval of unseasonably low temperatures. Overall, the chronology of emergence among sexes in chipmunks appears to be similar to that of ground squirrels, though data are relatively sparse and phenology is likely affected by food availability to a much greater degree.

Genetic variation

In many studies of free-living sciurids, phenotypic plasticity has been assessed as interpopulation differences in the timing of hibernation and/or reproduction. A clear limitation to explaining the results of this approach is the possibility that some or all of this variation is driven by genetic differences between populations. Phenological shifts in response to changes in environmental conditions over shorter time frames generally reflect phenotypic plasticity, but such plasticity has a theoretical limit, and microevolution of phenological traits is thought to be critical for the long-term persistence of populations faced with directional changes in their environment (Lande & Shannon, 1996; Visser, 2008). For microevolution to occur, there must be genetically heritable phenotypic variation, as well as selection acting on this variation. Lane (2012) reviews how to quantify heritability and selection estimates for phenological traits within hibernators using concepts and theory from quantitative genetics and animal breeding. Although the capacity to adjust phenology through physiological plasticity and microevolution is likely critical in determining population resilience to environmental change, we are only aware of a single study that has attempted to measure heritability of phenotypic traits in a hibernator. Using a multigenerational pedigree and phenotypic records on timing of emergence spanning 18 years, Lane *et al.* (2011) estimated quantitative genetic influences on the timing of emergence of free-living of Columbian ground squirrels and found that, after controlling for the influence of annual variation, c. 20% of the variation in emergence date of females was explained by additive genetic variance. Thus, there is evidence that heritable genetic variance in phenotypic traits exists, upon which selection could act. Currently, the main limitation in applying these approaches to hibernation studies is a lack of long-term datasets measuring individual variation in phenotypic traits in pedigreed populations (Lane, 2012). We encourage greater use of simple reciprocal transplant experiments or common garden experiments to establish whether differences may stem from local adaptations, although we recognize these approaches are imperfect because of the potential influences of maternal effects (Garland & Adolph, 1991). Questions associated with climate change can also be addressed using altitudinal transplants or by transplanting animals to a different longitude at the same latitude, but caution should be used

in interpreting results from latitudinal transplants because photoperiodic adjustment and seasonal adjustment will always be confounded (Bradshaw & Holzapfel, 2007).

Another approach for measuring adaptive change is use of molecular markers (reviewed in Hansen *et al.*, 2012). Although our lack of understanding regarding the molecular structure of the circannual clock currently limits the options for this approach in studies of seasonal timing, some progress has been made using circadian genes that influence phenological traits (e.g. Liedvogel *et al.*, 2009), though we are not aware of any studies in hibernating species.

Conclusions

Phenology of hibernation and reproduction in sciurid rodents is controlled by an endogenous rhythm entrained by the annual cycle of photoperiod, yet high levels of phenotypic plasticity in timing are evident and may contribute to resilience of populations to rapid climate change. Nonetheless, how environmental signals are integrated and interact with endogenous programming mechanisms remains unclear, and the molecular makeup of the circannual clock is unknown. Traditional field studies have demonstrated correlational links between environmental variables and population phenology, but establishing the mechanistic links will require more extensive analyses, better long-term datasets, more experimental field manipulations and use of methods that provide information on the duration of the below-ground euthermic intervals that precede and follow torpor-arousal cycles. The collection of long-term datasets on pedigreed populations is also needed to establish the amount of heritable variation in phenological traits and to determine whether selection is currently acting on this variation. Classic reciprocal transplant and common garden experiments, along with newly developed molecular marker approaches, will also shed light on the contribution of genotypic shifts to intra- and interpopulation differences in phenology.

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