
Hit Snooze: An Imperiled Hibernator Assesses Spring Snow Conditions to Decide Whether to Terminate Hibernation or Reenter Torpor

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ABSTRACT

Many animals follow annual cycles wherein physiology and behavior change seasonally. Hibernating mammals undergo one of the most drastic seasonal alterations of physiology and behavior, the timing of which can have significant fitness consequences. The environmental cues regulating these profound phenotypic changes will heavily influence whether hibernators acclimate and ultimately adapt to climate change. Hence, identifying the cues and proximate mechanisms responsible for hibernation termination timing is critical. Northern Idaho ground squirrels (*Urocitellus brunneus*)—a rare, endemic species threatened with extinction—exhibit substantial variation in hibernation termination phenology, but it is unclear what causes this variation. We attached geolocators to free-ranging squirrels to test the hypothesis that squirrels assess surface

conditions in spring before deciding whether to terminate seasonal heterothermy or reenter torpor. Northern Idaho ground squirrels frequently reentered torpor following a brief initial emergence from hibernacula and were more likely to do so earlier in spring or when challenged by residual snowpack. Female squirrels reentered torpor when confronted with relatively shallow snowpack upon emergence, whereas male squirrels reentered torpor in response to deeper spring snowpack. This novel behavior was previously assumed to be physiologically constrained in male ground squirrels by testosterone production required for spermatogenesis and activated by the circannual clock. Assessing surface conditions to decide when to terminate hibernation may help buffer these threatened squirrels against climate change. Documenting the extent to which other hibernators can facultatively alter emergence timing by reentering torpor after emergence will help identify which species are most likely to persist under climate change.

Keywords: behavioral plasticity, biologging, climate change, phenological optimization, physiological plasticity, seasonal environments, threatened species conservation.

Introduction

Many animals exhibit distinctive annual cycles wherein individuals undergo substantial seasonal changes in behavior and physiology to better match their phenotype to environmental conditions. The phenology of physiological states or behaviors within the annual cycle is often synchronous with seasonal variation in food availability (Cushing 1969; Visser and Gienapp 2019). Movement patterns of many large herbivores, for example, follow spring green-up (i.e., surfing the green wave; Aikens et al. 2020). Similarly, reproduction in many animals may be timed to maximize growth and/or survival of neonates (Kenagy et al. 1989; Ozgul et al. 2010). However, the optimal annual cycle for an animal depends on many ecological processes, and apparent phenological mismatches can occur as a result of trade-offs delineated by opposing selection pressures (McNamara and Houston 2008; Forrest and Miller-Rushing 2010; Williams et al. 2017b). Behavioral plasticity and physiological plasticity in response to environmental cues are important means by which animals modulate annual phenology in the face of interannual environmental variation, but the explicit mechanisms underlying phenological plasticity are often not well understood (Chmura et al. 2019).

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Hibernation in mammals (hereafter, “hibernators”) is arguably the most extreme example of seasonal change in animal physiology and behavior. Hibernators greatly reduce metabolic expenditure for portions of the year by reducing activity, suppressing basal metabolism, and (in small hibernators) allowing body temperature to fall via bouts of torpor that last for days or weeks (Geiser 2013; Ruf and Geiser 2015; table S1; tables S1–S3 are available online). These long torpor bouts are periodically interrupted by euthermic arousal episodes that generally last <24 h. Torpor bout length is negatively correlated with ambient temperature throughout much of hibernation in most animals (hibernators experiencing subfreezing hibernacula temperatures are rare and may establish thermogenesis to defend body temperatures; Barnes 1989; Geiser et al. 1990). However, individuals often enter a potentiation phase near the conclusion of seasonal hibernation that marks the transition from dormancy to activity and is characterized by shorter torpor bouts and longer arousal bouts (Geiser et al. 1990; Ruf and Geiser 2015; Williams et al. 2017a; Wilsterman et al. 2021). Although hibernation phenology is often assumed to be determined by ambient temperature and food availability (Humphries et al. 2003), optimal hibernation phenology balances trade-offs among these and several other selection pressures to maximize individual fitness (Michener 1983; Allison et al. 2023; Ruf and Bieber 2023). Indeed, predation risk and reproductive requirements often explain more intraspecific variation in hibernation phenology than thermal tolerance or food limitation (Stawski and Geiser 2010; Bieber et al. 2014; Williams et al. 2017a; Allison et al. 2023).

A consistent pattern among hibernators that mate in spring, following hibernation, is the emergence of reproductive males before females (Murie and Harris 1982; Michener 1983; Fagerstone 1988; Millesi et al. 1999; Sheriff et al. 2011; Bieber et al. 2018; Goldberg and Conway 2021). Males terminate seasonal heterothermy (i.e., torpor use) earlier than females to establish spermatogenesis, a process that requires euthermic body temperatures and high levels of testosterone and can take weeks to complete (Barnes et al. 1986; Michener 1992; Richter et al. 2017). Testosterone production inhibits torpor expression, resulting in earlier emergence from hibernation than is energetically optimal in males but allowing phenological synchrony between the sexes (i.e., simultaneous reproductive maturation; Lee 1990; Richter et al. 2017). However, many species shift hibernation phenology (especially hibernation termination and emergence timing; table S1) in response to environmental variation (e.g., ambient temperature and snowmelt; Michener 1977; Murie and Harris 1982; Inouye et al. 2000; Lane et al. 2012; Williams et al. 2017a; Kucheravy 2021; Allison et al. 2023; Chmura et al. 2023; Thompson et al. 2023). Given these patterns, male hibernators might be expected to plastically modulate emergence timing to maximize their status within intrasexual breeding hierarchies (e.g., by claiming and defending breeding territories) while avoiding starvation and maintaining reproductive synchrony with later-emerging females (i.e., emerging sufficiently early to establish spermatogenesis before female emergence from hibernacula; Thompson et al. 2023). Male northern Idaho ground squirrels (*Urocitellus brunneus*)—a rare, endemic species threatened with extinction—apparently adhere

