Abstract: All activity incurs costs, but animals can often alter the timing of their activity to reduce these costs. Metabolic costs of activity are especially high during seasons of energy deficits (such as winter), but the extent to which animals can adjust their activity timing to reduce metabolic costs is unclear. Here, we test the hypothesis that the timing of small mammal activity during winter minimizes heat loss. Using motion-activated cameras deployed under snow, we show that a widely distributed nocturnal small-mammal species (*Peromyscus leucopus*, white-footed mouse) shifted to diurnal activity in early winter, which reduced potential heat loss by 4%. *Myodes gapperi* (southern red-backed vole) also avoided cold temperatures, but did so by adjusting its activity timing at a broader temporal scale by minimizing activity on cold days. We conclude that plasticity in activity timing—at both 24-hour and multi-day temporal scales—is an important means of conserving energy during winter, and may need to be accounted for when forecasting species distributions, abundances, and interactions.

Keywords: activity pattern; diel activity; northern temperate forest; *Myodes gapperi*; *Peromyscus leucopus*; snow; subnivium

Introduction

The timing of activity determines the abiotic conditions an organism experiences, the resources it can obtain, and the likelihood of encountering mates, competitors, predators, or parasites (Kronfeld-Schor and Dayan 2003, Abu Baker and Brown 2014, Bennie et al. 2014, van der Vinne et al. 2019). As a result, individuals exhibit variation in activity patterns in response to their environment (e.g., predation risk, Connolly & Orrock, 2017; Courbin et al., 2019), which may affect demography, biotic interactions, and evolution (Bennie et al. 2014, Gaston et al. 2015). Recent evidence also documents the importance of activity timing in the context of rapid environmental change, such as invasive species (Guiden and Orrock 2019), climate change (Levy et al. 2019), and anthropogenic light (Gaston et al. 2017, Hopkins et al. 2018); such shifts in activity timing may lead to changes in population viability, shifts in competitive interactions, and lead to the emergence of novel predator-prey dynamics (Gaynor et al. 2018, Guiden et al. 2019a).

Despite an emerging understanding that activity timing can exhibit important seasonal dynamics (Guiden and Orrock 2019), our understanding of activity timing remains incomplete because it is often quantified exclusively during the growing season. For example, in high-latitude habitats, winter snow accumulation intercepts light (Evernden and Fuller 1972), decreases resource availability (Guiden et al. 2019b), and insulates air temperatures ("subnivium" formation, Pauli et al. 2013)—all of which might influence animal decisions about when to be active (Kronfeld-Schor and Dayan 2003). Activity patterns under snow might therefore differ greatly from growing-season activity patterns. While winter is commonly described as a season of energy deficits (Marchand 1987, Williams et al. 2014), there have been few studies investigating how organisms might adjust the timing of their activity to manage these deficits. This lack of data describing winter activity patterns is an important gap in our knowledge: 55% of the northern hemisphere experiences seasonal freezing temperatures, and climate change is disproportionately altering winter conditions in many of these habitats (Kreyling 2010).

Animals should be active as long as benefits of activity (e.g., foraging gains) outweigh the costs of activity (e.g., metabolic costs or predation risk, Brown 1988, Brown and Kotler 2004, Gaynor et al. 2019). Metabolic costs of foraging in cold environments can be extreme, especially for small homeotherms (Conley and Porter 1986). Thus, small mammals that must forage during winter should be under strong selection to minimize heat loss by reducing activity on cold days (Orrock and Danielson 2009). Alternatively, animals could minimize metabolic costs by shifting the timing of their activity (e.g., nocturnal animals could become active during the day (van der Vinne et al. 2019). We tested the hypothesis that activity patterns in two common small-mammal species (*Peromyscus leucopus*, white-footed mouse, and *Myodes gapperi*, southern red-backed vole) minimize heat loss, using a novel method of monitoring subnivean (“below-snow”) foraging activity (Soininen et al. 2015). Our data reveal unexpected shifts in small-mammal activity timing between summer and winter, highlighting the importance of behavior for reducing metabolic costs associated with extreme winter temperatures.

Methods

This study was conducted at 10 different sites characterized by mixed-deciduous forest in northern Wisconsin, USA. The 10 sites spanned a 45 km latitudinal gradient (45.80°N to 46.13°N). Data were collected concurrently with an experiment investigating small-mammal responses to changes in snow depth and woody debris (Guiden 2019, Appendix). We monitored small-mammal winter foraging activity with four subnivean camera traps (Soininen et al. 2015) per site, which allowed us to identify small-mammals to genus or species. Camera traps consisted of cameras placed in transparent plastic boxes (58 cm length × 41 cm width × 31 cm height), with 10 cm × 10 cm holes cut to allow small mammals to access the box (Appendix). Cameras were attached to the box ceiling with the lens pointed towards the ground (Soininen et al., 2015, Appendix). The environment within the camera boxes therefore mimicked environments typically encountered by small mammals in nature throughout the winter (e.g., areas under short shrubs that intercept snow, subnivean habitats characterized by loose snow at the soil-snow interface, Pauli et al. 2013, Petty et al. 2015, Zuckerberg and Pauli 2018), providing insight into how small mammals might use subnivean habitat. We placed 10 seeds of five temperate tree species (n = 50 seeds total) consumed by *P. leucopus* and *M. gapperi* (*Abies balsamea*, *Acer rubrum*, *Acer saccharum*, *Pinus resinosa*, *Quercus rubra*, Schnurr et al. 2002, 2004; Cramer 2014) in the leaf litter below each camera (Guiden 2019). Camera traps did not bias small-mammal activity timing by providing an artificial refuge (Appendix), and there was no evidence of small mammals nesting in the camera boxes. By the following spring, 78% of deployed seeds were removed (Guiden 2019).

In order to understand how winter climate influenced small-mammal activity timing, we tracked near-ground temperature and snow depth at our sites between 7 December 2017 and 20 February 2018. Daily snow depth observations were obtained from the closest weather station (Boulder Junction, WI, mean distance from study sites: 18.44 km), and provided an excellent fit to field measurements of snow depth ($r^2 = 0.83$, $P = 0.005$, d.f. = 46.77, Guiden 2019). Each camera box included an iButton thermochron (Maxim Integrated, San Jose CA) suspended 15 cm above the soil, which measured air temperature every four hours to quantify thermal conditions experienced by small mammals foraging within the box. Because snow depth and daily minimum temperatures were strongly correlated ($r = 0.56$, d.f. = 73, $P < 0.001$, Fig. 1B), we conducted a correlation-based principal components analysis to reduce these variables to a single principal component (see Results).

To test for an association between winter climate and small-mammal activity, we constructed a hurdle model with a truncated negative binomial distribution using the "glmmTMB" package in R (Brooks et al. 2017). This hurdle model had two components: a zero-inflation model that determined the probability of a small mammal being photographed, and a conditional model that modeled the number of photographs as a negative binomial distribution when the number of photographs > 0. This model allowed us to make inferences about the effects of winter climate conditions on two different processes: a) the probability of small mammals being active or not (i.e., the zero-inflation model), and b) for active small mammals, the magnitude of activity on a given day (i.e., the conditional model). Both the zero-inflation model and conditional model described *Myodes gapperi* and *Peromyscus leucopus* activity as a function of species, the climate principal component, a species × climate interaction, and a random intercept for site.

We estimated the amount of energy small mammals would lose as heat during periods of activity at two temporal scales: mean daily temperatures, and the approximate temperature (within two hours) of each small-mammal photograph. Heat loss (in watts) was estimated from a model accounting for the temperature gradient between the environment and core body temperature, the animal's size and shape, and the insulation provided by fur (Porter and Kearney 2009). We multiplied heat loss by 3600 seconds to estimate the amount of energy (in joules) a small mammal would lose as heat during one hour of activity.

