

## NOTE

# Sex-Dependent Phenological Plasticity in an Arctic Hibernator

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**ABSTRACT:** Hibernation provides a means of escaping the metabolic challenges associated with seasonality, yet the ability of mammals to prolong or reenter seasonal dormancy in response to extreme weather events is unclear. Here, we show that Arctic ground squirrels in northern Alaska exhibited sex-dependent plasticity in the physiology and phenology of hibernation in response to a series of late spring snowstorms in 2013 that resulted in the latest snowmelt on record. Females and nonreproductive males responded to the >1-month delay in snowmelt by extending heterothermy or reentering hibernation after several days of euthermy, leading to a >2-week delay in reproduction compared to surrounding years. In contrast, reproductive males neither extended nor reentered hibernation, likely because seasonal gonadal growth and development and subsequent testosterone release prevents a return to torpor. Our findings reveal intriguing differences in responses of males and females to climatic stressors, which can generate a phenological mismatch between the sexes.

**Keywords:** Arctic ground squirrel, behavioral flexibility, climate change, extreme weather, hibernation, mismatch, phenology.

## Introduction

Many organisms face rapid changes in the temporal availability or distribution of resources, and their capacity to adjust the timing of seasonal life-cycle events, including migration, hibernation, and reproduction, is likely a critical aspect of individual fitness and population resilience to climate change (Chevin et al. 2010). One of the most commonly reported responses to climate change involves warmer springs leading to earlier timing of life-history events, although climate-driven changes in precipitation patterns can also alter the temperature dependency of phenology (Lane

et al. 2012; Shen et al. 2015). Although phenological plasticity buffers many vertebrates from climate change, trophic mismatches may still occur if temporal shifts are insufficient to maintain synchrony among linked trophic levels (Visser and Both 2005; Post and Forchhammer 2008). In addition to directional changes in the seasonal timing and phasing of resource availability, climate change is predicted to increase both the frequency and the severity of extreme cataclysmic events, including storms, floods, and wildfires (Karl 2009). Yet how animals respond to these challenging events is understudied, particularly with respect to the potential for hibernation, the regulated suppression of metabolic rate to below basal levels, to act as a buffering mechanism (but see Nowack et al. 2015).

Hibernation, one of the most intriguing adaptations to seasonality, is characterized by profound reductions in metabolism, body temperature ( $T_b$ ), and activity. Hibernators that occupy high latitudes or high elevations appear particularly sensitive to snow cover, which affects forage availability in spring, with delays in snowmelt negatively affecting fitness (Morton and Sherman 1978; Ozgul et al. 2010; Lane et al. 2012). Linkages between climate-driven change in snowmelt and hibernation phenology have come principally from trapping studies focused on the timing of female emergence, but it remains unclear how animals sequestered within underground hibernacula assess surface conditions. Further, despite the pronounced energetic savings of torpor, it is unclear whether delayed emergence reflects a later end to torpor-arousal cycling, a longer interval of preemergent euthermy as animals remain at high  $T_b$  while sequestered in their hibernacula, or both.

To address these issues and develop a more mechanistic understanding of how hibernators adjust their phenology, we have been using  $T_b$  and light loggers to assess the timing of, and relationships among, key seasonal life-cycle events in free-living Arctic ground squirrels (AGS; *Urocitellus parryi*) at two sites, Toolik Lake (TL) and Atigun River (AR),

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in northern Alaska (Sheriff et al. 2011; Williams et al. 2011). Although these sites are only 20 km apart, they differ substantially in their snow-cover regimes, with drier conditions and the wind transport of snow at AR leading to consistently earlier ( $27 \pm 5$  [SE] days) snow loss in spring compared to TL (Sheriff et al. 2011). Over a 14-year interval, we found that while this consistent site difference in the timing of snowmelt had no effect on the date males ended torpor, AR females ended hibernation, emerged, and gave birth 13 days earlier than females at the late snowmelt site (Sheriff et al. 2011). Although we assume that this variation in phenology over a relatively small spatial scale is generated by plasticity of physiological mechanisms, we cannot discount the possibility that genetic differences between populations underlie phenological variation. However, interannual variability in snowmelt provides the opportunity to examine physiological and phenological plasticity.

