Changing Winters: the Effects of Snow and Land Cover on the Behavior, Physiology, and Survival of Ruffed Grouse

By

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To all the girls who love exploring and watching birds

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Dissertation Abstract

In temperate regions, winter is a time of scarcity during which animals must balance the need to find food, evade predators, and survive freezing temperatures. In doing so, animals display an array of adaptations ranging from seasonal migration to flexible overwintering strategies, including seeking out unique winter environments, such as the subnivium, or the microhabitat under the snowpack that provides a thermally stable environment and acts as a buffer from extreme winter weather. Little attention has been given to why some species flexibly use winter microrefugia, such as the subnivium, or the ecological conditions that drive this flexibility, particularly in the context of warming winters and the loss of seasonal snow cover due to climate change. The overarching goal of this dissertation is to provide greater insight into the use of the subnivium by a winter-adapted bird, the ruffed grouse (*Bonasa umbellus*), and whether behavioral plasticity can mediate the physiological and demographic costs of exposure to dynamic winter weather.

Each chapter of this dissertation is written and formatted for publication as a manuscript in a peer-reviewed journal. **Chapter 1** (prepared for *Behavioral Ecology*) examines the winter weather conditions that are associated with snow burrowing behavior and subnivium use by grouse. We monitored ruffed grouse roosting behavior in central Wisconsin using radio telemetry, and found non-linear relationships between roosting behavior and snow conditions: grouse were more likely to roost in snow burrows when snow was deep and powdery. Further, grouse experienced warmer temperatures in snow burrows than in other roost types. **Chapter 2** (Shipley et al. 2019, *Oecologia*) explores how behavioral flexibility and winter temperatures mediate grouse physiological stress, which is associated with both thermoregulation and perceived risk of predation. We measured ruffed grouse fecal corticosterone metabolites (FCMs),

a measure of stress, and found that FCMs were elevated at cold temperatures, but when grouse roosted in snow burrows they were effectively buffered from this cold-associated stress response. FCMs were high when snow was shallow but decreased rapidly as snow depth surpassed 20 cm; this is one of the first studies to explore how winter weather influences stress in a free-living cold-adapted vertebrate and its ability to mediate this relationship behaviorally. **Chapter 3** (prepared for *Landscape Ecology*) expands upon Chapter 2, and asks how winter weather interacts with land cover to influence physiological stress and create a landscape of stress, or “stress-scape”. Despite considerable spatiotemporal variation in snow depth, snow density, and temperature, we found regions across the landscape where grouse displayed highly predictable, consistently elevated FCM levels Finally, **Chapter 4** (Shipley et al. 2020, *Proceedings of the Royal Society B*) examines how grouse select their winter habitat and how individual personality mediates selection and influences overwinter survival. Grouse generally selected deeper snow and warmer areas, and those individuals found in shallower snow were less likely to survive the winter. Individuals that selected deep snow, however, improved their survival suggesting that the demographic consequences of selecting winter refugia are mediated by differences in personality.

This dissertation provides important insights into the extent that behavioral flexibility and use of a deteriorating winter microrefugium influence stress physiology and the demographics of a winter-adapted species. Loss of winter microrefugia due to warming winters and climate change may severely limit the use of behavioral flexibility for winter-adapted species.

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Seeking shelter: winter weather constrains the behavioral flexibility of a winter-adapted bird

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Prepared for *Behavioral Ecology*

Abstract

Behavioral flexibility is an important way in which animals respond to changing environmental conditions. Seeking out and accessing microrefugia is an important behavior that can protect animals from inclement weather, predation, and periods of rapid environmental change. During winter, snow is an important seasonal microrefugium that provides thermal insulation and protects overwintering species from predators. However, snow depth and quality can be highly variable throughout the winter, and it is unclear how species that use snow cover as a microrefugium adjust their behavior with changing environmental conditions and in complex landscapes. We documented roosting behavior of a winter-adapted bird, the ruffed grouse (*Bonasa umbellus*), and found significant non-linear relationships between roosting behavior and snow conditions: grouse were more likely to use snow burrows when snow was deep and powdery. Further, grouse experienced warmer temperatures in snow burrows than in other roost types. Contrary to our predictions, cover types did not influence snow roosting behavior, and grouse were not more likely to use snow burrows at colder temperatures, potentially because snow roosting may serve to protect grouse from predators in addition to serving as thermal refugia. However, both the snow conditions necessary for snow roosting, and the occurrence of snow roosting behavior, were relatively rare and declined over the course of our study. Loss of winter microrefugia due to warming winters and climate change may severely limit the use of behavioral flexibility for winter-adapted species.

Introduction

Phenotypic plasticity is a crucial pathway by which animals respond to changing environmental conditions (Piersma and van Gils 2011). Animals can respond to shifting environmental conditions in a variety of ways, including phenologically (e.g., altering the timing of migration, (Koleček, Adamík and Reif 2020), physiologically (e.g., lowering energy expenditure (Humphries et al. 2005) or increasing summit metabolic rates (Cooper 2002), or morphologically (e.g., increasing fat stores (Pokallus and Pauli 2016). However, responding to extremes in environmental conditions through behavioral flexibility may be particularly important (Sih et al. 2010, Beever et al. 2017). Responding behaviorally to environmental change may be advantageous because behavior is reversible over short time periods, and individuals are not committing to particular phenotypes when the future is uncertain (Chevin, Lande and Mace 2010). For example, desert wood rats (*Neotoma lepida*) shift the timing of when they leave their dens so they are not exposed to ambient night temperatures that are above their lethal physiological threshold (Murray and Smith 2012). Similarly, American Pikas (*Ochotona princeps*), which typically rely on cooler talus areas, are increasingly shifting to cooler forests to avoid extreme daytime temperatures (Beever et al. 2017).

Seeking out microrefugia, or localized patches of milder or more stable conditions, that can buffer animals from unsuitable climate, may be an important behavioral adaptation in a changing world. As such, the availability of microrefugia and the behaviors that promote the use of those refugia is important, especially if trade-offs with other competing behaviors exist. Microrefugia can naturally moderate climate extremes, and both terrestrial and aquatic animals often select microhabitats, such as rock interstices (Hall et al. 2016) or tree cavities (Coombs, Bowman and Garroway 2010). In fact, the degree to which microrefugia moderate the outside environment during the warm season is even more important than other habitat characteristics for predicting the occurrence of American Pika (Hall et al. 2016). The use of microrefugia are also important for reptiles that respond to warming ambient temperatures by sheltering to maintain body temperatures (Valdecantos et al. 2013, Carter, Goldizen and Heinsohn 2012). However, increased time spent inside refugia as an escape from extreme conditions may limit time spent on other important behaviors, such as foraging (Murray and Smith 2012).

Microrefugia may be particularly important in winter, which in temperate ecosystems is a time of resource scarcity and shifting environmental conditions. Reduced access to food and extreme cold results in increased energy expenditure (Shipley et al. 2019) and exposure to predators as a result of more time spent in the open foraging (Lima 1986). During the winter months, areas with warmer microclimates are associated with higher basal area in forests (Suggitt et al. 2011, Ashcroft and Gollan 2012, Ford et al. 2013), higher elevations due to cold air pooling (Sears, Raskin and Angiletta Jr 2011), or more contiguous forested landscapes (Latimer and Zuckerberg 2016). In temperate areas, snow cover provides important microrefugia that insulates and protects many species from harsh winter weather (Pauli et al. 2013). Deep snow can reduce physiological stress associated with cold temperatures (Shipley et al. 2019), and can increase survival for snow-adapted species, such as the ruffed grouse (Shipley, Cruz and Zuckerberg 2020). However, unlike land cover, snow is ephemeral (Thompson et al. 2018). The flexibility to seek cover and access ephemeral microrefugia may be more or less important in different environments where more predictable and persistent microrefugia exist. Temperature, snow depth, and snow density all change throughout the course of the winter, but it is unclear how species that use snow cover as a microrefugium adjust their behavior with changing environmental conditions.

Ruffed grouse are a winter-adapted bird species associated with temperate forests of North America. In winter, grouse can spend up to 80% of their time sedentary: roosting in trees, on the ground or on top of the snow, or completely or partially below the snow in snow burrows or snow bowls (Bump et al. 1947). Snow burrows are thought to provide superior insulation relative to other roost sites (Thompson and Fritzell 1988), allowing grouse to remain within their thermo-neutral temperature range (Marjakangas, Rintamaki and Hissa 1984), and are used by a number of species in the order *Galliformes*, including black grouse (Marjakangas et al. 1984), capercaillie (Marjakangas et al. 1984), partridge (*Perdix perdix;* Westerskov 1965), willow ptarmigan (Irving 1960) and greater sage-grouse (Back, Barrington and McAdoo 1987). Use of deep snow and roosting in snow burrows is an important behavioral adaptation that reduces physiological stress in ruffed grouse (Shipley et al. 2019), influences habitat selection (Shipley et al. 2020), and increases overwinter survival (Shipley et al. 2020). However, it is unclear how winter weather conditions and land cover interact to influence the behavioral decisions of grouse to use microrefugia at a given location, and in turn, how these behavioral decisions influence grouse exposure to cold temperatures.

We tested the hypotheses that winter temperature, snow depth, snow density and land cover influence behavioral shifts towards the use of thermal microrefugia, and that behavioral flexibility would mediate exposure to cold winter temperatures. Specifically, we predicted: *i*) snow roosting behavior would be more likely with increasing snow depth, more powdery snow, and colder temperatures; *ii*) snow roosting would be more likely in open habitat where there is less forest cover and fewer alternative microrefugia (such as tree roosts); and *iii*) grouse using snow roosts would experience reduced exposure to cold ambient temperatures.

Methods

Study site

Sandhill Wildlife Area (SWA; 44˚18´N, 90˚07´W) is a 3700 ha state wildlife area in central Wisconsin, and is a study site for a number of long-term monitoring programs for winter-adapted species. Vegetation at SWA is a mosaic of forested red and white pine (*Pinus resinosa* and *P. strobus*), tag alder (*Alnus serrulata*), aspen (*Populus tremuloides* and *P. gradidentata*), and oak (*Quercus* sp.), fragmented by open water and marshes. There were on average 47 winter nights each year when snow depth exceeded 20 cm (range 0-101 nights) between 2001-2015. Mean winter (December-March) temperature at SWA is − 9 °C ± 10.0 °C (range − 26.5 to 5.5 °C).

Grouse trapping, radio telemetry, and roost site observations

From September-November (2015-2017), we captured ruffed grouse in walk-in pens connected to drift fences made from chicken wire (Gullion 1965). We collected morphological measurements, identified age and sex of each grouse (Hale, Wendt and Halazon 1954), and tagged birds with 12-g necklace style radio transmitters (Advanced Telemetry Systems, Inc.). During three winters (1 December – 31 March 2015-2018, hereafter Years 1, 2, and 3), we found roost sites for each tagged grouse 1-2 times each week, between 0900 and 1700, by flushing the bird off the roost. We categorized roosting behavior as “snow burrow” if the grouse was roosting under the snow with at least a partial roof of snow (>75% covered), “snow bowl” if the roost was a bowl-shaped indentation in the snow without a roof, “tree roost” if the grouse was found in a deciduous or coniferous tree, or as “surface roost” if the roost was on the ground or on top of the snow without an indentation.

Environmental predictors of roosting behavior

We extracted land cover classes at each grouse roost site using our land cover map (Wilson et al. 2018, Shipley et al. 2020), which had a 5-m resolution and 5 land cover classes: Mature Forest, Aspen-Alder (hereafter, "Dense Cover"), Scrub Oak, Open (emergent vegetation, lowland brush/willow, and lowland grass), and Other (hereafter, "Marsh"). Marsh primarily consisted of open water and emergent vegetation, and we do not consider it habitat for grouse.

We measured snow depth at roost sites to the nearest half centimeter. We measured snow sink depth (an index of snow density) at roost sites by dropping a 200-gram cylinder (diameter: 8.5 cm) from 50 cm above the top of the snow and recording the sinking depth to the nearest half centimeter. Larger values indicate powdery, less dense snow. A value of zero indicates very hard snow. When snow was not present, snow density was recorded as "N/A". We did not include roost observations when snow was absent, as we wanted to test for the effect of snow sink depth.

To ensure accuracy, we discarded observations when snow depth was equal to snow sink depth (Thompson et al. 2021). For each grouse roost location, we extracted the minimum temperature from the previous day from daily temperature rasters. Minimum temperature from the previous day is an important predictor of corticosterone levels in ruffed grouse (Shipley et al. 2019), and thus likely to influence roosting behavior. Temperature rasters (10 m resolution) were created using regression kriging (Hengl, Heuvelink and Rossiter 2007) of data collected from temperature sensors spaced across SWA to capture differences in temperature according to land cover types and distances to forest edge (Shipley et al. 2020).

Grouse temperature exposure

To investigate how grouse roosting behavior impacts the temperatures that grouse are exposed to, we attached iButton temperature sensors (DS1922L; Maxim Integrated) to the radio transmitters of a subset of our tagged grouse. We attached sensors to the side of the transmitter facing away from the bird's body using steel-reinforced epoxy (JB Weld). Attaching iButtons to transmitters increased the mass of the transmitter from 12g to ~15.3 g, but total weight of the transmitter and iButton did not exceed 5% of birds' body mass. iButtons recorded temperature every half hour during winter.

Statistical analyses

We used a multinomial logistic model to model the effects of land cover and weather variables on the probability of different ruffed grouse roosting behaviors (snow burrow, snow bowl, surface, or tree). We tested for the effect of minimum temperature, snow depth, snow sinking depth, land cover, date, and time of day (minutes from midnight) on roosting behavior. Predictor variables (other than land cover) were scaled using a z-transformation to enable comparisons among predictors (presented as $\beta \pm SE$). We did not test for random effects due to model convergence issues, likely due to unequal observations across individual grouse. We developed a list of *a priori* candidate models (Table S1), which included combinations of 1-6 of the predictors and two-way interactions. We did not include predictor variables or their interactions in the same model if they exhibited multicollinearity (Dormann et al. 2013). We ranked models based on Akaike's Information Criterion corrected for small sample sizes (Burnham and Anderson 2002), and models were considered competitive if they were within 2 ΔAIC_c of the top model. If more than one model was competitive, we selected the model with the greatest AIC_c weight (w_i) for interpretation. We performed a residual analysis to confirm that statistical assumptions were met. We implemented the multinomial logistic model using the nnet package (Venables and Ripley 2002) version 7.3.14 in the R statistical platform (version 4.0.0).

To further explore the effects of land cover and snow depth on the probability of using snow for roosting (both snow burrows and snow bowls), we used a generalized linear model with a logit link function. We coded roosting behavior as 0 = "surface roosts" and "tree roosts" and 1 = "snow burrows" and "snow bowls", and included snow depth and land cover as main effects, and an interaction between snow depth and land cover. For both the multinomial model of all roosting behaviors and the binomial logistic model of snow burrows/bowls and other roosts, we visualized predictors with partial dependency plots, using ggplot2 (version 3.1.1), that related each predictor to the probability of roosting behaviors while keeping the other predictors conditional on their means.

To quantify the effect of roosting behavior on temperatures experienced by grouse, we used temperature data recorded by iButtons that were attached to grouse transmitters. For each roost observation of a grouse with an iButton, we extracted the median temperature from the bird's iButton during the previous 12 hours, representing temperature experienced by the grouse while at the roost. Galliforms usually defecate 1-3 solid feces per hour (Baltic et al. 2005), and the number of feces that we observed at ruffed grouse roosts ranged from 1-22. Twelve hours is therefore likely representative of the time grouse spend at roosts. We then extracted the minimum temperature from the previous day from our daily temperature rasters, and calculated the difference between the median grouse iButton temperature and the minimum ambient temperature. As minimum temperature usually occurs in the early morning hours, minimum temperature likely occurred during the twelve hours prior to the roost observation. We used a generalized linear model with a Gaussian error distribution to model the effect of roosting behavior on the difference in temperature between the median grouse iButton temperature and the minimum ambient temperature. Roosting behavior was categorized as “snow roost” (snow bowls and snow burrows were pooled due to small sample sizes of observed snow burrows by grouse with iButtons), “surface roost”, and “tree roost”. Mean values are given ± the standard deviation. We visualized the effects of the roosting behavior on the temperature difference between the grouse iButtons and ambient temperature using ggplot2 (version 3.1.1).

Results

From December to March 2015-2018, we observed 55 grouse using 17 snow burrows, 86 snow bowls, 565 surface roosts, and 86 tree roosts. We discarded 234 roost observations when snow depth was equal to zero, 25 observations when snow depth was equal to snow sink depth, and 36 observations when grouse were roosting in Marsh (7% of all roost observations, not typically considered ruffed grouse habitat). Our final dataset of roost observations included 17 snow burrows, 80 snow bowls, 289 surface roosts, and 73 tree roosts, representing 53 grouse (Figure 1). In Mature Forest, we found 7 snow burrows, 32 snow bowls, 126 surface roosts, and 48 tree roosts. In Dense Cover, grouse used 5 snow burrows, 31 snow bowls, 98 surface roosts, and 6 tree roosts. We found 2 snow burrows, 6 snow bowls, 24 surface roosts, and 1 tree roost in Open habitat. In Scrub Oak, grouse used 3 snow burrows, 11 snow bowls, 41 surface roosts, and 18 tree roosts.

Snow depth ranged from 13.0 to 44.0 cm ($\bar{x}$ = 23.9 ± 6.6 cm) at snow burrows, 3.0 to 40.0 cm ($\bar{x}$ = 15.8 ± 7.7 cm) at snow bowls, 0.5 to 39.0 cm ($\bar{x}$ = 11.4 ± 7.7 cm) at surface roosts, and 1.0 to 31.0 cm ($\bar{x}$ = 11.6 ± 6.6 cm) at tree roosts. At snow burrows, snow sink depth ranged from 4.0 to 15.0 cm ($\bar{x}$ = 9.5 ± 3.18 cm), 1.0 to 17.0 cm ($\bar{x}$ = 6.7 ± 2.5 cm) at snow bowls, 0.0 to 13.0 ($\bar{x}$ = 3.4 ± 2.4 cm) at surface roosts, and 0.0 to 17.0 cm ($\bar{x}$ = 4.7 ± 3.0 cm) at tree roosts.

Minimum temperature at snow burrows ranged from -26.7 to -4.3˚C (x̅ = -13.6 ± 6.7 ˚C), -28.1 to 1.0˚C (x̅ = -16.4 ± 7.6˚C) at snow bowls, -29.2 to 0.8˚C (x̅ = -13.8 ± 7.9˚C) at surface roosts, and -27.9 to 0.7˚C (x̅ = -14.7 ± 8.4˚C) at tree roosts.

We retrieved transmitters with iButtons from 8 individual ruffed grouse. During the time that the iButtons were collecting temperature data, we had a total of 75 roost observations of the grouse with iButtons. After extracting minimum temperature from the previous night from our daily temperature rasters, our final dataset had a total of 67 roost observations: 12 snow roosts (snow burrows and bowls pooled), 41 surface roosts, and 14 tree roosts. Temperature differences between grouse iButtons and ambient temperature ranged from 4.8 to 35.3˚C for grouse using snow roosts (x̅ = 18.6 ± 7.6˚C), 3.9 to 29.8˚C for grouse using surface roosts (x̅ = 14.2 ± 6.5˚C), and 7.9 to 20.7˚C for grouse using tree roosts (x̅ = 14.9 ± 4.2˚C).

Effects of land cover and winter weather on roosting behavior

We found strong support for the role of snow depth, snow sink depth, and land cover in influencing roosting behavior in ruffed grouse. The top model included snow depth, snow sink depth, land cover, and time of day (AIC_c weight = 0.39). An additional competitive model was identical to the top model but did not include time (Tables 1, S1). As snow depth increased, grouse were more likely to use snow burrows (β = 1.47, 95% CI: 0.80, 2.13) and snow bowls (β = 0.32, 95% CI: 0.03, 0.62) relative to surface roosts (Figure 2a). As snow sink depth increased, and snow became more powdery, grouse were much more likely to use snow burrows (β = 2.24, 95% CI: 1.61, 2.88), snow bowls (β = 1.41, 95% CI: 1.04, 1.77), and to a lesser extent, tree roosts (β = 0.71, 95% CI: 0.37, 1.05) relative to surface roosts (Figure 2b). While surface roosts were the most common roosting behavior across all land cover classes, grouse were more likely to roost in trees when they were in Mature Forest (*β* = 1.87, 95% CI: 0.97, 2.77) and Scrub Oak (*β* = 2.06, 95% CI: 1.04, 3.07) relative to Dense Cover (Figure 2c). Grouse were also more likely to use snow bowls later in the day (*β* = 0.32, 95% CI: 0.02, 0.61; Figure 2d).

We found evidence that land cover influenced the relationship between roosting behavior and snow depth. In our binomial model of snow roosting behavior, we found a significant main effect of snow depth (*β* = 2.02, 95% CI: 0.66, 3.96): grouse were more likely to use snow roosts (bowls or burrows) than other roosts (surface or tree roosts) as snow depth increased. However, we found a significant interaction between snow depth and land cover. As predicted, grouse were more likely to snow roost in shallower snow when they were in Open habitat as compared to Mature Forest (*β* = -1.44, 95% CI: -3.42, -0.03) and Scrub Oak (*β* = -1.48, 95% CI: -3.48, -0.01; Figure 3).

Effects of roosting behavior on temperature exposure

The difference between grouse temperature exposure and ambient temperature (i.e., the difference between temperature recorded on grouse iButtons and minimum ambient temperature) was significantly warmer when grouse used snow roosts as compared to surface roosts (*β* = -4.40, SE = 2.07, 95% confidence interval: -8.45, -0.34; Figure 4). Grouse experienced temperatures 4.4˚C warmer in snow roosts than on surface roosts. The difference between grouse temperature exposure and ambient temperature was warmer in snow roosts than in tree roosts, but this was not significant (*β* = -3.69, SE = 2.48, 95% confidence interval: -8.55, 1.17).

Discussion

Our study demonstrates how snow conditions and land cover influence animal behavior and the use of ephemeral winter microrefugia. Snow density and snow depth were the most important factors influencing roosting behavior, and grouse rapidly shifted behavior towards roosting in snow bowls and burrows as snow became more powdery and deeper. Temperature did not influence roosting behavior. Although the likelihood of snow roosting did not differ among land cover types, grouse were more likely to use snow roosts in open habitat at shallower snow depths, potentially indicating an increased importance of using snow roosts for protection from predators in open habitat or a lack of alternative roosts. Importantly, we note that while snow roosting resulted in grouse being less exposed to colder temperatures, snow burrows and the winter weather conditions that promote them were relatively rare, and snow burrowing only accounted for a very small proportion (0.4 to 8%) of observed roosting (Figure 5)

Effects of winter weather and land cover on roosting behavior

Grouse were more likely to use snow bowls and snow burrows than surface roosts as snow depth increased, but this behavioral flexibility in the use of microrefugia was distinctly nonlinear. While the probability that grouse would use snow bowls increased steadily between 0-35 cm, the probability that grouse would roost in snow burrows remained near 0% until snow depths reached 20-25 cm, and increased rapidly to nearly 50% when snow depths exceeded 40 cm. This rapid increase in the likelihood of using snow burrows when snow depth exceeds 25 cm, compared to the more gradual increase in the likelihood of using snow bowls with increasing snow depth, is indicative of the superior benefits of snow burrows over snow bowls. A snow depth of about 38 cm is needed before snow burrowing becomes more common than snow bowls, and 40 cm of snow is needed before snow burrowing becomes more common than surface roosts. The minimum snow depth that grouse used snow burrows was 13 cm, while we observed grouse using snow bowls with as little as 3 cm of snow. While grouse can roost in snow bowls when snow is shallow, roosting in shallower snow bowls with more of the bird’s body above the snow may not provide the same benefits as deeper snow bowls or snow burrows. In fact, we found that as snow depths approached 15 cm, grouse avoided deeper snow, and only began selecting for deeper snow at depths greater than 15 cm. Notably, exposure to deeper snow (close to 15 cm) is associated with increased winter mortality (Shipley et al. 2020) and may explain why the probability of grouse roosting in snow bowls only marginally increases with deeper snow.

Grouse were more likely to use snow bowls and snow burrows as compared to surface roosts as snow sink depth increased and snow became more powdery. The relative hardness of snow had a much stronger effect on the probability of snow roosting behavior than the effect of snow depth. Between 0-10 cm of sink depth (0.35 g/cm^3), the probability that grouse would roost in snow bowls increased from 0-60%, while the probability of surface roosting steeply declined to nearly zero when snow was very powdery. Snow burrowing probability only exceeded 0% when sink depths increased past 6 cm (0.59 g/cm^3), and then increased to about 50% at 15 cm sink depth (0.24 g/cm^3). A snow sink depth of about 8 cm (0.44 g/cm^3) was needed before snow bowls became more common than surface roosts, and a sink depth of 11 cm (0.32 g/cm^3) was needed before snow burrows became more common than surface roosts. The minimum snow sink depth that we observed grouse using snow burrows was 4 cm and 1 cm for snow bowls. As snow sink depth increased to 7 cm, the probability that grouse would use tree roosts increased, and then declined as snow sink depth exceeded 10 cm. Increased snow sink depth is associated with increased physiological stress in grouse (Shipley et al. 2019), likely due to increased energy required to move through more powdery snow. When snow sink depths increased towards 7 cm, grouse do not use snow burrows, and are relatively unlikely to roost in snow bowls. At these moderate sink depths, grouse may spend more time roosting in trees to avoid more powdery snow that may be more difficult to move through and increase stress levels. As sink depths increase beyond 10 cm, snow burrowing and snow bowls become more likely, and grouse are less likely to roost in trees. Even at the maximum snow sink depths that we observed, snow burrowing never surpassed snow bowls as the most common roosting behavior. This may indicate that deep snow bowls may have similar benefits to snow burrows, or that there may be some trade-offs associated with using snow burrows, such as the inability to visually observe surroundings. Regardless, the ability to use snow bowls or snow burrows under similar conditions further points to the importance of behavioral flexibility.

While minimum temperature is an important predictor of grouse stress (Shipley et al. 2019) and roost site selection (Shipley et al. 2020), we did not find an effect of temperature on roosting behavior. Snow burrowing is important for reducing the effect of cold temperatures on grouse stress (Shipley et al. 2019) and increases overwinter survival (Shipley et al. 2020). The benefits of snow roosting could therefore be relevant regardless of temperature, and grouse may increase their use of snow roosts as soon as minimum snow depth and snow sink depth conditions are met. Alternatively, or additionally, predator avoidance may also be an important benefit of snow roosting in addition to thermal insulation (Shipley et al. 2020), and grouse will continue to use snow roosts even when temperatures are warmer.

Land cover did not have an effect on the probability that grouse would use snow bowls or snow burrows, and surface roosts were the most common roosting behavior across cover types. Grouse were more likely to roost in trees in mature forest and scrub oak, likely due to the increased availability of large trees for roosting as compared to open areas and dense cover. However, in open habitat, as predicted, grouse were more likely to use snow roosts at shallower snow depths than in mature forest or scrub oak. Grouse stress increases with the size of open habitat patches (Shipley et al., Chapter 3), and grouse avoid open areas (Shipley et al. 2020). In this study, open habitat was not associated with lower minimum temperatures. Thus, the tendency to use snow roosts at shallower depths in open habitat may reflect increased perceived risk of predation, and a greater need to roost under the snow as a refuge from predators.

Effects of roosting behavior on temperature exposure

When grouse used snow roosts, they experienced temperatures 4.4˚C warmer than ambient temperature compared to when they used surface roosts. The temperatures recorded by the sensors attached to grouse transmitters were likely partially influenced by grouse body temperature, as temperatures recorded by sensors were considerably warmer than ambient temperature recorded at surface roosts. However, the effect of body heat would presumably have the same effect regardless of roosting behavior. Using a heated taxidermic mount, Thompson and Fritzell (1988) found that snow burrows were up to 7˚C warmer than other roost sites. Snow burrows clearly are important for heat retention and energy savings. The majority of our snow roosts observations were snow bowls, which are open on top, and thus our estimate of the heat retention of snow roosts is likely an underestimate, and would probably be more with a higher proportion of true snow burrows.

Deteriorating conditions for an adaptive behavioral strategy

Seeking refugia below the snow is an important behavioral adaptation that allows for exposure to warmer temperatures, reduces stress (Shipley et al. 2019), and is associated with increased overwinter survival (Shipley et al. 2020). However, the conditions that promote snow roosting: deep, powdery snow, are deteriorating. Across Wisconsin, average snow depths currently peak at 20 cm in mid-winter, and peak snow depths are projected to decline to 8-15 cm in the future (Notaro et al. 2011, Notaro et al. 2014), well below what is needed for snow burrowing to be more than a rare occurrence. An increase in the number of freeze-thaw events is also predicted (Mellander, Lofvenius and Laudon 2007, Sinha and Cherkauer 2010), resulting in a hardened snow layer that will further reduce the quality of the snow for snow roosting. Even during our relatively short 3-year study period, we observed fewer days with deep snow and fewer days with powdery snow each year, and a decline in the occurrence of snow roosting behavior. Each year, we observed a smaller proportion of winter days that met the minimum conditions for snow burrows, and only a very small number of winter days when snow burrowing was predicted to be more common than roosting on top of the snow (Figure 5a). Further, the occurrence of snow burrows declined each year to 0.4% of all roosts in Year 3, and surface roosts increased to 68% in Year 3 (Figure 5b). For species that use snow cover as a refuge from harsh winter conditions, the limits of this behavioral flexibility are being stretched as deep and powdery snow becomes less common with climate change.

Behavioral flexibility and snow roosting behavior have clear benefits for heat retention, stress reduction, and increased survival via predator avoidance, but the conditions that promote the use of these microrefugia are vanishing. While using snow bowls is currently possible for a large proportion of winter days (87-94% across years), roosting in shallower snow bowls may not provide the same benefits as deeper snow bowls or snow burrows. Importantly, the loss of snow cover is truncating the range of behavioral flexibility for this winter-adapted bird. Given these nonlinear behavioral responses to the use of this important winter microrefugia, it is likely that a rapidly changing winter climate poses a tipping point in this behavioral syndrome. While winters are expected to warm in the future, loss of snow cover may result in a functionally colder winter environment for snow-adapted species (Pauli et al. 2013, Zuckerberg and Pauli 2018) and reduce the effectiveness of evolved adaptations and behavioral flexibility.