We compared estimated energetic costs of activity between *P. leucopus* and *M. gapperi* using two linear mixed models. The first model compared heat loss between days when small mammals were active and days when small mammals were inactive. This model described mean daily energetic costs at each site as a function of species, a binary variable describing whether a species was observed or not, time period (early winter or late winter), and all possible interactions, and included a random intercept for site. 22 January 2018 was chosen as the division between early and late winter, because on this date a large snowstorm resulted in widespread subnivium formation, dramatically reducing the daily range of near-ground temperatures (Fig. 2A-2B). Because these animals are typically nocturnal, the second model used finer-scale temperature data to compare heat loss at the time of each photograph to heat loss at a random night-time temperature recorded within 24 hours of each photograph. This model described the amount of energy lost as heat as a function of species, a binary variable describing the type of activity timing (observed activity or random nocturnal activity), time period (early winter or late winter), and all possible interactions. This model also included a random intercept term for each paired comparison between observed and random times, which was nested within site. All mixed-effects models were constructed in R using the “lme4” package (Bates et al. 2015).

Results

Snow depth reached a maximum of 45.8 cm on 23 January 2018 (Fig. 1A). As snow depth increased, daily temperature ranges decreased ($r = 0.38$, $F_{1,73} = 39.59$, $P < 0.001$, Fig. 1B). Our principal component analysis identified one principal component that described 76% of the variance in climate data. This principal component was correlated with deep snow and warm daily minimum temperatures. 55% of deployed cameras recorded small-mammal activity (n = 1456 photographs); 66% of photographs could be identified to genus or species (n = 963). *Peromyscus leucopus* were the most commonly photographed species (n = 660), followed by *M. gapperi* (n = 296), *Napaeozapus insignis* (n = 5), and *Sorex* spp. (n = 2).

At a multi-day temporal scale, *P. leucopus* and *M. gapperi* showed distinct activity patterns (Fig. 1A). The probability of observing either small-mammal species increased with the climate principal component ($\beta = -0.61 \pm 0.14$, zero-inflated model: $z = 4.33$, $P < 0.001$). On cold days with little snow (25th percentile of climate principal component), the probability of observing a small mammal was 3.9%, but the probability of observing a small mammal more than doubled to 8.6% on warm days with deep snow (75th percentile of climate principal component). The probability of observing a small mammal was not affected by species ($\beta = 0.01 \pm 0.22$, $z = 0.01$, $P = 0.96$), but was marginally affected by the species × climate interaction ($\beta = 0.31 \pm 0.18$, $z = 1.71$, $P = 0.09$). However, the relationship between the number of photographs observed and the climate principal component differed strongly between the two species (conditional model species × climate principal component: $\beta = -0.92 \pm 0.23$, $z = 3.87$, $P = 0.001$). The number of *P. leucopus* photographs was greatest on days with shallow snow and/or low daily minimum temperatures (Fig. 1C), but *M. gapperi* activity was greatest on days with deep snow and relatively high daily minimum temperatures (Fig. 1D). On days when activity was observed, there were almost twice as many *P. leucopus* spp. photographs (10.96 ± 2.41) compared to *M. gapperi* photographs (5.86 ± 1.79, conditional model species main effect: $\beta = 0.62 \pm 0.26$, $z = 2.35$, $P = 0.02$). There was also a weak positive effect of climate principal component in the conditional model ($\beta = 0.23 \pm 0.18$, $z = 1.29$, $P = 0.19$). These species exhibited very different diel activity patterns: *Peromyscus leucopus* were primarily observed between 08:00 and 16:00 (Fig. 1E), while *M. gapperi* had a uniform diel activity pattern (Fig. 1F).

Near-ground air temperatures were colder and more variable in early winter compared to late winter (Fig. 2A), and we observed a seven-fold decrease in daily temperature range once snow accumulated > 45 cm (Fig. 2B). Small mammals reduced heat loss by avoiding activity on cold days (Fig. 2C-D). Based on mean daily temperatures, heat loss in early winter would have been 4% greater on days when small mammals were not photographed (3725 ± 61 J) compared to days when small mammals were photographed (3567 ± 68 J, Fig. 2C), but this difference in heat loss disappeared in late winter ($\beta = 113.55 \pm 100.93$, time period × photograph interaction: $F_{1,737.5} = 10.10$, $P = 0.001$, Fig 2D). The marginally significant species × time period × photograph interaction ($\beta = 241.48 \pm 144.63$, $F_{1,736.7} = 2.78$, $P = 0.09$) suggested that during early winter, *M.gapperi* was active on days with lower mean energetic costs than *P. leucopus* (Fig. 2C). Small mammals also minimized heat loss by adjusting their diel activity patterns (Fig. 2E-F). On average, heat loss was 1.6% lower during times of observed small mammal activity (3657 ± 11 J) compared to random nocturnal activity (3717 ± 11 J, $\beta = 110.58 \pm 22.11$, $F_{1,952} = 187.84$, $P < 0.001$), but this effect was more than twice as strong during early winter (activity timing × time period interaction: $\beta = -142.17 \pm 27.38$, $F_{1,952} = 75.49$, $P < 0.001$). Full model results are summarized in the Appendix.

Discussion

Temporal activity patterns are rarely quantified during winter, and consequently it is difficult to appreciate the adaptive value of decisions associated with the timing of activity. Moreover, activity patterns have historically been considered invariant (Bennie et al. 2014), but it is becoming increasingly clear that we often underestimate the plasticity of diel activity (Hazlerigg and Tyler 2019). Using a novel method to observe activity in free-ranging animals below snow cover, the data presented here support the hypothesis that the timing of foraging activity in two common small-mammal species (Fig. 1C-1F) minimizes metabolic costs incurred by activity during winter (Fig. 2E-2F). *Peromyscus leucopus*, a ubiquitous small mammal that is considered nocturnal across its range in eastern North America (Jackson 1961, Bruseo and Barry 1995, Whitaker and Hamilton 1998, Guiden and Orrock 2019, Appendix) was primarily diurnal throughout our winter study (Fig. 1E). *Myodes gapperi*, on the other hand, greatly reduced its activity on cold days with little snow cover (Fig. 1D). Such shifts in activity timing may be an important adaptation to thermally challenging environments (Kearney et al. 2009), allowing organisms to minimize heat loss during cold winter days (Fig. 2). Understanding how species shift foraging activity patterns at different temporal scales could provide a critical missing link in niche models (Roy-Dufresne et al. 2013). Day-time winter temperatures may best predict habitat suitability for species responding to temperature on a 24-hour scale, such as *P. leucopus*, whereas mean daily temperatures may best predict habitat suitability for species responding on a multi-day scale, such as *M. gapperi* (Fig. 2C-2D). Without accounting for species-specific behavioral plasticity during winter, ecologists risk mischaracterizing the thermal niche of species using subnivean habitats (Pauli et al. 2013) or reaching incorrect conclusions when comparing the energetic costs of activity in different mammal species (Fig. 2C-2F).

The different behavioral strategies employed by *P. leucopus* and *M. gapperi* might reflect differences in how snow accumulation affects each species. During winter, the subnivium provides an important thermal refuge as snow depth approaches 50 cm (Pauli et al. 2013, Petty et al. 2015), but is unlikely to form until several weeks after the first snowfall (Fig. 2A). When snow was deep enough to provide protective cover from visually hunting predators, but not deep enough to provide a stable thermal environment, *P. leucopus* shifted to diurnal behavior (Fig. 1E), leading to an estimated 4.4% reduction in heat loss compared to the nocturnal activity (Fig. 2E). While *M. gapperi* did not avoid nocturnal activity (Fig. 1F), it also minimized heat loss by avoiding activity on extremely cold days (Fig. 1D, Fig. 2C) while having no clear nocturnal or diurnal activity pattern (Fig. 1F). The pulse of *P. leucopus* activity in December (Fig. 1A) suggests this species may accept cold temperatures to forage for large seeds (e.g., *Quercus rubra*) before deep snow covers these resources (Anderson 1986), particularly given their ability to avoid the coldest time of day (Fig. 1E). *Myodes gapperi*, which likely does not cache seeds, did not exhibit a December activity pulse (Fig. 1A), and became most active when temperatures were mild in late January (Fig. 2A). The effect of snow on species-specific foraging strategies might therefore influence whether small mammals adjust their foraging activity at broad (day-to-day) or fine (diel) temporal scales.