Here, we describe how AGS altered their hibernation phenology and physiology in response to an extreme weather phenomenon that occurred throughout the Northern Hemisphere in 2013. Prolonged cold spells occurred across northern Europe in the spring of 2013, with strong northeasterly winds drawn from Siberia and heavy, unseasonable snowstorms breaking 400-year-old March snowfall records (Christidis et al. 2014; Gladalski et al. 2014). North of the Brooks Range in the Alaskan Arctic, where our study sites lie, winter snowfall in 2013 was the highest on record (2000–present), with cold and late spring snowstorms causing further delays in snowmelt (Stuefer et al. 2014; Krause et al. 2016b).

### Material and Methods

We estimated phenological events (termination of torpor and parturition) from patterns of  $T_b$  recorded by implanted or collar-borne data loggers in free-living AGS at two sites separated by 20 km in northern Alaska: TL ( $68^{\circ}38'N$ ,  $149^{\circ}38'W$ ; elevation 719 m) and AR ( $68^{\circ}27'N$ ,  $149^{\circ}21'W$ ; elevation 812 m) from 2009 to 2016 (for detailed methods, see Williams et al. 2011). Sample sizes are shown in table A1 (tables A1–A6 are available online). We began deploying light loggers affixed to collars in the summer of 2013, which provides information on when animals are above- versus belowground; these loggers also record skin temperatures, which closely approximate core  $T_b$  during hibernation (Williams et al. 2016). From 2010 to 2015, we assessed daily snow cover at both sites based on digital images from cameras mounted on 10-m towers provided by the University of Alaska Fairbanks' Toolik Field Station (Environmental Data Center 2016). The area imaged by each camera was similar between AR and TL, with a field of view of approximately 100 m width in the foreground and 500 m in the background. Percent snow cover in each image was quantified using the threshold tool in ImageJ (National Institutes of

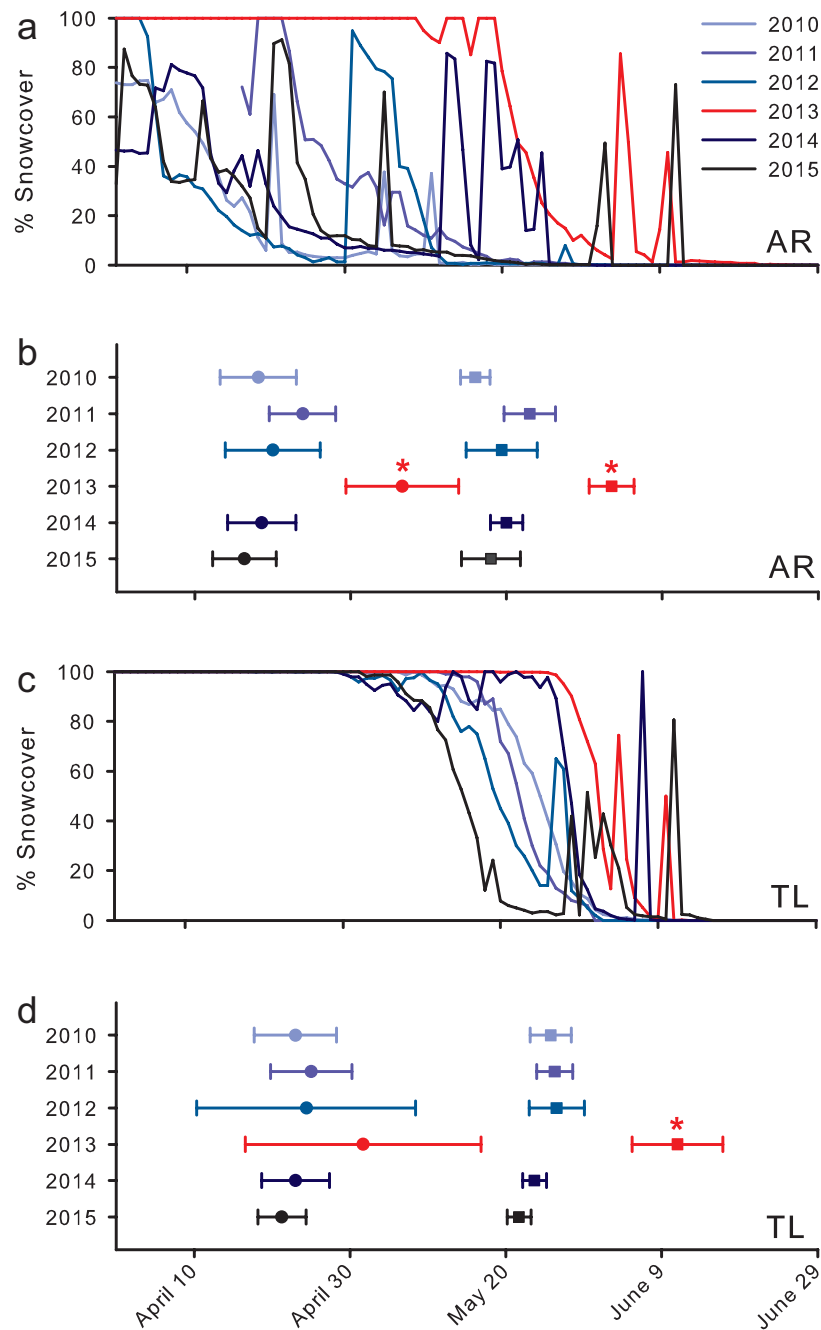
Health, Bethesda, MD). The image was first converted to eight-bit color, then white pixels were converted to red pixels, and then the total number of red pixels within the image was quantified to produce percent snow-covered ground.

