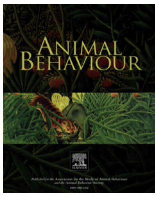
Animal Behaviour 164 (2020) 181–192

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Seasonal shifts in activity timing reduce heat loss of small mammals during winter

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ARTICLE INFO

Article history:
Received 14 January 2020
Initial acceptance 9 March 2020
Final acceptance 18 March 2020

MS. number: A20-00031

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

All activity imposes 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 (white-footed mouse, *Peromyscus leucopus*) shifted to diurnal activity in early winter, which reduced potential heat loss by 4%. The southern red-backed vole, *Myodes gapperi*, 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 h and multiday 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.

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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 (Abu Baker & Brown, 2014; Bennie, Duffy, Inger, & Gaston, 2014; Kronfeld-Schor & Dayan, 2003; 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, Duffy, & Bennie, 2015). Recent evidence also documents the importance of activity timing in the context of rapid environmental change, such as invasive species (Guiden & Orrock, 2019), climate change (Levy, Dayan, Porter, & Kronfeld-Schor, 2019) and anthropogenic light (Gaston, Davies, Nedelec, & Holt, 2017; Hopkins, Gaston, Visser, Elgar, & Jones, 2018); such shifts in activity timing may influence population viability and competitive interactions and lead to the emergence of novel predator–prey dynamics (Gaynor, Hojnowski, Carter, & Brashares, 2018; Guiden, Bartel, Byer, Shipley, & Orrock, 2019).

Despite an emerging understanding that activity timing can exhibit important seasonal dynamics (Guiden & 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 & Fuller, 1972), decreases resource availability (Guiden et al., 2019) and insulates air temperatures (‘subnivium’ formation; Pauli, Zuckerberg, Whiteman, & Porter, 2013) – all of which might influence animal decisions about when to be active (Kronfeld-Schor & Dayan, 2003). Activity patterns under snow might therefore differ greatly from those during the growing season. While winter is commonly described as a season of energy deficits (Marchand, 1987; Williams, Henry, & Sinclair, 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 & Kotler, 2004; Gaynor, Brown, Middleton, Power, & Brashares, 2019). Metabolic costs of

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https://doi.org/10.1016/j.anbehav.2020.04.014
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foraging in cold environments can be extreme, especially for small homeotherms (Conley & 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 & 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 (white-footed mouse, *Peromyscus leucopus*, and southern red-backed vole, *Myodes gapperi*) minimize heat loss, using a novel method of monitoring subnivean ('below-snow') foraging activity (Soininen, Jensvoll, Killengreen, & Ims, 2015). Our data reveal unexpected shifts in the activity timing of small mammals between summer and winter, highlighting the importance of behaviour 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, U.S.A. The 10 sites spanned a 45 km latitudinal gradient (45°48′N – 46°7′48″N). Data were collected concurrently with an experiment investigating responses of small mammals to changes in snow depth and woody debris (Guiden, 2019; see Appendix). We monitored winter foraging activity of small mammals with four subnivean camera