Plasticity in winter activity timing may have important ecological consequences. Small mammals that lose excessive energy to heat in cold temperatures can experience decreased reproductive success (Bult and Lynch 1997) and impaired immune responses (Nelson and Demas 1996). Thus, *P. leucopus* that exhibit shifts in activity timing and *M. gapperi* that reduce activity during cold days may increase their relative fitness in cold environments by avoiding these costs. A key question that arises from our findings is what proportion of the *P. leucopus* population switches to diurnal activity timing in early winter, given that our camera data are unable to distinguish among individual *P. leucopus*. Future research could use PIT-tags or live-trapping to determine if individual state (e.g., age or physiology, Clark 1994) or behavioral syndromes (e.g., bold individuals, Sih et al. 2004) makes animals more likely to shift foraging activity patterns, which could select for these traits in cold environments. Seasonal shifts in foraging activity patterns may also have a strong influence on species distribution and persistence, as activity timing also plays an important role in moderating winter biotic interactions. For example, *P. leucopus* may face elevated predation risk by diurnal predators (e.g., hawks, Smithers et al. 2005) during winter. Additionally, in the absence of a subnivium, competition between *P. leucopus* and *M. gapperi* (Lemaître et al. 2010) may be increasingly likely due to a compressed window of time where costs of activity are low. Once subnivium forms, thermal constraints on activity are relaxed (Fig. 1B), and species may be less likely to encounter one another.

The unexpected plasticity we observed in the timing of small-mammal foraging activity underneath the snow highlights the need for increased research on seasonal shifts in behavior. For example, while our study shows that small mammals alter foraging activity in response to cold temperatures, it is possible that these species also exhibit plasticity in other types of activity, such as social interactions or territory defense (Ostfeld 1985). Additionally, the degree to which this behavioral plasticity is taxonomically widespread remains unclear. Identifying which species respond at 24-hour temporal scales versus multi-day temporal scales to avoid high metabolic costs may help anticipate species responses to climate change (Kearney et al. 2009). It also remains unknown if predators of small mammals shift their activity patterns to track their prey, or if climate change (Creel et al. 2016) and human activity (Gaynor et al. 2018) constrain carnivore activity timing. As northern temperate forests warm and snow ceases to provide a thermal refuge for many species (Pauli et al. 2013, Seidl et al. 2017), behavioral plasticity in activity timing may become an increasingly important strategy to avoid extremely cold temperatures.

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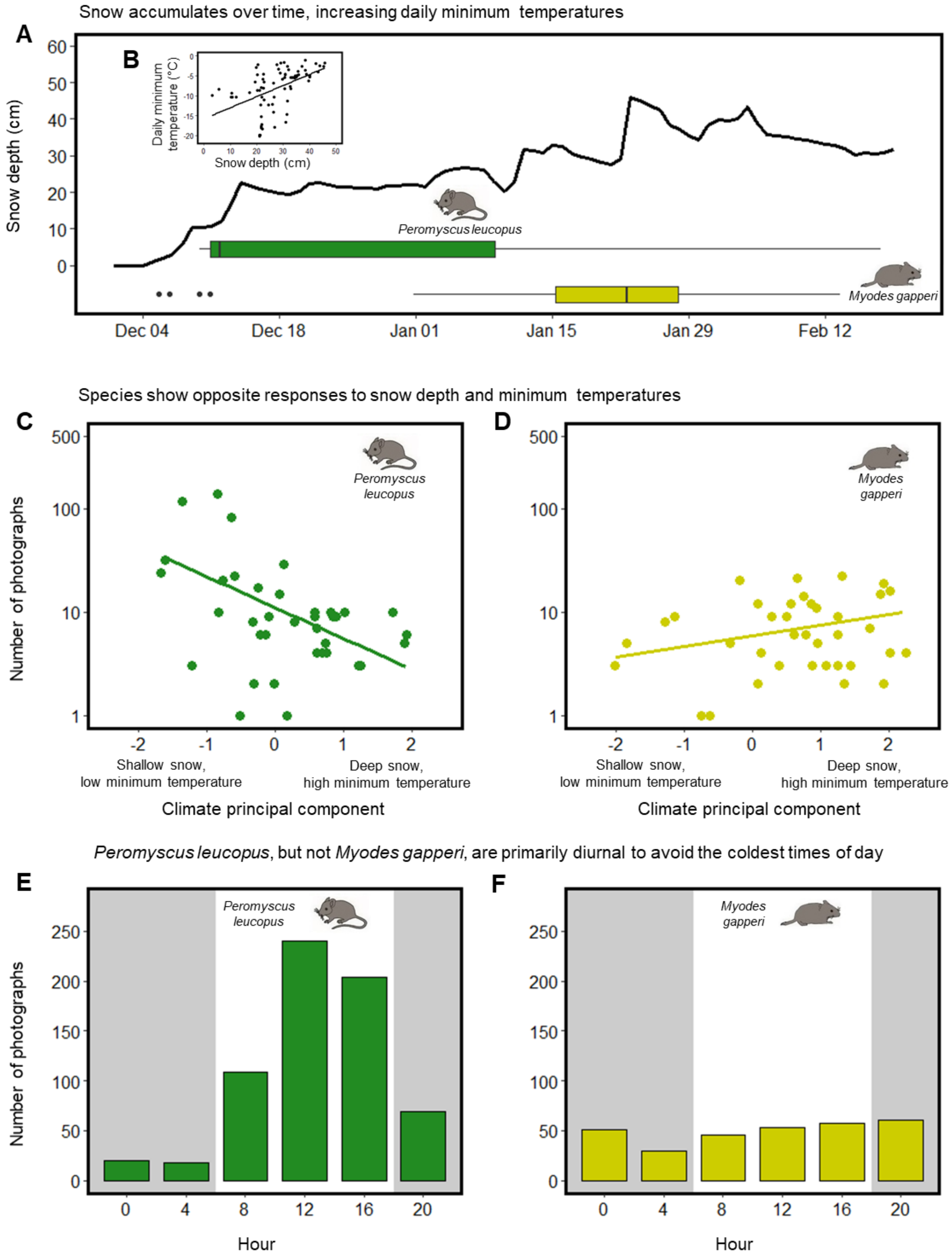
Fig. 1: A) Snow depth for each day of the study. Boxplots represent the distribution of *Peromyscus leucopus* (green) and *Myodes gapperi* (yellow) photographs through time. B) Daily minimum temperature as a function of snow depth. C) Number of *P. leucopus* and D) *M. gapperi* photographs per site per day as a function of the climate principal component (high values represent warmer days and/or deep snow). Curve represents hurdle model predictions. E) Number of *P. leucopus* and F) *M. gapperi* photographs binned in 4-hour intervals.

Fig 2: A) Maximum and minimum temperatures for each day of the study averaged across all sites. B) Diel temperature profiles for early winter (before 22 January 2018, orange points) and late winter (after 22 January 2018, blue points) averaged across all sites and dates. C) Estimated heat loss in early winter and D) late winter based on mean daily temperatures for *Peromyscus leucopus* (green) and *Myodes gapperi* (yellow). Points represent estimated marginal means for days where activity was not observed (open circles) and days where activity was observed (closed circle). E) Estimated heat loss during early winter and F) late winter based on the timing of small-mammal activity. Points represent estimated marginal means for the heat loss based on temperatures associated with each photograph of a small mammal (to the nearest two hours, closed circles). Because these species are nocturnal during the growing season, we also estimated heat loss for a random night-time temperature recorded by iButtons within 24 hours of each photograph (open circles). All error bars represent 95% confidence intervals.