We used linear mixed-effects models, fitted using REML in SAS PROC MIXED (SAS Institute, Cary, NC) with individual included as a random effect, to determine whether the date torpor is terminated or the date parturition occurred was different across years at each site. The data used in this analysis are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.47pf0> (Williams et al. 2017). Significant effects of year were investigated with post hoc tests comparing 2013 to all other years using Dunnett's procedure to adjust  $P$  values for multiple comparisons.

### Results and Discussion

During the spring of 2013, an extreme weather phenomenon characterized by a series of late spring snowstorms and persistent snow cover occurred across northern Europe and northern North America (Christidis et al. 2014; Gladalski et al. 2014; Stuefer et al. 2014). This meteorological event resulted in altered body condition, physiology, and phenology of migrant songbirds (Gladalski et al. 2014; Krause et al. 2016a, 2016b) and shorebirds (Senner et al. 2015). During this same period, we recorded substantial delays in spring snowmelt at both of our study sites, though the effect was much more pronounced at AR, the early snowmelt site (fig. 1). Consequently, patches of snow-free ground, important to ground squirrels for foraging, were not available at AR until mid to late May in 2013, approximately 1 month later than other years (fig. 1). Relative to other years, the termination of torpor in females was delayed in 2013 at AR ( $P < .0001$ ; table A2; fig. 1b) but not at TL ( $F_{5,18.4} = 1.07$ ,  $P = .41$ ; table A3; fig. 1d), although parturition occurred later at both sites ( $P \leq .0001$ ; tables A4, A5; fig. 1). Unlike adult males, who exhibited stereotypic  $T_b$  patterns during hibernation in 2013 (fig. 2a), the pattern of heterothermy in females that delayed the onset of their active season was distinct, with unusually long arousal episodes followed by one or more short (2–3-day) bouts of torpor. Abdominal  $T_b$  during these short torpor bouts was higher than is typical (fig. 2b), indicative of a higher hypothalamic  $T_b$  set point. Although adult males did not extend their use of torpor in 2013 relative to most other years (table A6), two yearling males that did not become reproductive exhibited similar  $T_b$  patterns as adult females, with longer arousals followed by repeated short bouts of torpor prior to the completion of heterothermy (fig. 2c).