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Tables

Table 1. Candidate models ($\Delta AIC_c \leq 6$) and the intercept null model evaluating the effects of winter weather variables and land cover on ruffed grouse roosting behavior. See Supplementary Materials for the full list of candidate models.

Model	k	AIC_c	ΔAIC_c	w_i
Snow Depth + Snow Sink Depth + Cover + Time	21	766.56	0.00	0.39
Snow Depth + Snow Sink Depth + Cover	18	767.03	0.48	0.31
Snow Depth*Snow Sink Depth + Cover + Time	24	769.05	2.49	0.11
Snow Depth*Snow Sink Depth + Cover	21	769.26	2.71	0.10
Snow Depth + Snow Sink Depth + Temp + Cover + Time	24	770.52	3.97	0.05
Snow Depth + Snow Sink Depth + Temp + Cover	21	771.11	4.55	0.04
NULL	3	933.47	166.91	0.00

Snow sink depth represents the depth that a weighted cylinder sinks into the snow when dropped and is a proxy for snow density; larger values indicate more powdery snow. Cover is a categorical land cover variable and includes Mature Forest, Dense Cover, Open habitat, and Scrub Oak. Temperature represents minimum temperature at the roost location during the previous 24 hours. Time is measured in minutes from midnight.

Figures

Fig. 1: Ruffed grouse roosting behavior and land cover categories at Sandhill Wildlife Area in central Wisconsin, USA. Snow burrows (a, purple), snow bowls (b, blue), surface roosts (c, black), and tree roosts (e, green). Surface roosts were most common, followed by snow bowls, tree roosts, and snow burrows.

Fig. 2: Partial dependency plots showing the effects of (a) snow depth (cm); (b) snow sink depth (cm; larger values indicate more powdery snow), (c) land cover classes, and (d) time (minutes from midnight; 700 corresponds to noon) on the probability of ruffed grouse using snow burrows (purple), snow bowls (blue), surface roosts (black), or tree roosts (green). Lines and shaded bands (a, b, d) and points and error bars (c) represent means and 95% confidence intervals. The probability of grouse using snow bowls increased steadily as snow depths increased from 0-35 cm, but the probability of snow burrowing increased considerably only between 20-40 cm of snow depth. Grouse also began using snow bowls with harder snow, and used snow bowls more as snow became more powdery, but grouse did not use snow burrows unless snow was considerably more powdery.

Fig. 3: Partial dependency plot showing the effect of an interaction between snow depth (cm) and land cover on the probability that ruffed grouse will use snow roosts (snow burrows and snow bowls pooled) over all other roost behaviors. Open habitat (light brown), Dense Cover (bright green), Mature Forest (dark green), and Scrub Oak (dark brown). Lines and shaded bands represent means and 95% confidence intervals. Grouse were more likely to use snow roosts at shallower snow depths in Open habitat than in Mature Forest or Scrub Oak.

Fig. 4: The effect of ruffed grouse roosting behavior on grouse exposure to winter temperatures. Snow roosts represent pooled observations of snow burrows and snow bowls. Temperature

increase (˚C) represents the difference between the median temperature recorded by iButtons attached to grouse radio transmitters during the 12 hours prior to the roost observation and the minimum ambient temperature during the previous 24 hours. Roost behaviors that do not share letters have 95% Confidence Intervals that do not overlap zero. Grouse in snow roosts experienced significantly warmer temperatures than grouse using surface roosts.

Fig. 5: The proportion of winter days that we observed snow roosting behavior in Year 1 (2015-2016), Year 2 (2016-2017), and Year 3 (2017-2018) that had the minimum conditions for snow bowls (blue) and snow burrows (purple) (a). The proportion of roosts in each year that were tree roosts (green), surface roosts (black), snow bowls (blue), and snow burrows (purple) (b). Even during our short 3-year study, suitable conditions for snow burrowing deteriorated, and the occurrence of snow burrowing behavior declined.

Figure 1

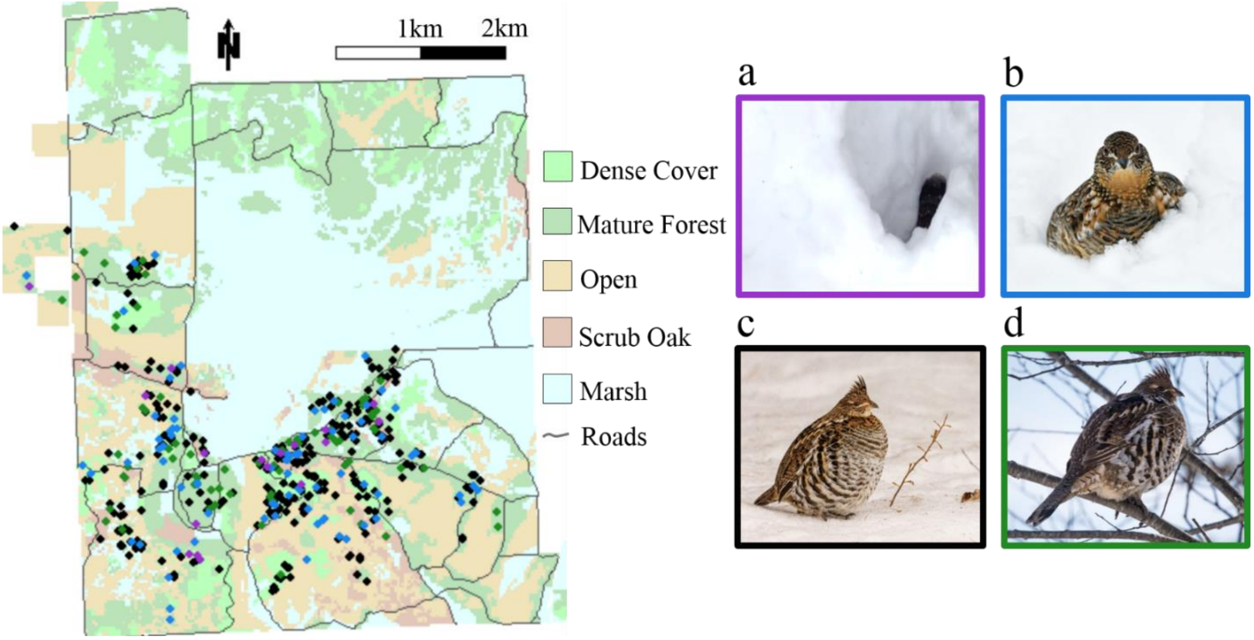

N
1km
2km
Dense Cover
Mature Forest
Open
Scrub Oak
Marsh
Roads
a
b
c
d

Figure 2

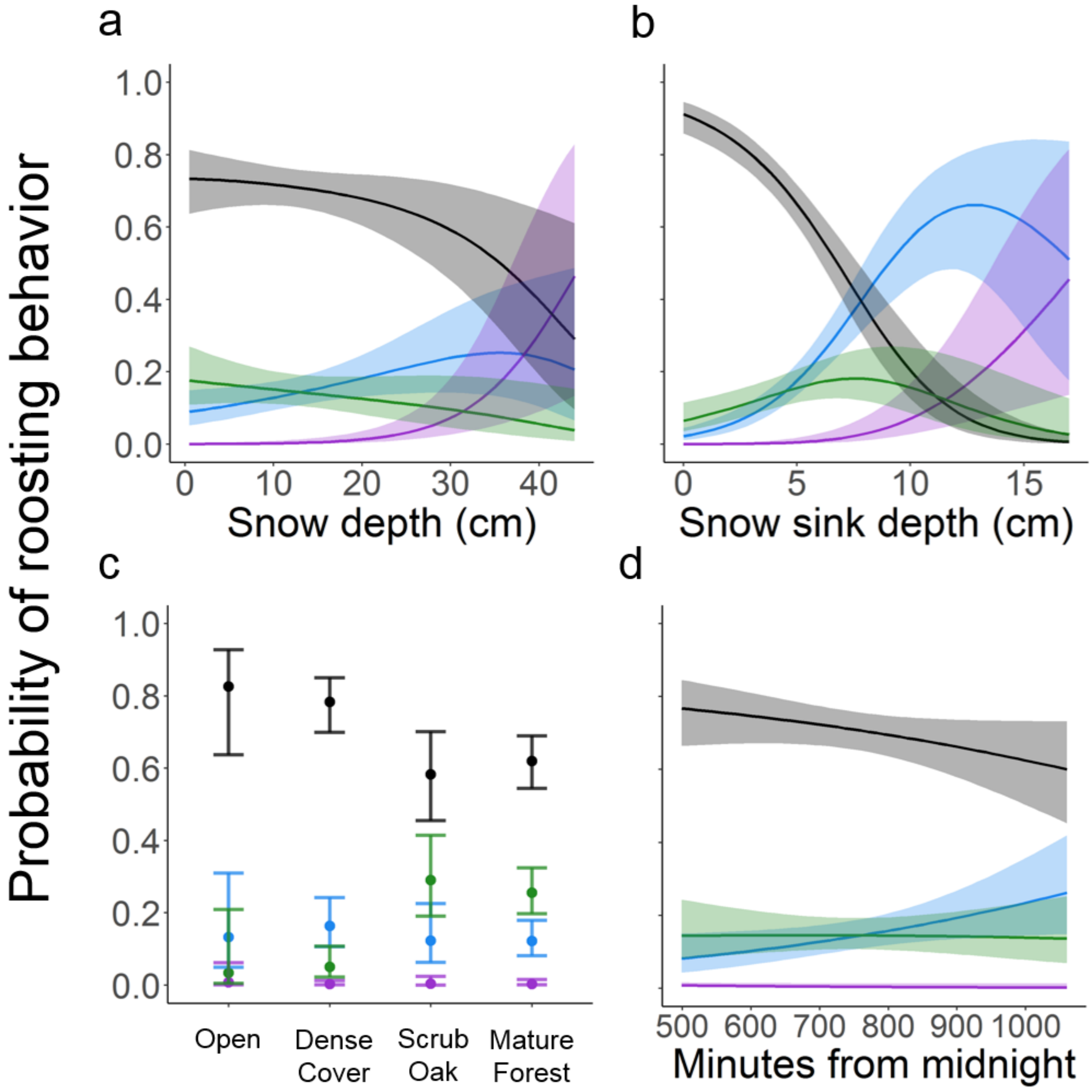

a
b
c
d
Probability of roosting behavior
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
Snow depth (cm)
0
5
10
15
Snow sink depth (cm)
Open
Dense Cover
Scrub Oak
Mature Forest
500
600
700
800
900
1000
Minutes from midnight

Figure 3

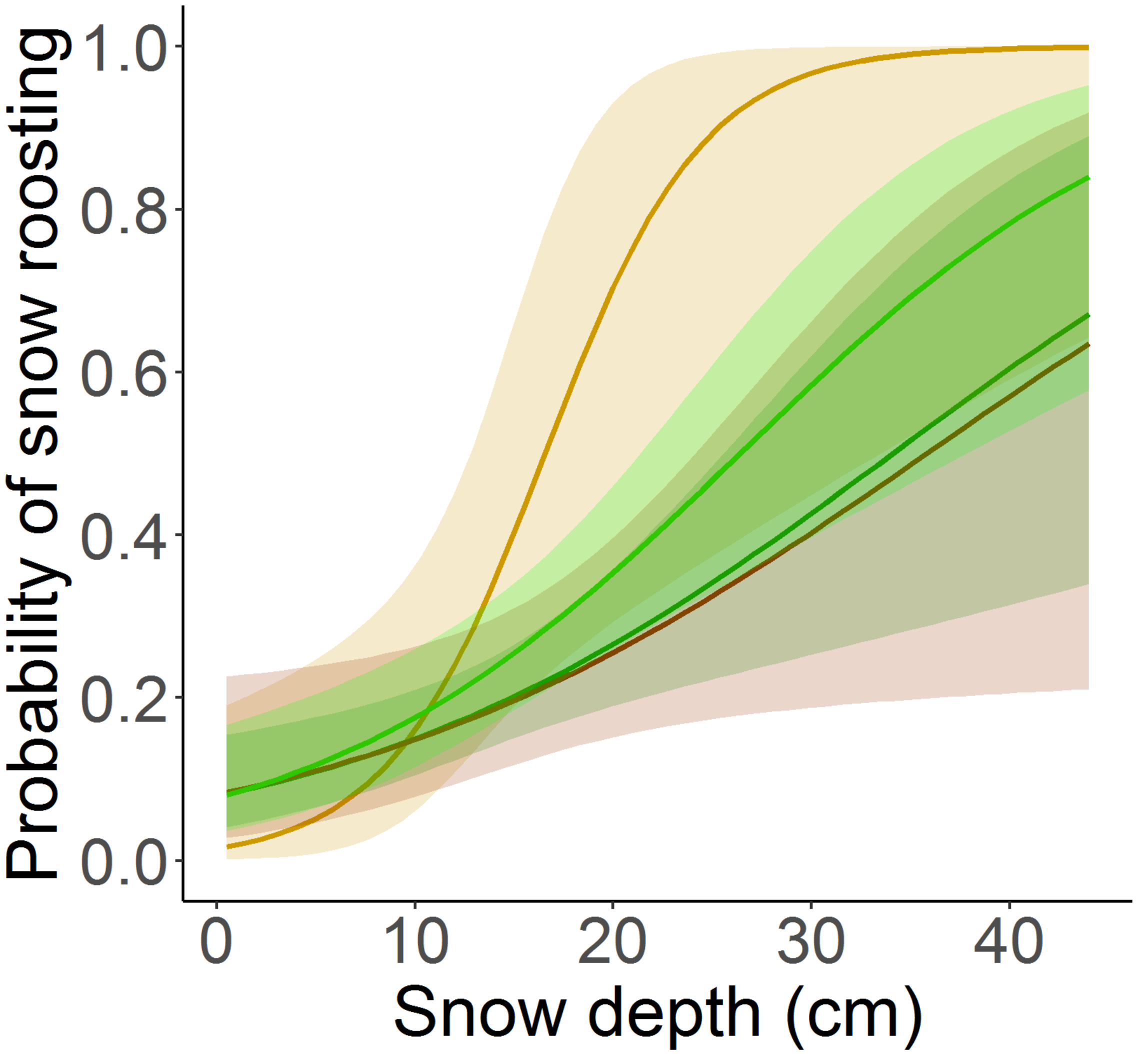

Probability of snow roosting
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
Snow depth (cm)

Figure 4

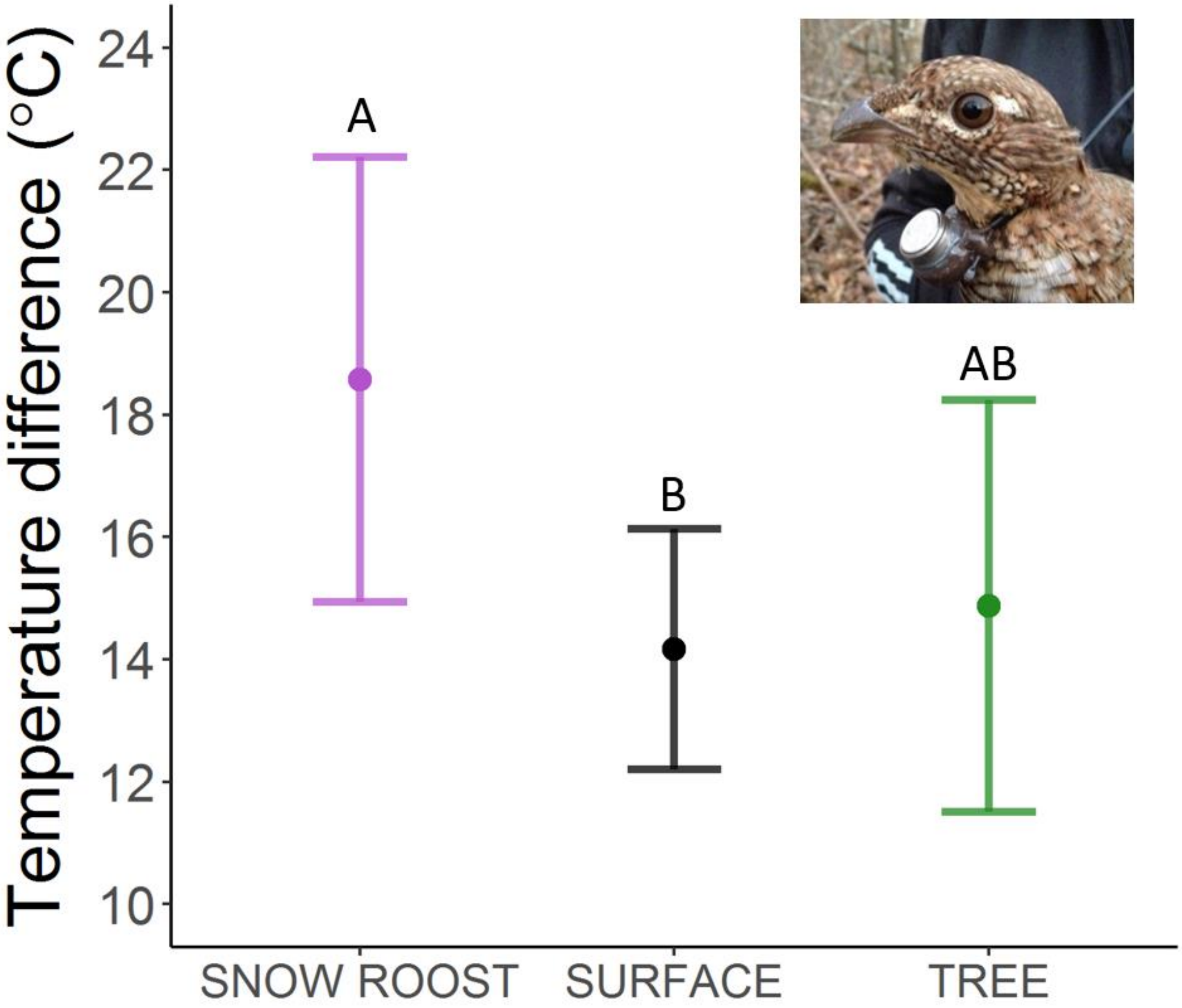
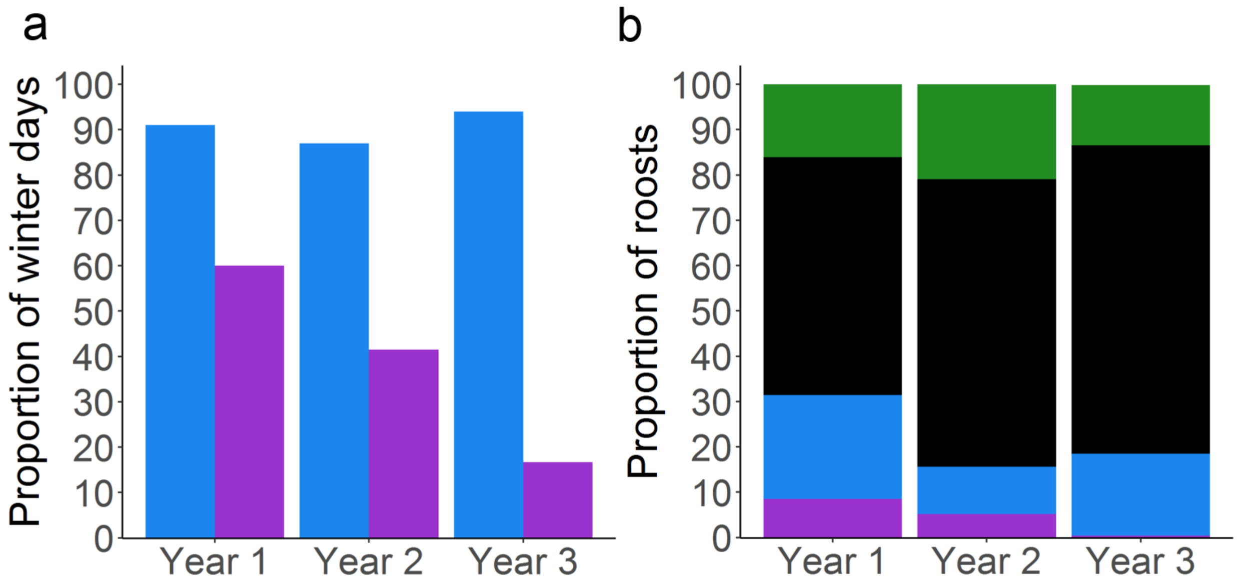

Temperature difference (°C)
24
22
20
18
16
14
12
10
A
B
AB
SNOW ROOST
SURFACE
TREE

Figure 5


a
Proportion of winter days
100
90
80
70
60
50
40
30
20
10
0
Year 1
Year 2
Year 3
b
Proportion of roosts
100
90
80
70
60
50
40
30
20
10
0
Year 1
Year 2
Year 3

Supplementary Materials

Table S1. Candidate models ($\Delta AIC_c \leq 6$) and the intercept null model evaluating the effects of winter weather variable and land cover on ruffed grouse roosting behavior.

Model	k	AIC_c	ΔAIC_c	w_i
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Snow Depth + Snow Sink Depth + Temp + Cover + Time	24	770.52	3.97	0.05
Snow Depth + Snow Sink Depth + Temp + Cover	21	771.11	4.55	0.04
Snow Depth + Snow Sink Depth*Cover	27	778.33	11.77	0.00
Snow Depth + Snow Sink Depth + Date	12	780.84	14.28	0.00
Snow Depth + Snow Sink Depth + Temp*Cover	30	781.28	14.72	0.00
Snow Depth*Cover + Snow Sink Depth	27	781.95	15.39	0.00
Snow Depth + Snow Sink Depth*Cover + Temp	30	782.33	15.77	0.00
Snow Depth*Cover + Snow Sink Depth + Time	30	782.35	15.79	0.00
Snow Depth + Snow Sink Depth + Time	12	783.33	16.77	0.00
Snow Depth + Snow Sink Depth	9	784.63	18.07	0.00
Snow Depth + Snow Sink Depth + Temp + Date	15	784.87	18.31	0.00
Snow Sink Depth + Cover + Time	18	785.77	19.21	0.00
Snow Depth*Cover + Snow Sink Depth + Temp	30	786.08	19.52	0.00
Snow Depth*Snow Sink Depth	12	786.21	19.66	0.00
Snow Sink Depth + Cover	15	786.62	20.06	0.00
Snow Depth + Snow Sink Depth + Temp + Time	15	787.02	20.46	0.00
Snow Depth + Snow Sink Depth + Temp	12	788.57	22.01	0.00
Snow Sink Depth	6	804.62	38.06	0.00
Snow Depth + Temp	9	890.61	124.05	0.00
Snow Depth	6	891.05	124.49	0.00
Cover + Temp + Time	18	914.10	147.55	0.00

Cover	12	916.13	149.57	0.00
Date	6	925.52	158.96	0.00
Time	6	931.56	165.00	0.00
Temp	6	932.64	166.09	0.00
NULL	3	933.47	166.91	0.00

Snow sink depth represents the depth that a weighted cylinder sinks into the snow when dropped and is a proxy for snow density; larger values indicate more powdery snow. Cover is a categorical land cover variable and includes Mature Forest, Dense Cover, Open habitat, and Scrub Oak. Temperature represents minimum temperature at the roost location during the previous 24 hours. Time is measured in minutes from midnight.

Snow roosting reduces temperature-associated stress in a wintering bird

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Abstract

Animals in temperate northern regions employ a variety of strategies to cope with the energetic demands of winter. Behavioural plasticity may be important, as winter weather conditions are increasingly variable as a result of modern climate change. If behavioural strategies for thermoregulation are no longer effective in a changing environment, animals may experience physiological stress, which can have fitness consequences. We monitored winter roosting behaviour of radio-tagged ruffed grouse (*Bonasa umbellus*), recorded snow depth and temperature, and assayed droppings for fecal corticosterone metabolites (FCM). Grouse FCM levels increased with declining temperatures. FCM levels were high when snow was shallow, but decreased rapidly as snow depth increased beyond 20 cm. When grouse used snow burrows, there was no effect of temperature on FCM levels. Snow burrowing is an important strategy that appears to allow grouse to mediate the possibly stressful effects of cold temperatures. This is one of the first studies to explore how variable winter weather conditions influence stress in a free-living cold-adapted vertebrate and its ability to mediate this relationship behaviourally. Animals that depend on the snowpack as a winter refuge will likely experience increased stress and possible fitness costs resulting from the loss of snow cover due to climate change.

Introduction

In temperate and northern regions, winter is a period when animals must balance increased thermoregulatory demands with reduced energy availability and intake (Anderson and Jetz 2005; Williams et al. 2015). While some species avoid winter by migrating (Somveille et al. 2015) or hibernating (Geiser 2013; Sheriff et al. 2011b), others confront the winter through a diversity of physiological adaptions including lowering energy expenditure (Humphries et al. 2005; Sheriff et al. 2009c; Sheriff et al. 2009d), increasing summit metabolic rates (Cooper 2002), engaging in heterothermy (Dammhahn et al. 2017), or altering morphological features (e.g., increasing fat stores; Pokallus and Pauli 2016). In addition to these physiological responses, overwintering species display a range of behavioural flexibility such as whether or not to cache food (Smith and Reichman 1984), nesting alone or communally (Williams et al. 2013), or seeking out winter refugia, such as within thermally stable areas under the snowpack (Pauli et al. 2013). Flexibility in either physiological or behavioural responses represents a potential capacity for individuals to respond to shifting environmental conditions (Beever et al. 2017).

Understanding the adaptations of animals that confront the winter is of particular importance as modern climate change is rapidly altering winter conditions. Temperate and northern ecosystems, in particular, are experiencing some of the most rapid changes in temperature (Post 2013). The Great Lakes region of the United States has experienced increasing winter temperatures of 0.5° per decade from 1970 to 2005 (Lorenz et al. 2009) and decreases in snow cover duration, particularly in early spring (Vaughan et al. 2013). These trends have reduced the snow season by 5.3 days per decade since the 1970s (Notaro et al. 2011), a trend that is expected to continue (Krasting et al. 2013). There is growing evidence that changing winter conditions are beyond the capacity of many resident species to respond. For example, reduced snow cover is increasing mismatch in coat color camouflage in snowshoe hares (*Lepus americanus*; (Mills et al. 2013), leading to reduced survival (Wilson et al. 2018; Zimova et al. 2016), and implicated in regional range contraction (Sultaire et al. 2016). When snow is present, rain-on-snow events and increasing freeze-thaw cycles create ice fields that prevent reindeer (*Rangifer tarandus platyrhyncus*) from accessing food below the snow (Hansen et al. 2011). Repeated thawing and refreezing events can be harmful for species that overwinter under the snowpack, such as freeze-tolerant amphibians, as many of these species undergo energy-intensive physiological processes to survive the winter months (Sinclair et al. 2013). Several studies have identified behaviours that help individual species cope with climate change (Kearney et al. 2009; Snell-Rood 2013), but there is a lack of information on the ecological contexts and consequences of behavioural flexibility in response to climate variability (Beever et al. 2017).

While there is a good understanding of the strategies animals have to cope with cold winter temperatures, relatively less is known about how animals may adapt to variable and changing winter conditions. The study of stress physiology in free-living animals has proven valuable for understanding how vertebrates adjust to environmental change and implement decisions on coping with the challenges of uncertain environments (Dantzer et al. 2014; Sheriff et al. 2011b). Glucocorticoid stress hormones (hereafter, GCs) play critical roles in performance and fitness (Sapolsky et al. 2000; Wingfield et al. 1998) and help animals cope with and respond to a variety of stressors including food shortages, inclement weather, or increased predator presence. Glucocorticoids are involved in a variety of physiological processes in animals, including cardiovascular activation, immune function, neurobiology, and reproduction (Sapolsky et al. 2000; Wingfield et al. 1998). Glucocorticoids also play a key role in regulating metabolism, and serve to increase circulating concentrations of glucose to provide for an animal’s energy needs

(Jimeno et al. 2018; Landys et al. 2006; Sapolsky et al. 2000). To enable these functions, GCs can modulate animal behaviour by increasing foraging behaviour (Astheimer et al. 1992; Nagra et al. 1963a; Nagra et al. 1963b; Wingfield and Ramenofsky 1999) or locomotor activity (Astheimer et al. 1992; Breuner et al. 1998; Wingfield and Ramenofsky 1999). However, if an animal cannot escape a stressor, GCs can remain chronically elevated, and can result in significant deleterious effects, including fat depletion and muscle atrophy (Marra and Holberton 1998; Romero and Wikelski 2001) and reduced reproductive output (Sheriff et al. 2009b) and survival (MacLeod et al. 2018a). This could occur either via continual "wear and tear" resulting from elevation of GCs beyond the range of normal seasonal variation (predictive homeostasis), or from extreme elevation into the range of homeostatic overload when the GCs themselves become pathological (Romero et al. 2009).

Elevated GC levels in free-living animals have been associated with inclement weather, and can have fitness consequences. For example, early spring snow storms during the parental care period of white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) were associated with greatly elevated corticosterone levels and brood losses (Wingfield et al. 1983). High GC levels were associated with a delayed return to the breeding grounds by mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) that had departed to snow-free lower elevations following spring storms (Hahn et al. 2004). Adelie penguins (*Pygoscelis adeliae*) subjected to experimentally elevated GC levels spent less time incubating eggs, which often led to egg loss, particularly during harsh weather (Thierry et al. 2013). All of these studies occurred during the breeding season, and investigated the interactive effects of harsh weather, stress physiology, and breeding performance. There is almost no information on how changing winter conditions influence stress hormone levels in wild animals (but see Sheriff et al. 2017), and little information on how snow cover and cold temperatures influence the stress physiology of animals adapted to cope with a winter environment.