to this prediction (Allison et al. 2023). Other ground squirrel species—notably, Arctic ground squirrels (*Urocitellus parryii*) and Richardson’s ground squirrels (*Urocitellus richardsonii*)—do not follow this pattern (Williams et al. 2017a; Kucheravy et al. 2021); males of these two species amass food caches before hibernation, which allow them to establish spermatogenesis while remaining ensconced in their hibernacula for extended periods before emergence (Michener 1992; Buck and Barnes 1999; Sheriff et al. 2011). Because northern Idaho ground squirrels hibernate underground, sheltered from ambient aboveground conditions, the proximate mechanisms regulating the termination of hibernation (and hence reproductive synchrony) are not known, but they may dictate how well this imperiled hibernator acclimates and ultimately adapts to climate change.

Male northern Idaho ground squirrels can potentially maintain synchrony of reproductive maturation with later-emerging females by using sensory assessment of aboveground conditions to determine when to terminate hibernation. In Arctic ground squirrels, for example, assessment of surface conditions allows females and nonreproductive yearling males to prolong hibernation in years with late spring snowmelt and thereby avoid harsh foraging conditions (Williams et al. 2017a). In contrast, adult male Arctic ground squirrels failed to display such plasticity under the same conditions (Williams et al. 2017a). Torpor reentry behavior (table S1) was thus assumed to be physiologically constrained in male ground squirrels due to the incompatibility of torpor and spermatogenesis triggered by the circannual clock (Lee 1990; Williams et al. 2014, 2017a; Richter et al. 2017). However, the onset of testosterone production for spermatogenesis need not coincide with initial spring emergence from hibernacula. The hypothesis that northern Idaho ground squirrels emerge from hibernacula to use sensory assessment of surface conditions to decide when to terminate seasonal heterothermy (i.e., the surface assessment hypothesis) may also explain female northern Idaho ground squirrel hibernation termination behavior in years with late spring snowpack, similar to female Arctic ground squirrels. The surface assessment hypothesis assumes that northern Idaho ground squirrels emerge from hibernacula in spring to assess surface conditions before deciding whether to terminate hibernation for the season (i.e., some squirrels emerge from hibernacula in spring but subsequently reenter torpor). Additionally, if snowpack is the environmental cue squirrels assess to determine when to terminate hibernation, then snow depth at initial emergence should positively influence the probability of a squirrel subsequently reentering torpor. We tested the above predictions of the surface assessment hypothesis that may explain intraspecific variation in the timing of spring termination of hibernation in northern Idaho ground squirrels.

Methods

Study Species and System

The northern Idaho ground squirrel is a small-bodied, semifossorial rodent endemic to west-central Idaho. Adult female body mass ranges seasonally from ~100 g at hibernation emergence in spring to ~180 g at hibernation immergence in summer; adult male body

mass ranges from ~120 g at hibernation emergence in spring to ~270 g at hibernation immergence in summer (Allison and Conway 2022). These rare squirrels are listed as federally threatened under the US Endangered Species Act due to population declines in the twentieth century (US Fish and Wildlife Service 2000; Sherman and Runge 2002; Yensen and Dyni 2020). Fewer than 3,000 free-ranging individuals are estimated to persist in small aggregations scattered throughout the species' limited historical distribution (Barbosa et al. 2021; Wagner and Struthers 2022).

Northern Idaho ground squirrels are fat-storing obligate hibernators, spending 8–10 mo hibernating annually. Hibernation phenology varies across populations due to climatic differences across the 1,000-m elevational gradient within the species' small range (Goldberg and Conway 2021; Allison et al. 2023). Neither sex caches food before hibernation (A. Z. T. Allison, personal observation); hence, both sexes are primarily income breeders that greatly deplete prehibernation fat stores before termination of hibernation in spring (see above). Females breed within a few days of hibernation emergence (Sherman 1989), meaning that late-emerging males may lose breeding opportunities. Accordingly, reproductive-aged males (≥ 2 yr old at emergence; reproductively mature yearlings have never been documented in this species) terminate hibernation and emerge from hibernacula ~2 wk before reproductive-aged females (≥ 1 yr old at emergence) on average (Allison et al. 2023). The earlier emergence of males relative to females is assumed to reflect the need for males to establish spermatogenesis, as in other hibernating ground squirrel species (Barnes et al. 1986; Lee 1990; Michener 1992; Richter et al. 2017). Unprofitable foraging and aboveground predation risk likely make it suboptimal for males to terminate hibernation and emerge from hibernacula earlier than is necessary for reproduction, such that male squirrels modulate emergence phenology in response to interannual variation in environmental conditions, including the timing of spring snowmelt (Allison et al. 2023). Females also alter hibernation emergence timing in response to environmental variation but may do so primarily to maximize annual recruitment of offspring (Allison et al. 2023). This makes sense because small mammalian income breeders are likely under strong selection to maintain tight synchrony between reproductive phenology and availability of energetic resources (Williams et al. 2017b).