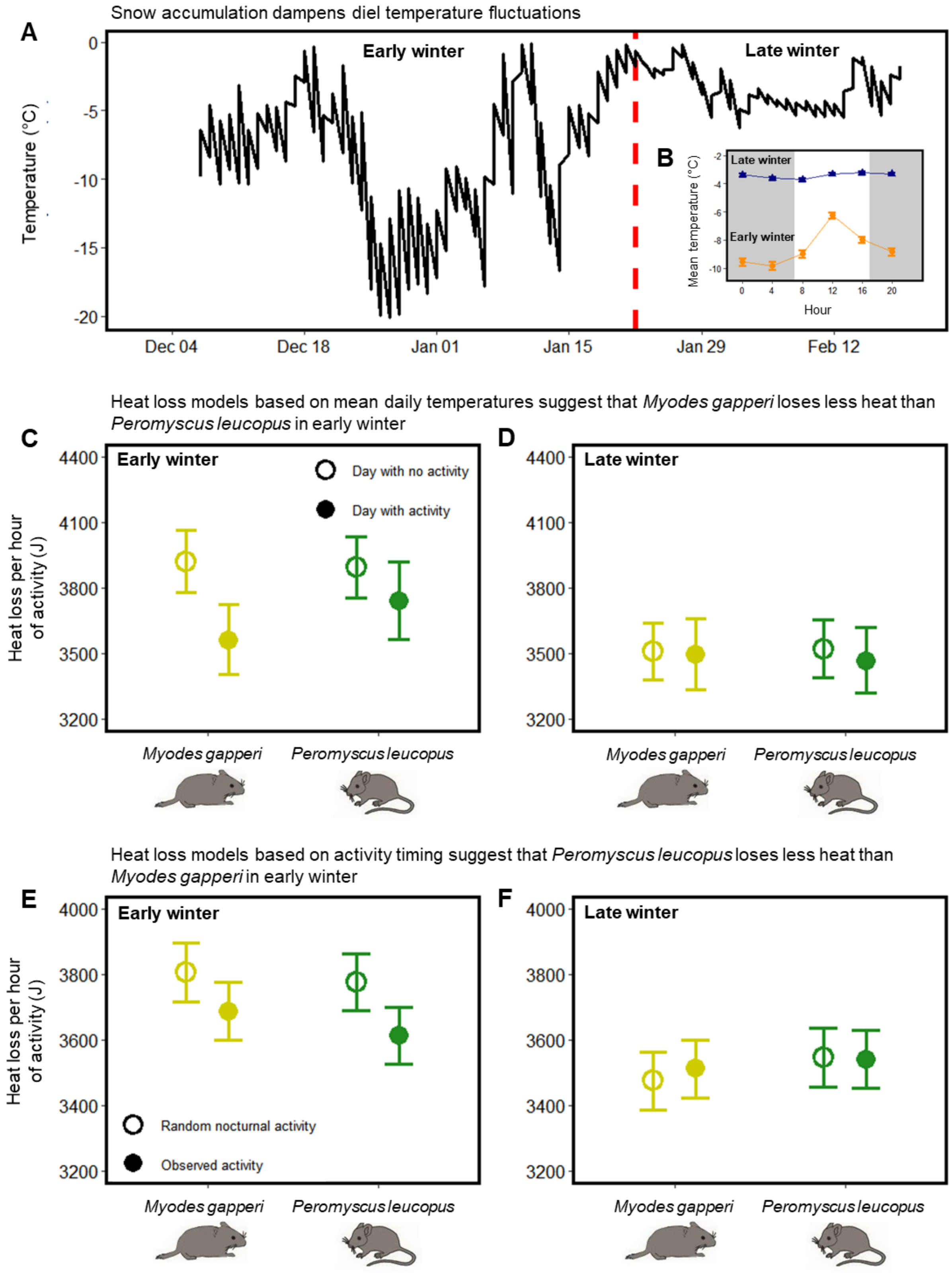


Snow accumulates over time, increasing daily minimum temperatures

Species show opposite responses to snow depth and minimum temperatures

Peromyscus leucopus, but not *Myodes gapperi*, are primarily diurnal to avoid the coldest times of day

Fig. 1



Snow accumulation dampens diel temperature fluctuations

Heat loss models based on mean daily temperatures suggest that *Myodes gapperi* loses less heat than *Peromyscus leucopus* in early winter

Heat loss models based on activity timing suggest that *Peromyscus leucopus* loses less heat than *Myodes gapperi* in early winter

Fig. 2

Appendix

Summer live-capture and activity data

In order to provide context for our estimates of small-mammal winter activity, we quantified small-mammal activity in the summer using live trapping. We established a 4 x 4 trapping grid at each site in July 2017. Grid points were spaced 10 m apart, and at each grid point we deployed two Sherman live-traps within 1 m of the grid point. We pre-baited traps (i.e., placed bait in traps but locked trap doors open) for one night in order to allow animals to acclimate to traps (Edalgo and Anderson 2007). Traps were deployed for four consecutive nights and checked around sunrise. All captured animals were identified to species, and given an ear tag with a unique number.

During summer live-trapping, we observed 240 capture events representing 114 unique individuals and 7 taxa (Table S1). *Peromyscus leucopus* was captured the most frequently at these sites (n = 119 captures) followed by *T. striatus* (n = 43 captures), *M. gapperi* (n = 30 captures), and *P. maniculatus* (n = 13). *Peromyscus leucopus* were captured at every site, whereas *M. gapperi* were captured at 7 out of 10 sites. The number of *Peromyscus* spp. photos at a site was strongly correlated with the *Peromyscus* spp. M_{t+1} (i.e., the number of individuals captured, Slade and Blair 2000) during summer ($F_{1,8} = 6.93$, $P = 0.03$). Additionally, we observed diurnal activity at 8 of our 10 sites where we trapped an average of 5.84 individual *Peromyscus* spp. during summer. These data, along with observations of *Peromyscus leucopus* extensively using snow-covered ground during winter as opposed to arboreal habitats (Nicholson 1941), suggests that shifts to diurnal activity may be a common phenomenon in northern *Peromyscus* spp. populations, rather than being driven by a handful of individuals. However, *Myodes gapperi* summer M_{t+1} did not predict the number of *M. gapperi* photographs in winter (r

= -0.41, $F_{1,8} = 0.02$, $P = 0.89$), and *M. gapperi* were detected at three sites in winter where they were not captured during summer.

Because *P. leucopus* and *P. maniculatus* are morphologically similar (Stephens et al. 2014), we did not attempt to distinguish between these species in our photograph analysis. In order to assess whether the single site with *P. maniculatus* was driving the patterns in Fig. 2 (main text), we repeated this analysis using only the 9 sites with only *P. leucopus*. Excluding the site with both *P. leucopus* and *P. maniculatus* does not qualitatively change our results (Fig. S1). Consequently, we can confidently conclude that *P. leucopus* can shift activity timing in winter. However, because it was impossible to say whether *P. leucopus* or *P. maniculatus* (or both) were photographed at the site where these species co-occurred, we cannot confidently conclude that *P. maniculatus* is also able to shift its activity timing during winter.

Table S1: Comparison of summer live-captures and winter photographs for several northern temperate small-mammal species. Measurements of activity for each species are pooled from 10 sites.