Ruffed grouse (*Bonasa umbellus*) are winter-adapted birds closely associated with the northern forests of North America, and despite extensive conservation efforts, grouse populations have declined by 50% over the last half century (Rusch et al. 2000). Winter is an important demographic bottleneck for grouse as they experience high rates of mortality, especially via predation (Small et al. 1991; Thompson and Fritzell 1989). Winter precipitation and temperature, in particular, are critical components of grouse dynamics and cycling (Pomara and Zuckerberg 2017). Despite the importance of winter on grouse ecology, it is a relatively understudied portion of their life cycle. During the winter, grouse are typically sedentary and spend up to 80% of the time roosting either on the ground, in trees, or when snow cover is sufficient, in burrows under the snow (Bump et al. 1947). Snow burrows provide superior thermal insulation as compared to other roost sites (Thompson and Fritzell 1988b). Indeed, snow burrows form microenvironments within thermo-neutral temperatures for grouse (Marjakangas et al. 1984), and are particularly important when grouse have low fat and protein reserves and relatively little metabolic tolerance to fasting (Thomas 1987). Roosting in snow burrows is a potentially important behavioural adaptation that grouse use to maintain energy reserves during harsh winter conditions. Use of snow burrows is primarily limited by the quantity and quality of available snow cover (Gullion 1970), and grouse need roughly 15-20 cm of powdery snow for burrowing (Blanchette et al. 2007; Gullion 1970; Heinrich 2017). Across Wisconsin, which encompasses the southern range boundary for grouse in the Great Lakes region, snow depth averages ~10 cm in December and March, and peaks at ~20 cm in midwinter when temperatures are coldest (Notaro et al. 2011), resulting in a brief, yet potentially critical, window of time when snow burrowing conditions are suitable.

Here, we tested the hypothesis that both winter temperature and snow depth influence the stress physiology of ruffed grouse, and that behavioural use of snow burrows allow grouse to mediate the influence of temperature on stress hormone levels. Specifically, we predicted i) corticosterone concentrations (as measured by fecal corticosterone metabolites, FCM) would increase as temperature decreased; ii) corticosterone concentrations would decrease as snow depth and snow compaction increased, and iii) ambient temperature would not influence corticosterone concentrations when grouse used snow burrows.

Methods

Study Site

Our work was conducted in Sandhill Wildlife Area (44°18′ N, 90°07′ W), a 3,700 ha state wildlife area located in central Wisconsin. Sandhill is a mosaic of naturally fragmented upland oak (*Quercus* sp.) and aspen (*Populus tremuloides* and *P. grandidentata*) forests interspersed by marshes and open water. It is actively managed by the Wisconsin Department of Natural Resources with selective logging to promote habitat for ruffed grouse and white-tailed deer (*Odocoileus virginianus*). Sandhill is surrounded by a 3.5 m tall fence, and a short 4-5 week ruffed grouse hunting season is limited and closely monitored in the southern half of the wildlife area in autumn. The mean winter temperature at Sandhill (December-March) is -9°C ± 10.0 °C (range -26.5 to 5.5 °C), and between 2001 and 2015, there were on average 47 nights each winter when snow depth exceeded 20 cm (range 0-101 nights).

Grouse trapping and radio telemetry

From Sep-2015 to Nov-2015, we trapped ruffed grouse in walk-in pens (“lily pad traps”) located at both ends of a 15 m chicken wire drift fence (Gullion 1965). At capture, we identified age and sex of grouse according to standard criteria (Hale et al. 1954), collected morphological measurements, fitted each bird with an aluminum leg band for identification (National Band and Tag Company), and attached a 12-g necklace-style radio transmitter equipped with a 4-hour mortality sensor (Advanced Telemetry Systems, Inc.). During the winter of 2015-2016 (01-Dec – 31-Mar), we located a roost site for each radio-tagged grouse approximately once per week, between 0900 and 1700, typically by flushing the bird off of its roost.

Roost site observations

We categorized roost site locations as “snow roosts” if they occurred in snow burrows (with at least a partial roof of snow [> 75% covered]) or snow bowls (bowl-shaped indentations in the snow without a roof). Alternatively, we used “other roosts” if the grouse were found in trees or sitting on top of the snow or the ground. If a roost location could not be determined during flushing, or there was evidence that the bird was not roosting when it was located (e.g., it was foraging), we relocated the bird 2-3 days later.

We calculated mean snow depth at the roost site by taking the average depth in centimeters from 7 locations that were equidistant from the roost site to the perimeter of a 0.04 ha circular plot: at the roost site, 3.6 m, 7.2 m, and 10.8 m North or South of the roost site, and 3.6 m, 7.2 m, and 10.8 m East or West of the roost site. We measured average snow compaction depth (an index of snow density) at the same 7 locations by dropping a 200-gram cylindrical weight with a diameter of 8.5 cm from 50 cm above the top of the snow and recording the sinking depth in cm. Higher values indicate powdery, less dense snow (i.e. increased compaction depth).

A value of zero for snow compaction depth indicates very hard snow. If no snow was present, we recorded “N/A” for snow compaction depth.

Fecal sample collection

To estimate grouse stress hormone levels, we collected feces from ruffed grouse roost sites across a roughly 1,000-ha area within Sandhill Wildlife Area. Fecal glucocorticoids closely mirror plasma GCs (Sheriff et al. 2010), and provide an accurate non-invasive method for assessing stress in wild populations (Dantzer et al. 2014; Sheriff et al. 2011a). In black grouse (*Tetrao tetrix*), FCMs peak between 1-4 hours after administering corticosterone intravenously (Baltic et al. 2005). We collected ruffed grouse fecal droppings from roost sites where individual grouse identity was known with certainty. We attempted to collect all fecal droppings (discarding cecal droppings; Zimmerman et al. 2013) from each roost site. Grouse did not reuse roost sites. All grouse droppings collected from a single roost location (range: 2-22 droppings, representing ~1-22 hours of roosting time for an individual grouse; (Baltic et al. 2005) were pooled and considered a sample. After collection, fecal samples were immediately put on ice and stored at -20 °C for later analysis of corticosterone metabolites. While there is evidence that FCM levels increase artificially when feces are not immediately stored on ice (e.g., Descovich et al. 2012; Khan et al. 2002), in our study droppings were usually deposited on snow. Additionally, our results show that grouse FCM levels actually decline with warmer temperatures (Fig. 1), further indicating that environmental degradation of samples is not a concern in this study.

Temperature data collection

Temperature data (°C) were recorded at a central location within the study site using an iButton data logger (DS1922L; Maxim Integrated). Temperature readings at 1-m above ground were recorded every 30 minutes throughout the winter. Minimum temperature from the previous night was used for each grouse roost observation. Minimum nightly temperature likely represents the maximum challenge to a bird's ability to cope with the cold (Frigerio et al. 2004) and also likely a factor influencing initial roost site selection.

Corticosterone assay protocol

We used a standard corticosterone I^{125} double-antibody radioimmunoassay (RIA) kit (MP Biomedicals, Solon, Ohio) to measure corticosterone metabolites (Millspaugh and Washburn 2004; Wasser et al. 2000) that has been validated for use in ruffed grouse (Zimmerman et al. 2013). We followed the manufacturer's instructions for the RIA assay, but halved all reagents (Wasser et al. 2000; Zimmerman et al. 2013). Briefly, we freeze-dried samples using a lyophilizer for 24 hours and finely ground and mixed using a mortar and pestle. We extracted corticosterone metabolites by adding 2 ml of 90% methanol to 200 mg of dried feces and vortexing for 30 min. We centrifuged samples at 1900*g* for 20 min, removed the supernatant, diluted (1:20) with assay buffer, and stored the samples at -20 °C until assayed with the RIA kit. The average intra-assay coefficient of variation was 2.38%. All samples were assayed in a single run, therefore we did not calculate an inter-assay coefficient of variation.

Statistical analyses

We used a generalized linear mixed effects model (GLMM) with a Gaussian error distribution (Zuur et al. 2009) to model the effects of environmental conditions and roost type on variation in grouse stress hormone levels. Each model was weighted by the log-transformed number of fecal droppings that were collected at each roost. We used number of droppings as a proxy for length of time that a bird spent at a roost, given that galliforms defecate 1-3 solid feces per hour (Baltic et al. 2005). The longer a bird spent at a roost, the more likely the environmental conditions of the roost would be reflected in its FCM levels. We tested for the effect of minimum temperature, snow depth, snow compaction depth, date, time of day, and roost type as fixed effects. Predictor variables (other than roost type) were scaled using a z-transformation to enable comparisons among predictors (presented as $\beta \pm SE$). Corticosterone metabolite concentrations were log-transformed, and individual bird ID was included as a random effect. We first performed analysis to test for important environmental variables that influence grouse FCM, independent of grouse roosting behaviour. For this first analysis we developed a list of *a priori* candidate models (Table 1), which included combinations of 1-5 of the abiotic factors: temperature, snow depth (linear and quadratic forms), compaction depth, date, time of day, and two-way interactions of the above factors. Time of day was included to account for the natural daily rhythm in FCM levels often seen in birds (e.g., Carere et al. 2003; Scheiber et al. 2017). We did not include predictor variables or their interactions in the same model if they exhibited multicollinearity (Pearson's correlation coefficient ≥ 0.6) or if the model had a variance inflation factor (VIF; measure of the degree of collinearity in a model) greater than five (Dormann et al. 2013). We ranked models based on Akaike's Information Criterion corrected for small sample sizes (AIC_c; (Burnham and Anderson 2002), and models were considered competitive if they were within 2 ΔAIC of the top model. If more than one model was competitive, we selected the model with the greatest AIC weight (w_i) for interpretation. We chose not to use model averaging of parameter estimates for competitive models, given recent concerns about model averaging of parameter estimates in model selection (Cade 2015). After identifying important abiotic factors that influenced grouse FCM (i.e., those variables in the top model), we ran a second analysis to test for the importance of individual grouse characteristics in mediating the influence of environmental variables on FCM levels. Therefore, in the second analysis we included all the important environmental factors retained from the first analysis, and included grouse roost type, which included two categories:

"snow roost" (snow bowls and snow burrows) and "not snow roost" (all other roost types), grouse age, grouse sex, and two-way interactions with abiotic predictors. We performed a residual analysis to confirm that statistical assumptions were met. We implemented GLMMs using the lme4 package (Bates et al. 2015) and calculated the conditional R^2 (Nakagawa and Schielzeth 2013) for the top model in each round of model selection using the MuMIn package (Barton 2018) in the R statistical platform (R Core Team, ver. 3.3.3). For brevity, we list the candidate models with a $\Delta AIC_c < 6$ in Tables 1 and 2, but for a complete list of candidate models used in both analyses, see the Supplementary Materials (Tables S1 and S2). Using estimates of the between-group variance and within-group variance obtained from our top model, we calculated repeatability (i.e. the proportion of the total variation in FCM levels accounted for by differences between individual grouse; intraclass correlation coefficient) (Roche et al. 2016). We used the non-parametric Mann-Whitney U test to test for differences in environmental variables between snow roosts and other roosts. Mean values are given ± the standard deviation.

To display the results of our top model, we used the *visreg* function in the *visreg* package to compute partial residuals (Breheny and Burchett 2017). Partial residual plots hold all parameters in the statistical model that are not being displayed constant (at the median value of each parameter). Partial residual plots are an appropriate way to visualize the data because both the plotted points and the model's estimate of the effect of the predictor on the response variable take into account the other variables in the model (Breheny and Burchett 2017; Rohr et al. 2018). Plots with raw data values can be found in Supplementary Materials (Figs. S5-S7).

Results

We measured fecal corticosterone metabolites in droppings collected from 70 roost sites used by ruffed grouse during Jan-2016 to Mar-2016 (Fig. S1). We created a subset of the dataset for subsequent analysis to only include data points with values for snow compaction depth (i.e., snow depth > 0 cm). Further, at five roost sites we did not record the number of fecal droppings that we collected, and these observations were removed so that all observations in the final dataset could be weighted by number of droppings. Our final dataset included fecal samples from 50 roost sites (15 snow roosts and 35 other roosts; roost sites were never re-used by individual grouse), representing 15 radio-tagged individuals. The mean number of samples (i.e., roost sites) per individual grouse was 3.3 (range: 2-5). The number of droppings at roosts ranged from 2 to 22 ($\bar{x}$ = 11.04 ± 6.09). Minimum air temperature ranged from -26.5 to 2.0 °C ($\bar{x}$ = -10.4 ± 9.3 °C; Fig. S2). Snow depth ranged from 2.4 to 39.6 cm ($\bar{x}$ = 21.0 ± 10.5 cm; 27 out of all 50 roost sites (including all roost types) we observed had snow depths greater than 20 cm). Snow compaction depth ranged from 0 to 9.8 cm ($\bar{x}$ = 4.6 ± 3.2 cm). We included date in the model set as a single predictor to test for a temporal effect of winter conditions that might influence stress levels in grouse, but are not captured by our weather variables (e.g., food availability). Snow depth and snow compaction depth were correlated (r = 0.77), but our top models from the first (Table 1) and second rounds (Table 2) of model selection had VIFs less than five (4.17 and 4.42, respectively), and we chose not to exclude snow depth and snow compaction depth from the same models. While we recognize that there is likely a mechanistic relationship between snow compaction depth and temperature, we did not find a statistical correlation in our dataset. The repeatability (proportion of variation in FCM levels due to inter-individual differences between grouse) was 0.00, suggesting that the variation in corticosterone metabolites was due to environmental effects not differences among individual grouse.

Effects of ambient temperature and snow on FCM levels

We found strong support for the role of ambient temperature and snow depth on grouse FCM levels, and the top model included minimum temperature, the quadratic form of snow depth, snow compaction depth, and time of day (AIC_c weight = 0.34; $R^2 = 0.24$; Table 1). An additional competitive model was identical to the top model, but did not include time. FCM concentrations increased as ambient temperature became colder (Table 3, Fig. 1), and generally decreased with greater snow depth, but this relationship was nonlinear as evidenced by the inclusion of the quadratic form of snow depth (Table 3, Fig. 2). As snow depth increased to 15 cm, FCM concentrations remained stable, but as snow depth increased beyond 15-20 cm, FCM concentrations rapidly decreased. Contrary to our predictions, and independent of snow depth, there was a positive relationship between snow compaction depth and FCM concentrations (Table 3; Fig. 2). As snow became increasingly powdery and less dense (increased snow compaction depth), grouse FCM concentrations increased. FCM levels were highest earlier in the day (Table 3).

Mediating effects of snow roosting

We found that flexible roosting behaviour tended to modify the relationship between grouse FCM levels and winter conditions. The single competitive model obtained from the second round of model selection included time of day, the quadratic of snow depth, snow compaction depth, and an interaction between temperature and roost type (AIC_c weight = 0.65; $R^2 = 0.34$; Table 3). When grouse used snow roosts there was no effect of temperature on FCM levels, but if they used any other roost type the strong negative relationship between FCM levels and ambient temperature remained (Fig. 3). At the coldest temperatures (-26.5 °C), roosting in snow burrows reduced grouse FCM levels by 45% (138.15 ng/g in other roosts vs. 74.70 ng/g in snow burrows).

Further, we found very similar results when we restricted the dataset to observations with 8 or more fecal droppings (n = 35 roost observations): the top model remained the same and the relationships between FCMs and temperature (β = -0.53, SE = 0.09), roost type (β = 0.10, SE = 0.19, snow depth (β = -2.50, SE = 0.80), the quadratic of snow depth (β = -1.38, SE = 0.41), snow compaction depth (β = 0.42, SE = 0.13), time of day (β = -0.17, SE = 0.06), and the interaction between temperature and roost type (β = 0.62, SE = 0.16) were essentially unchanged (Table 3).

Additionally, we found no differences in minimum temperature or the number of droppings between snow roosts and other roosts. The number of droppings at snow roosts and other roosts ranged from 2 to 21 and 2 to 22, respectively ($\bar{x}$ = 11.2 ± 6.3 and 11.0 ± 6.1 droppings, W = 254.5, p = 0.87). Minimum air temperature ranged from -25.5 to -2.5 °C and -26.5 to 2.0 °C for snow roosts and other roosts, respectively ($\bar{x}$ = -11.3 ± 8.2 and -10.0 ± 9.8 °C, W = 293.5, p = 0.52). The numbers of snow roost sites and other roost sites located for each individual grouse are given in Figures S3 and S4, respectively. Snow was deeper at snow roosting sites, ranging from 12.7 to 39.6 cm and 2.4 to 31.4 cm for snow roosts and other roosts, respectively ($\bar{x}$ = 29.7 ± 9.0 cm and 17.3 ± 8.8 cm, W = 80, p < 0.001). Snow compaction depth was greater (i.e. snow was more powdery) at snow roosting sites, ranging from 1.8 to 9.8 cm and 0 to 9.1 cm for snow roosts and other roosts, respectively ($\bar{x}$ = 7.2 ± 2.6 cm and 3.4 ± 2.7 cm, W = 84.5, p < 0.001).

Discussion

Our study is a novel exploration of the influence of winter conditions on the stress physiology of a wild bird and the behavioural responses used to mediate such a relationship. We found that wintering ruffed grouse had greater FCM levels (indicative of greater plasma corticosterone levels) when ambient temperatures were low and when snow was shallow. Further, we found that the use of snow burrows eliminated the relationship between ambient temperature and FCM levels, and grouse roosting in snow burrows had lower FCM levels than those roosting outside of snow burrows. For species that overwinter in temperate and northern areas, physiological and behavioural adaptations that maximize energy conservation during winter are critical (e.g., Humphries et al. 2005; Pokallus and Pauli 2016; Sheriff et al. 2009c; Sheriff et al. 2009d).

The influence of ambient temperature

During the winter season, we found that grouse had higher FCM levels during periods of cold ambient temperatures. We suggest that cold-induced increases in FCM levels are associated with animals' need to increase energy expenditure. For example, corticosterone metabolites in greylag geese (*Anser anser*) increased with decreasing minimum ambient temperature, reflecting the role of corticosterone in thermoregulation (Frigerio et al. 2004). At extreme cold temperatures, more energy is required for thermoregulation, and increases in circulating glucocorticoids may help mediate increased metabolic demand (Jimeno et al. 2018; Sapolsky et al. 2000). For example, in captive birds, variation in GCs has been shown to be a reflection of increased energy expenditure, independent of psychological stress (Jimeno et al. 2018). A changing winter environment, including drops in temperature, combined with loss of snow cover (see below), may increase stress hormone levels as a result of higher metabolic demands for thermoregulation in winter-adapted species.

The mediating effects of snow depth and snow burrow use

Snow cover is a critical seasonal characteristic of many temperate environments, and deep snow was associated with lower FCM levels in grouse, but this relationship was nonlinear. Grouse FCM levels remained stable, but high, as snow depth increased to 15 cm, and rapidly decreased thereafter as snow depth increased beyond 15 cm. Interestingly, ~15-20 cm is often cited as the minimum depth required for grouse to use snow burrows (Gullion 1970; Heinrich 2017; Thompson and Fritzell 1988a). As snow depth increases beyond 20 cm the prevalence and ability to use snow burrows may increase, resulting in lower energetic costs and FCM levels for grouse. When winter temperatures were low we found snow burrowing behaviour mediated the effect of cold temperatures on FCM levels, and grouse in snow burrows had lower FCM levels than those outside of snow burrows regardless of temperature. For example, during the coldest temperatures we recorded (-26.5 °C), birds that used snow burrows had 45% lower FCM levels than those that did not. Thus, we believe that the use of snow burrows decouples the strong negative relationship between FCM levels and ambient temperature because it alleviates some of the costs of thermoregulation. However, we acknowledge that there may be important ecological differences between true snow burrows and snow bowls. In this study, we pooled snow burrows and bowls due to a small sample size of burrows (12 snow bowls and 3 snow burrows). True snow burrows are likely even more insulative than snow bowls (which are open on top), and the reduction in FCM levels through the use of true snow burrows is likely even greater than what we documented.

Other northern species have been shown to use behaviour to modify their thermoregulatory costs during winter. For example, female red squirrels (*Tamiasciurus hudsonicus*), which are typically asocial, are more likely to nest communally during cold temperatures to conserve heat (Williams et al. 2013). Given that snow burrows can retain more heat and result in temperatures approximately 7 °C warmer than other roost sites (Marjakangas et al. 1984; Thompson and Fritzell 1988a), they likely provide a significant energy savings as reflected in lower grouse FCM levels. The lower critical temperature for ruffed grouse (below which they must increase their metabolic rate to keep up with environmental demands) has been estimated as -0.3 °C (Rasmussen and Brander 1973) and as 1.5 °C (Thompson and Fritzell 1988a). Given that average winter temperatures were -10 °C, the use of snow burrows may allow grouse to remain at or close to their lower critical temperature, and within their thermal neutral zone.

An alternative explanation for the reduced corticosterone levels in grouse using snow burrows is the evidence that snow burrows provide a refuge from predators, particularly raptors (Gullion 1970; Heinrich 2017; Marjakangas 1986). Grouse in snow burrows are often completely concealed, and snow that is not deep enough for burrowing may result in grouse being more visible to predators and possibly increase their risk of predation. Perceived risk of predation is associated with greater stress hormone levels in many species (Sheriff et al. 2009b; Sheriff and Thaler 2014), and grouse roosting outside of snow burrows may perceive increased vulnerability. In fact, rock ptarmigan (*Lagopus mutus*) soil their white feathers to become less conspicuous after snow melt and prior to spring molt, indicating the ability to perceive increased risk due to camouflage mismatch (Montgomerie et al. 2001). While not being in a snow burrow might result in grouse being more exposed to predators, the loss of snow’s thermal protection may also increase foraging activities to compensate for energy loss, resulting in the possible synergistic consequences of increased predation risk and energy deficits due to low snow cover. Again, there may be differences in predation risk for birds roosting in true snow burrows and those using snow bowls, and snow burrows likely provide more protection from predators. Similar to the thermoregulatory benefits of snow burrows, if the decrease in FCM levels shown here for birds in snow roosts is due to a decrease in perceived predation risk, this effect is likely to be even greater for grouse using true snow burrows.

We found powdery, uncompacted snow was associated with increased grouse FCM levels, which was unexpected, as grouse need light, powdery snow for burrowing (Blanchette et al. 2007; Gullion 1970). Less dense snow, however, may increase energy expenditure because birds must “snowplow” through deep powdery snow as they walk. The effect of powdery snow may be especially costly when snow is not sufficiently deep for burrowing, but is powdery enough that birds must push their way through it, or resort to flying, which is also energy intensive (Gallagher et al. 2017). The influence of snow quality warrants further exploration.

Interpreting fecal corticosterone metabolite concentrations

There has been much work in assessing the usefulness of FCM concentrations as indicators of plasma GCs in wildlife (Dantzer et al. 2014; Dickens and Romero 2013; Goymann 2012; Sheriff et al. 2011a; Washburn and Millspaugh 2002). However, several confounding factors that can alter FCM levels and limit its usefulness are often overlooked. In our study factors related to the interaction between sample integrity and environmental temperatures may have influenced FCM levels. For example, it has been shown that fecal samples exposed to rainfall, elevated temperatures (> 22 °C) (Descovich et al. 2012; Khan et al. 2002), or freeze thaw cycles (Washburn and Millspaugh 2002) can exhibit artificially elevated FCM concentrations. Increased microbial activity due to rain events (Washburn and Millspaugh 2002) or excessive heat (Millspaugh et al. 2003) has been suggested to influence FCM levels. However, these factors are unlikely to have altered our results because we designed our field protocol to avoid sample collection during rainfall, elevated temperatures, or freeze-thaw events. Further, we found that increasing temperatures resulted in lower FCM concentrations, and as a result, if ambient temperature had any effect on our samples, our results would be considered conservative. Ambient temperature may also have affected our FCM concentrations indirectly with lower temperatures causing animals to increase food intake and ultimately ‘diluting’ FCM levels because of increased fecal bulk (Goymann 2012), however the rate of metabolite secretion may be proportional to the rate of fecal excretion (Randall et al. 2000; Sheriff et al. 2009a; Touma et al. 2003; Wasser et al. 1994). If this factor influenced our FCM concentrations, our results would again be a conservative estimate because we would expect our FCM concentrations to be ‘diluted’ at lower temperatures, but we found lower temperatures increased FCM concentrations. Finally, it is possible that “baseline” differences in FCMs exist between individual grouse, but repeatability (Roche et al. 2016) was zero, and we found little evidence of appreciable differences in FCMs between individual grouse. Thus, although we believe our methodology accounted for factors that could influence FCM levels, if such factors were influential our results are a conservative estimate of the influence of temperature on FCM levels and the ability of grouse to behaviorally mediate such a relationship.

Implications of future losses in snow cover

Most studies on the behavioural shifts in response to climate variability focus on directional stimuli (e.g., increases in average summer temperature, earlier spring conditions) and behavioural changes over extended timescales (e.g., multiple seasons) (Beever et al. 2017). For example, many studies have shown that climate-induced advances of spring conditions have created a mismatch between animal phenology and their environment, with potential consequences to fitness (e.g., Both et al. 2006; Both et al. 2009; Sheriff et al. 2017). However, far fewer studies have investigated animal responses to rapidly shifting and ephemeral climate stressors (i.e., within season changes in temperature and snow cover), which could play an equally important role in species’ ability to cope with a changing climate (Beever et al. 2017).

During the winter of 2015-16, only 27 out of the 70 roost sites we discovered had snow depths greater than 20 cm. Average mid-winter snow depth across Wisconsin currently peaks at 20 cm (Notaro et al. 2011). Future climate projections predict that peak midwinter snow depths will decline to 8-15 cm (Notaro et al. 2014; Notaro et al. 2011), with an increase in the number of freeze-thaw events (Mellander et al. 2007; Sinha and Cherkauer 2010) resulting in a shallow and hardened snow layer, which will nearly eliminate the possibility of snow burrowing. A mid-winter thaw resulting in snow melt, followed by low temperatures, may be particularly hazardous, as these winter-adapted birds may lose an important seasonal refuge that allows them to escape cold temperatures and predation. Consequently, while winters are expected to become warmer in the future, the loss of snow cover will result in a functionally colder environment for many snow-adapted species (Pauli et al. 2013; Zuckerberg and Pauli 2018).

For species that require snow for thermoregulation or to reduce predation risk (e.g., Pauli et al. 2013; Sinclair et al. 2013), or for organisms that molt white in winter for crypsis (Mills et al. 2013), the loss of snow, even for short periods of time, can result in a significant fitness cost via stress hormone-induced reductions in body condition, growth, and immunity (Boonstra 2013). Further, temperature-induced increased energy expenditure for thermoregulation and associated increases in stress hormone levels during the winter may also carry over to increase an individual’s vulnerability to subsequent stressors during the breeding season (MacLeod et al. 2018b). Overwintering species have evolved a number of behavioural adaptations in using winter refugia to minimize the physiological consequences of seasonality, but a rapidly changing winter environment and the loss of snow cover could stretch the limits of behavioural flexibility.

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Tables

Table 1. Model selection for abiotic factors influencing Ruffed Grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI. TEMP = minimum temperature, DEPTH = snow depth, CDEPTH = snow compaction depth, TIME = time of day, DATE = date, k = number of parameters in the model, AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = change in AIC_c from the model above, w_i = Akaike weight. Only models with a $\Delta AIC_c < 6$ are shown. The full list of candidate models can be found in Supplementary Materials.

Model	k	AIC_c	ΔAIC_c	w_i
TEMP + DEPTH^2 + CDEPTH + TIME	8	86.46	0.00	0.34
TEMP + DEPTH^2 + CDEPTH	7	87.48	1.02	0.21
TEMP + DEPTH^2	6	88.80	2.35	0.11
TEMP*CDEPTH	6	88.90	2.44	0.10
TEMP	4	89.82	3.36	0.06
TEMP + DEPTH^2 + TIME	7	90.05	3.59	0.06
TEMP*CDEPTH + TIME	7	91.00	4.54	0.04
TEMP + TIME	5	91.41	4.95	0.03
TEMP + CDEPTH	5	92.05	5.59	0.02

* indicates an interaction

Table 2. Model selection for abiotic and biotic factors influencing Ruffed Grouse corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, Wisconsin, USA. TEMP = minimum temperature, DEPTH = snow depth, CDEPTH = snow compaction depth, TIME = time of day, ROOST = roost type, SEX = grouse sex, AGE = grouse age, k = number of parameters in the model, AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = change in AIC_c from the model above, w_i = Akaike weight. Only models with a $\Delta AIC_c < 6$ are shown. The full list of candidate models can be found in Supplementary Materials.

Model	k	AIC_c	ΔAIC_c	w_i
TEMP*ROOST + $DEPTH^2$ + CDEPTH + TIME	10	80.63	0.00	0.65
TEMP*ROOST + ROOST*$DEPTH^2$ + CDEPTH + TIME	12	84.89	4.25	0.08
TEMP + $DEPTH^2$ + CDEPTH + TIME + SEX	9	85.62	4.99	0.05
TEMP + $DEPTH^2$ + CDEPTH + TIME + AGE	9	85.72	5.09	0.05
TEMP + $DEPTH^2$ + CDEPTH + TIME	8	86.46	5.83	0.04

* indicates an interaction

Table 3. Relationships between fecal corticosterone metabolite concentrations and environmental predictors and roost type for Ruffed Grouse at Sandhill Wildlife Area, Wood County, Wisconsin, USA. Only variables in the top model (based on AIC model selection of a list of generalized linear mixed-effects models) are presented here. Individual bird ID was included as a random effect to control for non-independence among individuals in the population. β = beta estimate, SE = standard error, 95% CI = 95% Confidence Interval, TEMP = minimum temperature, DEPTH = snow depth, CDEPTH = snow compaction depth, TIME = time of day, ROOST = roost type (snow roost = 1, other roost = 0).

Fixed Effects	β	SE	95% CI
Intercept	3.86	0.08	3.86, 3.92
TEMP	-0.50	0.08	-0.50, -0.49
ROOST	0.15	0.17	0.15, 0.17
DEPTH	-2.43	0.85	-2.43, -2.35
DEPTH^2	-1.13	0.44	-1.14, -1.09
CDEPTH	0.29	0.11	0.29, 0.31
TIME	-0.11	0.06	-0.11, -0.10
TEMP*ROOST	0.55	0.15	0.55, 0.57

* indicates an interaction

Figures

Fig. 1: Partial residual plot of ambient temperature and ruffed grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI. Shaded areas represent 95% confidence intervals.

Fig. 2: Partial residual plots of snow depth and snow compaction depth and ruffed grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI. Shaded areas represent 95% confidence intervals.