We tested the surface assessment hypothesis at nine study sites that spanned much of the extant geographic (fig. S1; figs. S1–S3 are available online) and elevational (1,275–2,275 m asl) range occupied by northern Idaho ground squirrels. Northern Idaho ground squirrel hibernation phenology is apparently adapted to local climates (Barbosa et al. 2021; Allison et al. 2023), but each of the study sites during the 8-yr study (2016–2023) experienced significant interannual variation in the timing of spring snowmelt (table S2). The forbs and grasses that comprise the species' diet (Dyner and Yensen 1996; Yensen et al. 2018; Goldberg et al. 2020b) begin to green-up within days of snowmelt, and exposed soil patches immediately provide opportunities for squirrels to excavate and consume nutritious plant roots (e.g., *Lomatium* spp. and *Allium* spp.; A. Z. T. Allison, personal observation). This variation in the timing of snowmelt, and hence food availability, allowed us to explicitly test whether the surface assessment hypothesis ex-

plains how northern Idaho ground squirrels decide when to terminate hibernation.

Data Collection

To test the surface assessment hypothesis, we captured northern Idaho ground squirrels in baited Tomahawk traps (Tomahawk Live Trap, Hazelhurst, WI) and via focal animal trapping (Allison and Conway 2022). We attached VHF radio collars (Holohil Systems, Ottawa, Ontario; Lotek, Newmarket, Ontario) and geolocators (Migrate Technology, Cambridge) to 207 adult (≥ 1 yr old in the year they were collared) squirrels (92 males and 115 females; table S3). Geolocators recorded the maximum ambient light intensity during 5-min intervals, allowing us to ascertain whether a squirrel emerged aboveground during a given 5-min sampling interval (Goldberg and Conway 2021; Allison and Conway 2022). We considered any light intensity reading > 0 lux to indicate that a squirrel had emerged to the surface because northern Idaho ground squirrels plug hibernacula such that no light penetrates the burrow system until the squirrel surfaces. Geolocators also recorded squirrel skin temperature every 15 min (ground squirrel skin temperature measured by geolocators closely approximates ground squirrel core body temperature during hibernation; Williams et al. 2012), which enabled us to document torpor expression. We considered skin temperatures of $< 25^\circ\text{C}$ lasting for ≥ 24 h to indicate reentry into torpor (i.e., an extension of hibernation) following an initial spring emergence event (table S1). Thus, we were able to distinguish between the timing of emergence to the surface from hibernacula and the annual termination of hibernation and hence test a key assumption of the surface assessment hypothesis. We programmed VHF transmitters to emit a signal only on certain days during the summer they were deployed and the subsequent spring following squirrel emergence from hibernacula, thereby spreading the limited battery life (~43 d) of these necessarily small transmitters ($\leq 2.5\%$ of squirrel body mass) across two ground squirrel active seasons. This allowed us to monitor collared squirrels before hibernation, locate hibernacula, and recover geolocators more efficiently following hibernation, which was necessary to download the recorded data. We recovered 76 geolocators that recorded hibernation termination phenology for adult northern Idaho ground squirrels (44 males and 32 females).

We downloaded daily snow depth data (1-km²-resolution Snow Data Assimilation System data; National Operational Hydrologic Remote Sensing Center 2004) for each study site from 2016 to 2023, which were the finest-scale-resolution snow depth data available for our remote study sites. Northern Idaho ground squirrels often move up to 300 m away from active-season foraging patches to hibernate (Goldberg et al. 2020a), such that snowmelt at the scale of a few hundred meters squared may be more relevant to hibernation termination timing in this species than snow conditions within only a few meters of hibernacula. The combination of geocator and snow depth data facilitated an explicit test of the predicted influence of snowpack on hibernation termination phenology under the surface assessment hypothesis. We also recorded the reproductive status of all captured squirrels to determine whether any animals that reentered torpor after emerging from hibernacula

subsequently underwent seasonal puberty and reproductively matured or whether torpor reentry necessarily deferred reproduction until the following year. We recorded male squirrels as scrotal (descended testes and pigmented penis) or nonreproductive based on visual inspection of genitalia; we recorded female squirrels as visually pregnant (distended abdomen), lactating (enlarged nipples with hairless patches), or nonreproductive (Sherman and Runge 2002). We assumed all scrotal males were physiologically capable of reproduction, although we could not assess individual reproductive success.

Statistical Analyses

We constructed generalized linear mixed effects models via the lme4 package (Bates et al. 2015) in R (ver. 4.2.2; R Core Team 2023) to test whether snow depth influenced the probability of northern Idaho ground squirrels reentering torpor following initial spring emergence to the surface (determined via geolocator data). We used a logit link function to model the probability of reentering torpor as a binomial distribution. Our global model included fixed effects of day of year (Julian day), study site elevation (m), and the two-way interaction between site-specific snow depth (cm) at initial emergence and squirrel sex (binary). The global model also included random intercepts for study site and year. The interaction term allowed us to test for sex-specific responses to snowpack upon emergence. We compared all subsets of the global fixed effects structure based on Akaike information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) via the MuMIn package in R (Bartoń 2022; table 1). We considered the top competing model ($\Delta\text{AICc} < 2.00$) that did not include any uninformative predictor variables (i.e., those for which the 85% confidence interval overlaps zero; Arnold 2010) to be the most parsimonious model explaining variation in torpor reentry behavior.