Species	Live-captures (summer)	Photographs (winter)
Blarina brevicauda	14	0
Glaucomys volans	5	0
Myodes gapperi	30	256
Napaeozapus insignis	3	5
Peromyscus spp.	135	591
Sorex spp.	10	2
Tamias striatus	43	0

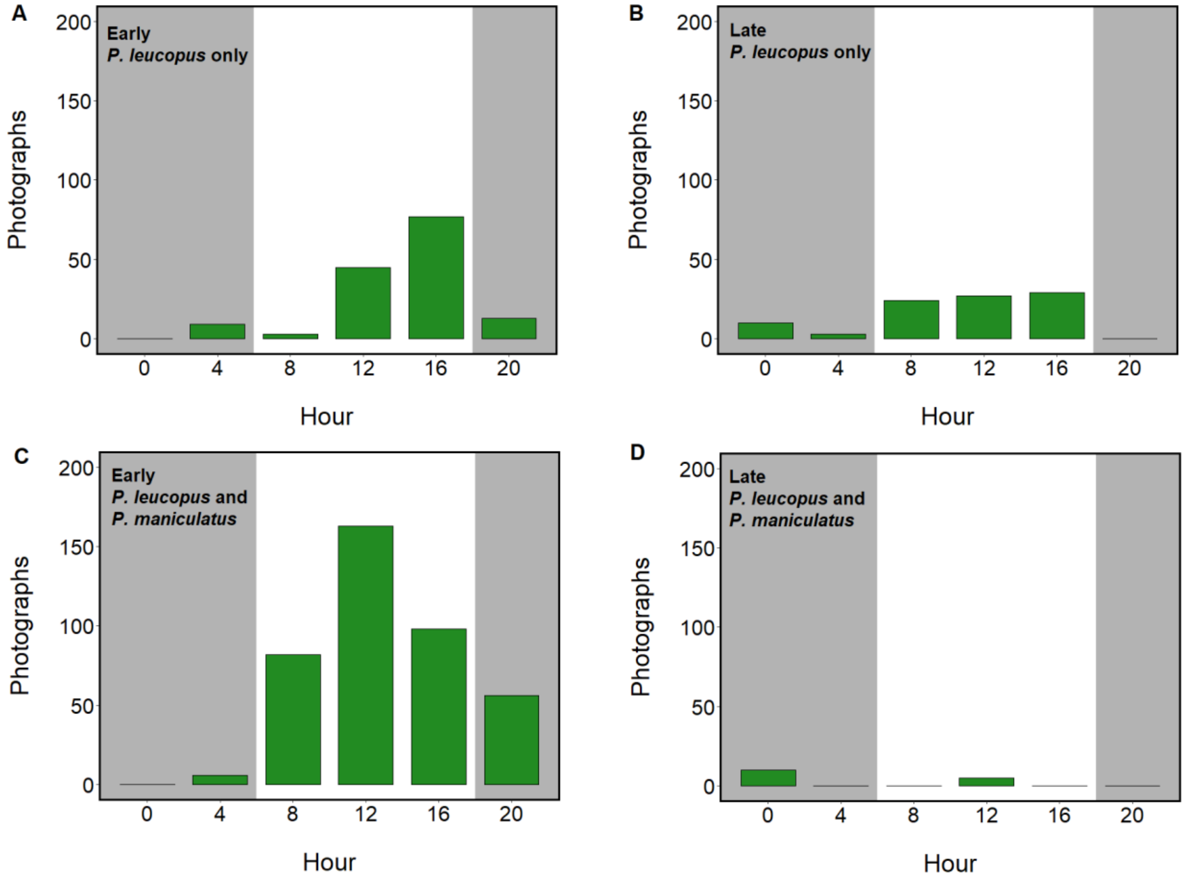


Fig. S1: Diel activity patterns during winter determined by photographs of *Peromyscus* spp. (green bars). A) At sites where only *P. leucopus* was captured (n = 9), we primarily observed diurnal activity in early winter, and B) no clear activity pattern in late winter (see main text Results). C) At the 1 site where *P. leucopus* and *P. maniculatus* were captured, we also primarily observed diurnal activity in early winter and D) no clear activity pattern in late winter. However, it is unclear whether *P. leucopus* or *P. maniculatus* (or both species) is driving the activity patterns in C) and D).

Camera boxes did not modify Peromyscus leucopus *behavior*

We chose to construct our camera boxes out of transparent plastic, because the dark environment created by metal or wooden camera boxes (Soininen et al. 2015) may create an artificially strong refuge for small mammals. To ensure that the shifts in activity timing we observed (Fig. 1E, main text) were due to increases in snow cover, and not an artifact of refuge introduced by our camera boxes, we deployed cameras in a snow-free environment. Cameras were deployed for one week, starting 14 April 2019, at a temperate forest at the University of Wisconsin Arboretum (43.0429°N, 89.4243°W). *Peromyscus leucopus* are the dominant small-mammal species at the arboretum, but *P. maniculatus* does not occur in this study area (Guiden and Orrock 2019). As expected, *P. leucopus* were almost exclusively nocturnal in the absence of snow at the UW Arboretum (Fig. S2), compared to the strong shift to diurnal activity underneath snow during winter at the northern WI site (Fig. S2, Fig. 1E-1F main text).

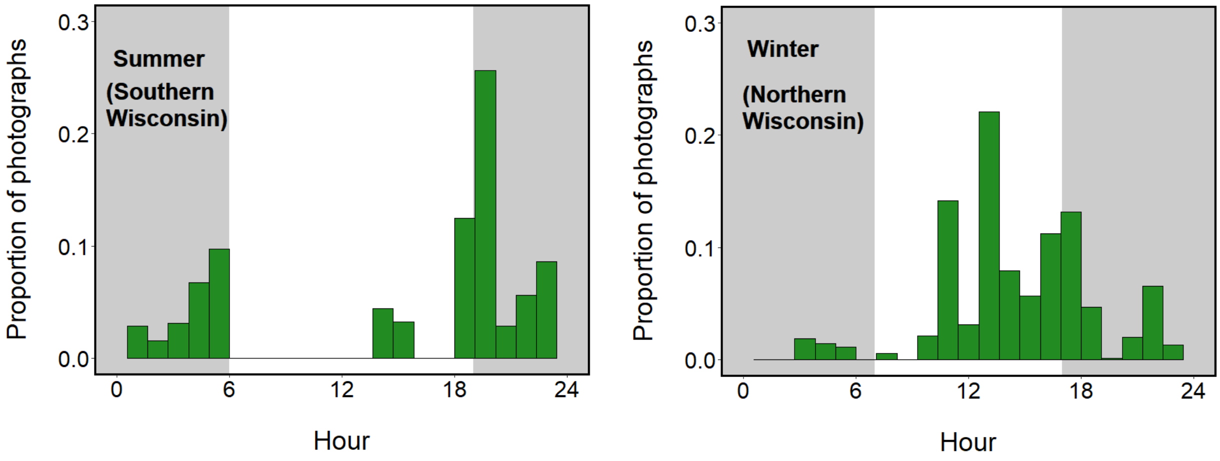


Fig. S2: Comparison of diel activity patterns for *Peromyscus leucopus* in summer (14 April 2019 to 21 April 2019) and *Peromyscus maniculatus* and *Peromyscus leucopus* in winter (7 December 2017 to 20 February 2018). Summer photographs were taken at the University of Wisconsin

Arboretum (43.0429°N, 89.4243°W). *Peromyscus* spp. were much more likely to exhibit diurnal activity during winter, underneath the cover of snow.

Analysis of unidentified animals

Because we could not identify the small-mammal species in a proportion of photographs, we assessed the activity patterns of these unidentified photographs to determine whether unidentified animals were exhibiting patterns of activity similar to identified ones and to be certain that our conclusions for identified animals are not driven by shifts in identification (e.g., if nocturnally active animals of *P. leucopus* were less likely to be identifiable). There was no clear bias in the date or time of activity in these photographs (Fig. S3). Rather, photographs showed a mix of activity peaks in early and late winter (Fig. S3A), and a mix of diurnal and nocturnal activity (Fig. S3B). For comparison, we provide similar figures with *P. leucopus* and *M. gapperi* activity combined showing the date (Fig. S4C, data from Fig. 1A) and hour (Fig. S4D, data from Fig. 1C-1D, main text) of activity from photographs were the species could be identified. This suggests that unidentified photographs were a mix of the two most common species, *P. leucopus* and *M. gapperi*, rather than predominantly consisting of one of these species.