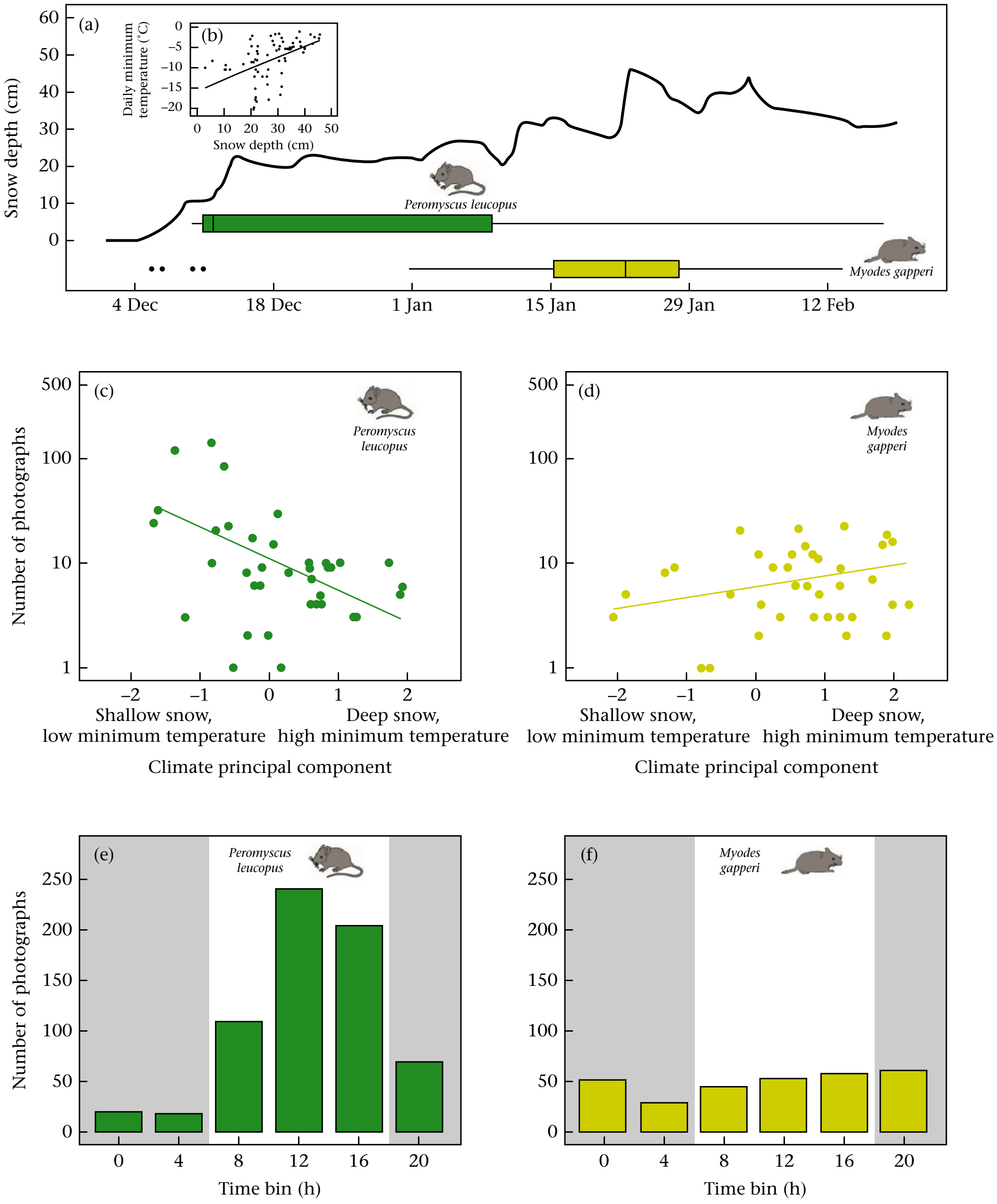

Figure 1. (a) Snow depth for each day of the study. Box plots represent the distribution of *Peromyscus leucopus* and *Myodes gapperi* photographs through time. (b) Daily minimum temperature as a function of snow depth. (c) Number of *P. leucopus* and (d) *M. gapperi* photographs per site per day as 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 h intervals across nocturnal (grey) and diurnal (white) activity.

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 × 41 cm and 31 cm tall), with 10 × 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, Zuckerberg, & Pauli, 2015; Zuckerberg & 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*; Cramer, 2014; Schnurr, Canham, Ostfeld, & Inouye, 2004; Schnurr, Ostfeld, & Canham, 2002) in the leaf litter below each camera (Guiden, 2019). Camera traps did not bias activity timing of small mammals 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).

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, U.S.A.; mean distance from study sites: 18.44 km) and provided an excellent fit to field measurements of snow depth ($r^2_{46.77} = 0.83$, $P = 0.005$; Guiden, 2019). Each camera box included an iButton thermochron (Maxim Integrated, San Jose, CA, U.S.A.) suspended 15 cm above the soil, which measured air temperature every 4 h to quantify thermal conditions experienced by small mammals foraging within the box. Because snow depth and daily minimum temperatures were strongly correlated (Pearson correlation: $r_{73} = 0.56$, $P < 0.001$; 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 modelled 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: (1) the probability of small mammals being active or not (i.e. the zero-inflation model), and (2) for active small mammals, the magnitude of activity on a given day (i.e. the conditional model). Both the zero-inflation model and the conditional model described *M. gapperi* and *P. 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 2 h) of each small mammal photograph. Heat loss (W) 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 & Kearney, 2009). We multiplied heat loss by 3600 s to estimate the amount of energy (J) a small mammal would lose as heat during 1 h 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. We chosen 22 January 2018 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 (see Results, Fig. 2a, b). 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 h 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, Maechler, Bolker, & Walker, 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. Fifty-five per cent 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* ($N = 296$), woodland jumping mouse, *Napaeozapus insignis* ($N = 5$) and *Sorex* spp. ($N = 2$).