Results

Adult male northern Idaho ground squirrels frequently reentered torpor following initial spring emergence from hibernacula (15 of 44, 34.1%; fig. 1), as assumed by the surface assessment hypothesis. We also documented reentry into torpor following emergence from hibernacula in female northern Idaho ground squirrels (5 of 32, 15.6%), albeit less frequently than in males. At least one squirrel at each of the nine study sites and in six of the 8 yr of the study reentered torpor after experiencing surface conditions. Nine of the 20 (45.0%) squirrels that reentered torpor did so after only a single <10-min emergence bout, whereas the other 11 squirrels (55.0%) emerged on multiple days (typically only once per day, for <10 min d⁻¹) before reentering torpor. One male reentered torpor following emergence to the surface during three successive euthermic arousal bouts (fig. 1C); another male emerged from its hibernaculum and remained active (i.e., regularly surfaced) for nearly 3 wk before reentering torpor following a spring snowstorm that added 24 cm of new snow across a week on top of 14 cm of residual snowpack (fig. 1D). These results explicitly illustrate the plasticity of hibernation termination phenology in these threatened squirrels.

Table 1: Model selection table for generalized linear mixed effects candidate models constructed to explain variation in whether free-ranging adult northern Idaho ground squirrels reentered torpor or terminated hibernation after initial spring emergence

Model	ΔAICc	w_i
Sex × snow + J day + (site) + (year)	0	.65
Sex × snow + J day + elevation + (site) + (year)	1.91	.25
Sex + snow + J day + (site) + (year)	6.18	.03
Snow + J day + (site) + (year)	6.34	.03
Sex + snow + J day + elevation + (site) + (year)	7.67	.01
Snow + J day + elevation + (site) + (year)	8.22	.01
J day + elevation + (site) + (year)	9.34	.01
Sex × snow + elevation + (site) + (year)	9.97	.00
Sex × snow + (site) + (year)	10.73	.00
Sex + J day + elevation + (site) + (year)	10.90	.00
Snow + (site) + (year)	11.07	.00
Snow + elevation + (site) + (year)	11.13	.00
Sex + snow + (site) + (year)	12.84	.00
Sex + snow + elevation + (site) + (year)	13.48	.00
J day + (site) + (year)	14.81	.00
J day + sex + (site) + (year)	16.81	.00
Sex + (site) + (year)	16.94	.00
Sex + elevation + (site) + (year)	18.52	.00
(Site) + (year)	18.84	.00
Elevation + (site) + (year)	20.59	.00

Note. All candidate models are included. The global model is shown in bold, and the random intercept-only model is shown in italics. Random intercepts are in parentheses. $n = 76$ free-ranging adult northern Idaho ground squirrels. AICc = Akaike information criterion corrected for small sample sizes; sex = squirrel sex; snow = snow depth at initial emergence; J day = Julian day of initial emergence; elevation = study site elevation; site = study site; w_i = Akaike model weight.

The mean length of torpor bouts immediately following initial spring emergence from hibernacula was only 3.0 ± 0.7 d (mean \pm SD) and ranged from 1.8 to 5.4 d. We did not document any torpor bouts lasting <24 h following initial emergence to the surface (i.e., all such torpor bouts constituted multiday events). These relatively short torpor bouts were often part of the series of shorter torpor bouts at the end of the hibernation period making up the potentiation phase of hibernation (Wilsterman et al. 2021). By comparison, the longest midwinter torpor bout—before the potentiation phase—lasted 20–35 d. Adult male northern Idaho ground squirrels first emerged from hibernacula 2.4 ± 2.1 d (range: 0–9 d) after terminating seasonal heterothermy. Some males emerged only briefly each day for as much as 10 d before gradually becoming more active, while others exhibited high levels of daily aboveground activity almost immediately after terminating seasonal heterothermy. Adult females first emerged 0.9 ± 0.6 d (range: 0–2 d) after terminating seasonal heterothermy and generally resumed high levels of activity within a day or two of emergence. One female that reentered torpor following