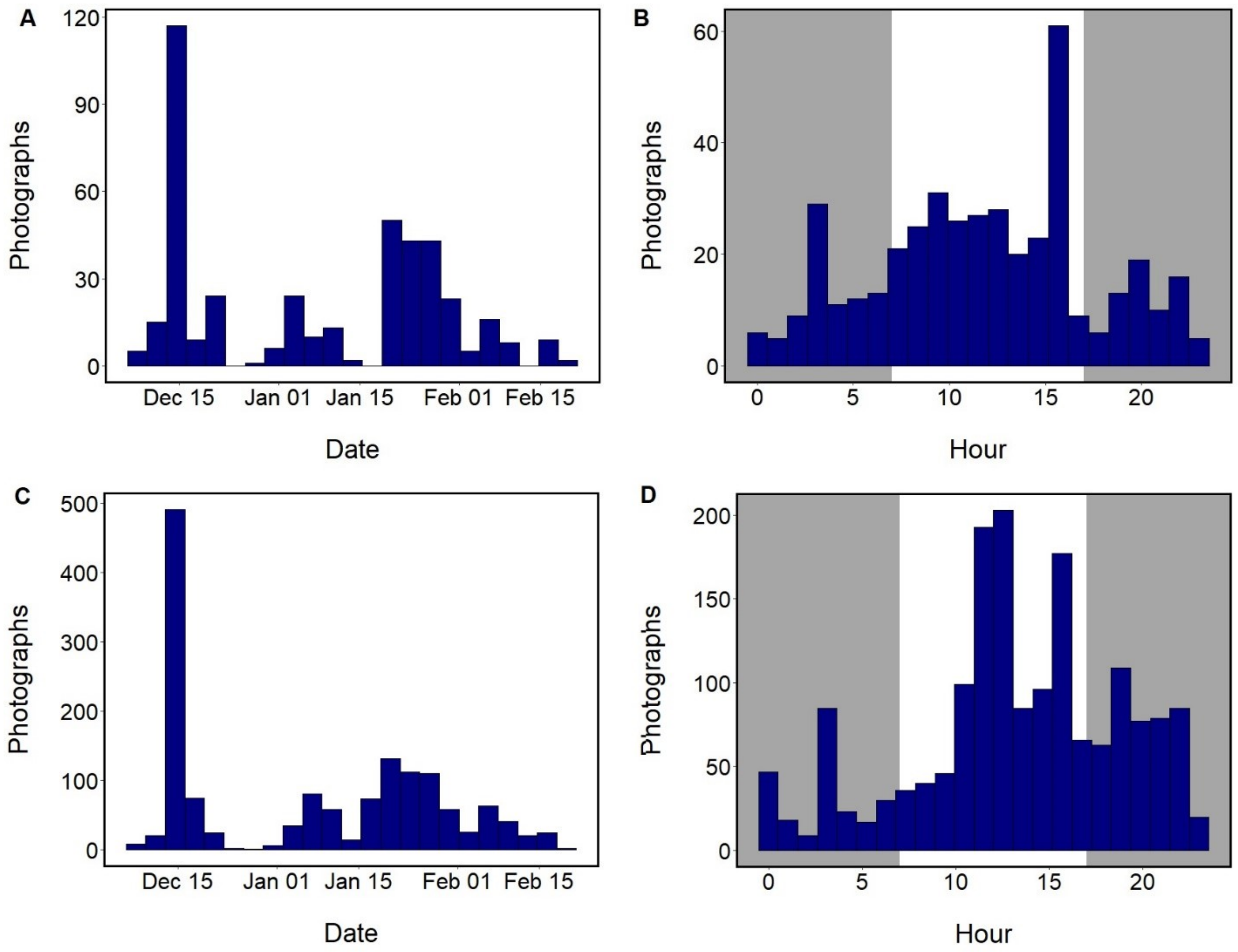


Fig. S3: Temporal distributions of photographs of unidentified animals (n = 425) at A) seasonal and B) diel scales. Most photographs are likely from *P. leucopus* and *M. gapperi* (see main text), and therefore represent a combination of activity patterns from these species. C) For comparison, combined temporal distribution of *P. leucopus* and *M. gapperi* at the seasonal scale using data from photographs where species could be identified. D) combined temporal distribution of *P. leucopus* and *M. gapperi* at the diel scale using data from photographs where species could be identified.

Camera trap set-up, woody debris manipulation, and snow removal experiment

We attached motion-activated cameras (Bushnell Essential E3, Overland Park KS) to a transparent plastic box, so that the camera was suspended approximately 31 cm above the soil surface, facing the soil (Fig. S4). We chose a transparent box to reduce the likelihood that small-mammals would perceive the box itself as a refuge, thus obscuring possible effects of our woody debris and snow removal treatments on small-mammal behavior. We cut out a 10 cm x 10 cm hole cut on two ends of the box, allowing small mammals to freely pass through. This box was placed in the center of the plot upside-down and anchored into the soil with turf staples. These cameras use infrared flash if photos are taken in dark conditions, which is calibrated to illuminate objects much farther away than the 31 cm used in our camera-trap design. In order to reduce wash-out caused by the infrared flash, we covered the majority of the infrared flash bulbs with duct tape. Cameras were deployed on 7 December 2017 and collected 5 May 2018, but very few photographs were taken after we initiated our snow removal treatment (20 February 2018). This is because cameras in snow removal plots continuously took photos until their batteries died. However, even in control plots, very little small-mammal activity was observed from mid-February to snow retreat. This likely reflects either a) small-mammal abundances declining over winter (Merritt and Merritt 1978), or b) depletion of food resources in our patches (Brown and Kotler 2004). Alternatively, disturbance caused by our snow shoveling treatment may have also diminished small-mammal activity, but this explanation seems less likely because we had visited sites consistently throughout winter, and because declines in small-mammal activity were evident before snow shoveling began (Fig. 1A).

This study was conducted in conjunction with an experiment to investigate the potential interactive effects of reduced snow and woody debris. In August 2017, we delineated four 2 m x 2 m plots at each site. All data used in this study were collected before snow was experimentally removed starting in February 2018, as cameras used to document rodent activity became increasingly non-functional after 20 February 2018 due to battery and data-storage limitations (Guiden 2019). In July 2017, all woody debris within the plots, as well as a 0.5 m radius around the plot, was removed. Half of the plots were randomly selected to have woody debris added, and half of the plots were left as a control with no woody debris. In October 2017, woody-debris addition plots received a standardized volume of untreated pine lumber (approximate dimensions: 10 cm × 10 cm × 100 cm); this volume corresponded to the median volume of woody debris removed from plots. Starting in December 2017, we measured snow depth in each plot approximately every three weeks.