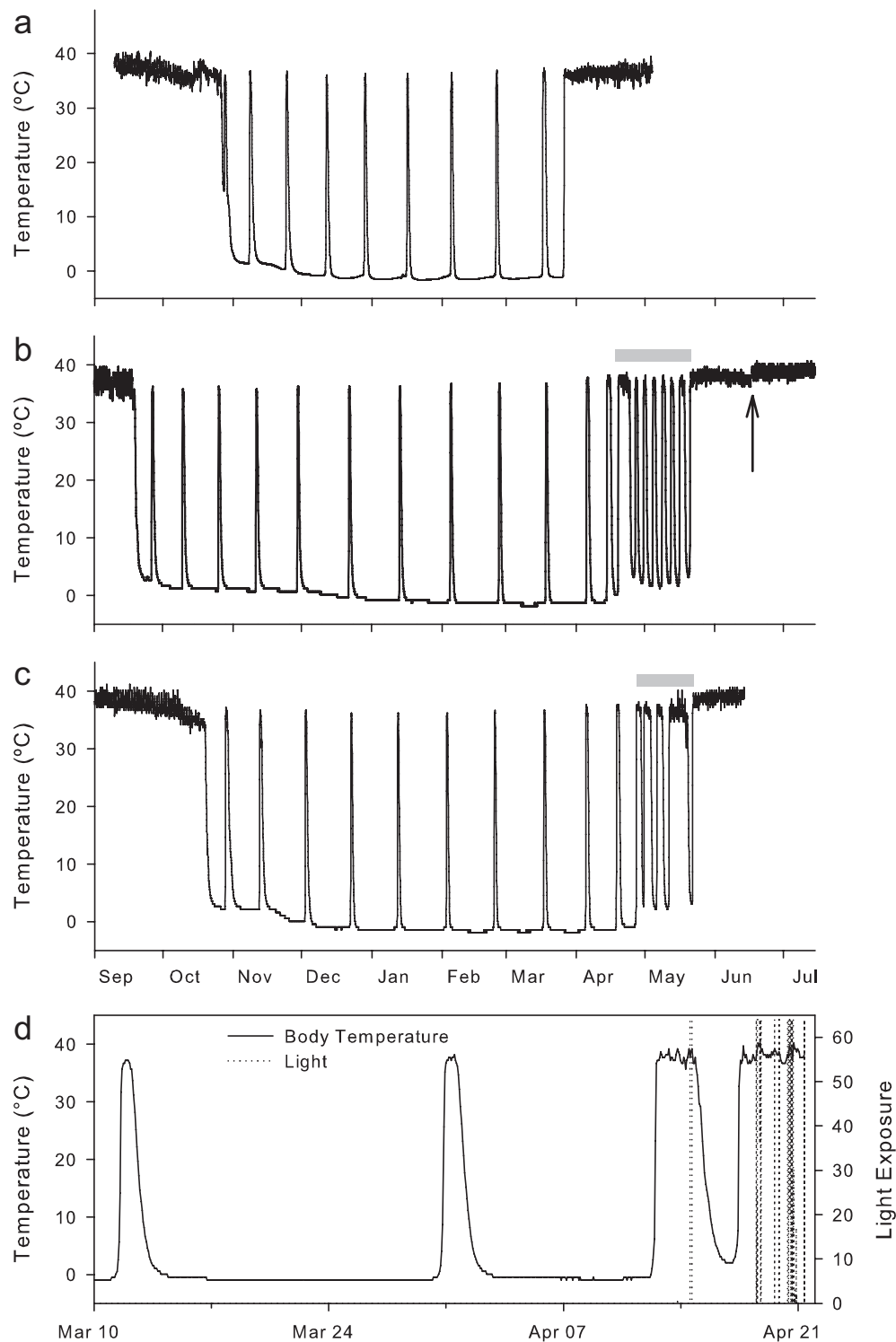
Reproductive males typically emerge 11–14 days earlier than females after an extended 15–25-day bout of belowground euthermia, during which time they consume a food hoard and replenish lipid and protein stores lost throughout hibernation as they undergo gonadal growth and sper-



**Figure 1:** Percent snow cover and female Arctic ground squirrel phenology versus day of year at Atigun River (AR; *a, b*) and Toolik Lake (TL; *c, d*) study sites from 2010 to 2015. In 2013 (red), late spring snowstorms delayed snowmelt, resulting in a later end to torpor (circles; mean  $\pm$  SD) and parturition (squares). Asterisks indicate significant delays ( $P < .0001$ ) in 2013 relative to all other years.

matogenesis (Barnes 1996; Sheriff et al. 2011, 2013). An endogenous circannual clock activates the reproductive axis leading to increased circulating testosterone, which prevents reentry into torpor following arousal, leading to an earlier termination of hibernation in males (Williams et al. 2014; Richter et al. 2017). This strategy allows males to be-

come fertile, establish territories, and compete with other males for access to receptive females as they subsequently emerge from hibernation (Buck and Barnes 2003). However, because testosterone brings about an earlier end to heterothermy in spring (Richter et al. 2017) and inhibits hibernation (Lee et al. 1990), gonadal development and accompanying