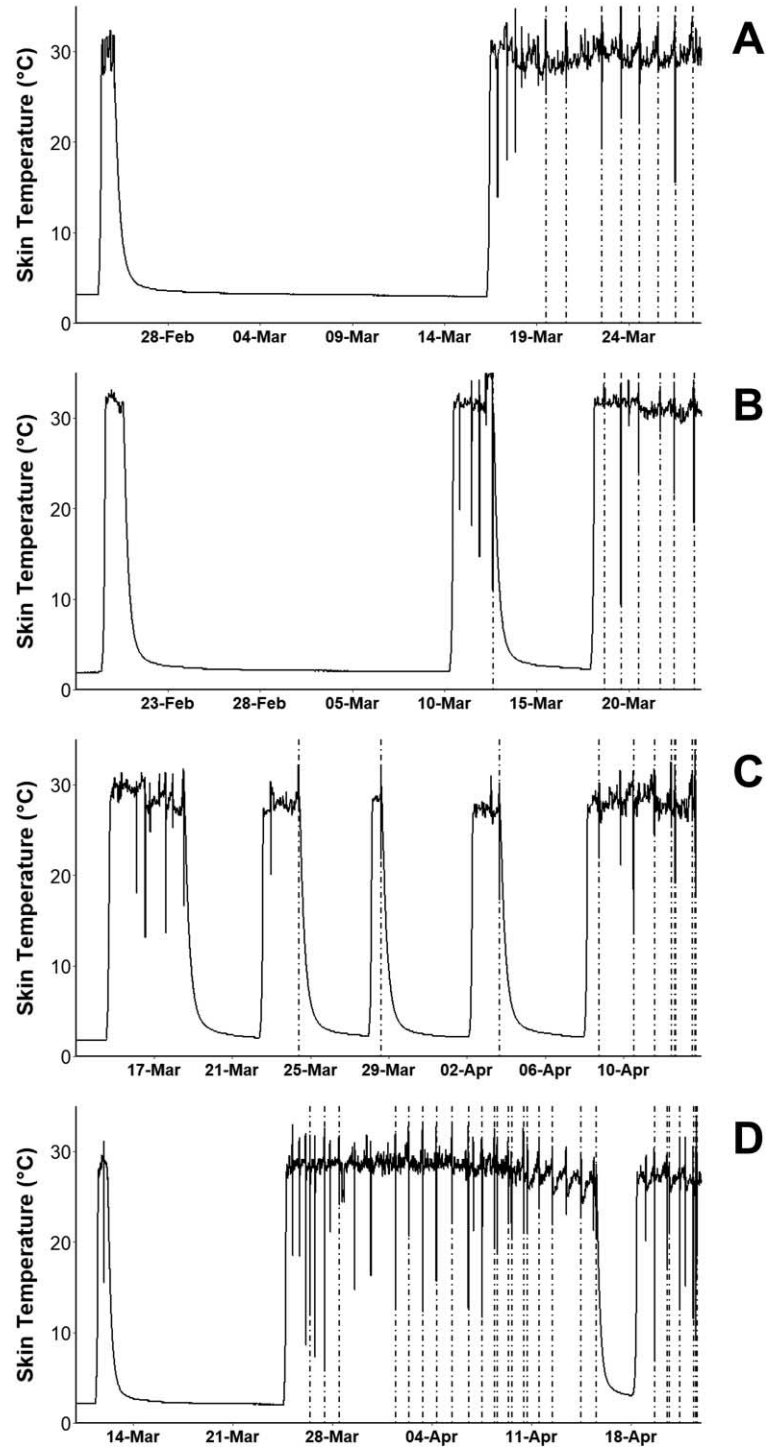


Figure 1. Changes in skin temperature (solid lines) illustrating hibernation termination behavior for four free-ranging, adult male northern Idaho ground squirrels. Vertical dot-dashed lines are instances when a geolocator detected that a squirrel emerged to the surface. The squirrel in *A* terminated hibernation following a final long torpor bout and did not reenter torpor following initial spring emergence to the surface. The squirrel in *B* emerged to the surface on March 12 before reentering torpor for 5 d, after which the squirrel terminated hibernation. The squirrel in *C* emerged to the surface during three successive euthermic bouts (on March 24, March 28, and April 3) before reentering torpor for 2–4 d, after which the squirrel terminated hibernation. The squirrel in *D* remained euthermic and emerged to the surface regularly across a ~3-wk period starting on March 24 before reentering torpor for 3 d on April 15 following a persistent snowstorm that dropped 24 cm of new snow between April 9 and April 15 on top of 14 cm of residual snowpack.

emergence to the surface died in its hibernaculum nest during the subsequent torpor bout. The recovered carcass (which had not significantly decayed at the time of recovery) weighed just 69 g, lighter than would be expected of a healthy adult female northern Idaho ground squirrel at emergence (all captured females ≥ 2 yr of age weighed >85 g).

Mean snow depth on the day of hibernation termination (the final date of seasonal torpor use) was 58.4 ± 51.4 cm for male northern Idaho ground squirrels and 29.5 ± 36.2 cm for females. The mean day of hibernation termination was 14.0 ± 12.3 d before snowmelt (the first day after March 1 with a snow depth of 0 cm) in males and 0.4 ± 12.9 d before snowmelt in females. A majority of females (17 of 32, 53.1%) did not emerge from hibernacula until less than 2 cm of snow remained at a site. Snow depth at initial spring emergence from hibernacula positively influenced the probability of reentering torpor in both sexes (table 2; fig. 2A), which supports a second prediction of the surface assessment hypothesis. The effect of snow depth differed between males and females (table 1): females more readily reentered torpor at lower levels of snowpack than did males (table 2; fig. 2A). The day of year on which a squirrel initially emerged from its hibernaculum negatively influenced the probability of subsequently reentering torpor (table 2; fig. 2B). We failed to detect an effect of elevation on the probability of reentering torpor following initial spring emergence, although snow depth at emergence and study site are correlated with elevation and were both in the top model explaining variation in torpor reentry behavior (table 1). The fixed effects in our top model explained 47.7% of the variation in torpor reentry behavior; the full model (including random effects) explained 77.6% of the observed variation.