At a multiday 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* 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: *P. leucopus* were primarily observed

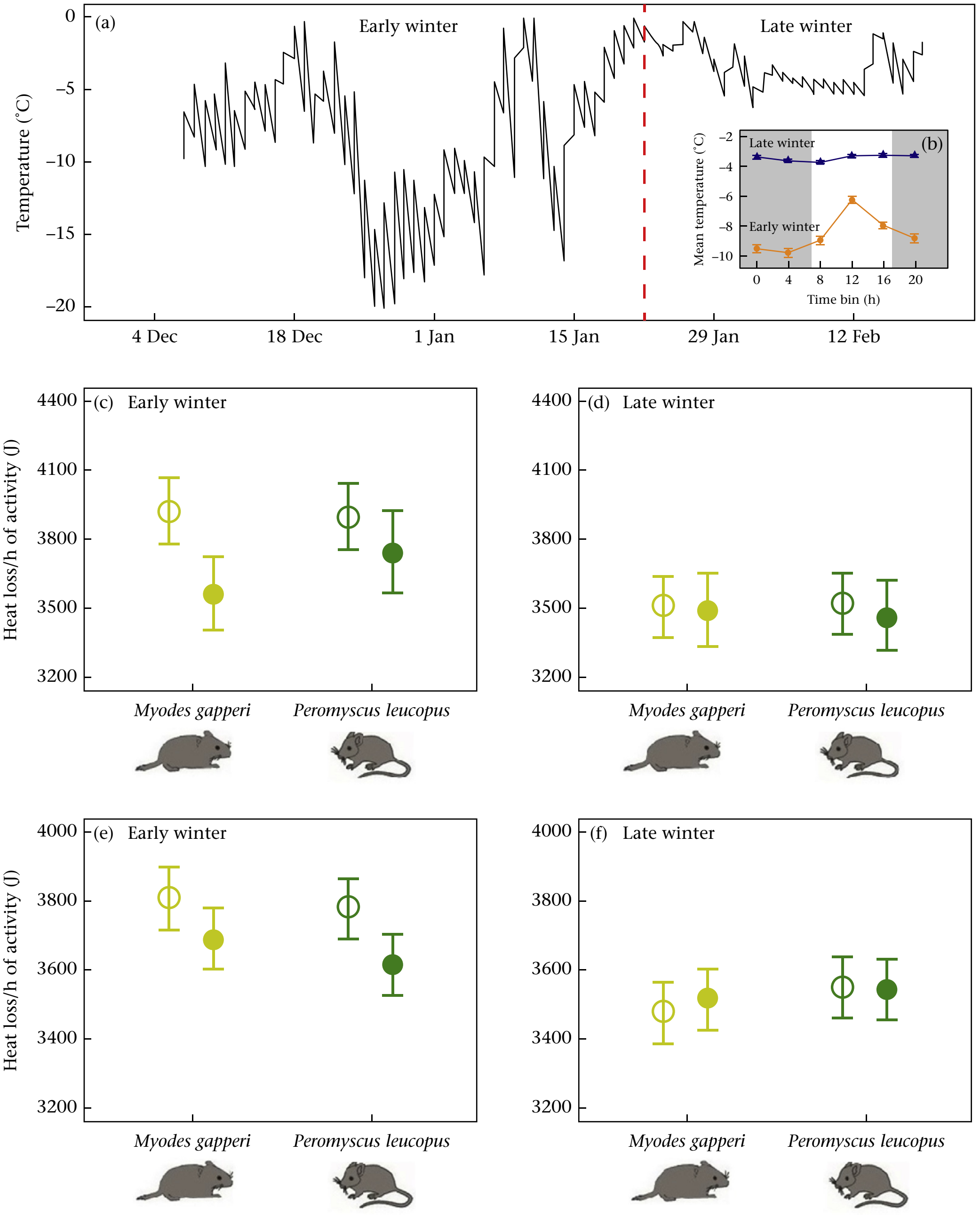

Figure 2. (a) Maximum and minimum temperatures for each day of the study averaged across all sites. (b) Diel temperature profiles, showing nocturnal (grey) and diurnal (white) activity, for early winter (before 22 January 2018, orange points) and late winter (after 22 January 2018, blue points) averaged across all sites and dates. Estimated heat loss in (c) early winter and (d) late winter based on mean daily temperatures for *Peromyscus leucopus* and *Myodes gapperi*. Points represent estimated marginal means for days where activity was not observed (open circles) and days where activity was observed (closed circles). Estimated heat loss during (e) 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 2 h, 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 h of each photograph (open circles). All error bars represent 95% confidence intervals.

between 0800 and 1600 hours (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 (Tables A3, A4).

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 & 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–f) minimizes metabolic costs imposed by activity during winter (Fig. 2e, f). *Peromyscus leucopus*, a ubiquitous small mammal that is considered nocturnal across its range in eastern North America (Bruseo & Barry, 1995; Guiden & Orrock, 2019; Jackson, 1961; Whitaker & Hamilton, 1998; 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, Shine, & Porter, 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, Logan, Simon, Chmura, & Millien, 2013). Daytime winter temperatures may best predict habitat suitability for species responding to temperature on a 24 h scale, such as *P. leucopus*, whereas mean daily temperatures may best predict habitat suitability for species responding on a multiday scale, such as *M. gapperi* (Fig. 2c, d). Without accounting for species-specific behavioural 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–f).

The different behavioural strategies used 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 it 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 behaviour (Fig. 1e), leading to an estimated 4.4% reduction in heat loss compared to 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 (Figs. 1d, Figs. 