Fig. 3: Partial residual plot of the interaction between ambient temperature and roost site and ruffed grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI. The dashed and solid lines indicate the effect of temperature on corticosterone for ruffed grouse using snow roosts vs. using other roosts, respectively. Circles and triangles represent partial residuals for ruffed grouse using snow roosts vs. using other roosts, respectively. Shaded areas represent 95% confidence intervals.

Figure 1

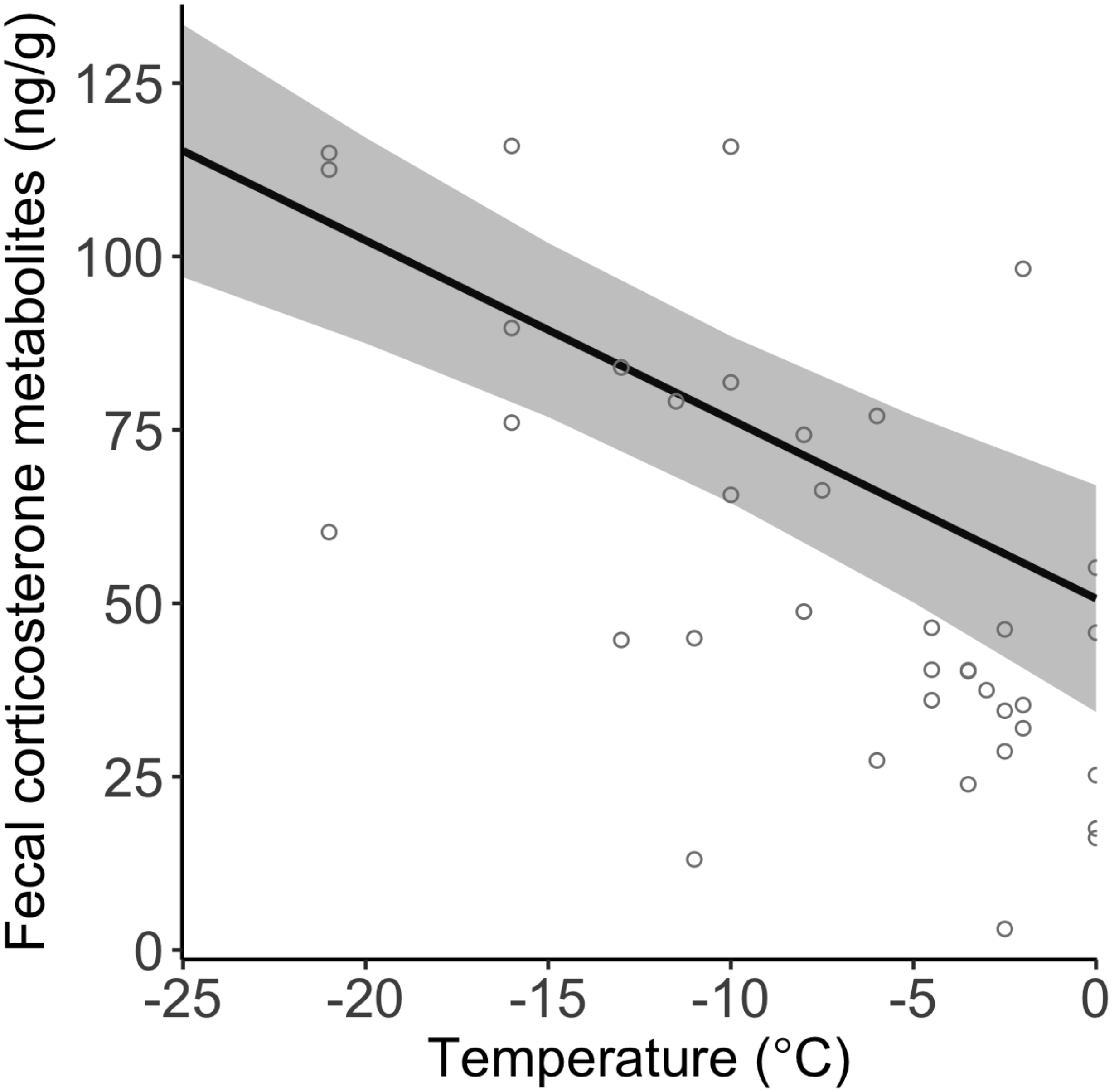

Fecal corticosterone metabolites (ng/g)
125
100
75
50
25
0
-25
-20
-15
-10
-5
0
Temperature (°C)

Figure 2

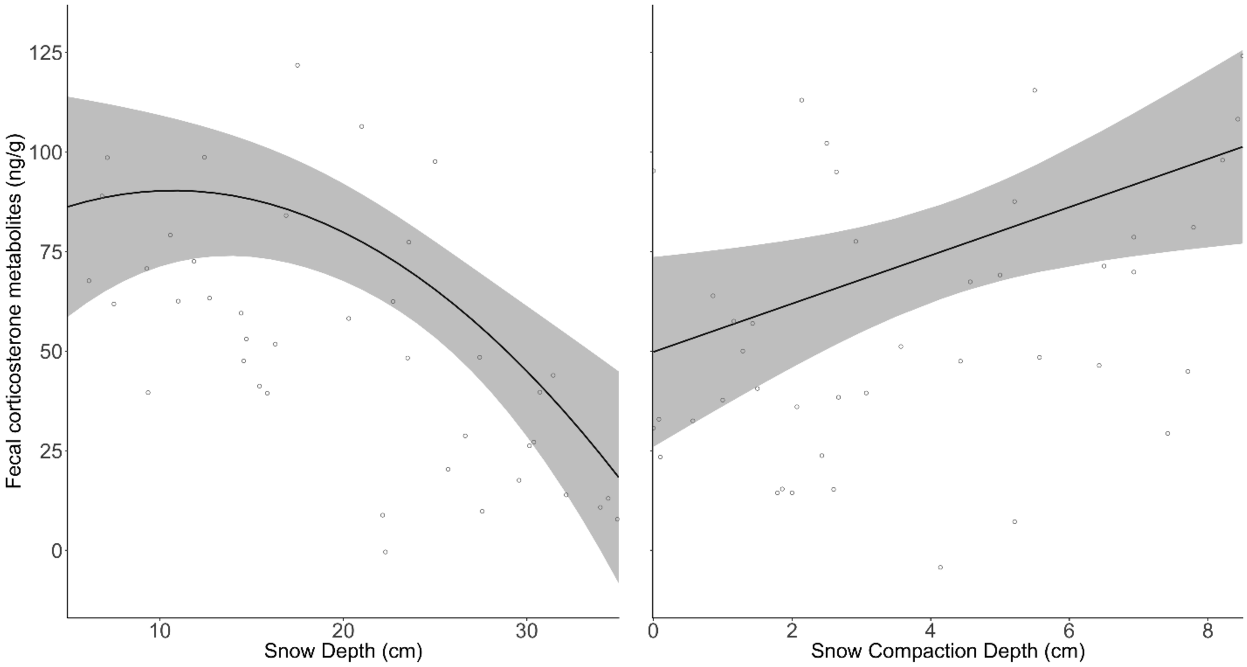
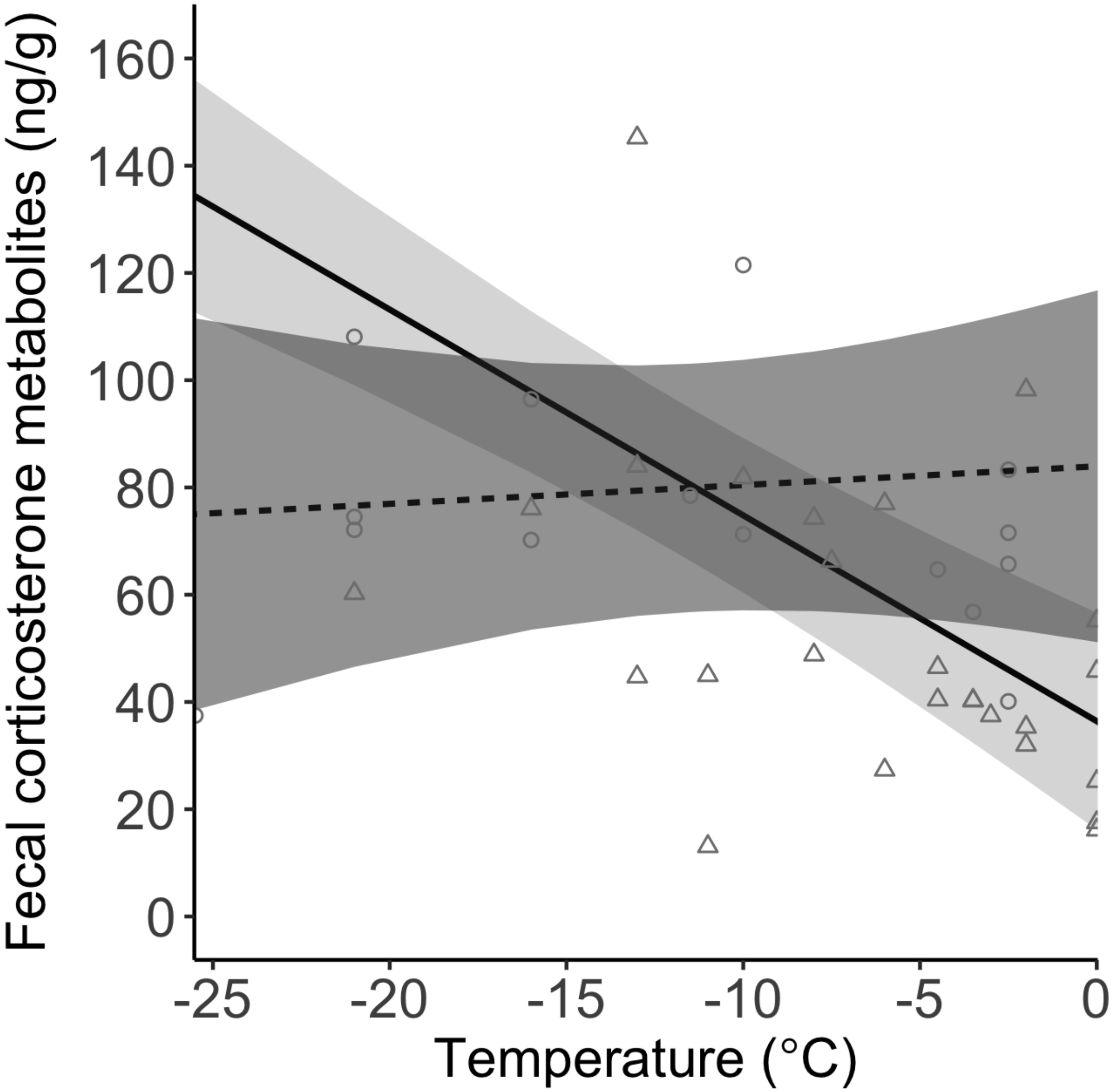

Fecal corticosterone metabolites (ng/g)
125
100
75
50
25
0
10
20
30
Snow Depth (cm)
0
2
4
6
8
Snow Compaction Depth (cm)

Figure 3


Fecal corticosterone metabolites (ng/g)
160
140
120
100
80
60
40
20
0
-25
-20
-15
-10
-5
0
Temperature (°C)

Supplementary Materials

Table S1. Model selection for abiotic factors influencing Ruffed Grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI. TEMP = minimum temperature, DEPTH = snow depth, CDEPTH = snow compaction depth, TIME = time of day, DATE = date, k = number of parameters in the model, AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = change in AIC_c from the model above, w_i = Akaike weight.

Model	k	AIC_c	ΔAIC_c	w_i
TEMP + $DEPTH^2$ + CDEPTH + TIME	8	86.46	0.00	0.34
TEMP + $DEPTH^2$ + CDEPTH	7	87.48	1.02	0.21
TEMP + $DEPTH^2$	6	88.80	2.35	0.11
TEMP*CDEPTH	6	88.90	2.44	0.10
TEMP	4	89.82	3.36	0.06
TEMP + $DEPTH^2$ + TIME	7	90.05	3.59	0.06
TEMP*CDEPTH + TIME	7	91.00	4.54	0.04
TEMP + TIME	5	91.41	4.95	0.03
TEMP + CDEPTH	5	92.05	5.59	0.02
TEMP*$DEPTH^2$	8	93.07	6.60	0.01
TEMP + CDEPTH + TIME	6	93.74	7.28	0.01
$DEPTH^2$	5	94.98	8.52	0.00
TEMP*$DEPTH^2$ + TIME	9	95.00	8.54	0.00
$DEPTH^2$ + TIME	6	97.08	10.62	0.00
NULL	3	99.10	12.64	0.00
DATE*CDEPTH + TIME	7	99.27	12.81	0.00
DATE*CDEPTH	6	99.62	13.17	0.00
DATE	4	100.78	14.32	0.00
CDEPTH	4	101.03	14.57	0.00
TIME	4	101.16	14.70	0.00

DATE + TIME	5	102.70	16.24	0.00
DATE + CDEPTH	5	102.90	16.43	0.00
CDEPTH + TIME	5	103.18	16.72	0.00
DATE + CDEPTH + TIME	6	104.93	18.47	0.00

* indicates an interaction.

Table S2. Model selection for abiotic and biotic factors influencing Ruffed Grouse corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, Wisconsin, USA. TEMP = minimum temperature, DEPTH = snow depth, CDEPTH = snow compaction depth, TIME = time of day, ROOST = roost type, SEX = grouse sex, AGE = grouse age, k = number of parameters in the model, AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = change in AIC_c from the model above, w_i = Akaike weight.

Model	k	AIC_c	ΔAIC_c	w_i
TEMP*ROOST + $DEPTH^2$ + CDEPTH + TIME	10	80.63	0.00	0.65
TEMP*ROOST + ROOST*$DEPTH^2$ + CDEPTH + TIME	12	84.89	4.25	0.08
TEMP + $DEPTH^2$ + CDEPTH + TIME + SEX	9	85.62	4.99	0.05
TEMP + $DEPTH^2$ + CDEPTH + TIME + AGE	9	85.72	5.09	0.05
TEMP + $DEPTH^2$ + CDEPTH + TIME	8	86.46	5.83	0.04
TEMP*AGE + $DEPTH^2$ + CDEPTH + TIME	10	86.96	6.32	0.03
TEMP + SEX*$DEPTH^2$ + CDEPTH + TIME	11	88.51	7.88	0.01
TEMP*ROOST + ROOST*$DEPTH^2$ + ROOST*CDEPTH + TIME	13	88.54	7.90	0.01
TEMP + SEX*CDEPTH + $DEPTH^2$ + TIME	10	88.56	7.92	0.01
TEMP + $DEPTH^2$ + CDEPTH + ROOST + TIME + AGE + SEX	11	88.79	8.15	0.01
TEMP + AGE*CDEPTH + $DEPTH^2$ + TIME	10	88.79	8.15	0.01
TEMP*SEX + $DEPTH^2$ + CDEPTH + TIME	10	88.86	8.23	0.01
TEMP + AGE*$DEPTH^2$ + CDEPTH + TIME	11	88.96	8.33	0.01
TEMP + $DEPTH^2$ + CDEPTH + TIME + ROOST	9	89.44	8.81	0.01
TEMP + ROOST*CDEPTH + $DEPTH^2$ + TIME	10	90.73	10.09	0.00
TEMP*AGE + AGE*$DEPTH^2$ + CDEPTH + TIME	12	91.15	10.51	0.00
TEMP + SEX*$DEPTH^2$ + SEX*CDEPTH + TIME	12	92.10	11.47	0.00
TEMP*SEX + SEX*$DEPTH^2$ + CDEPTH + TIME	12	92.13	11.50	0.00
TEMP + AGE*$DEPTH^2$ + AGE*CDEPTH + TIME	12	92.53	11.90	0.00
TEMP*AGE + AGE*$DEPTH^2$ + AGE*CDEPTH + TIME	13	94.54	13.90	0.00
TEMP + ROOST*$DEPTH^2$ + CDEPTH + TIME	11	94.69	14.05	0.00

TEMP*SEX + SEX*DEPTH^2 + SEX*CDEPTH + TIME	13	95.95	15.32	0.00
TEMP + ROOST*DEPTH^2 + ROOST*CDEPTH + TIME	12	96.21	15.58	0.00
NULL	3	99.10	18.47	0.00

* indicates an interaction.

Supplementary Figures

Fig. S1: Number of ruffed grouse fecal samples collected for fecal corticosterone metabolite analysis, Sandhill Wildlife Area, Wood County, Wisconsin, USA, January-March 2016. 1 = January 1, 2016.

Fig. S2: Number of ruffed grouse fecal samples collected at different ambient minimum temperatures for fecal corticosterone metabolite analysis, Sandhill Wildlife Area, Wood County, Wisconsin, USA, January-March 2016.

Fig. S3: Number of snow roosts located for 15 individual ruffed grouse, Sandhill Wildife Area, Wood County, Wisconsin, USA, January-March 2016.

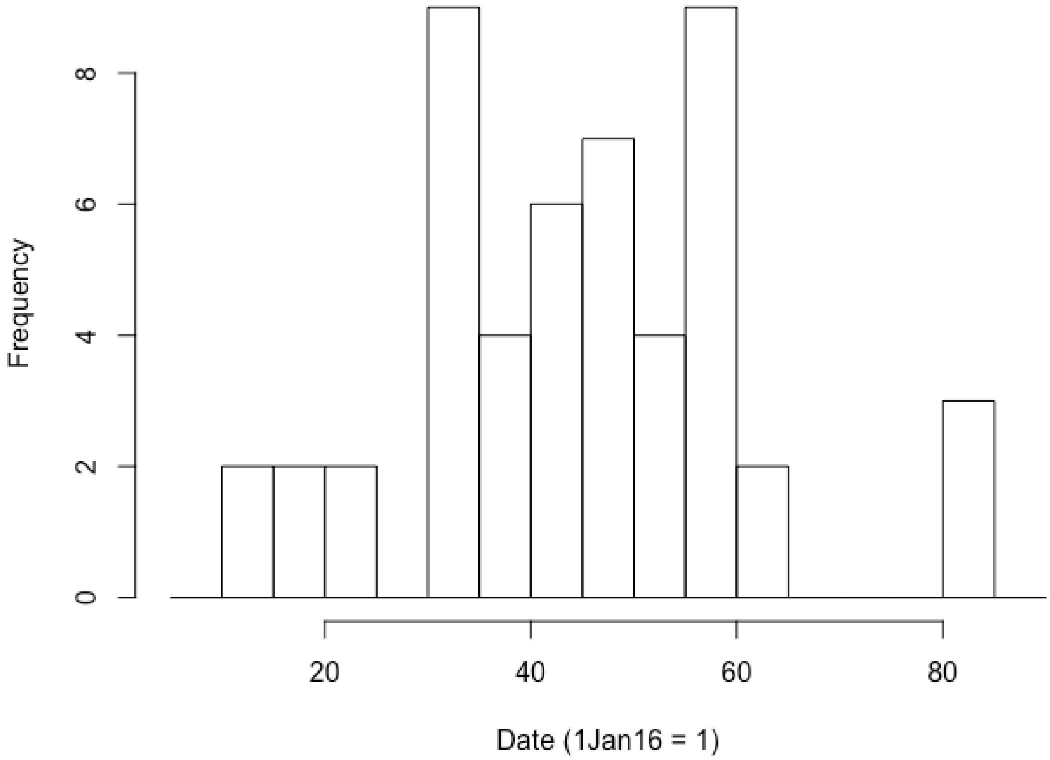
Fig. S4: Number of other roosts located for 15 individual ruffed grouse, Sandhill Wildlife Area, Wood County, Wisconsin, USA, January-March 2016.

Fig. S5: The relationship between ambient temperature and ruffed grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI, USA. Shaded areas represent 95% confidence intervals. Circles represent raw values.

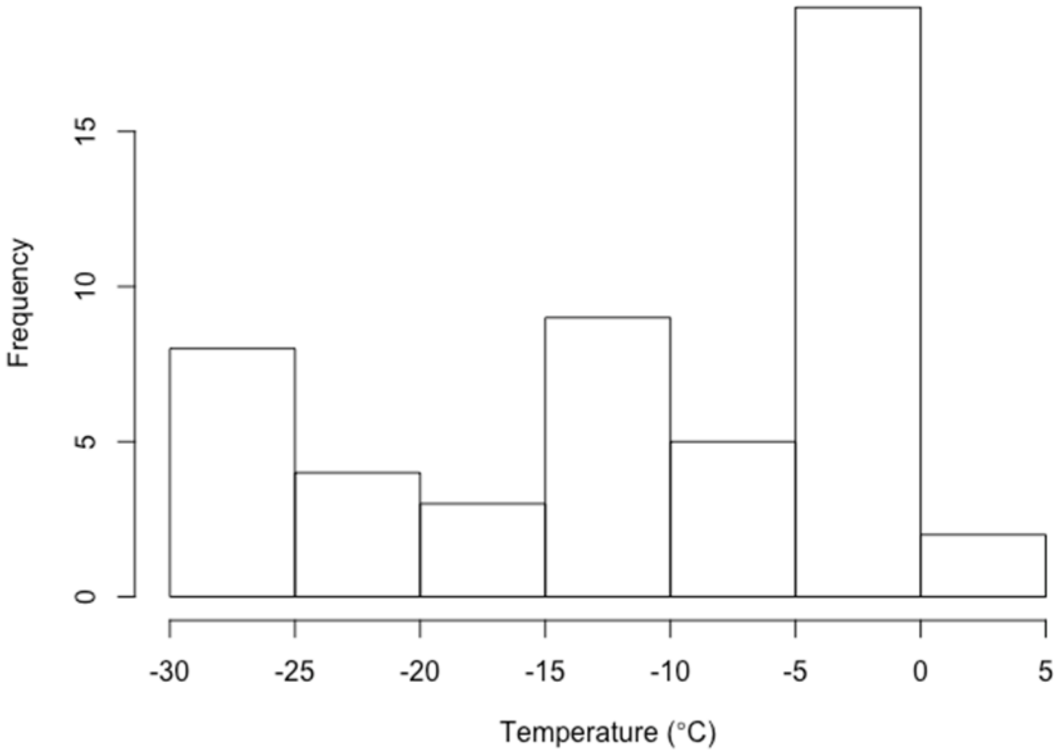
Fig. S6: The relationship between snow depth and snow compaction depth and ruffed grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI, USA. Shaded areas represent 95% confidence intervals. Circles represent raw values.

Fig. S7: The effect of the interaction between roost site and temperature on ruffed grouse fecal corticosterone metabolite concentrations, January-March 2016, Sandhill Wildlife Area, Wood County, WI, USA. The dashed and solid lines indicate the effect of temperature on corticosterone for ruffed grouse using snow roosts vs. using other roosts, respectively. Circles and triangles represent raw values for ruffed grouse using snow roosts vs. using other roosts, respectively. Shaded areas represent 95% confidence intervals.