We recaptured eight of the 15 adult male squirrels that reentered torpor following emergence from hibernacula 2–4 wk following the termination of hibernation, the period during which we expected these squirrels to be reproductively mature. Seven of those eight males were scrotal when captured, demonstrating that torpor reentry does not necessarily result in the loss of the sole annual reproduction opportunity for male northern Idaho ground

squirrels. We similarly recaptured two of the five adult females that reentered torpor 4–6 wk after terminating hibernation, at which time both squirrels were lactating.

Discussion

We found support for a key assumption of the surface assessment hypothesis: some male and female northern Idaho ground squirrels reentered torpor following initial spring emergence from hibernacula. Moreover, most of the squirrels that reentered torpor following emergence subsequently reproductively matured. Thus, torpor reentry following apparent surface assessment suggests that hibernation termination phenology is partially the outcome of an animal's attempts to balance the costs and benefits of euthermia and the timing of reproductive maturation. Reentry into torpor for as few as 2 d specifically implies that the fitness costs of terminating hibernation too early or too late are substantial and further supports the idea that torpor reentry does not necessarily defer reproduction to the following year. The costs of terminating hibernation and emerging too early likely include increased predation risk during aboveground activity (reducing the probability of surviving to reproduce; Allison et al. 2023, 2024), increased thermoregulatory costs, and decreased body condition resulting from low forage availability (Allison and Conway 2022), whereas the costs of terminating hibernation and emerging too late presumably involve diminished reproductive success (Sherman 1989; Viblanc et al. 2022; Thompson et al. 2023). This novel facultative reentry into torpor contradicts the assumption that endogenous circannual rhythms (e.g., in testosterone production and establishment of spermatogenesis) entirely constrain plasticity in hibernation termination phenology in reproductive male ground squirrels (Williams et al. 2014, 2017a; Richter et al. 2017; Kucheravy et al. 2021). In fact, we documented extreme plasticity in the use of torpor by reproductive adult male northern Idaho ground squirrels, at least in part as a response to snow conditions. This suggests that testosterone production in male northern Idaho ground squirrels is not entirely regulated by the circannual clock or spring emergence from hibernacula. That is, northern Idaho ground squirrels may be able to facultatively reduce or delay testosterone production based on the environmental conditions encountered upon emergence from hibernacula and thereby extend hibernation and delay the establishment of spermatogenesis.

Snow depth positively influenced the probability of a squirrel reentering torpor after initial spring emergence to the surface, with females reentering torpor at shallower snow depths than males on average. The difference between the sexes in the raw prevalence of torpor reentry is primarily explained by the fact that females often did not emerge from hibernacula until all or most of the snow at a site had melted. Thus, although females emerging into snowy conditions can reenter torpor, females may also respond to some other cue(s) (e.g., increases in soil temperature following snowmelt) in years with early spring snowmelt. Alternatively, the circannual clock in females may often dictate initial emergence only after complete snowmelt. Different snow depth–response thresholds between the sexes are expected if

Table 2: Estimates of β for predictor variables included in the top generalized linear mixed effects model designed to explain variation in whether free-ranging adult northern Idaho ground squirrels reentered torpor or terminated hibernation following initial spring emergence

Predictor variable	β	SE	<i>P</i>
Sex (male)	−.19	1.52	.90
Snow depth	.10	.03	.00
Julian day	−.16	.06	.01
Sex \times snow depth	−.06	.03	.02

Note. Female squirrels represent the baseline sex to which the effect of being male is compared. We recorded snow depth and Julian day on the day of initial spring emergence to the surface. Study site and year were also included in the top model as random intercepts, and the displayed predictor variables were included as the fixed effects. $n = 76$ free-ranging adult northern Idaho ground squirrels.