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 & Lynch, 1997) and impaired immune responses (Nelson & 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 were unable to distinguish among individual *P. leucopus*. Future research could use PIT tags or live trapping to determine whether individual states (e.g. age or physiology; Clark, 1994) or behavioural syndromes (e.g. bold individuals; Sih, Bell, & Johnson, 2004) make 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, Boal, & Andersen, 2005) during winter. Additionally, in the absence of a subnivium, competition between *P. leucopus* and *M. gapperi* (Lemaître, Fortin, Morris, & Darveau, 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 behaviour. 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 defence (Ostfeld, 1985). Additionally, the degree to which this behavioural plasticity is taxonomically widespread remains unclear. Identifying which species respond at 24 h temporal scales versus multiday temporal scales to avoid high metabolic costs may help anticipate species responses to climate change (Kearney et al., 2009). It also remains unknown whether predators of small mammals shift their activity patterns to track their prey, or whether climate change (Creel, Creel, Creel, & Creel, 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), behavioural plasticity in activity timing may become an increasingly important strategy to avoid extremely cold temperatures.

Conflict of Interest

None.

Acknowledgments

We thank the University of Wisconsin-Madison (UW) Trout Lake Field Station and the UW Arboretum for supporting field work. R. Eddy and W. Wood provided assistance with field experiments; S. Bartel, B. Connolly and J. Cruz provided helpful comments on earlier drafts of this manuscript. J. Guiden contributed illustrations for the figures. This work was funded by a National Science Foundation (NSF) Dissertation Improvement Grant (DEB-1701506). P.W.G. was supported by an NSF IGERT award (DGE-1144752) and by the Wisconsin Alumni Research Foundation; J.L.O. was supported by a UW Vilas Fellowship.

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Appendix

Summer Live-capture and Activity Data

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 × 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 prebaited 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 & Anderson, 2007). Traps were deployed for four consecutive nights and checked around sunrise. All captured animals were identified to species, and given an eartag with a unique number. Protocols for small mammal live trapping were approved by the Institutional Animal Care and Use Committee of the University of Wisconsin-Madison (IACUC No. L005041).