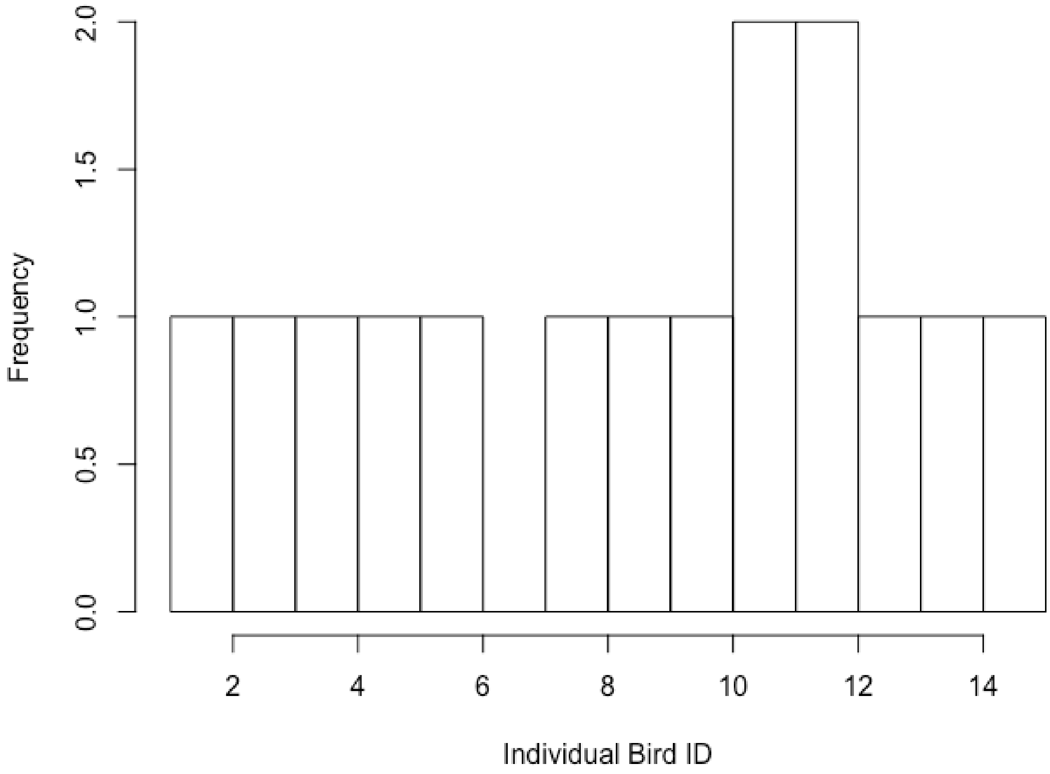
Supplementary Figure 1



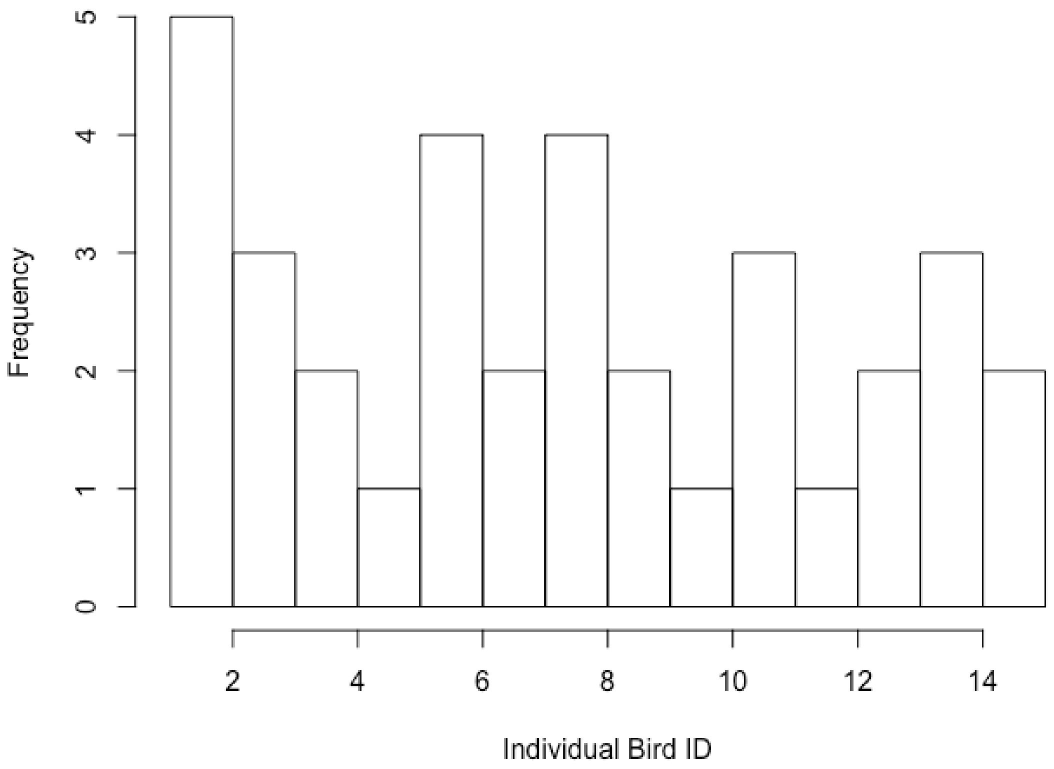
Supplementary Figure 2



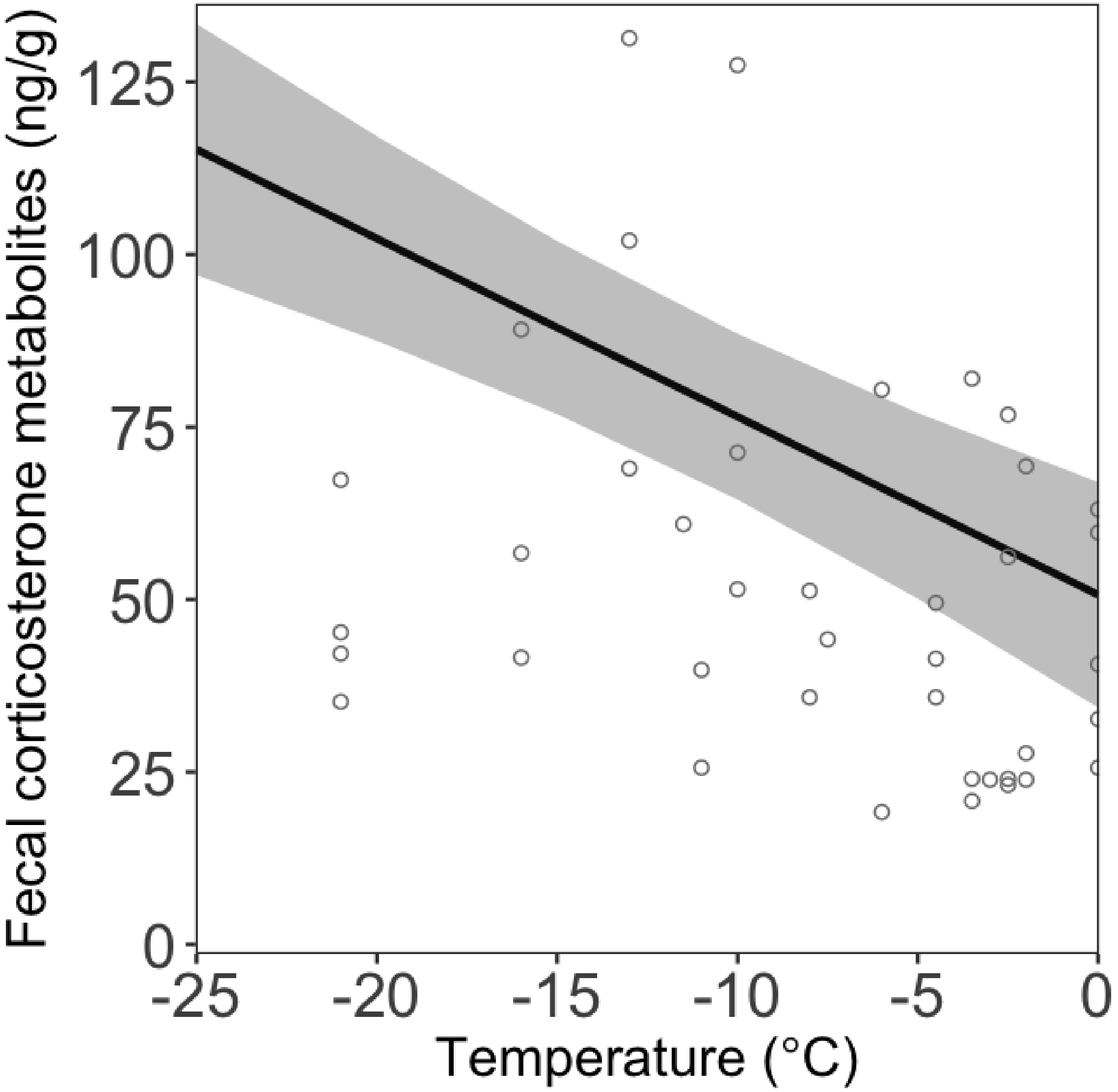
Supplementary Figure 3



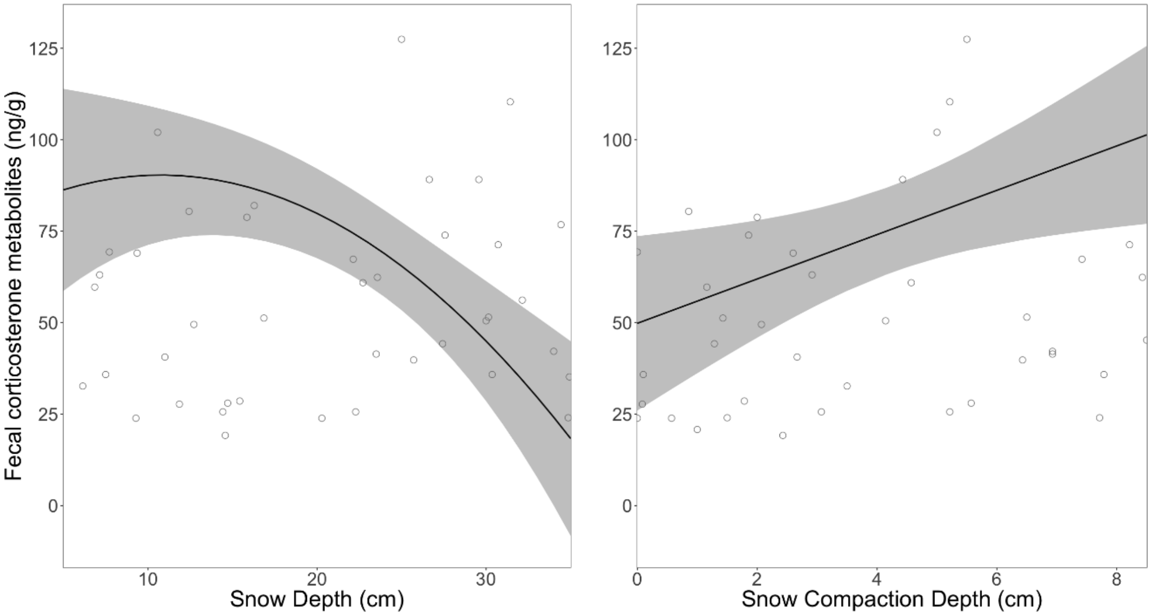
Supplementary Figure 4



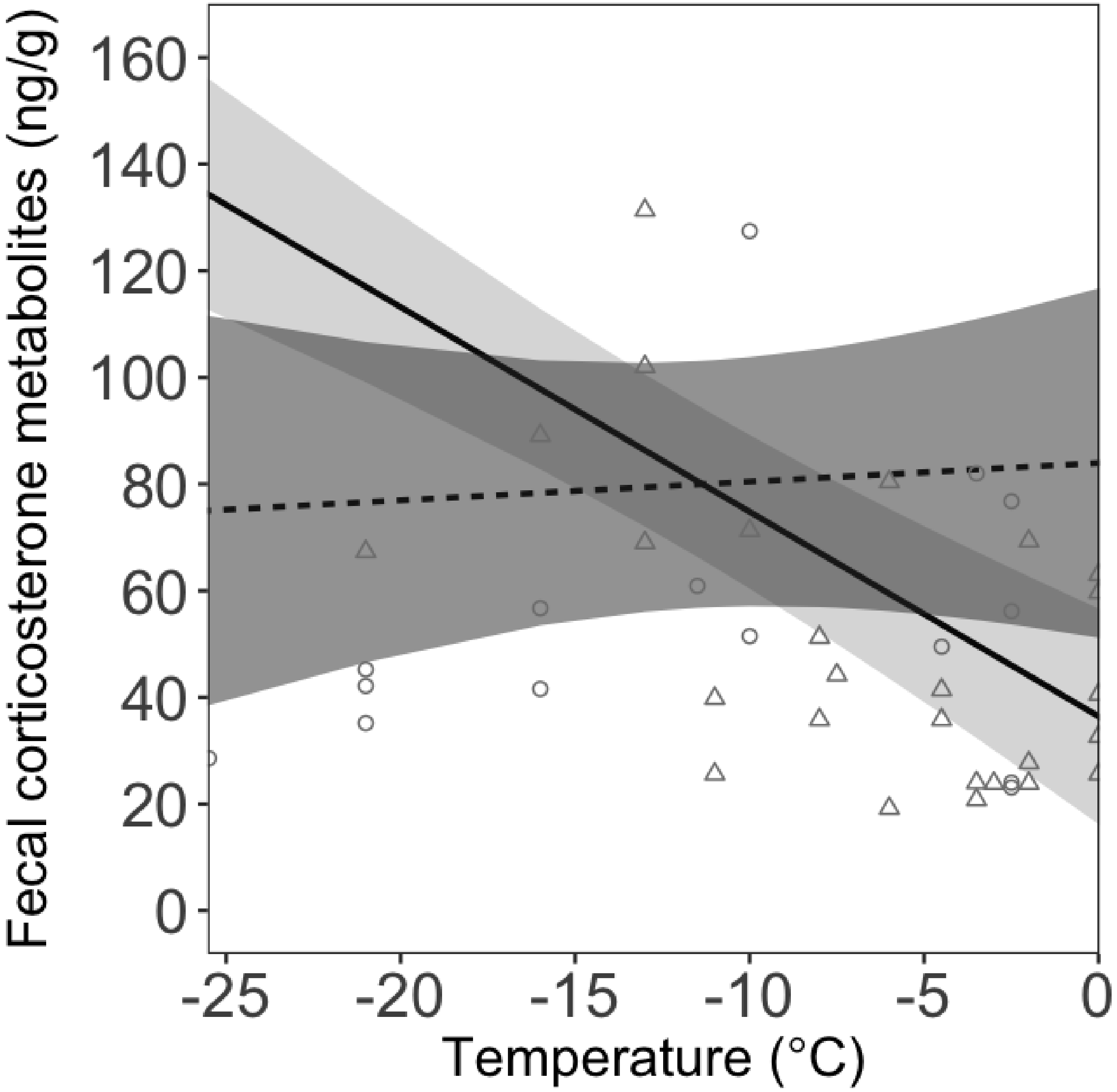
Supplementary Figure 5



Supplementary Figure 6



Supplementary Figure 7



Weather and land cover create a predictable “stress-scape” for a winter-adapted bird

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Prepared for *Landscape Ecology*

Abstract

Variability in temperature and snow cover are characteristics of high-latitude environments that impose significant pressures on overwintering species. To cope with increased energetic demands and decreased resources, winter-adapted species occupying seasonal environments often seek out refugia that can buffer them from inclement conditions. Ruffed grouse (*Bonasa umbellus*) are one such species that roosts in the thermally stable microhabitat beneath deep snow, and by accessing this microrefugium, is buffered from the negative effects of cold temperatures on physiological stress (glucocorticoid hormone levels). Despite the physiological advantages of accessing warmer refugia during winter, it is unknown how land cover and winter climate promote the occurrence of such refugia over space and time. Analogous to the landscape of fear, which mediates how some animals navigate spatial variation in predation risk, mapping a landscape of stress, or stress-scape, may provide insights into hotspots where ecological or environmental stressors persist. We assayed droppings for fecal corticosterone metabolites (FCMs; stress hormones) collected from radio-tagged ruffed grouse over three winters and developed a spatial model of daily FCM concentrations across the extent of our study area, thus quantifying a stress-scape. FCMs increased with shallower snow depths, less dense snow, and colder ambient temperatures. Additionally, FCMs were higher in areas with more open habitat. However, despite considerable spatiotemporal variation in snow depth, snow density, and temperature, regions of consistently elevated FCM levels were highly consistent and predictable across years. Mapping stress-scapes offers a unique tool for understanding and quantifying the indirect effects of environmental stressors. In the case of ruffed grouse, promoting habitats associated with deep snow and minimizing open habitat may provide spatial refugia associated with lower stress levels and a path for mitigating the impacts of snow cover loss for winter-adapted species.

Introduction

The way in which animals navigate through a landscape is a critical, yet complex, component of animal ecology. Many features of the landscape affect how species explore and use their habitats, such as the composition and configuration of land cover (Rosalino, Macdonald and Santos-Reis 2004, Da Silveira et al. 2016), topography (Johnson, Seip and Boyce 2004, Squires et al. 2013), presence of predators (Hebblewhite, Merrill and McDonald 2005, Kittle et al. 2008), presence of conspecifics (Fletcher 2006, Campomizzi et al. 2008), and the human footprint (Preisler, Ager and Wisdom 2006, Leblond, Dussault and Ouellet 2013, Stabach et al. 2016). However, many landscape features, such as temperature, are dynamic. The way in which static landscape features such as land cover interact with temporally-variable features may create, in essence, landscapes that are dynamic across time and space. Recent work has shown that some species move according to least-cost pathways associated with an "energetic landscape" (Shepard et al. 2013, Mosser et al. 2014) resulting from static factors such as topography and temporally-variable factors such as wind speed (Shepard et al. 2013). Similarly, the "landscape of fear" (Laundre, Hernandez and Altendorf 2001, Kohl et al. 2018, Gaynor et al. 2019) predicts that animals reduce risk by accounting for the spatiotemporal activity of predators and the distribution of cover types associated with those predators. Trade-offs can exist when navigating an energetically-costly landscape when predation risk varies spatially, but animals can potentially adjust their movements to avoid risky areas (Pokallus and Pauli 2016).

Physiological stress, often measured by glucocorticoid hormones (GCs), is an important component of animal biology. GCs are associated with a variety of physiological processes from cardiovascular activation to reproduction (Sapolsky, Romero and Munck 2000, Wingfield et al. 1998) that are relevant to how animals navigate landscapes, and play an important role in metabolism and energetic needs by increasing the concentrations of circulating glucose (Jimeno, Hau and Verhulst 2018, Landys, Ramenofsky and Wingfield 2006, Sapolsky et al. 2000). GCs help animals respond to a variety of stressors such as energetic stress resulting from food shortages, inclement weather, and increased predator presence. Importantly, elevated GC levels are associated with increased risk of predation (Sheriff, Krebs and Boonstra 2009b, Sheriff et al. 2011, Sheriff and Thaler 2014). To respond to these stressors, GCs moderate animal behavior by increasing locomotor activity (Astheimer, Buttemer and Wingfield 1992, Wingfield and Ramenofsky 1999) or foraging (Astheimer et al. 1992, Nagra, Meyer and Breitenbach 1963). However, if the animal cannot escape the stressor, GCs remain elevated, which can ultimately result in serious consequences, including the loss of fat and muscle atrophy (Marra and Holberton 1998, Romero and Wikelski 2001) as well as reduced reproductive output (Sheriff et al. 2009b) and survival (MacLeod et al. 2018).

Both consistent and fluctuating landscape features are associated with changes in GCs in animals. For example, mule deer *(Odocoileus hemionus*) show decreases in GCs in areas with vegetation closer to peak forage quality during spring green-up, but elevated GCs in areas with increased human disturbance (Jachowski et al. 2018). Similarly, areas with new vegetative growth and low human disturbance are associated with decreased GCs in wildebeest (Stabach et al. 2016). In some cases, changing landscape features, such as changes in forage quality or productivity as measured by normalized difference vegetative index (NDVI), were more important predictors of GCs in wild impala (*Aepyceros melampus*) than static features like land cover or proxies for human disturbance (Hunninck et al. 2020). While static and dynamic landscape features have been associated with changes in GCs, it is unknown how these features interact spatially and temporally to produce a “landscape of stress”.

For many species of mid- and high-latitude environments, winter is a period of increased thermoregulatory demands and highly variable weather conditions associated with increased GC levels. Cold temperatures and reduced food availability can increase energy expenditure and exposure to predators while foraging (Pokallus and Pauli 2016). While many landscape features that influence animal GCs vary across broad scales (Jachowski et al. 2018, Hunninck et al. 2020), fine-scale variation in topography and land cover can create localized pockets of warmer conditions (Morelli et al. 2016) that can influence animal GCs (Shipley et al. 2019). In spatially heterogeneous environments, such as forests, warmer microclimates can be created through structural complexity (Suggitt et al. 2011, Ashcroft and Gollan 2012, Ford et al. 2013), reduced fragmentation (Latimer and Zuckerberg 2016), or higher elevations (Sears, Raskin and Angiletta Jr 2011). These microrefugia may be particularly important in winter for buffering animals from extreme conditions (Latimer and Zuckerberg 2019) but vary considerably over fine geographic scales and over the course of the winter. While forest cover and topography create stable microclimates (Dobrowski 2011, Ford et al. 2013), snow cover is ephemeral. Snow is an important microhabitat that insulates and protects many species from the harsh effects of winter (Pauli et al. 2013), but snow depth and density, and the relative benefits that snow can provide for winter-adapted species, is highly variable and difficult to predict (Thompson et al. 2018, Thompson et al. 2021, Shipley, Cruz and Zuckerberg 2020).

Ruffed grouse (*Bonasa umbellus*) are a winter-adapted bird species associated with northern forests of North America. In winter, grouse are relatively sedentary and spend up to 80% of the time roosting on the ground, in trees, or in burrows under the snow (Bump et al. 1947). Snow burrows provide excellent thermal insulation relative to other roost sites (Thompson and Fritzell 1988), forming microenvironments within thermo-neutral temperatures for grouse (Marjakangas, Rintamaki and Hissa 1984) that can be particularly important during winter when grouse have reduced somatic stores and little ability to tolerate metabolic fasting (Thomas 1987). Use of snow burrows is limited to time periods and areas where snow is deep (>15 cm) and powdery (Blanchette et al. 2007, Gullion 1970, Heinrich 2017, Shipley et al., *unpublished data*). Use of snow burrows greatly reduce cold temperature-induced increases in GC levels during winter (Shipley et al. 2019). Further, individual grouse that select areas with deep snow (>15 cm) and use snow burrows are more likely to avoid predation (Shipley et al. 2020). This indicates that snow burrows provide an environment that decreases both thermoregulatory stress and the risk of predation.

The relationship between ruffed grouse GCs and winter microrefugia that vary across space and time represent an ideal scenario for modeling the landscape of stress, or “stress-scape”. Here, we present a first-ever quantification of the stress-scape as an empirically-derived spatial model of stress. Our objectives were to: 1) develop a spatially-explicit model of ruffed grouse GCs (as measured by fecal corticosterone metabolites, FCM) informed by static and dynamic predictors, and based on these relationships; 2) use model-based predictions to map a stress-scape. Our approach centered on collecting fecal samples from ruffed grouse at roost locations, extracting spatial predictors (e.g., land cover, minimum temperature, and snow cover), and developing a spatial model to interpolate daily and annual stress-scapes (Fig. 1). We hypothesized that changes in grouse FCMs would be primarily influenced by temperature and snow cover, with grouse FCMs increasing with cold temperatures and shallow snow conditions, but that regions of high forest cover, warm microclimates, and deep snow would support spatial refugia that reduce grouse FMC levels.

Methods

Study site

Sandhill Wildlife Area (SWA; 44˚18´N, 90˚07´W) is a 3700 ha state wildlife area in central Wisconsin, and is a study site for a number of long-term monitoring programs, including winter-adapted species and climate change impacts. Vegetation at SWA is a mosaic of forested tag alder (*Alnus serrulata*), aspen (*Populus tremuloides* and *P. gradidentata*), oak (*Quercus* sp.), and red and white pine (*Pinus resinosa* and *P. strobus*), fragmented by marshes and open water. There were on average 47 winter nights each year when snow depth exceeded 20 cm (range 0-101 nights) between 2001-2015. Mean winter (December-March) temperature at SWA is − 9 °C ± 10.0 °C (range − 26.5 to 5.5 °C).

Grouse trapping, radio telemetry, and roost site observations

From September-November (2015-2017), we captured ruffed grouse in passive walk-in pens connected to chicken wire drift fences (Gullion 1965). We identified age and sex of each grouse (Hale, Wendt and Halazon 1954), collected morphological measurements, and tagged birds with 12-g necklace style radio transmitters (Advanced Telemetry Systems, Inc.) equipped with 4-hr mortality sensors. During three winters (1 December – 31 March 2015-2018, hereafter Years 1, 2, and 3), we found roost sites for each tagged grouse 1-2 times each week, between 0900 and 1700, by flushing the bird off the roost. We calculated snow depth at roost sites as the average depth (cm) from 7 locations that were equidistant from the roost site to the perimeter of a 0.04 ha circular plot: at the roost, 3.6 m, 7.2 m, and 10.8 m North or East of the roost, and 3.6 m, 7.2 m, and 10.8 m South or West of the roost. We measured average snow compaction depth (an index of snow density, hereafter “snow density”) at the same 7 locations by dropping a 200-gram cylinder (diameter: 8.5 cm) from 50 cm above the top of the snow and recording the sinking depth in cm. Larger values indicate powdery, less dense snow. A value of zero indicates very hard snow. When snow was not present, snow density was recorded as "N/A". Roost site locations were categorized as "snow roosts" if they were either snow burrows (with at least a partial snow roof, i.e. > 75% covered) or snow bowls (indentations in the snow without a roof). Roosts were categorized as "other" if grouse were sitting on top of the snow or ground, or were in trees.

Fecal sample collection and corticosterone assays

Fecal glucocorticoids provide an accurate, non-invasive method to assess stress in wild animals (Dantzer et al. 2014, Sheriff et al. 2009a, Sheriff et al. 2011), and closely track plasma GCs (Sheriff, Krebs and Boonstra 2010). We collected feces from ruffed grouse roost sites covering a ~ 1,000-ha area within SWA, and only collected fecal droppings where the identity of the individual grouse was known. Grouse do not reuse individual roost locations. We attempted to collect all droppings (Zimmerman et al. 2013) from each roost. FCMs peak between 1-4 hours after intravenous corticosterone is administered in black grouse (Baltic et al. 2005), thus, our disturbance did not alter FCM levels in the droppings we collected. All droppings from a single roost were pooled and considered a sample. Fecal samples were immediately put on ice and stored at -20 °C until they were assayed. FCM levels can artificially increase if feces are not stored on ice immediately, but grouse usually deposit droppings on snow, and previous research has shown that environmental degradation of samples is not a concern in this system (Shipley et al. 2019). We used a standard corticosterone I^{125} double-antibody radioimmunoassay (RIA) kit (MP Biomedicals, Solon, Ohio) to measure FCMs (Millspaugh and Washburn 2004, Wasser et al. 2000), validated for use in ruffed grouse (Zimmerman et al. 2013) and one we have used previously (Shipley et al. 2019). The average intra-assay coefficient of variation was 2.64% and the average inter-assay coefficient of variation was 12.86%.

Environmental predictors for corticosterone

Land Cover

Our land cover map (Wilson et al. 2018, Shipley et al. 2020) had a 5-m resolution and 5 land cover classes: Aspen-Alder (hereafter, “Dense Cover”), Mature Forest, Scrub Oak, Open (emergent vegetation, lowland brush/willow, and lowland grass), and Other (hereafter, “Marsh”). Marsh consisted primarily of a mix of emergent vegetation and open water, and we do not consider it habitat for grouse. Using this land cover map (Fig. 2), we calculated the area of the largest patch of Dense Cover within 309 m of each roost, the area of the largest patch of Mature Forest within 309 m of each roost, and the area of the largest patch of Open habitat within 309 m of each roost. We used 309 m as it is the average distance moved between successive grouse observations, and we consider it the area available to an individual grouse on a given day (Arthur et al. 1996, George et al. 2017, Shipley et al. 2020). We did not consider patch size of Scrub Oak, as Scrub Oak accounts for a relatively small proportion of SWA habitat (4.28%), it is not a habitat type that is used in management at SWA, and importantly, is not a strong predictor of habitat use in grouse (Shipley et al. 2020).

Temperature

We used maps of daily winter minimum temperature (10 m resolution) that covered the extent of SWA. Temperature maps were created using regression kriging (Hengl, Heuvelink and Rossiter 2007) of data collected from temperature sensors spaced across SWA to capture differences in temperature among land cover types and distances to forest edge (Shipley et al.

2020). Further, we created annual maps of spatial variance in daily temperature by stacking daily temperature rasters and calculating variance for each cell.

Snow depth and density

We used maps of snow depth and density (10-m resolution) that were created using regression kriging of snow depth and density data that were collected from both grouse roost locations and from measurements every two weeks at temperature sensor stations. Prior to kriging, all snow depth and density measurements were separated into snowfall periods based on the timing of snowfall events. Final snow depth and density maps represent depth and density for each snowfall period (Shipley et al. 2020). We further created annual maps of spatial variance by stacking snowfall period rasters and calculating the variance for each cell for snow depth and for snow density.

Statistical analyses

We used a generalized additive mixed effects model (Zuur et al. 2009) to model the effects of land cover and dynamic weather conditions on grouse stress hormone levels and to test for possible non-linear relationships among FCMs and predictors. For every fecal sample assayed, we first extracted minimum daily temperature, Dense Cover patch size, Mature Forest patch size, Open habitat patch size, annual temperature variance, annual snow depth variance, and annual snow density variance from the kriged maps (Fig. 1). We included snow depth and snow density as measured at roost sites when fecal samples were collected. We included time of day (number of minutes from midnight) when each sample was collected to account for the natural daily rhythm in avian FCM concentrations (Carere et al. 2003, Scheiber et al. 2017, Shipley et al. 2019). We did not include multiple predictors in the model if they were highly correlated (Dormann et al. 2013). Snow depth variance and snow density variance were highly correlated ($r = 0.86$), and we thus excluded snow density variance from the model. We also excluded snow depth variance due to data sparsity and to facilitate model convergence. As our goal was to maximize predictive accuracy (as opposed to finding the most parsimonious model), we did not implement a model selection approach and used a global model with all covariates. Corticosterone metabolite concentrations were log-transformed. In the final model, we tested for linear or non-linear fixed effects of latitude and longitude (UTMs, included as a bivariate smooth), snow depth, snow density, temperature, temperature variance, and time of day. The final model also included linear fixed effects of Dense Cover patch size, Mature Forest patch size, Open habitat patch size, and roost type. We included year and individual bird ID as random effects. Predictor variables (other than roost type) were scaled using a z-transformation to enable comparisons among predictors. We used the package mgcv (Wood 2011)(Wood 2011) version 1.8.33 in Program R (version 4.0.0) for model development. We visualized predictors with partial prediction plots, using ggplot2 (version 3.1.1), that related each predictor to FCM concentrations while keeping the other predictors at their mean values.

Mapping the stress-scape

Using the model of grouse FCMs, we mapped daily predictions of FCMs (stress-scapes) across our study site (Fig. 1). To do so, we created a grid of 277,056 points spaced 10 m apart across SWA. Across the prediction grid, we extracted temperature, temperature variance, snow depth, snow density, Dense Cover patch size, Mature Forest patch size, and Open habitat patch size. We used a consistent value of 720 minutes from midnight (i.e., noon) for time. As roost type was a binary categorical predictor, we chose to create daily stress-scapes as if all roosts were “other roosts”, i.e., not snow roosts. Using the global model with unscaled versions of the predictors, we predicted daily log-transformed FCMs across the grid. We show back-transformed predictions of FCMs, thus stress-scapes are expressed as ng/g of FCMs. We summarized daily stress-scapes into annual winter stress-scapes by stacking daily stress-scapes and taking the average of each cell. Finally, we created maps of annual variance in stress-scapes by stacking daily stress-scapes and calculating the variance of each cell.

Results

Fecal sample collection

We measured corticosterone metabolites in fecal droppings collected from 443 ruffed grouse roost sites during the winters of 2015-2016, 2016-2017, and 2017-2018. We subset the data for further analysis to only include observations with values for snow density (i.e., snow depth > 0 cm). Our resulting dataset included fecal samples from 396 roost sites (69 snow roosts and 327 other roosts), representing 44 radio-tagged individuals. The mean number of roost sites samples per individual grouse was 9 (range: 2-30). Snow depth at roost sites ranged from 0 to 39.58 cm ($\bar{x}$ = 12.48 ± 7.90 cm), and snow density ranged from 0 to 16 cm ($\bar{x}$ = 4.20 ± 2.84 cm).

Temperature, snow depth, and snow density

Daily temperature maps showed considerable spatial variation, with as much as 8.39 °C differences on a single day (mean = 2.74 °C, range = 0.24 to 8.39 °C; Fig. 3a-c). Average winter temperatures did not overlap across years: Year 1 was the warmest (-8.85 to -7.03 °C), Year 2 was somewhat cooler (-9.88 to -8.57 °C), and Year 3 was the coldest overall (-13.92 to -11.58 °C). Variance in daily minimum temperature was greater across years than spatially within years, with Year 1 showing the most overall variation. Variance in daily minimum temperature ranged from 67.02 to 81.76 °C, 57.61 to 68.76 °C, and 55.11 to 68.34 °C in Years 1, 2, and 3, respectively (Figure S1a-c). Due to lack of data in some portions of the winter, we only report on snow depth and density for time periods when maps for both depth and density are available, and subsequent predicted stress-scapes are limited to: 29 December – 1 March, 12 December – 30 January and 24 February – 5 March, and 9 December – 5 March in Years 1, 2, and 3, respectively. Snow depth was highly variable within each snowfall period, with as much as 25.17 cm of spatial variation within a single snowfall period (mean = 17.59 cm, range = 4.28 to 25.17 cm; Fig. 3d-f). Similar to variance in temperature, variance in snow depth was greater across years than spatially within years. Year 2 showed both the greatest magnitude in overall variance in snow depth and the greatest spatial differences (Fig. S1d-f). Snow density also showed considerable variation within each snowfall period (mean = 7.71 cm, range = 3.88 cm to 12.67 cm; Fig. 3g-i). The magnitude of variance in snow density was greatest in year 2, which is when the greatest spatial differences occurred within a single year (Fig. S1g-i).

Effects of land cover and weather on FCM levels

We found significant effects of temperature, snow density, and time, and a marginally significant effect of snow depth on ruffed grouse winter FCM levels (Table S1, Fig. 4a-h). FCM concentrations increased non-linearly as temperatures became colder (edf = 2.09, $p < 0.001$) and as snow density increased (i.e., became more powdery, edf = 1.0, $p = 0.01$), but decreased in deeper snow (edf = 1.0, $p = 0.08$). Additionally, FCMs increased with the size of open habitat patches ($\beta = 0.18$, SE = 0.07, $p = 0.01$). Grouse FCMs were greatest in the morning and the evening (edf = 2.55, $p = 0.01$). Additionally, we found a significant effect of latitude and longitude (edf = 12.12, $p = 0.02$). Roost type, patch size of Dense Cover, patch size of Mature Forest, and annual temperature variance were not important predictors of grouse FCMs (Table S1).

Stress-scapes

Daily stress-scapes showed consistent patterning of predicted areas of high and low stress (Fig. 1), despite less consistent spatial patterning of temperature and snow conditions, likely reflecting, in part, the influence of static land cover on FCM concentrations. Areas of low and high FCMs were consistent across years (Fig. 5a-c). Areas of high predicted FCMs are located in the south-central and southeast portions of the study region, whereas areas of low FCM levels are located in the west and northwest areas, which may be indicative of important refugia. The range of spatial variation in annual stress-scapes was 15.94 ng/g to 108.39 ng/g in Year 1, 17.12 ng/g to 115.58 ng/g in Year 2, and 19.00 ng/g to 130.89 ng/g in Year 3. Overall mean FCM concentrations across annual stress-scapes were 47.81 ng/g, 50.99 ng/g, and 58.29 ng/g in Years 1, 2, and 3. Year 1 had the least overall variance in daily stress-scapes (Fig. S2a-c). Years 2 and 3 had more areas of high variance in daily stress-scapes, with Year 2 showing the most spatial patterning in variance of daily stress-scapes.

Discussion

Here, we demonstrate the potential of static land cover and dynamic winter weather characteristics to create spatially explicit predictive maps of physiological stress for a winter-adapted bird. Ruffed grouse FCMs increased with the size of open habitat patches, cold temperatures, and shallow and more powdery snow. Despite considerable spatial and temporal variation in snow depth, snow density, and temperature, annual stress-scapes displayed highly consistent areas of elevated levels of grouse FCMs, indicative of predictable regions of potentially high chronic stress.