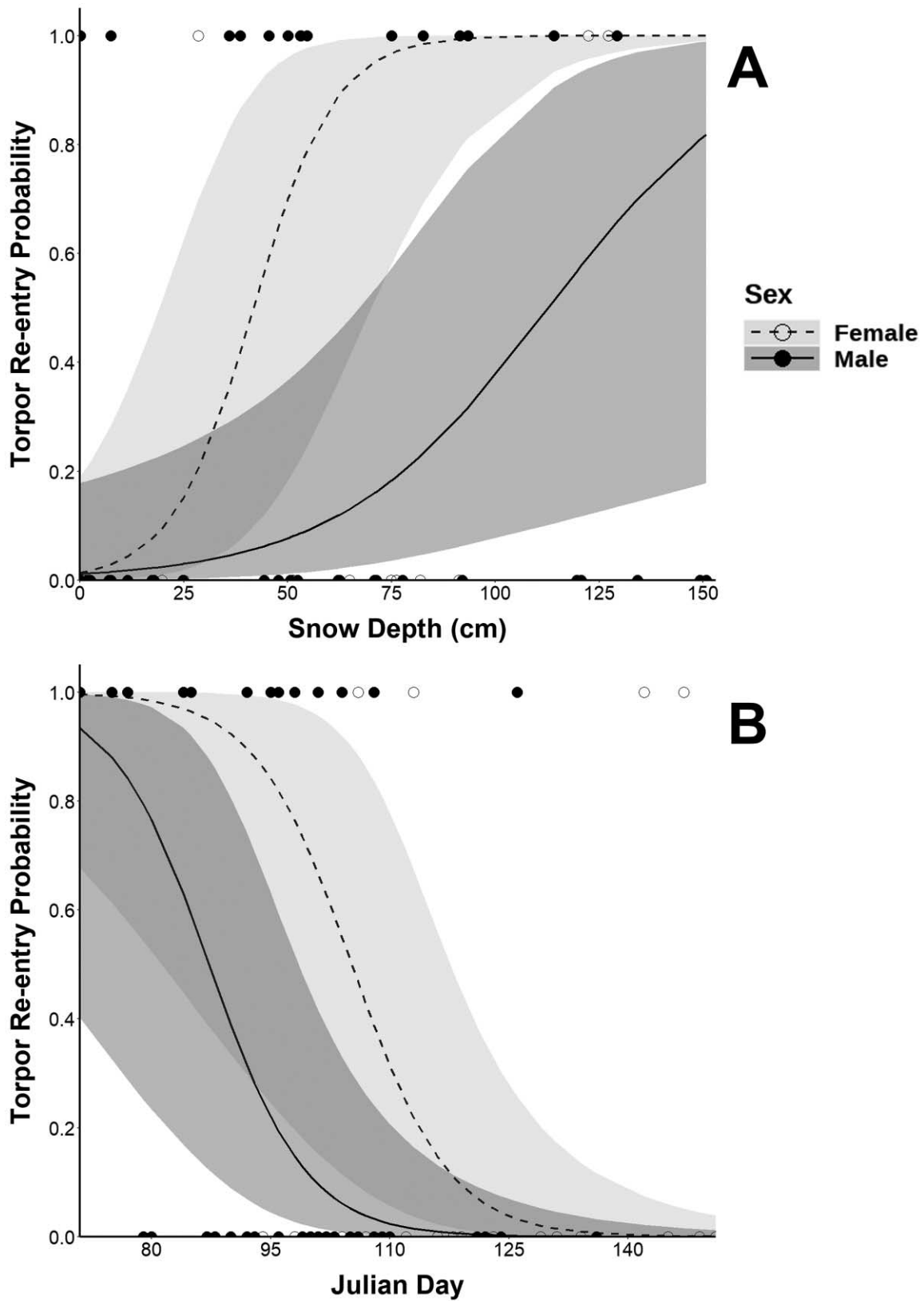


Figure 2. Marginal effects (\pm 95% confidence intervals) derived from the top generalized linear mixed effects model designed to explain why some northern Idaho ground squirrels reentered torpor following initial emergence ($n = 76$). Points represent raw torpor reentry outcomes following initial spring emergence (i.e., squirrels with values of 1 on the y-axis are those that reentered torpor, and squirrels with values of 0 did not reenter torpor). Snow depth (A) and day of year (Julian day; B) at initial spring emergence influenced the probability of reentering torpor. The explicit effect of snow depth was dependent on sex.

females optimize hibernation termination phenology (and hence reproductive phenology) to maximize pup growth and pup survival by maintaining synchrony with forage availability (Ozgul et al. 2010; Allison et al. 2023) and males optimize hibernation termination phenology to maximize their status in mating hierarchies while maintaining synchronous reproductive maturation with later-emerging females (Allison et al. 2023; Thompson et al. 2023). Finer-grained snow depth data (if/when such data become available) may explain even more variation in torpor reentry behavior, as ground squirrels may respond to snow conditions at a finer scale than 1 km² when deciding whether to terminate hibernation (Tamian et al. 2022). Additionally, snow depth may be a proxy for snow cover, which is assumed to reduce foraging opportunities for generalist herbivores like northern Idaho ground squirrels (Dyni and Yensen 1996; Yensen et al. 2018; Goldberg et al. 2020b) that rely on exposed surface patches to readily access food. This might explain why one male squirrel in 2022 reentered torpor when challenged by a persistent spring snowstorm following a nearly 3-wk euthermic period with daily aboveground activity.

Julian day was also in our top model, where it was negatively associated with torpor reentry probability independent of snow conditions. This suggests that the circannual clock influences decision-making regarding whether to reenter torpor after initial emergence from hibernacula. One possible ultimate explanation for this timekeeping pattern is that any residual snowpack encountered upon later emergence will, on average, melt faster under the influence of warmer temperatures than the same amount of snow earlier in the season. Endogenous fat reserves at the time of emergence may also influence the likelihood of subsequently reentering torpor. If early emergence is preferable when possible—as is suggested by other studies of hibernating ground squirrels (Ozgul et al. 2010; Lane et al. 2012; Viblanc et al. 2022; Thompson et al. 2023)—then squirrels in better condition that are better able to withstand harsh spring conditions may be less likely to reenter torpor following emergence (McNamara and Houston 1996). Squirrels that reenter torpor following emergence may then suffer from suboptimal reproductive synchrony with emerging females and consequently reduced reproductive success in that year compared to squirrels in better condition. The brevity of emergence bouts before torpor reentry suggests that ambient aboveground temperature (which is highly variable within and among days) is an unlikely hibernation termination cue, although squirrels emerging for multiple days before reentering torpor may have sampled ambient temperature directly or indirectly by assessing daily snowmelt. The most parsimonious explanation for the brevity of initial aboveground visits is that squirrels can rapidly assess cues attainable only at the surface (e.g., snowpack and/or snowmelt). However, the mechanism triggering initial emergence from hibernacula remains unknown. Possibly, rising soil temperature could cause squirrels to assess the suitability of surface conditions, although this would seem unlikely in the many cases where squirrels emerged while hibernacula (and often entire study sites) were snowbound. A more likely explanation for the timing of initial emergence is endogenous programming (i.e., the circannual clock), which may trigger increased testosterone production (Williams

et al. 2014). If so, squirrels reentering torpor must subsequently override that endogenous trigger.