During summer live trapping, we observed 240 capture events representing 114 unique individuals and seven taxa (Table A1). *P. leucopus* was captured the most frequently at these sites ($N = 119$ captures) followed by *Tamias striatus* ($N = 43$ captures), *M. gapperi* ($N = 30$ captures) and *Peromyscus 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 number of individual *Peromyscus* spp. captured, M_{t+1} (i.e. Slade & 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 *P. 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, the number of individual *M. gapperi* captured during 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, Anderson, Wendt, & Meece, 2014), we did not attempt to distinguish between these species in our photograph analysis. 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 nine sites with only *P. leucopus*. Excluding the site with both *P. leucopus* and *P. maniculatus* does not qualitatively change our results (Fig. A1). 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.

Camera Boxes Did Not Modify Peromyscus leucopus *Behaviour*

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 artefact of refuge introduced by our camera boxes, we deployed cameras in a snow-free environment. Cameras were deployed for 1 week, starting 14 April 2019, at a temperate forest at the University of Wisconsin Arboretum (43°2′34″N, 89°25′27″W). *Peromyscus leucopus* are the dominant small mammal species at the arboretum, but *P. maniculatus* does not occur in this study area (Guiden & Orrock, 2019). As expected, *P. leucopus* were almost exclusively nocturnal in the absence of snow at the University of Wisconsin Arboretum (Fig. A2), compared to the strong shift to diurnal activity underneath snow during winter at the northern Wisconsin site (Fig. A2, Fig. 1e, f).

Analysis of Unidentified Animals

Because we could not identify the small mammal species in some 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. A3). Rather, photographs showed a mix of activity peaks in early and late winter (Fig. A3a), and a mix of diurnal and nocturnal activity (Fig. A3b). For comparison, we provide similar figures with *P. leucopus* and *M. gapperi* activity combined showing the date (Fig. A4c; data from Fig. 1A) and hour (Fig. A4d; data from Fig. 1c, d) of activity from photographs where 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.

Camera Trap Set-up, Woody Debris Manipulation and Snow Removal Experiment

We attached motion-activated cameras (Bushnell Essential E3, Overland Park, KS, U.S.A.) to a transparent plastic box, so that the camera was suspended approximately 31 cm above the soil surface, facing the soil (Fig. A4). 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 behaviour. We cut out a 10 × 10 cm hole cut on two ends of the box, allowing small mammals to freely pass through. This box was placed in the centre 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. To reduce washout 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 (1) small mammal abundances declining over winter (Merritt & Merritt, 1978), or (2) depletion of food resources in our patches (Brown & Kotler, 2004). Alternatively, disturbance caused by our snow shovelling 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 shovelling 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 × 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 nonfunctional 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 × 10 × 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 3 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 (Figs A5, A6). In our main text analysis, we used photograph data from plots with woody debris and woody debris controls (Fig. 1c–f). Similarly, woody debris addition did not alter small mammal heat loss. Using a linear mixed model with a random intercept for site, we modelled 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 ($\beta = 262.12 \pm 145.08$, $F_{1,12.8} = 0.51$, $P = 0.50$) and no significant interaction with time period ($\beta = 65.07 \pm 40.29$, $F_{1,12.0} = 0.23$, $P = 0.65$) or species ($\beta = -148.34 \pm 50.32$, $F_{1,942.6} = 0.27$, $P = 0.60$).

Calculating Minimum and Maximum Possible Heat Loss

To understand whether timing of small mammal activity was optimal for reducing heat loss, we also estimated heat loss (Porter & Kearney, 2009) at the warmest and coldest possible times observed at the same site within 24 h of each photograph. Optimal activity timing should approach minimum possible heat loss, particularly when temperatures are low. We modelled the amount of energy lost as heat at the time of each photograph (i.e. iButton reading within 2 h, ‘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 A2).

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 was slightly lower (3604 ± 77 J, 10% less than mean heat loss at the coldest time of day) than *M. gapperi* heat loss (3662 ± 80 J, 8% less than mean heat loss at the coldest time of day; pairwise comparison: $t_{914.5} = 2.49$, $P = 0.01$; Fig. 2e). The difference in heat loss between the two species in late winter was not statistically significant (pairwise comparison: $t_{915.2} = 1.68$, $P = 0.33$; 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 A2).

Table A1
Comparison of summer live captures and winter photographs for several northern temperate small mammal species

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

Measurements of activity for each species are pooled from 10 sites.