Effects of land cover and weather on stress

Estimates of FCM for ruffed grouse were influenced by both static land cover and dynamic snow and temperature conditions. Land cover is a static characteristic of the landscape important for predicting grouse FCMs. Larger patches of open habitat were associated with increased grouse stress levels. While open areas may also be colder than other cover types, temperature was included in our model, and thus the effect of open habitat is independent of the effect of temperature. Open habitat provides less cover than other habitat types and may increase the threat of predation (Wolff 1980, Mysterud and Ostbye 1999). In fact, only 7% of grouse roost sites were in open habitat, and in open habitat grouse were more likely to seek cover in snow roosts at shallower snow depths than in other cover types (Shipley *unpublished data*), potentially indicating increased need for protection in open areas, or lack of alternative refugia. Increased grouse stress levels in open areas may, therefore, be more closely associated with perceived risk of predation than thermoregulatory costs.

Temperature, snow depth, and snow density, all dynamic predictors, varied over the course of the winter season and across the landscape. Cold temperatures, and shallow and powdery snow, were associated with increased stress in ruffed grouse. Extreme cold temperatures result in increased energy needed for thermoregulation, and increases in GCs may mediate increased metabolic demand (Jimeno et al. 2018, Sapolsky et al. 2000). Deep snow and the use of snow burrows can mediate the negative effects of cold temperatures on grouse FCM levels (Shipley et al. 2019), and the use of snow burrows is associated with increased survival in ruffed grouse (Shipley et al. 2020). Deep snow may therefore reduce grouse FCM levels through both decreased metabolic needs due to the insulating nature of snow, and a decrease in the risk of predation for grouse seeking cover under the snow (Shipley et al. 2020). Finally, powdery snow was associated with high grouse FCM levels. Grouse forage primarily while walking, and powdery snow that allows birds to sink through it may result in grouse expending more energy to move through it while foraging. While cold temperatures are often associated with powdery snow, there was no correlation between temperature and snow density in our study. In winter, grouse grow “toe bristles” that function as snowshoes and increase foot surface area by 17% and reduce sinking depth in powdery snow by 57% (Westerskov 1965, Hohn 1977), highlighting the potential energetic cost of moving through powdery snow. Interestingly, the relationships between grouse FCMs and dynamic and static predictors mirrored the patterns of grouse habitat selection; grouse selected for deep snow and warm microclimates, and avoided open areas (Shipley et al. 2020), all of which also reduced FCMs, highlighting possible synergies between habitat selection and environmental factors that contribute to elevated stress levels.

Mapping stress-scapes

Considering both static (e.g., land cover and climate) and dynamic (e.g., weather) predictors is known to be important for other types of spatial predictions, including species distribution modeling (Bateman, VanDerWal and Johnson 2012, Bateman et al. 2016). In our study, daily temperature maps and bi-weekly snow depth and density maps were highly variable, both in magnitude and in the locations of microclimates and snow depth. Despite this variability, the spatial patterning of areas of high predicted GCs was remarkably similar among daily stress-scapes, although some days had higher overall predicted GC levels than others; there was little spatial variation in annual stress-scapes. While the size of open habitat patches was an important static predictor of GCs, this factor does not alone explain the consistent spatial patterning of areas of high predicted GCs, as temperature, snow density, and to a lesser extent snow depth, were also important predictors of GCs. Interestingly, the areas with the lowest annual levels of predicted GCs were also the most variable in daily magnitude, and the areas of high predicted GCs were always high.

Relatively little variability in areas of high and low predicted GCs across daily and annual stress-scapes may mean that these areas are predictable for animals, and therefore, there may be useful for a variety of applications to explore how animals navigate their landscapes. For example, could a stress-scape be used to predict resource selection, dispersal, or home range size? There are also other questions that could be explored that may increase the utility of stress-scapes. For example, quantifying stress-scapes of other co-occurring, winter-adapted species, such as snowshoe hare (*Lepus americanus*), would allow a comparison of landscapes of stress across an entire community of species.

Management implications

While there is growing interest in incorporating physiological metrics with conservation efforts (Wikelski and Cooke 2006, Madliger and Love 2015, Madliger et al. 2016, Cooke and Suski 2008, Cooke and O'Connor 2010, Ames et al. 2020), physiological stress in animals is rarely considered during landscape-level planning for conservation. Mapping a stress-scape represents a useful visual representation of how static landscape features intersect with dynamic landscape features to produce areas of low or high predicted glucocorticoids. If the intersection of certain habitat types, topography or other landscape features, and pockets of milder weather conditions create refugia from extreme stress, it may be more effective to conserve these specific areas rather than creating or restoring specific habitat types elsewhere. Alternatively, considering the effects of both static and dynamic landscape features on the stress levels of free-living animals may prove useful. Further, for some prey species, a stress-scape could potentially be a composite of perceived risk of predation and thermoregulatory stress. Linking stress physiology with landscape-level conservation planning may yield understanding about how species perceive and are affected by the landscape somewhere in between species occurrence or abundance estimates and mortality. Quantification and visualization of the landscape of stress is an opportunity to gain new insights into another component of how species interact with their landscape and navigate complex and dynamic environments.

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Figure Legends

Fig. 1: Model development and mapping stress-scapes. Glucocorticoid samples were collected from ruffed grouse locations, and spatial predictors including land cover, minimum temperature, and snow cover were extracted from ruffed grouse locations to develop a generalized additive mixed model (GAMM) of glucocorticoids (1). Spatial predictors were extracted from a systematically generated grid of points across the extent of the study site (2). The GAMM was used to predict daily glucocorticoids across the study site over three winters (nanograms of fecal corticosterone metabolites per gram of dry feces) (3). Daily stress-scapes were averaged to create yearly stress-scapes (4).

Fig. 2: Land cover categories across Sandhill Wildlife Area in central Wisconsin, USA. Dense cover (a), mature forest (b), open (c), scrub oak (d), and marsh (e).

Fig. 3: Example maps of daily minimum temperature, biweekly snow depth, and biweekly snow density for Year 1 (2015-2016). Temperature in early (30 December), mid (19 January), and late (20 February) winter (a-c, respectively); biweekly snow depth (d-f) and biweekly snow density (g-i) in early (29 December – 6 January), mid (19 January – 2 February), and late (17 February – 1 March) winter, respectively; larger snow density values indicate more powdery snow. Temperature, snow depth, and snow density maps show considerable spatial variation. Differences in scale bars in each row demonstrate temporal variation in temperature, snow depth, and snow density in each time period.

Fig. 4: Partial dependency plots showing concentrations of ruffed grouse fecal corticosterone metabolites (FCMs) in relation to (a) snow depth (cm); (b) snow density (cm); (c) minimum temperature (˚C); (d) size of open habitat patch (ha); (e) size of mature forest patch (ha); (f) size of dense cover patch (ha); (g) time of day; and (h) annual variance in minimum temperature.

Black lines and grey bands represent means and 95% confidence intervals. FCM concentrations decreased with increasing snow depth and temperature and increased with more powdery snow and in larger open habitat patches.

Fig. 5: Annual winter stress-scapes displaying predicted ruffed grouse fecal corticosterone metabolites (FCMs) based on a generalized additive mixed model. Annual stress-scapes for Years 1 (a), 2 (b), and 3 (c). Despite variability in spatial predictors, annual stress-scapes show consistent spatial patterns in areas of predicted high FCMs.

Figure 1

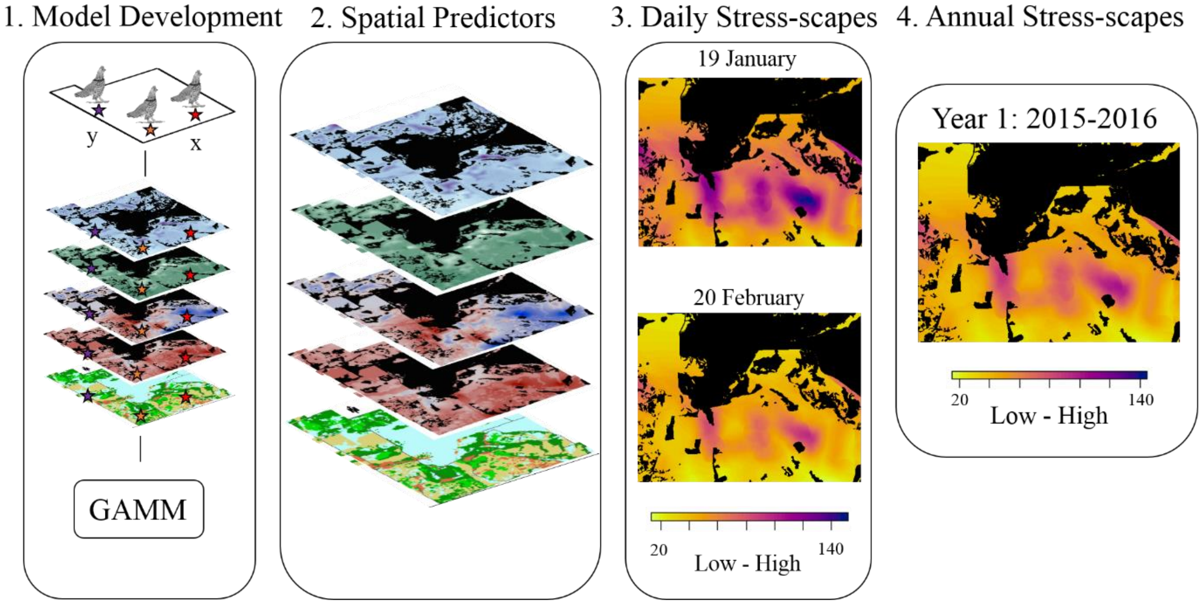

1. Model Development
2. Spatial Predictors
3. Daily Stress-scapes
4. Annual Stress-scapes
y
x
GAMM
19 January
20 February
20
140
Low - High
Year 1: 2015-2016
20
140
Low - High

Figure 2

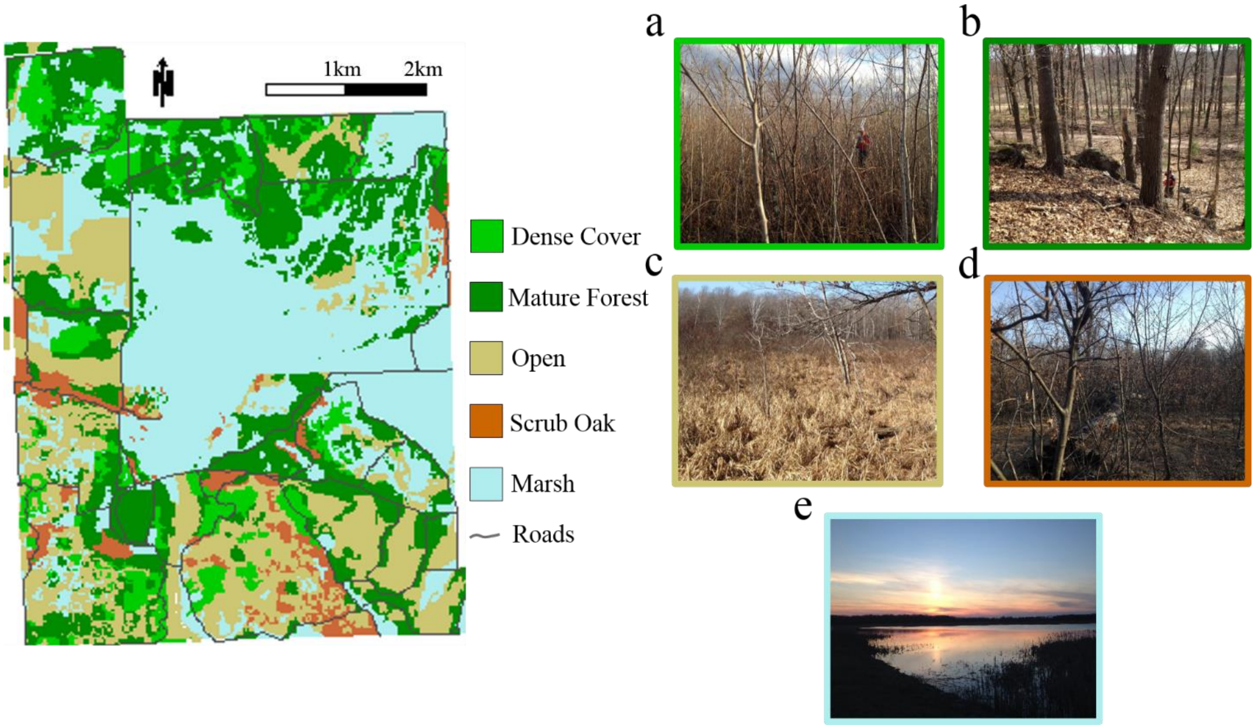

N
1km
2km
Dense Cover
Mature Forest
Open
Scrub Oak
Marsh
Roads
a
b
c
d
e

Figure 3

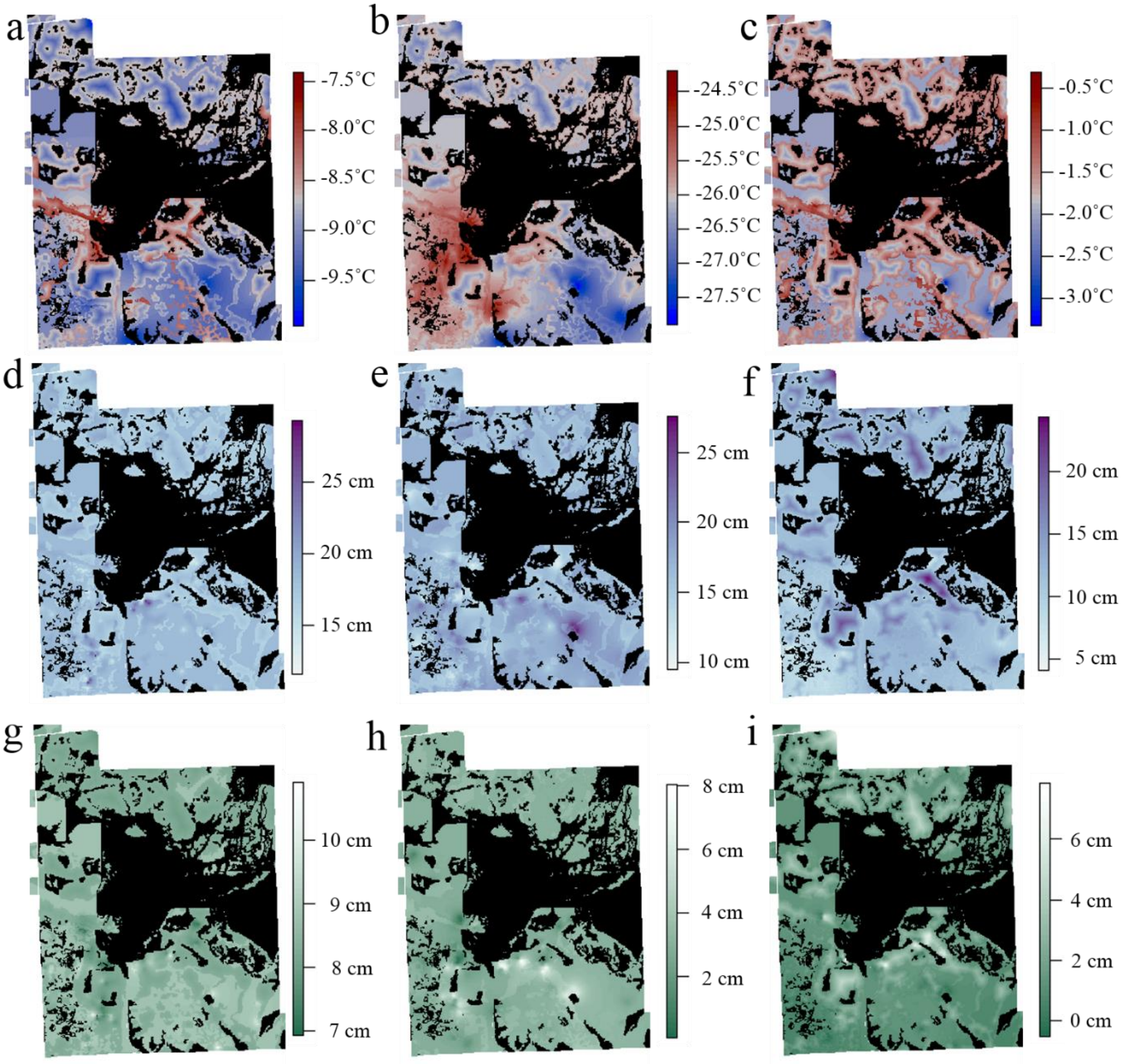

a
-7.5°C
-8.0°C
-8.5°C
-9.0°C
-9.5°C
b
-24.5°C
-25.0°C
-25.5°C
-26.0°C
-26.5°C
-27.0°C
-27.5°C
c
-0.5°C
-1.0°C
-1.5°C
-2.0°C
-2.5°C
-3.0°C
d
25 cm
20 cm
15 cm
e
25 cm
20 cm
15 cm
10 cm
f
20 cm
15 cm
10 cm
5 cm
g
10 cm
9 cm
8 cm
7 cm
h
8 cm
6 cm
4 cm
2 cm
i
6 cm
4 cm
2 cm
0 cm

Figure 4

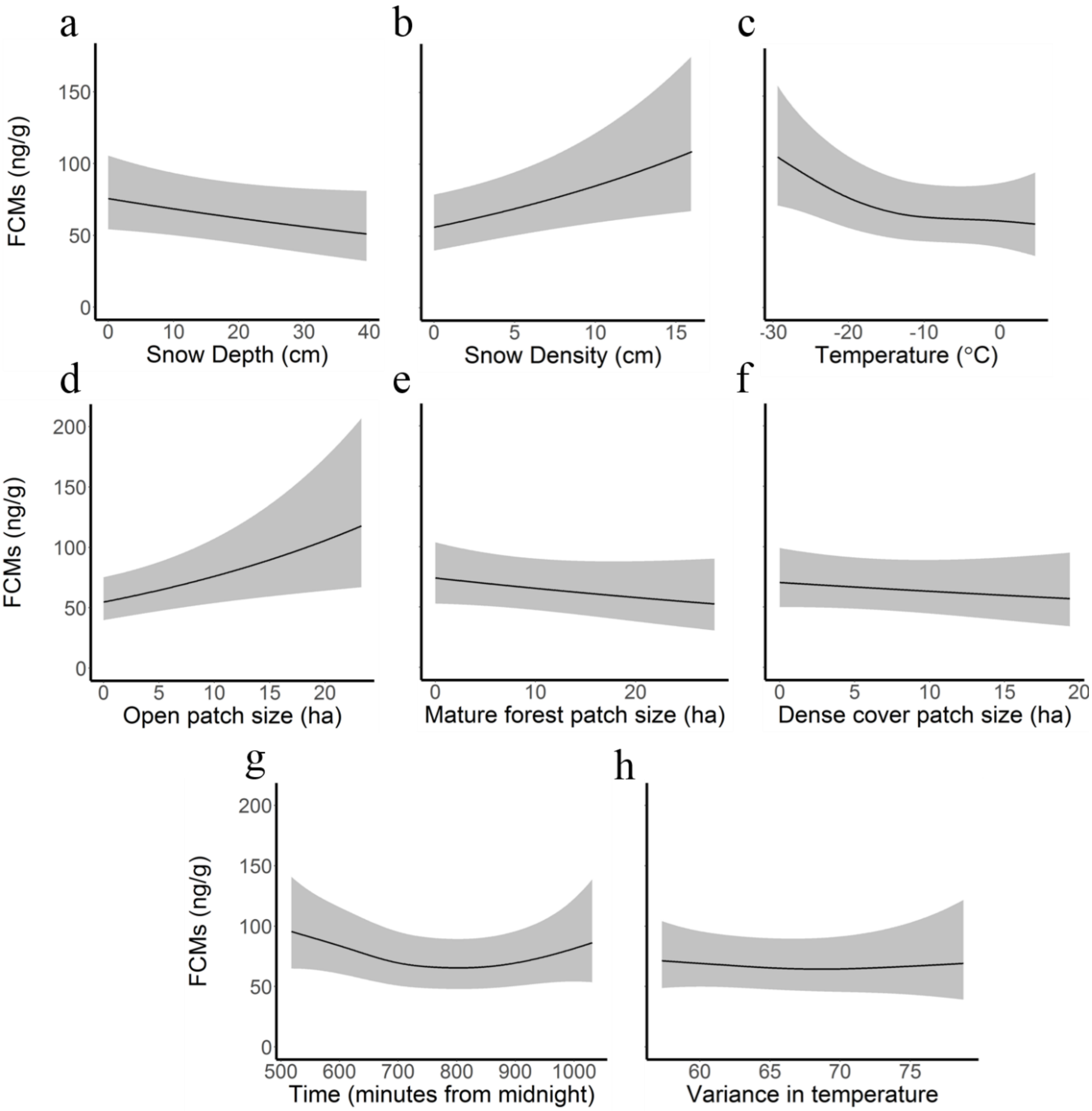
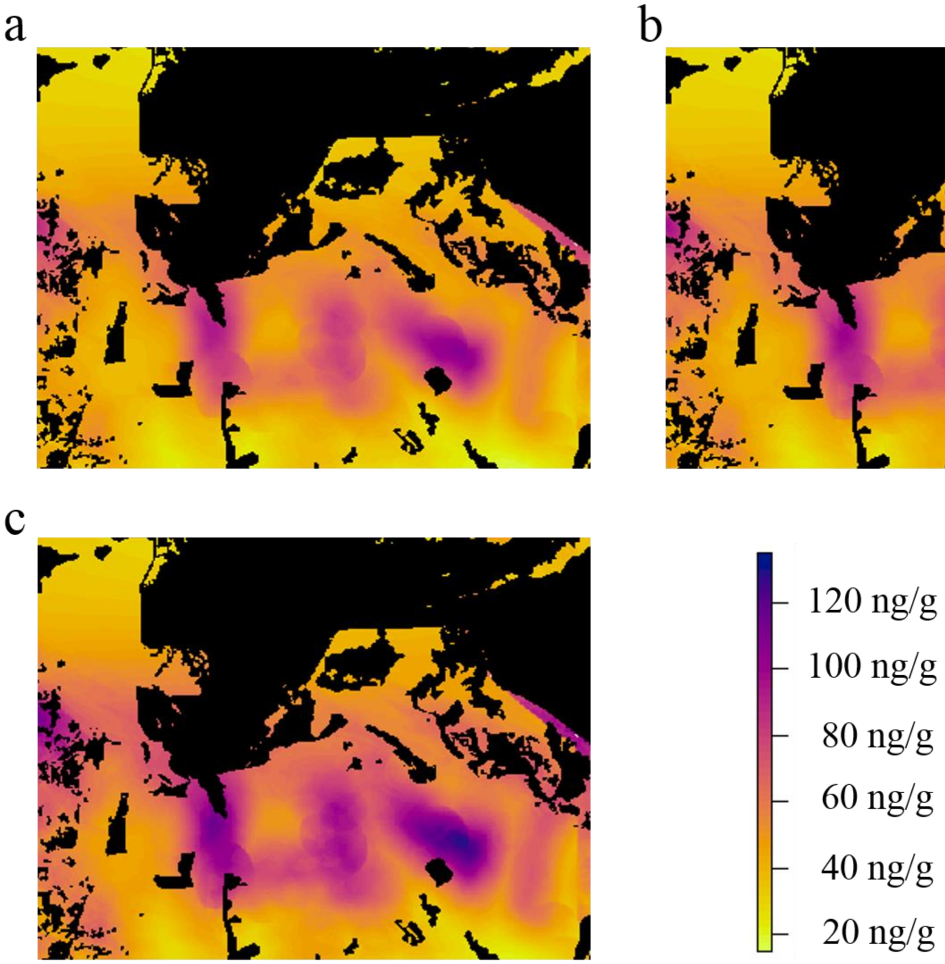

a
b
c
FCMs (ng/g)
150
100
50
0
0
10
20
30
40
Snow Depth (cm)
0
5
10
15
Snow Density (cm)
-30
-20
-10
0
Temperature (°C)
d
e
f
FCMs (ng/g)
200
150
100
50
0
0
5
10
15
20
Open patch size (ha)
0
10
20
Mature forest patch size (ha)
0
5
10
15
20
Dense cover patch size (ha)
g
h
FCMs (ng/g)
200
150
100
50
0
500
600
700
800
900
1000
Time (minutes from midnight)
60
65
70
75
Variance in temperature

Figure 5



Supplementary Materials

Table S1. Relationships between fecal corticosterone metabolite concentrations and environmental predictors and roost type for Ruffed Grouse at Sandhill Wildlife Area, Wood County, Wisconsin, USA, based on a generalized additive mixed model. Individual bird ID was included as a random effect to control for non-independence among individuals in the population. β = beta estimate, SE = standard error, edf = estimated degrees of freedom.

Fixed Effects	β	edf	SE	*p*-value
Intercept	4.09	-	0.06	< 0.001
Roost Type	-0.12	-	0.11	0.274
Dense Cover	-0.07	-	0.10	0.345
Open	0.17	-	0.07	0.008
Mature Forest	-0.08	-	0.07	0.234
Latitude, Longitude	-	12.12	-	0.020
Snow Depth	-	1.00	-	0.080
Snow Density	-	1.00	-	0.009
Temperature	-	2.09	-	0.000
Temperature Variance	-	1.38	-	0.769
Time	-	2.56	-	0.012

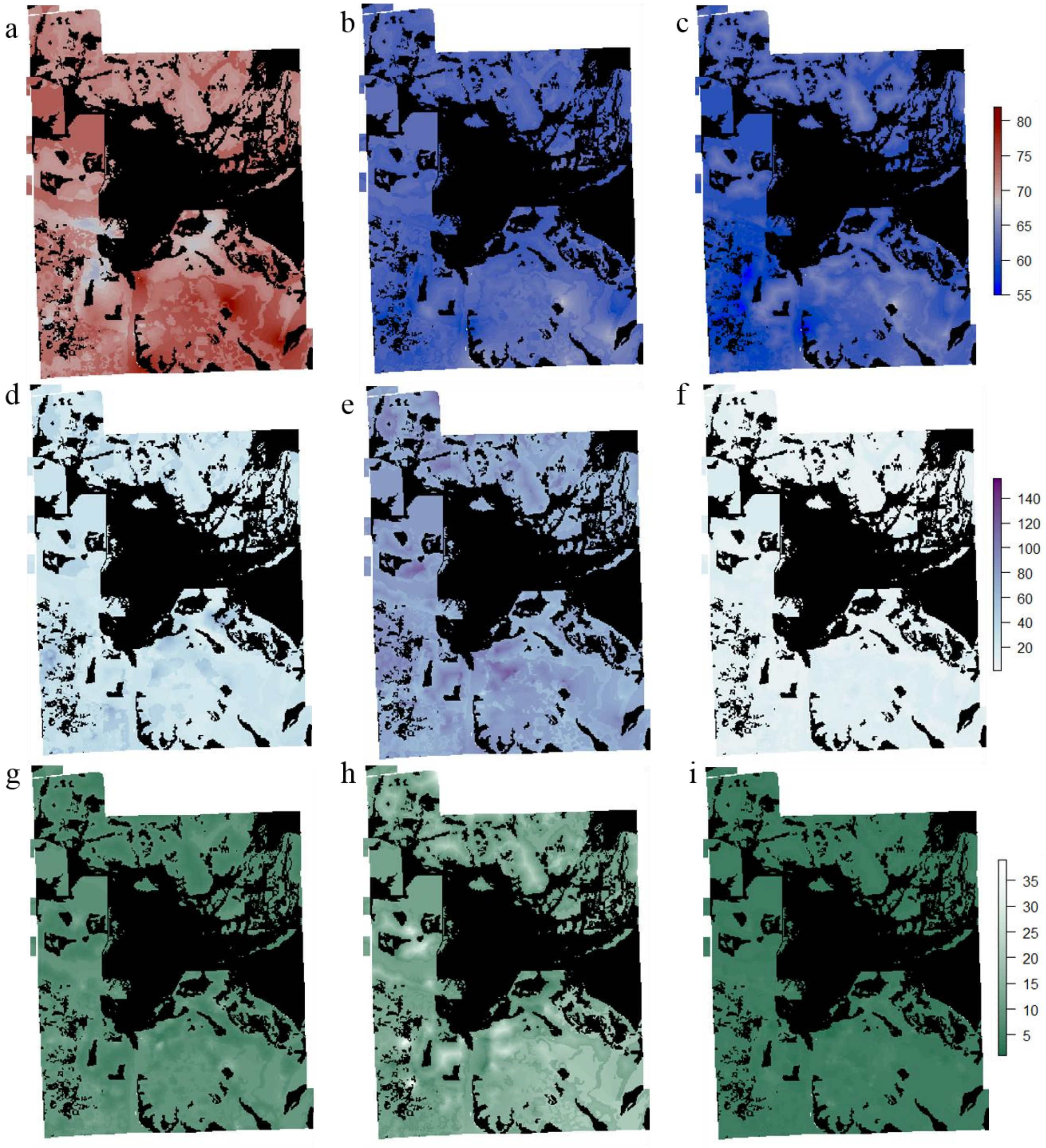
Roost Type is coded as 0 = “other roosts”, 1 = “snow roosts”. Snow density represents the depth that a weighted cylinder sinks into the snow when dropped and is a proxy for snow density; larger values indicate more powdery snow. Dense Cover, Open, and Mature Forest are measured as the area of the largest patch of each cover type within 309 m of each roost site. Temperature represents minimum temperature at the roost location during the previous 24 hours. Time is measured in minutes from midnight.

Supplementary Figures

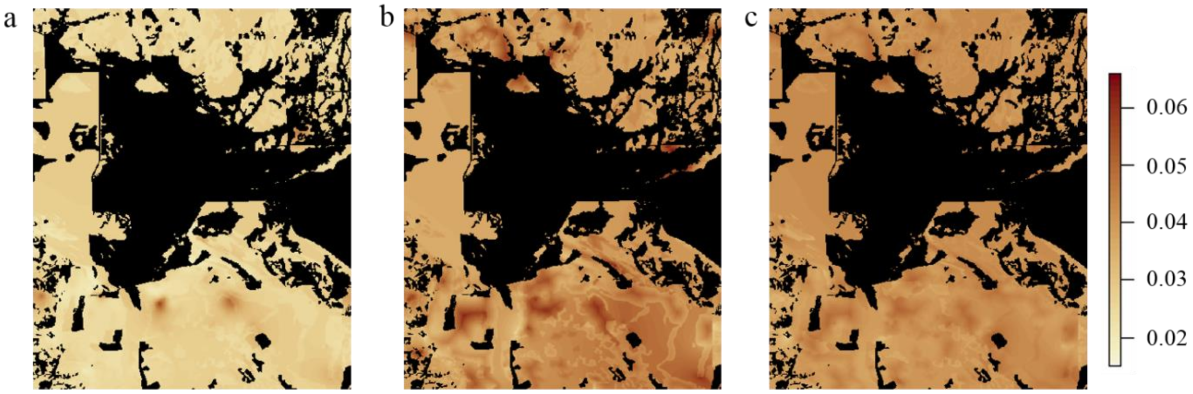
Figs S1: Variance in daily minimum temperature for winters 1, 2, and 3 (a-c, respectively), variance in biweekly snow depth for each winter (d-f, respectively), and variance in biweekly snow compaction depth for each winter (g-i, respectively). Year 1 showed the most overall variance in temperature, with clear spatial patterns in temperature variance. Year 2 showed the most overall variance in snow depth and snow density, and also showed clear spatial patterns in variance in snow depth and snow density.