**Figure 2:** Core abdominal body temperature ( $T_b$ ) of a reproductive male (a), a reproductive female (b), and a nonreproductive yearling male (c) in 2013. In response to late spring snowstorms, females and nonreproductive males reentered or extended hibernation in spring (shown below gray bars), resulting in delayed termination of heterothermy and later parturition (indicated by an arrow in the female trace). In 2015, combined measurement of  $T_b$  (solid line) and light (dashed vertical bars; arbitrary units) revealed that some females evaluate conditions on the surface prior to reentering torpor (d).

elevated testosterone levels also likely prevent males from using torpor as a mechanism to escape the energetic demands of late spring snowstorms. In years of delayed springs, this potentially leads to a temporal mismatch between the sexes, with males ready to mate well ahead of the interval in which receptive females are available.

Having observed a plastic response in the physiology and phenology of hibernation in females but not reproductive males, our next objective was to determine whether females were adjusting their phenology and patterns of heterothermy after assessing conditions on the surface. Simultaneous measurement of  $T_b$  and light exposure during hibernation and spring emergence in 2014 and 2015 revealed three instances (of 22) where females had arousal episodes that exceeded 48 h (58, 74, and 166 h). Light logger data indicate that these three females were exposed to light during these extended arousal episodes, indicating aboveground activity before reentering torpor (fig. 2d). We believe that these aboveground forays were used by females to determine the extent of snowmelt, their potential for foraging, and whether to end hibernation and initiate reproduction. No exposure to light was measured during heterothermy for the other 19 females, all of which had only short penultimate arousal episodes of  $30.7 \pm 1.9$  (SE) h (range: 14.4–44.1 h).

Altogether, our findings indicate that female and nonreproductive male Arctic ground squirrels can extend or reenter hibernation to avoid late spring snowstorms, similar to recent findings that some mammals will use torpor to increase survival during natural disasters, including cyclones (Nowack et al. 2015) and wildfires (Stawski et al. 2015; Nowack et al. 2016). Interestingly, we found that plasticity in the use of heterothermy in spring did not extend to reproductive males, likely owing to the requirement of more time for sexual maturation combined with sexual selection on early emergence for mating advantages. Interestingly, these explanations are also invoked to explain protandrous emergence timing in reptiles (reviewed in Morbey and Ydenberg 2001), but whether phenological plasticity also differs between the sexes is unclear. In migratory birds, protandry in arrival timing has led to sex differences in the environmental regulation of reproductive physiology (Ball and Ketterson 2008), and sexual selection has been shown to alter phenological responses to climate change (Spottiswoode et al. 2006). Climate change can also intensify selection for increased phenological plasticity (Nussey et al. 2005), though whether and how sexual selection affects this process has not been examined.

The pace and effects of climate change have been most pronounced in the Arctic (Hinzman et al. 2005; Karl 2009), and the consequences may also be amplified, owing to the short growing season that limits time for juvenile growth, fattening, and preparation for winter. Although the overall trend and prediction is for snowmelt to advance in the Arctic in re-

sponse to warming, increases in precipitation are predicted for the Arctic, and some regions might experience a deeper snowpack, an increase in late spring snowfall events, and later snowmelt (Hinzman et al. 2005; Hobbie et al. 2017). Additionally, Arctic shrubs are increasing under climate change, and they can cause local increases in winter snowpack by trapping wind-drifting snow and reducing sublimation (Sturm et al. 2001). At our study site in northern Alaska, the initiation of the growing season has been delayed by an average of 11 days from 2000 to 2010 compared to the previous decade (Cherry et al. 2014), and our results indicate that the sexes can differ in their responses to delayed snowmelt. The consequences of sex-dependent plasticity and mismatch remain unclear, although the lack of flexibility exhibited by males may have important implications for survival, population sex ratios, or microevolutionary responses to climate changes. Populations may be buffered to some degree, however, by the subset of yearling males that do not become reproductive and utilize torpor to avoid late spring snowstorms.

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