Table A2
Estimated marginal means and 95% confidence intervals describing heat loss of small mammals during winter activity

Model/Species	Time period	Estimated 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

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 h period of each photograph, and one that estimated heat loss at the coldest time within a 24 h period of each photograph. All models included main effects for species and time period (early versus late winter), a species∗time period interaction, and a random intercept term for site.

Table A3
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

Species	Time period	Active/ Inactive	Estimated 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

Heat loss for a given day was modelled 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 Methods in the main text.

Table A4
Estimated marginal means and 95% confidence intervals describing heat loss for small mammals during winter activity, comparing heat loss at the time of activity to heat loss at a random time at night

Species	Time period	Activity timing	Estimated 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

Heat loss was modelled 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 Methods in the main text.

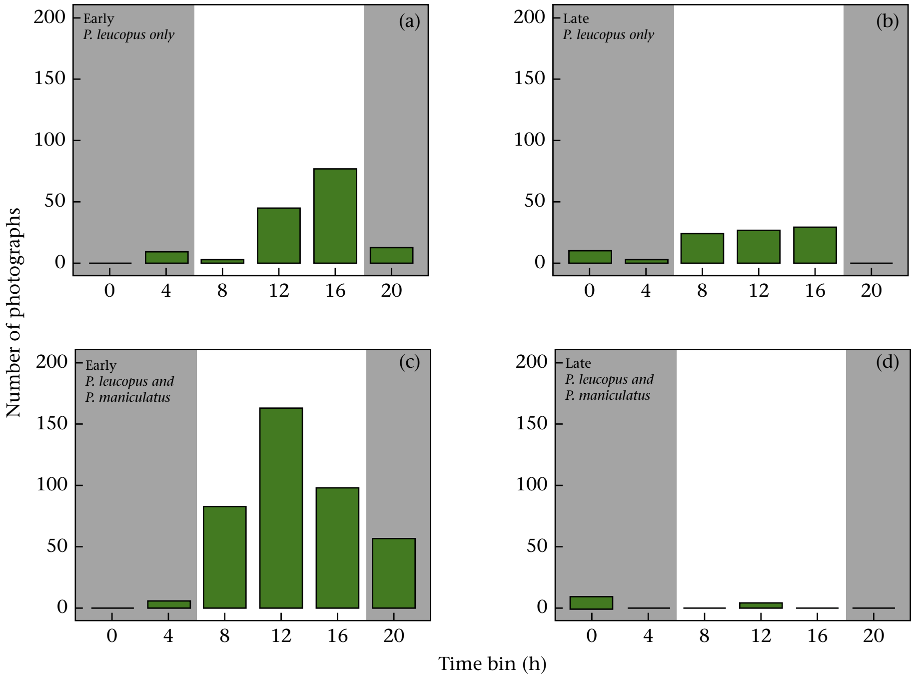

Figure A1. Diel activity patterns (nocturnal: grey; diurnal: white) during winter determined by photographs of *Peromyscus* spp. taken (a, b) at sites where only *P. leucopus* was captured ($N = 9$) and (c, d) at the one site where both *P. leucopus* and *P. maniculatus* were captured in early winter and late winter, respectively.

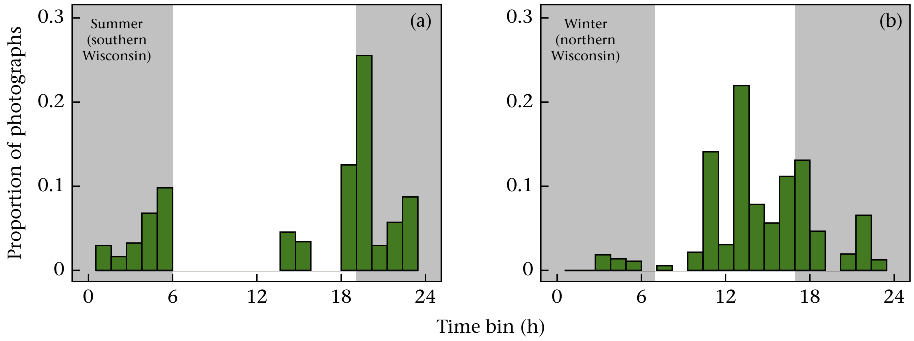

Figure A2. Comparison of diel activity patterns (nocturnal: grey; diurnal: white) for (a) *Peromyscus leucopus* in summer (14 April 2019 to 21 April 2019) and (b) *Peromyscus maniculatus* and *P. leucopus* in winter (7 December 2017 to 20 February 2018). Summer photographs were taken at the University of Wisconsin Arboretum (43°2′34″N, 89°25′27″W).