Fig. S2: The variance in daily stress-scapes for Years 1, 2, and 3 (a-c). Spatial patterning of areas of elevated predicted FCM concentrations are highly consistent from year to year. Years 2 and 3 show increased variance in daily FCM concentrations as compared to year 1, but areas that have the highest daily FCM variance are the same among years.

Supplementary Figure 1



Supplementary Figure 2



Personality differences in the selection of dynamic refugia have demographic consequences for a winter-adapted bird

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Abstract

For overwintering species, individuals' ability to find refugia from inclement weather and predators likely confers strong fitness benefits. How animals use their environment can be mediated by their personality (e.g., risk-taking), but does personality mediate how overwintering species select refugia? Snow cover is a dynamic winter characteristic that can influence crypsis or provide below-the-snow refugia. We explored how wintering ruffed grouse (*Bonasa umbellus*) selected snow roosting sites, a behavior that reduces stress and cold exposure. We linked selection for ~700 roosts with survival of 42 grouse, and showed that grouse generally selected deeper snow and warmer areas. Grouse found in shallow snow were less likely to survive winter. However, individuals that selected deep snow improved their survival, suggesting that demographic consequences of selecting winter refugia are mediated by differences in personality. Our study provides a crucial, and seldom addressed, link between personality in resource selection and resulting demographic consequences.

Introduction

Variability in functional traits across individuals is crucial to a population's ability to persist in stochastic environments (Piersma and van Gils 2011). Unlike functional traits that remain relatively stable within a single individual (e.g., bill size), behaviors such as cooperativeness and risk-taking may be highly variable among and within individuals in response to changing environmental conditions (Dall, Houston and McNamara 2004, Reale et al. 2007, Biro and Stamps 2008). For example, individual eastern chipmunks (*Tamias striatus*) that engaged in periodic heterothermy more frequently during winter in resource-rich years were more likely to survive winter (Dammhahn et al. 2017). Since behavioral traits are often heritable (Dingemanse et al. 2002), understanding and quantifying variation in behavior, and its possible demographic consequences, is critical for predicting population-level responses to environmental change (Piersma and van Gils 2011).

An important component of how individuals respond to environmental variability is by selecting resources critical for survival. Resource selection, in which animals use a resource in higher proportion to its availability (Johnson 1980, Lele et al. 2013), has been studied at the population level since the 1970s. Until recently, individual variation in resource selection has largely been treated as a nuisance, contributing to error within population-level estimates. However, there is growing interest in quantifying individual differences in resource selection (Bastille-Rousseau and Wittemyer 2019, Muff, Signer and Fieberg 2019). Individual differences in resource selection can be conceptualized as behavioral reaction norms that illustrate both *personality* and *plasticity* (Dingemanse et al. 2010). Behavioral reaction norms are similar to functional responses in resource selection, where selection changes as a function of resource availability (Hebblewhite and Merrill 2008, Moreau et al. 2012), but behavioral reaction norms plot resource selection across an environmental gradient for every individual. In a behavioral reaction norm, *personality* reflects an individual's mean behavioral response to an environmental gradient whereas *plasticity* is the individual's change in response (i.e., slope); with steeper slopes suggesting that an individual's behavior is highly plastic (Dingemanse et al. 2010). Reaction norms, which can be linear or non-linear (Rocha and Klaczko 2012), are thus a useful tool to describe how individuals' personalities and plasticity mediate resource selection (Leclerc et al. 2016, Bastille-Rousseau and Wittemyer 2019). Differences in personality and plasticity in behaviors other than resource selection have important consequences for survival (Smith and Blumstein 2008, Biro and Stamps 2008, Boon, Reale and Boutin 2008, Krams et al. 2013, Dammhahn et al. 2017). For example, bighorn sheep (*Ovis canadensis*) with bolder personalities had higher probability of surviving predation (Reale and Festa-Bianchet 2003), although avoiding predation may come at the cost of missed foraging opportunities and growth for bold individuals (Stamps 2007).

How animals select resources has clear implications for survival. Woodland caribou (*Rangifer tarandus caribou*) experience higher survival when they select habitat farther from anthropogenic disturbance (DeCesare et al. 2014, DeCesare et al. 2012). However, fitness consequences have yet to be linked to individual differences in personality or plasticity in resource selection (Bastille-Rousseau and Wittemyer 2019). Incorporating personality and behavioral plasticity into resource selection studies, and determining if there are fitness consequences, may be particularly important in the face of stochastic environmental conditions (Dingemanse and Wolf 2013, Bastille-Rousseau and Wittemyer 2019, Segev and Foitzik 2019). When resources vary across a landscape in space and/or time, individuals with greater behavioral plasticity can potentially exploit novel resources, and avoid competing with more behaviorally rigid individuals (Wolf, van Doorn and Weissing 2008). Consequently, a diversity of behavioral reaction norms (e.g., variation in personalities or plasticity) may be a key factor in determining whether a population will persist during rapid environmental change or in dynamic environments (Wolf et al. 2008, Wolf and Weissing 2012).

For resident species in mid- and high latitude ecosystems, especially those that do not hibernate, winter is a time of resource scarcity and shifting environmental conditions. Extreme cold and reduced access to food can result in increased energy expenditure and exposure to predators due to more time foraging (Lima 1986). In response to these elevated risks, individuals can select microrefugia, or localized pockets of milder conditions, to buffer against winter's effects (Coombs, Bowman and Garroway 2010) and reduce their need for thermoregulation (Shipley et al. 2019). In heterogenous environments, such as forests, areas with warmer microclimates can be created by structural complexity (Suggitt et al. 2011, Ashcroft and Gollan 2012, Ford et al. 2013), higher elevations (Sears, Raskin and Angiletta Jr 2011), or reduced fragmentation (Latimer and Zuckerberg 2016).

Unlike relatively stable microclimates created by forest cover or topography (Dobrowski 2011, Ford et al. 2013), snow is ephemeral. As snow depth changes during winter, this variability imparts potentially different costs and benefits. For example, snowshoe hare (*Lepus americanus*) that have molted white for winter are vulnerable to predation when the ground is snow-free (Zimova, Mills and Nowak 2016, Wilson et al. 2018), but experience increased probability of survival when snow is present and they are better camouflaged (Wilson et al. 2018). For species that do not molt white in winter, even slight differences in coloration can influence the effectiveness of crypsis in snow, with consequences for overwinter survival. For example, brown morph tawny owls (*Strix aluco*) are more visible than gray morph individuals against a snow-covered landscape (Koskenpato et al. 2019), and are less likely to survive during snowy winters

(Karell et al. 2011). For other winter-adapted species, such as ruffed grouse (*Bonasa umbellus*), which has brown plumage year-round, snow cover may result in phenotypic mismatch, exposing grouse to predators. The influence of snow, however, may shift from reducing crypsis at shallow depths to becoming a refuge after snow becomes sufficiently deep to allow creation and use of snow roosts. Deeper snow contributes to development of the subnivium - a thermally stable environment between the soil and snowpack - that serves as critical protection for many overwintering species (Pauli et al. 2013, Williams, Henry and Sinclair 2015). Changes in subnivium quality mediate population cycling in alpine rodents (Kausrud et al. 2008), and survival for tundra voles (Korslund and Steen 2006) and freeze-tolerant wood frogs (Sinclair et al. 2013, Fitzpatrick et al. 2019). For species such as ruffed grouse, availability and use of the subnivium can provide significant thermal benefits and reduce temperature-associated stress (Shipley et al. 2019).

Our goal was to test the broader hypothesis that individual animals differ in their personality (mean selection) and plasticity (slopes) in selecting dynamic winter refugia and that these individual differences have important consequences for overwinter survival. To test this hypothesis, we focus on individual variation in ruffed grouse winter roosting behavior. When snow conditions are sufficient (at least 15 cm), ruffed grouse can roost in snow burrows (Gullion 1970), reducing their physiological stress (Shipley et al. 2019), and potentially, their predation risk. Alternatively, when snow depths are below 15 cm, grouse cannot use snow burrows, and may be more visible and vulnerable to predation. Our objectives were to determine whether: 1) individual grouse are more or less likely to select winter refugia (deep snow or warmer temperatures) (personality); 2) individual grouse alter their selection of winter refugia as conditions change (behavioral plasticity); and 3) these individual differences have consequences for overwinter survival. Given the benefits of snow burrowing for this winter-adapted bird, we predicted grouse will generally seek out deeper snow when snow depths are suitable for burrowing (> 15 cm), but when snow is < 15 cm, grouse will avoid snowy areas that may increase their vulnerability to predators. However, we expect individuals will show a high degree of plasticity in their selection of winter refugia. Ultimately, we expect individual grouse that are able to avoid snow when it is shallow, but select deeper snow when burrowing is possible, and use deep snow for burrowing, will experience increased survival. Our study provides the crucial, and seldom addressed, link between individual variation in resource selection and resulting demographic consequences.

Methods

Study site

Our research was conducted in central Wisconsin, within Sandhill Wildlife Area (SWA; 44˚18´N, 90˚07´W), a 3700 ha state wildlife area. Vegetation within SWA consists of patches of oak (*Quercus* sp.), aspen (*Populus tremuloides* and *P. gradidentata*), tag alder (*Alnus serrulata)*, and red and white pine (*Pinus resinosa* and *P. strobus*), interspersed with marshes and open water. Between 2001-2015, there were on average 47 winter nights each year when snow depth surpassed 20 cm (range 0-101 nights). Mean winter (December-March) temperature at SWA is − 9 °C ± 10.0 °C (range − 26.5 to 5.5 °C).

Grouse trapping, radio telemetry, and roost site observations

From September-November (2015-2017), we trapped ruffed grouse in walk-in pens connected to a drift fence (Gullion 1965). We determined age and sex of each grouse (Hale, Wendt and Halazon 1954), measured body mass and tarsus length, and tagged grouse with radio transmitters (12-g, necklace-style; Advanced Telemetry Systems, Inc.) equipped with 4-hr mortality sensors. During three winter seasons (1 December – 31 March 2015-2018), we located roost sites for each radio-tagged grouse 1-2 times per week. Grouse do not reuse roost sites. We calculated mean snow depth at roost sites as the average depth (cm) from 7 locations that were equidistant from the roost site to the perimeter of a 0.04 ha circular plot: at the roost site, 3.6 m, 7.2 m, and 10.8 m North or East of the roost, and 3.6 m, 7.2 m, and 10.8 m South or West of the roost. Every two days during winter, we checked if any active grouse radio tags were emitting a mortality signal. If a mortality signal was detected, we collected grouse remains and used bite wounds, tracks, and feces to determine predator species.

Environmental predictors

Land Cover: In addition to being a potentially important predictor of both snow cover and temperature (Ashcroft and Gollan 2012, Ford et al. 2013, Sears et al. 2011), we chose to consider land cover because dense cover, particularly young aspen stands, are known to influence ruffed grouse presence (Gullion and Alm 1983). Our land cover map (see (Wilson et al. 2018), Appendix S1) had a 5 m-resolution and 5 land cover classes: Aspen-Alder (referred to as Dense Cover), Mature Forest, Scrub Oak, Open (emergent vegetation, lowland brush/willow, and lowland grass), and Other. “Other” mostly consisted of marsh and open water, and we do not consider it available habitat for grouse.

Temperature: We deployed an array of 58 iButton temperature sensors (DS1922L; Maxim Integrated) equipped with solar shields across roughly 1,000-ha of SWA, arranged in groups of three and spaced to capture differences in temperature at various distances from the forest edge. One iButton in each group was placed on the forest edge, the second at 20 m into the forest, and the third at 250 m into the forest or at the forest fragment’s center, whichever was closer. iButtons recorded temperature every half hour during winter (December-March) for three years: 2015-2016, 2016-2017, and 2017-2018. We used minimum daily temperature recorded at each iButton station, which was an important predictor of corticosterone levels in ruffed grouse (Shipley et al. 2019), and thus likely to influence roost site selection.

We used regression kriging to interpolate minimum daily temperature across SWA as a 10-m resolution raster for each winter day (hereafter daily temperature) (Hengl, Heuvelink and Rossiter 2007). To determine if there were areas that were consistently cold or warm throughout each winter, we similarly interpolated winter temperature (°C) on a yearly basis (Appendix S2).

Snow depth: Snow depth measurements were collected every two weeks at iButton stations using the same method as at roost sites, except there were 13 measurements at each station (collected in all four cardinal directions). Snow depth measurements were averaged to a single depth value for every iButton station every two weeks from December-March. To minimize the impact of additional snow accumulating between measurements, most snow depth measurements were collected within two-day periods, and we additionally separated all depth measurements into snowfall periods based on snowfall events (Appendix S3). We used regression kriging to interpolate snow depth (Appendix S2) for each snowfall period.

Behavioral reaction norms -personality and behavioral plasticity- in resource selection We estimated behavioral reaction norms for individual grouse in their selection for roost conditions by comparing roost site conditions against available conditions, using resource selection functions with random slopes (Muff et al. 2019). We defined conditions available to an individual grouse as occurring within buffers with a radius equal to the mean distance that a grouse normally moves between successive observations (Arthur et al. 1996, George et al. 2017), which for our population was 308 m. We extracted daily temperature, winter temperature, and snow depth estimates for each roost (used) and five matching random locations (available) within this mean distance. We then used smaller, 100-m buffers around used and available locations to calculate proportions of the five land cover classes.

Resource selection functions were estimated by a Poisson point-process model that included stratum-specific intercepts (where each stratum is a roost site and its matching, available locations); random individual intercepts, which accounted for lack of independence amongst roost sites belonging to the same individual; and fixed and random slopes for the environmental predictors, which quantified population- and individual-level plasticity in selection for these environmental conditions (Muff et al. 2019). We relied on this conditional Poisson model rather than more traditional conditional logistic approaches, because it allowed easy incorporation of random slopes (Muff et al. 2019). Combined slopes (sum of fixed effect and random individual slope) represent the individual's behavioral plasticity estimate in response to each environmental predictor (Leclerc et al. 2016). The mean probability of selection for each individual across the range of each environmental predictor for the population represents the individual's personality in selection (Dingemanse et al. 2010). Models were developed using package glmmTMB ((Brooks et al. 2017) version 3.5.1 in Program R (version 4.0.0).

We included individual- (random slopes) and population-level (fixed slopes) plasticity for all environmental conditions (including snow depth and its quadratic, daily temperature, winter temperature, and land cover classes) in a global model. We scaled all predictors using a z-transformation, and did not include predictors in the model if they were highly correlated (Pearson's correlation coefficient ≥ 0.7) (Dormann et al. 2013). When negligible variances (< 0.05) for a random slope indicated little evidence for individual plasticity for its associated predictor, we removed the corresponding random slope (i.e., only left population-level plasticity estimates based on the fixed coefficient). We identified important predictors at the population level based on 95% confidence intervals of fixed coefficients not overlapping zero, or only marginally overlapping zero. Important predictors at the individual level were selected when the corresponding random slopes had variance greater than one. We displayed individual-level behavioral reaction norms (summarizing their plasticity and personality) as partial prediction plots that kept other model predictors at their mean values.

Although random slopes aim to capture between-individual differences in their responses (i.e., differences in their plasticity), they may also inadvertently capture variation in the conditions the individuals were exposed to (i.e., in the predictors). We tested this by partitioning these sources of variation following Equation 3 in (van de Pol and Wright 2009), which we modified for a random slopes scenario by combining it with Equation 5 (van de Pol and Wright 2009). We added additional fixed slopes for the means of each z-transformed predictor across the range available to each individual bird to our model. These fixed slopes estimate how much the differences between individuals are due to predictor difference. We found all were non-significant, with 95% confidence intervals overlapping zero (Table S2), suggesting that the random slopes are indeed capturing differences in individuals' responses (i.e., in their plasticity). We thus simplified our model by removing these additional predictors, which simplified inference and reduced potential for over-parameterization.

Repeatability estimates the ratio of among-individual to within-individual variance (Leclerc et al. 2016, Bell, Hankison and Laskowski 2009). However, we do not calculate repeatability here because the winter environment is highly dynamic, and we do not have multiple observations for each individual when the combination of environmental conditions are the same. The resource selection framework, with available points unique to each used point, as well as the chosen Poisson model, also limit our ability to estimate within-individual variance.

We recognize that not generating a repeatability estimate may limit comparison with other studies.

Survival models

We used known-fate survival models with staggered entry (Laake 2013) to construct models in Program MARK (White and Burnham 1999) using RMark (version 2.2.6) to estimate ruffed grouse weekly survival during winter. We used a z-transformation to scale predictors, and did not include predictors in the same model if they were highly correlated. We related each grouse's overwinter survival to its personality and plasticity for selecting important environmental conditions at roost sites by including individual estimates of personality and plasticity in selection of environmental conditions as individual covariates in survival models. We also included each individual's exposure to these environmental conditions at used roost sites as individual covariates in survival models, to assess how environmental conditions that each individual experienced influenced survival, regardless of their response to these conditions.

We expected the effect of snow to differ depending on whether snow burrowing was possible, so we quantified personality and plasticity separately for snow depths above and below 15 cm; this cutoff is generally considered the minimum depth needed for grouse to snow burrow (Blanchette, Bourgeois and St-Onge 2007, Gullion 1970). We defined personality in selection for shallow snow as the mean probability of use below 15 cm of snow for each individual ($SSE<15_M$), and plasticity in selection for shallow snow as the change in probability of use between the minimum snow depth available to the individual and 14.9 cm ($\Delta SSE<15$). Similarly, we defined personality in selection for deep snow as the mean probability of selection between 15 cm and the population-level maximum available snow depth ($SSE>15_M$), and plasticity in selection for deep snow as the change in probability of selection between 15 cm and the maximum snow depth available to the individual (ΔSSE>15). Finally, exposure to shallow (SEXP<15) and deep snow (SEXP>15) were estimated as an individual's median snow depth at used roost sites for observations when snow depth was <15 cm and ≥ 15 cm, respectively. Because the range of winter temperature varied considerably from year to year, we define personality in selection for winter temperature as the individual's mean probability of use across the range of temperatures available that winter (WTSE_{M}).

We evaluated important predictors using model selection from a set of candidate models that included all biologically plausible combinations of uncorrelated predictors. We could not use a global model approach because of sample size limitations. We ranked candidate models using Akaike Information Criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson 1998). Models were considered competitive if within 2 ΔAIC_c of the top model. Predictors were considered important if they were in the top model and their 95% confidence intervals did not overlap zero, or only marginally overlapped zero (Burnham and Anderson 2002). We visualised important predictors via partial prediction plots, using ggplot2 (version 3.0.0), that related each predictor to survival while keeping remaining predictors at their mean values.

Sensitivity of survival analysis to error propagation

Using slopes and mean estimates of selection from behavioral reaction norms as predictors in the survival analysis ignores potential issues with error propagation (Hadfield et al. 2010, Houslay and Wilson 2017). We conducted a sensitivity analysis using a Bayesian approach (Muff et al. 2019) that evaluated how robust the survival analysis was to potential error in estimates from the behavioral reaction norms by incorporating moderate error and evaluating whether it influenced inference from the top survival model (see Appendix S4).

Roosting behavior

As a final step, we tested whether grouse that were more likely to use deep snow were more likely to roost in snow burrows or bowls. We categorized roosting behavior as 1 = roosting in snow burrow or snow bowl, or 0 = roosting on other roosts (e.g., on ground or tree). We modeled roosting behavior using snow depth at roost sites and $SSE{>}15_M$ as predictors with a generalized linear mixed model (GLMM) with a logit link function including individual bird ID as a random effect. All predictors were scaled using a z-transformation. We did not include predictors in the same model if they exhibited multicollinearity (Pearson's correlation coefficient ≥ 0.7). Analyses were conducted in R (R Core Team 2013) using package glmm (version 1.3.0).

Results

Temperature and snow depth

We found a high degree of spatial variation in both daily and winter temperature, and snow depth across SWA (Fig. 1). Daily temperature varied by as much as 8.39 °C on a single day (mean = 2.74 °C, range = 0.24 to 8.39 °C). Winter temperature, the average minimum temperature across winter, had a similar degree of spatial variation each winter (mean = 1.82 °C, range = 1.31 to 2.34 °C), but winter temperature conditions did not overlap across years (-8.85 to -7.03 °C, -9.88 to -8.57 °C, and -13.92 to -11.58 °C in Years 1, 2, and 3, respectively). We separated winter into 11 snowfall periods each year based on snowfall events. The mean spatial variation in snow depth for a given snowfall period when snow was present was 18.16 cm (range 4.60 to 30.93 cm).

Roost observations

We monitored roost site selection for 54 grouse during three winters. We removed nine birds from the dataset with fewer than five roost observations because the bird died, or because the roost observation occurred on a date when we were unable to interpolate snow depth due to low sample size for that snowfall period. The mean number of roost observations for each of the remaining 45 grouse was 16 (range = 5 to 45). The total number of roost observations was 683.

Population-level resource selection

At the population level, winter temperature, snow depth, and proportions of mature forest (β = 0.21, SE = 0.12, CI = -0.01, 0.44; marginally overlapping zero) and open habitat (β = -0.38, SE = 0.17, CI = -0.69, -0.02) were important predictors of roost site selection (Fig. 2, Table S1). Winter temperature (β = 4.06, SE = 0.81, CI = 2.46, 5.66) and snow depth (linear: β = -2.01, SE = 0.41, CI = -2.82, -1.20; quadratic: β = 1.48, SE = 0.20, CI = 1.08, 1.88) were the strongest predictors of roost site selection (Fig. 2, Table S1). During low snow periods (< 15 cm), grouse actively avoided snowy areas (Fig. 3A). At the population level, grouse were much more likely to use areas characterized by warmer temperatures (Fig. 3B).

Individual personality and behavioral plasticity in resource selection

Personality and plasticity in roost site selection varied widely among individual grouse (Fig. 3C, 3D). When snow depths were between 0-15 cm there was relatively little variation in $SSE{<}15_M$ or $\Delta SSE{<}15$ (all individuals consistently avoided snowy areas), but at snow depths > 15 cm, some individuals strongly selected for deep snow, and others avoided it (Fig. 3C). There was considerable variation in individual winter temperature selection (Fig. 3D); while all individuals selected for warmer winter temperatures, the range of winter temperatures available to them differed across years (Fig. 3D). Variance associated with random slopes for snow depth, the quadratic of snow depth, and winter temperature were 3.70, 0.24, and 4.64, respectively (Table S1).

Relationships between personality, plasticity, exposure, and survival

Of the 45 grouse included in the resource selection analysis, we removed six individuals from the survival analysis that were not exposed to or did not have access to snow > 15 cm. Of the 39 individuals included in the survival analysis, 10 individuals were killed by predators (2 by owls [*Strix varia* or *Bubo virginianus*], 5 by unidentified raptors, 1 by coyote [*Canis latrans*], and 2 by unidentified mammalian predators). No mortalities were attributed to causes other than predation. We included $\mathrm{SSE>15_{M}}$ and ΔSSE>15 and exposure to winter temperature (WTEXP) in separate survival models as they were highly correlated (-0.80 and 0.81, respectively).

Exposure to, and selection for, snow were important predictors of overwinter survival (Tables 1, S3, S4). As exposure to shallow snow (SEXP<15) increased, grouse survival sharply declined (β = -1.99, SE = 0.62, CI = -3.21, -0.77; Fig. 4A), but exposure to deep snow (SEXP>15) did not influence survival. Importantly, grouse with high values for $\mathrm{SSE>15_{M}}$ were more likely to be found in snow burrows or bowls (n = 769 roost observations; β = 0.26, SE = 0.13, CI = 0.00, 0.52) when snow was deep (β = 1.25, SE = 0.13, CI = 1.00, 1.50), and were more likely to survive winter (β = 0.70, SE = 0.43, CI = -0.14, 1.54; Fig. 4B). While $\mathrm{SSE>15_{M}}$ was an important predictor of overwinter survival (Tables 1, S4), $\mathrm{SSE<15_{M}}$ did not predict overwinter survival (Table S3). Further, neither ΔSSE<15 nor ΔSSE>15 influenced survival (Table S3). Finally $\mathrm{WTSE_{M}}$, ΔWTSE, WTEXP, and exposure to mature forest and open areas (FEXP, OEXP) did not influence overwinter survival (Tables 1, S3).

Sensitivity of survival analysis to error in random slopes

We found that the survival analysis was robust to moderate error propagation carried over from using random slope estimates from the behavioral reaction norms. The top model included $SSE>15_M$ and $SEXP<15$, regardless of the error-scenario used (Appendix S4, Tables S3-S6). Further, the beta estimates and confidence intervals of these two predictors in the top model of all versions of the survival analysis were remarkably similar (Tables S4, S6).

Discussion

By tracking individual variability in roost site selection, we found overwintering grouse changed their behavior in response to dynamic snow depth and winter temperature conditions, with important demographic consequences. Snow and winter temperature were important predictors of roost site selection and 13-20 times greater than the effect of land cover. Importantly, the role of snow in mediating roost site selection and survival varied throughout winter. At lower snow depths, snow-covered areas were associated with reduced survival, and grouse generally avoided these areas. However, once snow was deep enough for burrowing, individual grouse demonstrated strong plasticity in selecting deep snow and those with personalities for selecting deep snow were more likely to use snow burrows and survive the winter. Individual variation in resource selection can thus have important demographic consequences, and may be an adaptive strategy for temperate species seeking out refugia in dynamic, seasonal environments.

Personality and behavioral plasticity in roost site selection

Grouse demonstrated a high degree of individual variation in personality and behavioral plasticity in selection of ephemeral winter microrefugia. Despite some individual variation, most grouse tended to select roost sites with warmer winter air temperatures. Selecting warmer areas is likely adaptive, as less energy is needed for thermoregulation. These warmer areas buffer birds against cold temperatures, and may be particularly important when snow is scarce. While overall winter temperature was a significant predictor of population and individual-level selection, daily temperature was not. It is likely daily fluctuations in warm and cold locations may be too variable to predict, and it may be more reliable to seek out locations consistently warmer throughout winter.

Individual grouse varied considerably in the direction and magnitude of their response to differences in snow depth, but this was most evident during deep snow periods. When snow depths were too shallow to snow burrow, nearly all individuals were more likely to select areas with very shallow or no snow. This consistent behavior among grouse indicates no snow may be preferable because reddish-brown grouse are more cryptic against a snowless background. Deeper snow (that is still relatively shallow) is less suitable, likely because grouse are visible to predators via phenotypic mismatch, and navigating through this deeper snow may be a hindrance, potentially requiring more energy to move, and may make foraging more difficult. When snow becomes deep enough for burrowing, individual grouse diverge in the direction and magnitude of their plasticity. Some individuals selected very deep snow, and others strongly avoided it. Further, grouse exhibited a wide diversity of personalities in selecting for deep snow. Grouse that strongly selected areas with deep snow were more likely to roost in snow burrows and bowls, whereas grouse that avoided deep snow were more likely to roost on top of snow, in trees, or under protective cover. These differences in personality and plasticity in selection for deep snow may represent different behavioral strategies that allow grouse populations to persist in seasonal environments (Sih, Bell and Johnson 2004).

Exposure to and selection for microrefugia predict overwinter survival

Exposure to shallow snow and personality in selection for deep snow were important predictors of overwinter survival. It is likely there are survival costs associated with the presence of snow on the ground, possibly due to phenotypic mismatch (Karell et al. 2011, Koskenpato et al. 2019). Interestingly, exposure to deep snow did not influence overall survival, but individuals that selected deep snow were more likely to survive the winter. Selection for deep snow was associated with increased snow burrowing behavior, an adaptation that potentially allowed these individuals to reduce their predation risk. In snow bowls and burrows, grouse are more concealed from view than if they were in the open. In addition to direct concealment from predators, snow burrow roosts may also potentially reduce energy loss through thermoregulation, which in turn reduces the need to forage and be exposed to predators (Gilliam and Fraser 2001, Larsen and Boutin 1994, Metzgar and Boyd 1988).

While we found individuals that selected deep snow experienced increased survival, a diversity of personalities for snow selection exist. If seeking out deep snow benefits survival, why do some individuals avoid it? Importantly, the strong negative relationship between exposure to shallow snow and overwinter survival closely matches the behavior among grouse to avoid roosting in snowy areas when snow is relatively shallow. The negative effect of exposure to shallow snow on survival was more than twice as strong as the positive effect of seeking out deep snow. Because avoiding shallow snow (up to 15 cm) is more important for survival than seeking out deep snow, this may constitute a “runaway effect” or “behavioral inertia” that may explain why not all individuals seem capable of switching their behavior from avoiding shallow snow to selecting for deep snow when snow cover switches from representing a hazard to a refuge. Alternatively, or perhaps additionally, because deep snow is ephemeral in this system, switching behavioral strategies to seek out deep snow when snow burrowing becomes possible for a short time may not provide enough of a benefit for all individuals. It is possible a time-lag could exist, wherein some individuals with significant “behavioral inertia” would eventually switch strategies and seek out deep snow if it was available for longer time periods.