Woody debris addition had no effect on the magnitude or timing of small-mammal activity. We constructed a linear mixed model that treated the number of photographs in each plot as a function of species, woody debris addition, and a species × woody debris interaction. This model included a random intercept term for site (n = 40 plots). The number of photographs in each plot was not affected by woody debris addition ($\beta = -1.83 \pm 32.71$, $F_{1,67} = 0.77$, $P = 0.38$), species ($\beta = 3.38 \pm 32.71$, $F_{1,67} = 0.68$, $P = 0.41$), or a species × woody debris interaction ($\beta = -1.61 \pm 32.21$, $F_{1,67} = 0.54$, $P = 0.46$). *Peromyscus leucopus* exhibited a similar shift to diurnal activity in plots with woody debris added and control plots with no woody debris (Fig. S5-S6). In our main text analysis, we used photograph data from plots with woody debris and woody debris controls (Fig. 1C-1F). Similarly, woody debris addition did not alter small-mammal heat loss. Using a linear mixed model with a random intercept for site, we modeled heat loss as a function of woody debris treatment (woody debris addition or control), time period (early or late winter), and species (*P. leucopus* or *M. gapperi*) and all possible interactions. There was no significant main effect of woody debris treatment ($\beta = 262.12 \pm 145.08$, $F_{1,12.8} = 0.51$, $P = 0.50$), nor significant interactions with time period ($\beta = 65.07 \pm 40.29$, $F_{1,12.0} = 0.23$, $P = 0.65$) or species ($\beta = -148.34 \pm 50.32$, $F_{1,942.6} = 0.27$, $P = 0.60$).

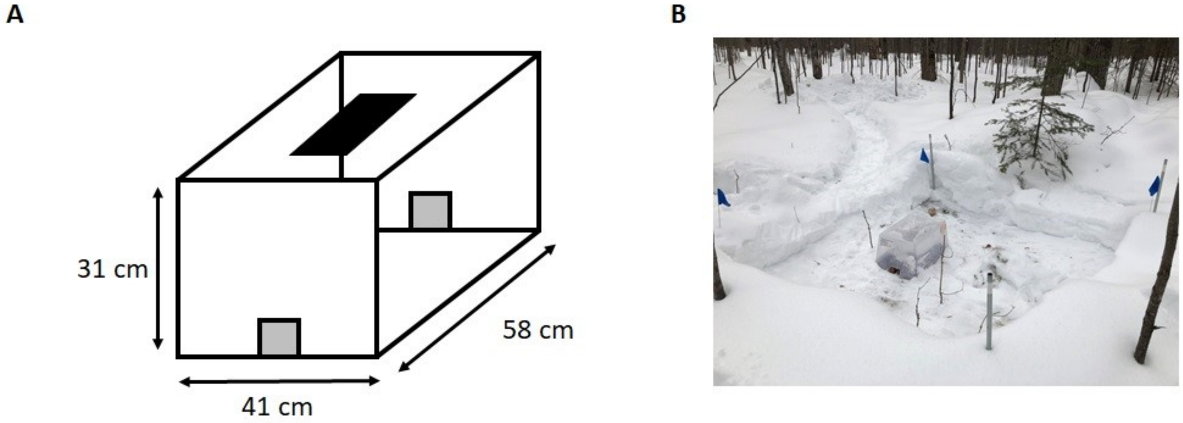


Fig. S4: A) Camera box design (adapted from Soininen *et al.* 2015). The camera box consisted of a transparent plastic box, with holes (grey) cut on either end to allow small mammals to pass through. A camera (black) was secured to two holes cut on the top of the box, allowing the camera to point down into the inside of the box. B) Photograph of a deployed camera box taken after the snow shoveling treatment began. Data were collected before the snow shoveling treatment began, spanning a period of snow accumulation from approximately 10 cm to 45 cm, so that the boxes were completely covered by snow at the end of the study.

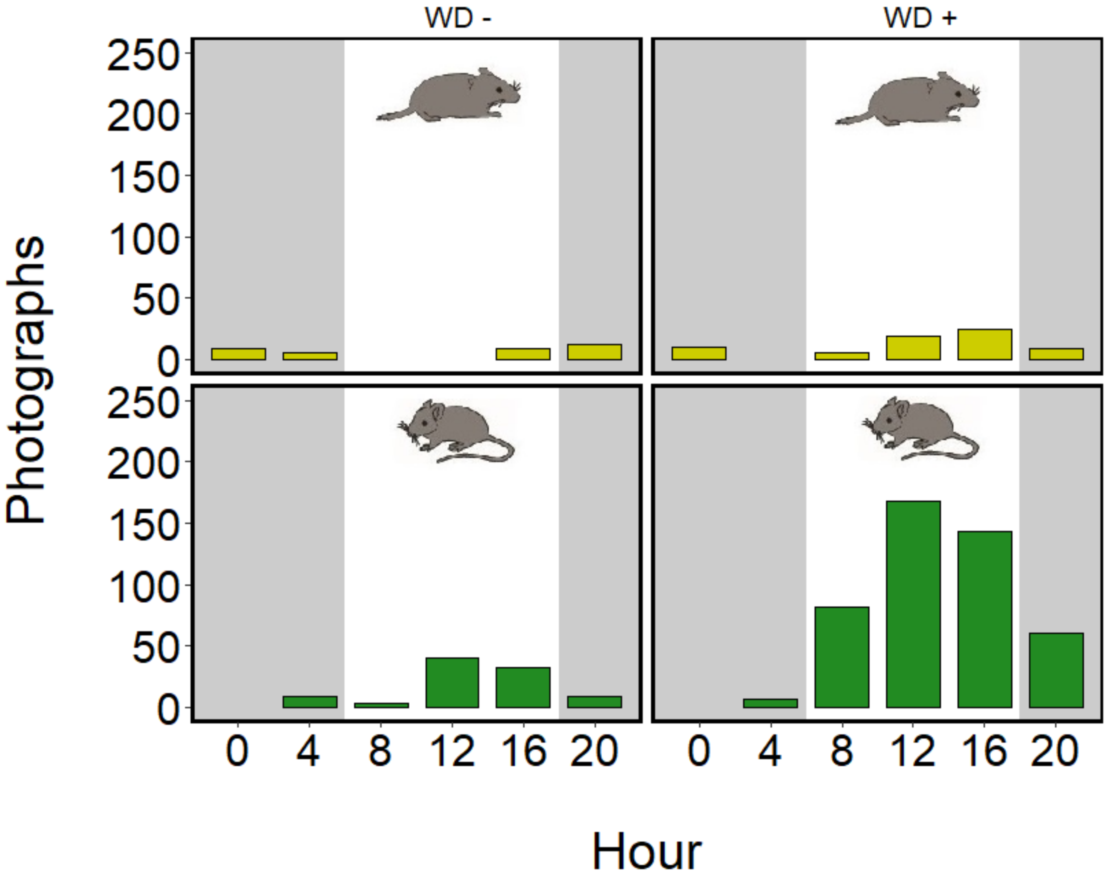


Fig. S5: Early winter diel activity patterns for *Myodes gapperi* (top row) and *Peromyscus leucopus* (bottom row) subset by woody debris treatment. Control plots with no woody debris added are shown in the left column, while woody debris addition plots are shown in the right column. Note that in both woody debris treatments, *P. leucopus* activity timing is primarily diurnal.