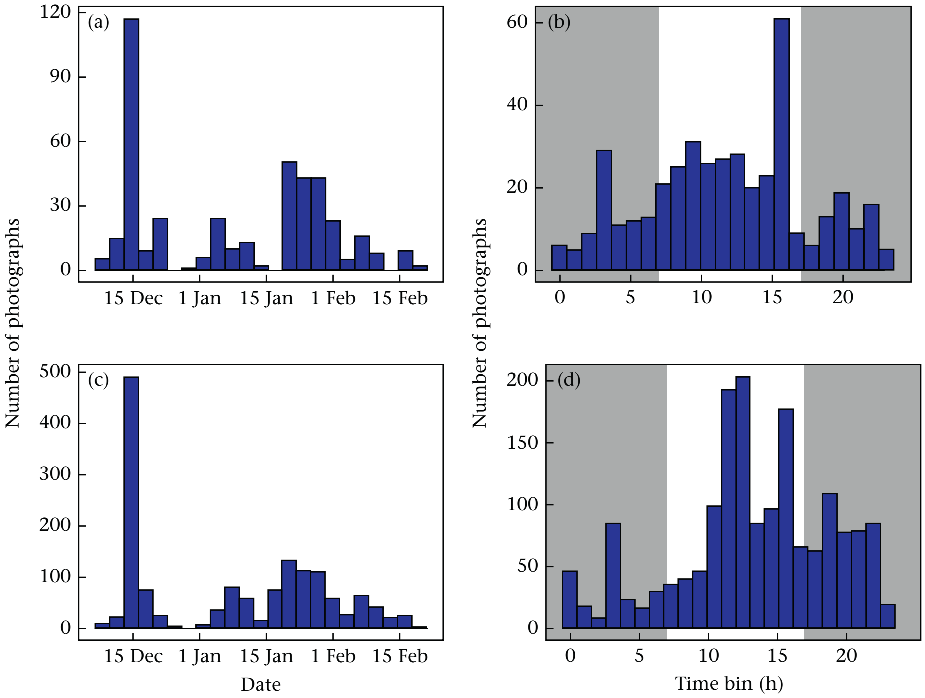

Figure A3. Temporal distributions of photographs of unidentified animals ($N = 425$) at (a) seasonal and (b) diel scales, showing nocturnal (grey) and diurnal (white) activity. Most photographs are likely from *Peromyscus leucopus* and *Myodes gapperi* (see main text), and therefore represent a combination 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.

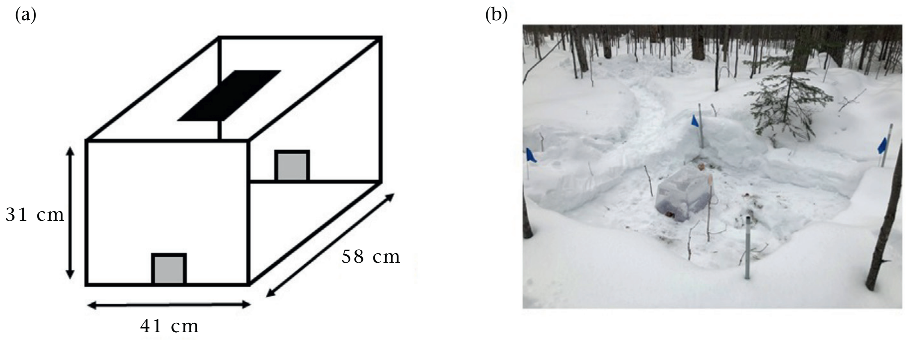

Figure A4. (a) Camera box design (adapted from Soininen et al., 2015). The camera box consisted of a transparent plastic box, with holes (grey) cut on either end to allow small mammals to pass through. A camera (black) was secured to two holes cut on the top of the box, allowing the camera to point down into the inside of the box. (b) Photograph of a deployed camera box taken after the snow shovelling treatment began. Data were collected before the snow shovelling 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.