Assessment of surface conditions before deciding whether to terminate hibernation potentially underlies the plasticity necessary for male northern Idaho ground squirrels to maintain reproductive synchrony with plastic females in a variable climate. That is, torpor reentry behavior in males may reflect expected female emergence timing under a given set of environmental conditions, such that males minimize the costs of early hibernation termination while still emerging with sufficient time to establish spermatogenesis before female emergence. Conversely, species exhibiting sex-dependent phenological shifts in response to climatic variation may suffer reduced fecundity as a result of phenological mismatches under future climate change (Williams et al. 2022). Sex-dependent phenological plasticity in response to extreme spring weather has been documented in two sister taxa to northern Idaho ground squirrels: Arctic ground squirrels (Williams et al. 2017a; Chmura et al. 2023) and Richardson's ground squirrels (Kucheravy et al. 2021). These species may instead be buffered against unpredictable spring foraging conditions by male food-caching behavior (Michener 1992; Buck and Barnes 1999). Food caches amassed in late summer or early autumn (i.e., breeding capital) allow male Arctic and Richardson's ground squirrels to consistently terminate hibernation and establish spermatogenesis early in spring regardless of surface conditions. This life history strategy, however, may leave these species vulnerable to intersexual mismatches in the timing of reproductive maturation under extreme weather conditions that are predicted to become more frequent under climate change (Williams et al. 2022; IPCC 2023). The lack of food-caching behavior in northern Idaho ground squirrels (i.e., their status as income breeders) also proximately explains why males of this species must emerge from hibernacula to forage soon after the termination of hibernation (Williams et al. 2017b).

Moreover, differences in life history strategies among these congeners suggest that divergent selection pressures act on the timing of hibernation termination among Holarctic ground squirrels (*Marmotini*). Food-caching species (i.e., capital breeders) may benefit from early termination of hibernation, perhaps because early arrival on breeding grounds confers a reproductive advantage via higher-quality territory or social status (i.e., the arrival time hypothesis; Ketterson and Nolan 1976; Allison et al. 2023; Thompson et al. 2023). Male northern Idaho ground squirrels compete for mates primarily through search effort and ability (i.e., scramble polygamy) rather than establishment of territories or social displays (although males will fight for mates when multiple males locate a sexually receptive female; Sherman 1989). Hence, differences in the contours of mate limitation may ultimately underlie the divergent hibernation strategies among these congeners. Alternatively, greater climatic variability across evolutionary time may have selected for male northern Idaho ground squirrels to evolve a more flexible mechanism regulating hibernation emergence phenology than that of some congeners to prevent frequent phenological mismatches with females. To our knowledge, the necessary data to test these alternative hypotheses via interspecific comparative studies do not yet exist, but the

recent development of biologging technology (e.g., geolocators) makes possible the collection of detailed phenological data in free-ranging individuals of additional hibernating species.

Despite the plasticity in hibernation termination timing that we documented, plastic phenological responses to climatic variation are presumably bounded in northern Idaho ground squirrels. The ability to delay hibernation emergence when challenged by late spring snowpack is undoubtedly constrained by endogenous energetic reserves, as illustrated by the low body mass of the female squirrel that possibly starved following reentry into torpor. The circannual clock may help these squirrels optimize hibernation phenology by preventing squirrels from emerging too early. Specifically, the circannual clock may regulate the transition from the maintenance phase to the potentiation phase of hibernation (Williams et al. 2014; Wilsterman et al. 2021). For instance, no squirrels emerged from hibernacula during occasional periods of total snowmelt in December, January, and February at our study sites. This makes sense because thermal conditions, food limitation, and the high probability of subsequent snowfall from December to February makes terminating hibernation and initiating reproduction a poor choice. Thus, adaptive evolutionary responses—particularly in endogenous circannual rhythms—will likely be necessary for these imperiled squirrels to persist under a warming climate wherein winter snowpack is predicted to decline (Lute et al. 2015; IPCC 2023). If we assume that the plasticity in hibernation termination timing that we documented is adaptive—but imperfect—such flexibility may facilitate the adaptation to novel climatic conditions that is likely necessary for these threatened squirrels to persist by bridging the divide between historical and future adaptive peaks (Ghalambor et al. 2007).

We elucidated a novel behavior with implications for our understanding of behavioral and physiological plasticity and the optimization of annual cycles as well as the conservation of a threatened species. Whether male subterranean hibernators of other species are capable of surface assessment before the termination of obligate hibernation remains to be seen and likely depends on the suite of selection pressures ultimately regulating hibernation phenology. Documenting the extent of plasticity (i.e., reaction norms) of phenological traits, such as hibernation, and the cues animals use to exercise that plasticity is increasingly important as we strive to identify which species require conservation interventions to endure novel climatic conditions and which will likely persist on their own.

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120629 and 37330), and US Fish and Wildlife Service recovery permit (TE94776A). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government. Data and code utilized for this study are permanently archived on figshare (<https://figshare.com/s/e665c3be41b54833a93b>).

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