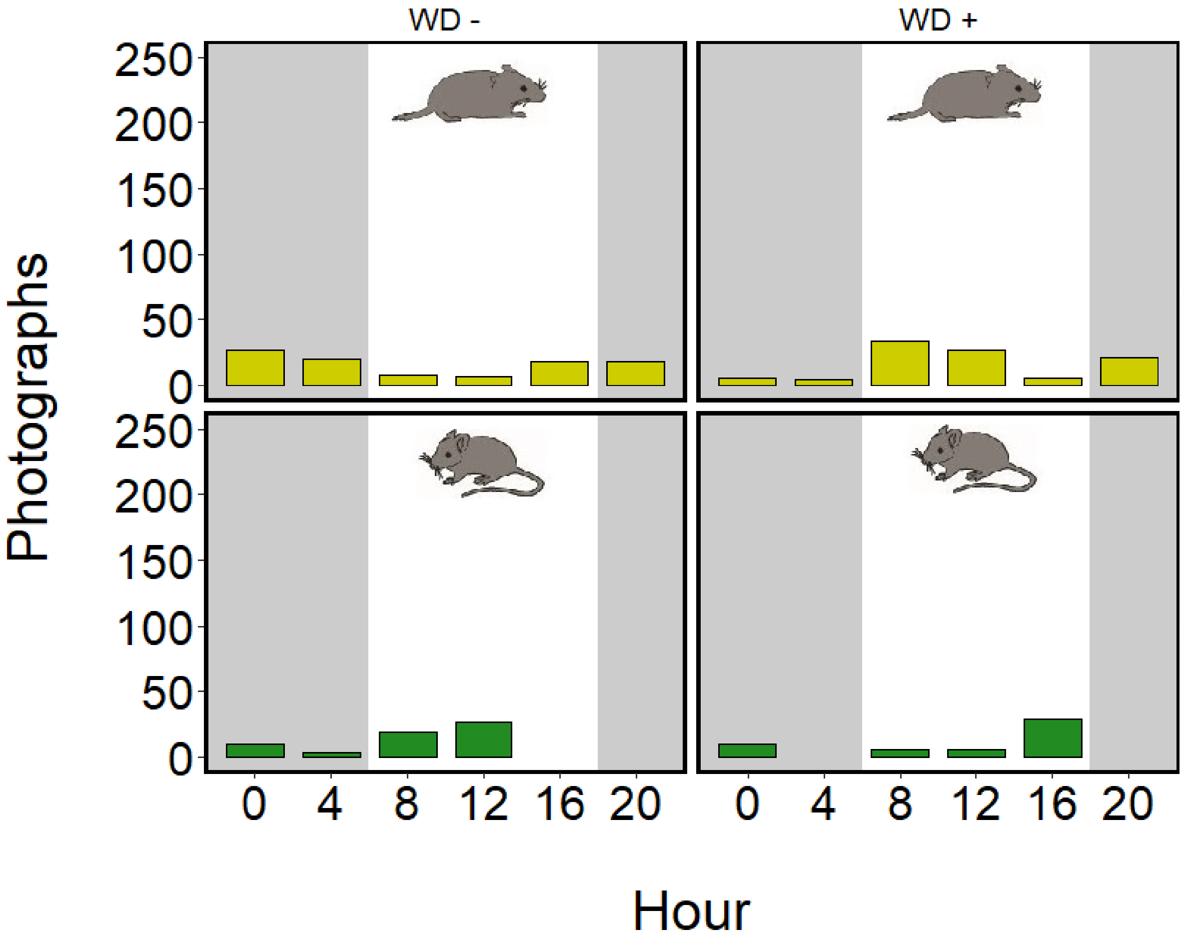


Fig. S6: Late winter diel activity patterns for *Myodes gapperi* (top row) and *Peromyscus leucopus* (bottom row) subset by woody debris treatment. Control plots with no woody debris added are shown in the left column, while woody debris addition plots are shown in the right column. Note that in both woody debris treatments, there is no distinct activity pattern for either species.

Calculating minimum and maximum possible heat loss

In order to understand whether small-mammal activity timing was optimal for reducing heat loss, we also estimated heat loss (Porter and Kearney 2009) at the warmest possible and coldest possible times observed at the same site within 24 hours of each photograph. Optimal activity timing should approach minimum possible heat loss, particularly when temperatures are low. We modeled the amount of energy lost as heat at the time of each photograph (i.e., iButton reading within two hours, "observed heat loss"), the maximum possible heat loss, and the minimum possible heat loss as function of species, time period, and a species × time period interaction (n = 3 models). We calculated estimated marginal means and 95% confidence intervals for each model using the "emmeans" package in R, which differs from ordinary marginal means by accounting for imbalanced designs (Lenth 2016, Table S2).

Given the colder average temperatures in early winter, the average heat loss at the coldest time of day was 6% greater in early winter (3996 ± 70 J) compared to late winter (3763 ± 63 J). Correspondingly, the estimated heat loss at the time of small-mammal activity was 4% greater in early winter (3633 ± 77 J), when the coldest temperatures occurred at night (Fig. 2B), compared to late winter (3501 ± 75 J, $F_{1,951.5} = 54.31$, $P < 0.001$), when minimum temperatures where warmer and there was less diel temperature fluctuation (Fig. 2B). A significant species × time period interaction ($F_{1,949.8} = 9.09$, $P = 0.002$) suggested that during early winter, *P. leucopus* heat loss (3604 ± 77 J, 10% less than mean heat loss at the coldest time of day) was slightly lower than *M. gapperi* heat loss (3662 ± 80 J, 8% less than mean heat loss at the coldest time of day; pairwise comparison: t = 2.49, P = 0.01, Fig. 2E). The difference in heat loss between the two species in late winter was not statistically significant (pairwise comparison: t = 1.68, P = 0.33, Fig. 2F). There was no main effect of species on heat loss ($F_{1,951.5} = 0.28$, $P = 0.59$). During both early winter and late winter, mean *M. gapperi* and *P. leucopus* heat loss estimated at the time of photographs did not differ from the minimum possible heat loss (Table S2).

Table S2: Estimated marginal means and 95% confidence intervals describing heat loss for small-mammal winter activity. Heat loss was determined using three models: one that estimated heat loss using the temperature data associated with each small-mammal photograph, one that estimated heat loss at the warmest time within a 24-hour period of each photograph, and one that estimated heat loss at the coldest time within a 24-hour period of each photograph. All models included main effects for species and time period (early vs. late winter), a species × time period interaction, and a random intercept term for site.

Model	Species	Time Period	Estimate marginal mean	Lower confidence limit (95% CI)	Upper confidence limit (95% CI)
Observed heat loss	*Myodes gapperi*	Early	3643	3533	3755
		Late	3470	3368	3576
	Peromyscus leucopus	Early	3632	3527	3740
		Late	3523	3418	3632
Lowest possible heat loss	*Myodes gapperi*	Early	3570	3428	3718
		Late	3344	3212	3482
	Peromyscus leucopus	Early	3441	3305	3582
		Late	3418	3282	3560
Highest possible heat loss	*Myodes gapperi*	Early	3994	3856	4137
		Late	3762	3637	3891
	Peromyscus leucopus	Early	3997	3859	4140
		Late	3764	3639	3893

Detailed model results

Table S3: Estimated marginal means and 95% confidence intervals comparing heat loss on days when small mammals were active to days when small mammals were not active, based on mean daily temperatures. Heat loss for a given day was modeled as a function of time period (early versus late winter), species, whether or not a small mammal was active (i.e., whether species were photographed), and all possible interactions. The model also included a random intercept term for site. For full model description, see the main text Methods.

Species	Time Period	Active or Inactive?	Estimate marginal mean	Lower confidence limit (95% CI)	Upper confidence limit (95% CI)
Myodes gapperi	Early	Active	3568	3389	3748
		Inactive	3945	3801	4089
	Late	Active	3462	3289	3635
		Inactive	3523	3374	3671
Peromyscus leucopus	Early	Active	3746	3558	3933
		Inactive	3920	3776	4063
	Late	Active	3490	3306	3674
		Inactive	3512	3364	3660

Table S4: Estimated marginal means and 95% confidence intervals describing heat loss for small-mammal winter activity, comparing heat loss at the time of activity to heat loss at a random time at night. Heat loss was modeled as a function of time period (early versus late winter), species, activity timing (observed activity or random nocturnal activity), and all possible interactions. The model also included a random intercept term for site. For full model description, see the main text Methods.

Species	Time Period	Activity timing	Estimate marginal mean	Lower confidence limit (95% CI)	Upper confidence limit (95% CI)
Myodes gapperi	Early	Observed	3750	3698	3802
		Random	3861	3809	3912
	Late	Observed	3533	3496	3571
		Random	3502	3464	3539
Peromyscus leucopus	Early	Observed	3741	3719	3763
		Random	3904	3882	3926
	Late	Observed	3604	3554	3654
		Random	3602	3552	3652

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