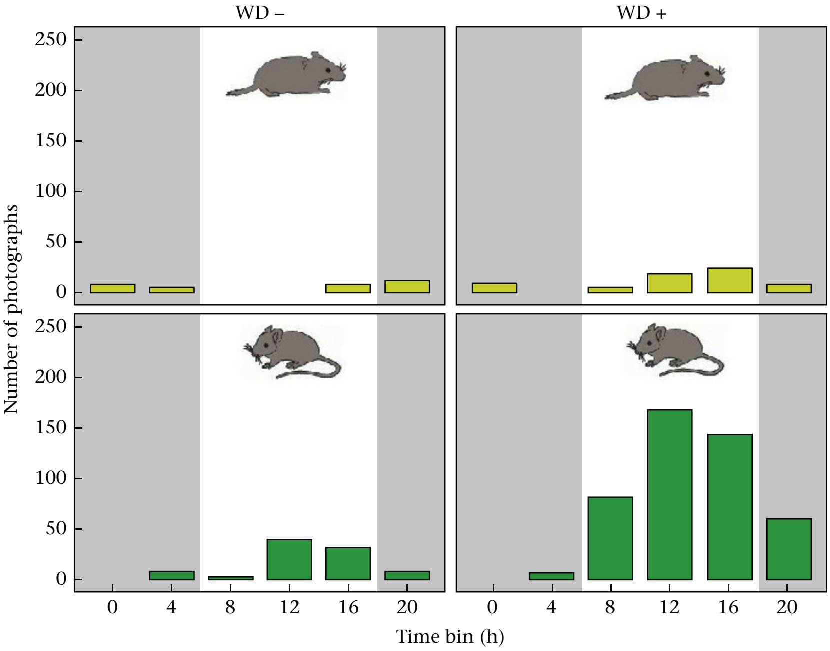

Figure A5. Early winter diel activity patterns (nocturnal: grey; diurnal: white) for *Myodes gapperi* (top row, yellow bars) and *Peromyscus leucopus* (bottom row, green bars) subset by woody debris treatment. Control plots with no woody debris added are shown in the left column (WD -); woody debris addition plots are shown in the right column (WD +).

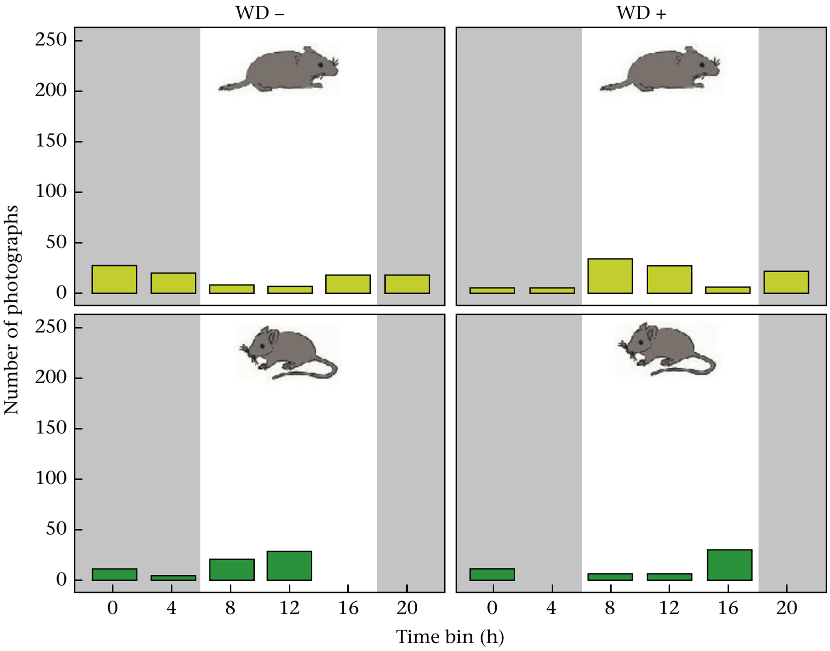

Figure A6. Late winter diel activity patterns (nocturnal: grey; diurnal: white) for *Myodes gapperi* (top row, yellow bars) and *Peromyscus leucopus* (bottom row, green bars) subset by woody debris treatment. Control plots with no woody debris added are shown in the left column (WD -); woody debris addition plots are shown in the right column (WD +).