Implications for future loss of snow cover and an adaptive behavioral strategy

Winter temperatures and snow cover are becoming increasingly variable, and snow cover extent and duration is rapidly declining throughout the Northern Hemipshere due to modern climate change (Notaro et al. 2011, Chen, Liang and Cao 2016, Vaughan et al. 2013). In Wisconsin, average snow depths currently peak at 15 cm in mid-winter, and are projected to decline to an average of 8-12 cm (Notaro et al. 2011). We have shown here that individuals consistently avoid shallow snow and suffer higher mortality in shallow snow. Importantly, when snow depths increase, individuals with personalities for selecting and using deep snow for roosting can improve their chances of survival. As winter temperatures are expected to climb in coming decades, deep snow is becoming less common, which may push winter-adapted species to the limits of their capacity to respond through behavioral adaptation.

Personality and plasticity in resource selection

To our knowledge, this is the first study to link individual differences in personality or plasticity in selection of dynamic refugia to fitness outcomes. It is worth noting that by considering resource selection within the lens of behavioral reaction norms, we found personality in resource selection had a larger impact on survival than plasticity in resource selection. When considering individual variation, plasticity is often what is assessed, but researchers interested in exploring individual variation in resource selection have the potential to miss important relationships if the effects of differences in personality are not assessed.

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Tables

Table 1. Top candidate models ($\Delta AIC_c \leq 2$) and the intercept null model evaluating ruffed grouse over-winter survival. Plasticity (i.e., change in probability of selection) and personality (i.e., mean probability of selection) covariates for each individual were derived from a resource selection function. See Supplementary Materials for the full list of candidate models.

Model	k	AIC_c	ΔAIC_c	w_i
$SSE>15_M$[a] + SEXP<15	3	99.20	0.00	0.14
SEXP<15	2	100.02	0.81	0.09
$SSE>15_M$ + SEXP<15 + SEXP<15	4	100.99	1.79	0.06
$SSE>15_M$ + SEXP<15 + $WTSE_M$	4	101.19	1.99	0.05
$SSE>15_M$ + SEXP<15 + ΔWTSE	4	101.20	2.00	0.05
NULL	1	115.07	15.87	0.00

[a] ΔSSE>15 = change in probability of selection between 15 cm and the maximum snow depth available to each individual, $SSE>15_M$ = mean probability of selection between 15 cm and the population-level maximum available snow depth, ΔWTSE = change in probability of selection across winter temperature conditions available to each individual. $WTSE_M$ = mean probability of selection across the range of winter temperature conditions available to the population in a given year. SEXP<15 = the median snow depth at an individual's used roost sites for snow depths < 15 cm. SEXP>15 = the median snow depth at an individual's used roost sites for snow depths ≥ 15 cm.

Figures

Fig. 1: Examples of spatial variability of environmental predictors in models estimating individual and population-level roost site selection and survival in ruffed grouse. (A) Land cover variation; (B) winter temperature (December – March, 2015-2016) as average minimum air temperature and; (C) average snow depth (January – February 2016).

Fig. 2: Beta estimates of environmental covariates included in a resource selection function estimating individual and population-level winter roost site selection in ruffed grouse. Important predictors (*) of roost site selection had 95% confidence intervals not-overlapping zero (represented by error bars). Snow and winter temperature were more important to roost site selection than land cover.

Fig. 3: Behavioral reaction norm plots of resource selection by roosting ruffed grouse in response to changing snow depth (A, C) and winter temperature (B, D). Top panels show population-level mean responses (black lines) and variability (grey bands) as 95% confidence intervals. Bottom panels show behavioral reaction norms for individual grouse. For snow depth (C), filled circles represent $\text{SSE}<15_{\text{M}}$ (left) and $\text{SSE}>15_{\text{M}}$ (right). For winter temperature (D), filled circles represent WTSE_{M}. Grouse strongly selected for sites with very shallow or no snow, but showed a high degree of plasticity (ΔSSE>15) and diverse personalities in deeper snow ($\text{SSE}>15_{\text{M}}$) (A, C). Individual grouse differed less in plasticity (ΔWTSE) and personality (WTSE_{M}) when selecting winter temperatures (B, D).

Fig. 4: Partial prediction plots showing over-winter survival probability of individual ruffed grouse in relation to SEXP<15 (A) and $\text{SSE}>15_{\text{M}}$ (B). In general, grouse exposed to shallower snow were less likely to die during winter, but when snow was deep enough (≥ 15 cm), individuals that selected for deeper snow improved their probability of survival, presumably

benefiting from snow burrowing. Black lines and grey bands represent population-level means and 95% confidence intervals.

Figure 1

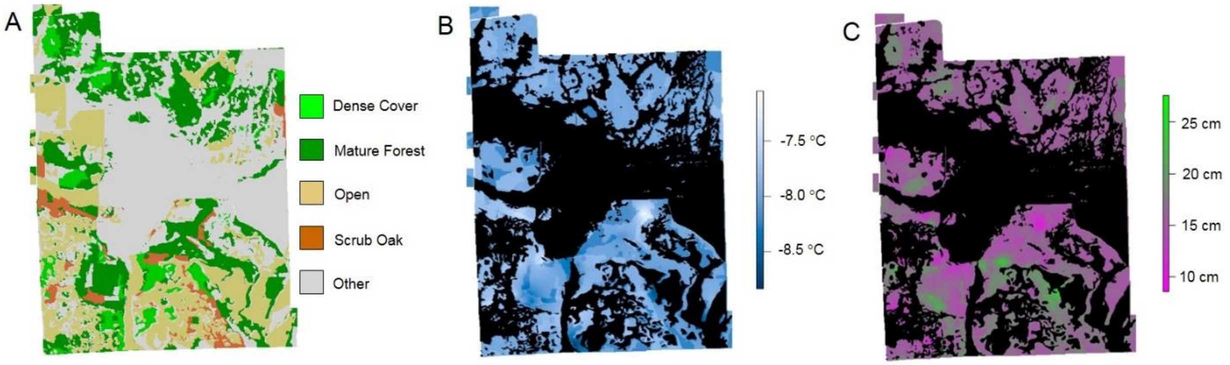

A
Dense Cover
Mature Forest
Open
Scrub Oak
Other
B
-7.5 °C
-8.0 °C
-8.5 °C
C
25 cm
20 cm
15 cm
10 cm

Figure 2

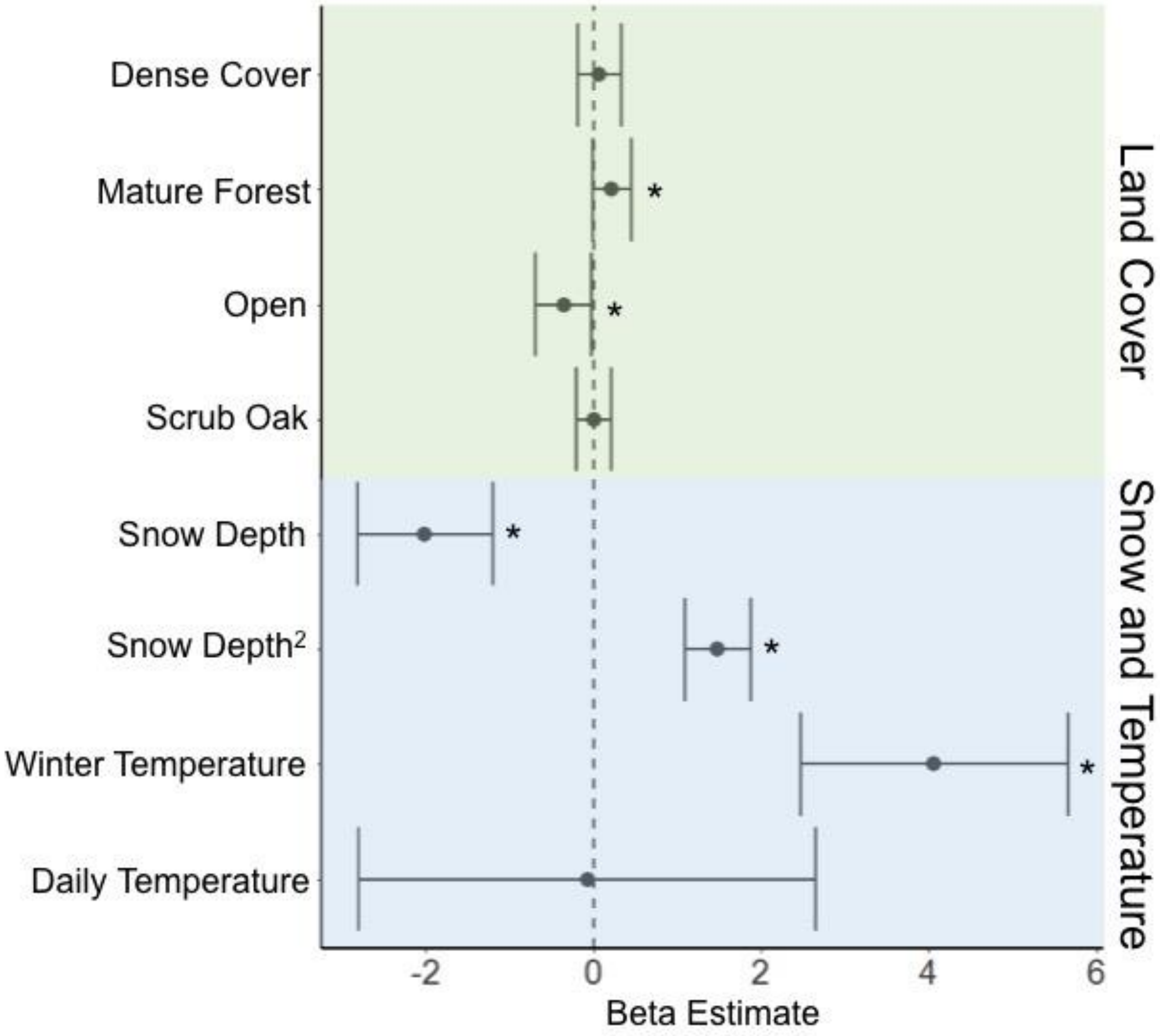

Dense Cover
Mature Forest
Open
Scrub Oak
Snow Depth
Snow Depth²
Winter Temperature
Daily Temperature
*
*
*
*
*
Land Cover
Snow and Temperature
-2
0
2
4
6
Beta Estimate

Figure 3

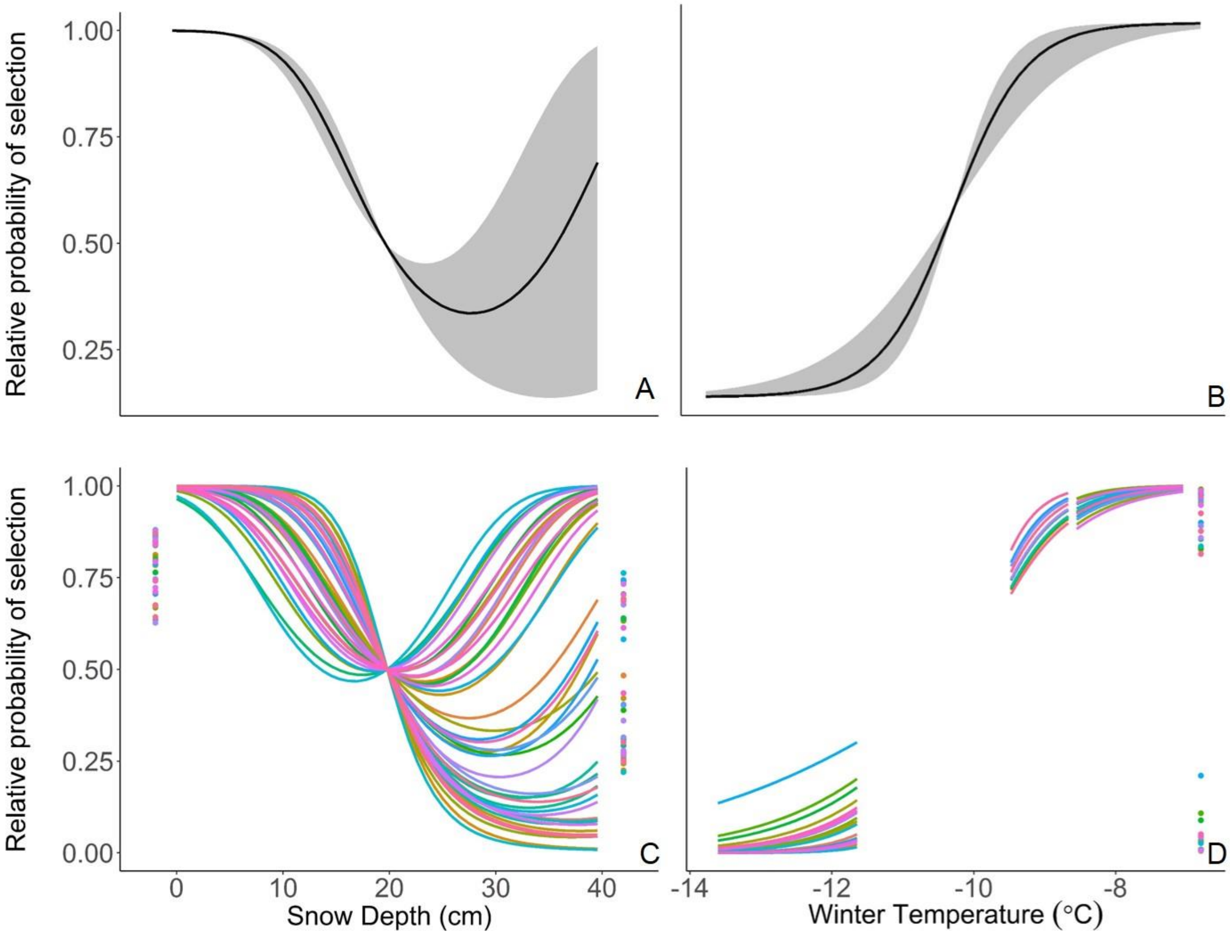
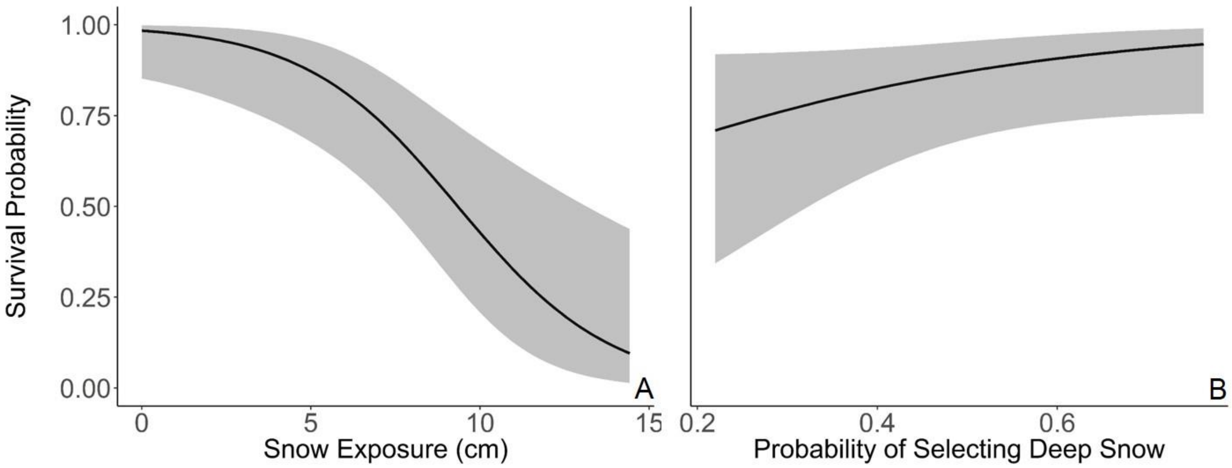

1.00
0.75
0.50
0.25
Relative probability of selection
A
B
1.00
0.75
0.50
0.25
0.00
Relative probability of selection
C
D
0
10
20
30
40
Snow Depth (cm)
-14
-12
-10
-8
Winter Temperature (°C)

Figure 4


Survival Probability
1.00
0.75
0.50
0.25
0.00
0
5
10
15
Snow Exposure (cm)
A
0.2
0.4
0.6
Probability of Selecting Deep Snow
B

Supplementary Materials

Appendix S1

Land Cover Classification

To classify land cover, we began with a forest inventory map of Sandhill (Wisconsin DNR, WISFIRS) with 31 habitat types. Using a combination of fine-scale vegetation surveys and a principal component analysis, we reclassified land cover into 5 classes: Aspen-Alder, Mature Forest, Clearcut, Open, and Other. After examining the number of used and available roost sites in each land cover class, we grouped "Clearcut" with "Other" (due to a low number of sites in Clearcut), removed "Scrub Oak" from "Other" and created a separate class for Scrub Oak. Our final land cover map had a 5 m- resolution and 5 land cover classes: Aspen-Alder (referred to as Dense Cover), Mature Forest, Scrub Oak, Open (emergent vegetation, lowland brush/willow, and lowland grass), and Other.

Appendix S2

Regression kriging to interpolate environmental predictors

We used regression kriging to interpolate minimum daily temperature across SWA. Predictors in the kriging regression included land cover classes and distance to forest edge (edge was considered the boundary between marsh or open water and any of the other cover types). All predictors were scaled using a z-transformation. We did not include predictors in the same model if they exhibited multicollinearity (Pearson's correlation coefficient ≥ 0.7). We again used regression kriging to interpolate winter temperature (°C). We averaged the minimum daily temperature for each of the 58 iButtons across each winter, to obtain seasonal values for each iButton, for each of the three winters. Predictors included land cover and distance to edge. Results were summarized as a 10 m-resolution raster of average minimum temperature (hereafter winter temperature) for each of the three winter seasons. To interpolate snow depth, we used regression kriging, and included land cover classes, distance to forest edge, and both the minimum and maximum average temperatures for each snowfall period as predictors.

Appendix S3

Snowfall Event Classification

Snowfall events likely drive snow depth, so we used daily snow depth measurements from a single NOAA weather station located at SWA to determine when they occurred. We defined a snowfall event as snow depth increasing by at least 7 cm from one day to the next. All snow depth measurements were grouped into periods such that snowfall events did not occur within a snowfall period. However, this was limited by the number of snow depth measurements available for that snowfall period. For example, if 8 cm of snow fell on 1 January, and another 10 cm of snow fell on 3 January, but only 3 snow depth measurements were taken in between the snow fall events, we could not separate these into two snowfall periods, and the 2 days in between were removed from the analysis. To maximize the number of snow depth measurements available across the study area, and in any given time period, we used snow depth measurements from grouse roost sites in addition to snow depth measurements collected at iButton stations.

Appendix S4

Sensitivity of survival analysis to error propagation

We obtained estimates of error in the random and fixed slopes from their posterior distributions using a Bayesian approach by re-running the step-selection function with uninformative priors using the R-INLA package (version 20.05.12), in R. We extracted the 0.4, 0.5, and 0.6 quantiles from the posterior distributions of the random and fixed slopes to recalculate estimates of personality and plasticity predictors for each individual under three alternative scenarios that represent moderate levels of error propagation. We re-ran the survival analyses using these three alternatives, and compared the top model in each scenario, and the beta estimates and confidence intervals of the predictors in each top model, with the top model from the original survival analysis to assess how moderate error propagation influenced our survival results.

Table S1. Candidate predictors potentially influencing winter roost site selection by Ruffed Grouse at the individual and population-level included in a step-selection function with random intercepts and slopes. Important predictors (in bold) had 95% confidence intervals not overlapping zero. Spatially-explicit estimates during winter for SnowDepth = snow depth, WinterTemperature = minimum air temperature, DailyTemperature = daily air temperature, DenseCover = proportion of dense cover, Oak = proportion of scrub oak, MatureForest = proportion of mature forest, and Open = proportion of open habitat. β = Fixed coefficient estimate, SE = standard error, 95% CI = 95% Confidence Interval.

Candidate predictors	β	SE	95% CI	*Variance of Random Coefficients*
Intercept	-4.33	3.87	-11.92, 3.26	
SnowDepth	-2.01	0.41	-2.82, -1.20	3.70
SnowDepth^2	1.48	0.20	1.08, 1.88	0.24
WinterTemperature	4.06	0.81	2.46, 5.66	4.64
DailyTemperature	-0.08	1.39	-2.80, 2.65	-
DenseCover	0.07	0.13	-0.18, 0.32	0.11
Oak	0.00	0.11	-0.20, 0.21	0.05
MatureForest	0.21	0.12	-0.01, 0.44	-
Open	-0.38	0.17	-0.69, -0.02	0.38

Table S2. Candidate predictors potentially influencing winter roost site selection by Ruffed Grouse at the individual and population-level included in a step-selection function with random intercepts and slopes to evaluate whether random slopes were inadvertently capturing variation in conditions the individuals were exposed to (i.e. the predictors). Important predictors (in bold) had 95% confidence intervals not overlapping zero. Spatially-explicit estimates during winter for SnowDepth = snow depth, WinterTemperature = minimum air temperature, DailyTemperature = daily air temperature, DenseCover = proportion of dense cover, Oak = proportion of scrub oak, MatureForest = proportion of mature forest, and Open = proportion of open habitat. Predictors that begin with "d" estimate how much the differences between individuals are due to predictor difference, and predictors without a "d" represent the within-subjects effects (van de Pol and Wright 2009). β = Fixed coefficient estimate, SE = standard error, 95% CI = 95% Confidence Interval.

Candidate predictors	β	SE	95% CI	*Variance of Random Coefficients*
Intercept	-4.52	6.75	-17.75, 8.71	
SnowDepth	-2.01	0.41	-2.83, -1.20	3.73
dSnowDepth	1.93	31.93	-60.67, 64.53	
SnowDepth^2	1.48	0.20	1.08, 1.88	0.24
dSnowDepth^2	1.17	33.20	-63.89, 66.26	
WinterTemperature	4.19	0.84	2.54, 5.84	5.00
dWinterTemperature	-5.52	12.75	-30.52, 19.47	
DailyTemperature	-0.02	1.40	-2.77, 2.71	0.001
dDailyTemperature	1.15	26.62	-51.02, 53.32	
DenseCover	0.06	0.13	-0.18, 0.32	0.11
dDenseCover	-0.30	13.70	-37.12, 26.60	
Oak	0.00	0.11	-0.20, 0.21	0.05
dOak	-0.26	13.78	-21.03, 20.52	
MatureForest	0.21	0.12	-0.01, 0.44	0.07
dMatureForest	0.59	17.14	-33.00, 34.18	
Open	-0.36	0.17	-0.69, -0.02	0.39

dOpen	0.41	12.10	-23.29, 24.11

Table S3. Candidate models evaluating Ruffed Grouse over-winter survival. Plasticity (i.e., change in probability of selection) and personality (i.e., mean probability of selection) covariates for each individual were derived from a step-selection function. Exposure covariates are the median values across all roost sites used by an individual. ΔSSE>15 = change in probability of selection between 15 cm and the maximum snow depth available to each individual. ΔSSE<15 = change in probability of selection between the minimum snow depth available to each individual and 14.9 cm. SSE>15$_M$ = mean probability of selection between 15 cm and the population-level maximum available snow depth. SSE<15$_M$ = mean probability of selection between the population-level minimum available snow depth and 14.9 cm. SEXP<15 = the median snow depth at an individual's used roost sites for snow depths < 15 cm. SEXP>15 = the median snow depth at an individual's used roost sites for snow depths ≥ 15 cm. ΔWTSE = change in probability of selection across winter minimum temperature conditions available to each individual. WTSE$_M$ = mean probability of selection across the range of winter minimum temperature conditions available to the population in a given year. WTEXP = the median winter minimum temperature at an individual's used roost sites. OEXP = the median proportion of open habitat at an individual's used roost sites. FEXP = the median proportion of mature forest habitat at an individual's used roost sites. k = number of parameters in the model, AIC$_c$ = Akaike's Information Criterion corrected for small sample sizes, ΔAIC$_c$ = change in AIC$_c$ from the top model, w_i = Akaike weight.

Model	k	AIC$_c$	ΔAIC$_c$	w_i
SSE>15$_M$ + SEXP<15	3	99.20	0.00	0.14
SEXP<15	2	100.02	0.81	0.09
SSE>15$_M$ + SEXP<15 + SEXP>15	4	100.99	1.79	0.06
SSE>15$_M$ + SEXP<15 + WTSE$_M$	4	101.19	1.99	0.05
SSE>15$_M$ + SEXP<15 + ΔWTSE	4	101.20	2.00	0.05
SEXP<15 + ΔWTSE	3	101.41	2.21	0.05
SEXP<15 + SEXP>15	3	101.71	2.50	0.04
SSE<15$_M$ + SEXP<15 + ΔSSE>15	4	101.72	2.51	0.04
SSE<15$_M$ + SEXP<15	3	101.99	2.79	0.03
ΔSSE<15 + SEXP<15 + WTEXP	4	102.30	3.10	0.03
ΔSSE>15 + SEXP<15 + WTEXP	4	102.39	3.19	0.03
SSE>15$_M$ + SEXP<15 + SEXP>15 + ΔWTSE	5	103.02	3.81	0.02
SSE>15$_M$ + SEXP<15 + SEXP>15 + WTSE$_M$	5	103.02	3.82	0.02
SSE<15$_M$ + SEXP<15 + ΔWTSE	4	103.12	3.92	0.02
SSE>15$_M$ + SEXP<15 + WTSE$_M$ + ΔWTSE	5	103.20	4.00	0.02
SSE<15$_M$ + SEXP<15 + SEXP>15 + ΔSSE>15	5	103.35	4.15	0.02
SEXP<15 + SEXP>15 + ΔWTSE	4	103.37	4.16	0.02
SEXP<15 + WTSE$_M$ + ΔWTSE	4	103.44	4.24	0.02

SSE<15$_{M}$ + SEXP<15 + SEXP>15	4	103.49	4.29	0.02
SSE<15$_{M}$ + SEXP<15 + WTSE$_{M}$ + ΔSSE>15	5	103.52	4.32	0.02
SSE<15$_{M}$ + SEXP<15 + ΔWTSE + ΔSSE>15	5	103.54	4.34	0.02
SEXP<15 + SEXP>15 + WTSE$_{M}$	4	103.69	4.49	0.01
ΔSSE<15 + SEXP<15 + WTEXP + ΔSSE>15	5	103.88	4.68	0.01
SSE<15$_{M}$ + SEXP<15 + WTSE$_{M}$	4	104.01	4.81	0.01
ΔSSE<15 + SEXP<15 + ΔWTSE + WTEXP	5	104.16	4.96	0.01
ΔSSE<15 + SEXP<15 + WTSE$_{M}$ + WTEXP	5	104.32	5.12	0.01
ΔSSE<15 + SEXP<15 + SEXP>15 + WTEXP	5	104.33	5.13	0.01
ΔSSE>15 + SEXP<15 + SEXP>15 + WTEXP	5	104.33	5.13	0.01
ΔSSE>15 + SEXP<15 + ΔWTSE + WTEXP	5	104.37	5.17	0.01
ΔSSE>15 + SEXP<15 + WTSE$_{M}$ + WTEXP	5	104.42	5.21	0.01
SSE<15$_{M}$ + SEXP<15 + SEXP>15 + ΔWTSE	5	104.92	5.72	0.01
SSE>15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE	6	105.05	5.85	0.01
SSE<15$_{M}$ + SEXP<15 + WTSE$_{M}$ + ΔWTSE	5	105.08	5.88	0.01
SSE<15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔSSE>15	6	105.23	6.03	0.01
SSE<15$_{M}$ + SEXP<15 + SEXP>15 + ΔWTSE + ΔSSE>15	6	105.30	6.10	0.01
SSE<15$_{M}$ + SEXP<15 + WTSE$_{M}$ + ΔWTSE + ΔSSE>15	6	105.31	6.11	0.01
SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE	5	105.38	6.18	0.01
SSE<15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$	5	105.52	6.31	0.01
ΔSSE<15 + SEXP<15 + ΔWTSE + WTEXP + ΔSSE>15	6	105.82	6.62	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + WTEXP + ΔSSE>15	6	105.82	6.62	0.00
ΔSSE<15 + SEXP<15 + WTSE$_{M}$ + WTEXP + ΔSSE>15	6	105.85	6.64	0.00
ΔSSE<15 + SEXP<15 + WTSE$_{M}$ + ΔWTSE + WTEXP	6	106.15	6.95	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + ΔWTSE + WTEXP	6	106.19	6.99	0.00
ΔSSE>15 + SEXP<15 + SEXP>15 + ΔWTSE + WTEXP	6	106.33	7.13	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + WTSE$_{M}$ + WTEXP	6	106.36	7.15	0.00
ΔSSE>15 + SEXP<15 + SEXP>15 + WTSE$_{M}$ + WTEXP	6	106.37	7.16	0.00
ΔSSE>15 + SEXP<15 + WTSE$_{M}$ + ΔWTSE + WTEXP	6	106.40	7.20	0.00
SSE>15$_{M}$ + SEXP<15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP	7	106.53	7.33	0.00
SSE<15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE	6	106.94	7.73	0.00
SSE<15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE + ΔSSE>15	7	107.16	7.96	0.00
ΔSSE<15 + SEXP<15 + WTSE$_{M}$ + ΔWTSE + WTEXP + ΔSSE>15	7	107.75	8.54	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + ΔWTSE + WTEXP + ΔSSE>15	7	107.78	8.58	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + WTSE$_{M}$ + WTEXP + ΔSSE>15	7	107.79	8.59	0.00
ΔSSE<15 + SEXP<15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP	7	107.91	8.71	0.00
ΔSSE>15 + SEXP<15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP	7	107.95	8.75	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE + WTEXP	7	108.19	8.99	0.00
ΔSSE>15 + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE + WTEXP	7	108.36	9.16	0.00
SSE>15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP	8	108.40	9.20	0.00
SSE<15$_{M}$ + SEXP<15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP	7	108.87	9.67	0.00
SSE<15$_{M}$ + SEXP<15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP + ΔSSE>15	8	109.08	9.88	0.00
ΔSSE<15 + SEXP<15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP + ΔSSE>15	8	109.45	10.25	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE + WTEXP + ΔSSE>15	8	109.72	10.51	0.00
ΔSSE>15 + SEXP<15 + SEXP>15 + WTSE$_{M}$ + ΔWTSE + FEXP + OEXP	8	109.94	10.74	0.00

ΔSSE<15 + SEXP<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP	8	109.95	10.75	0.00
ΔSSE<15	2	110.09	10.89	0.00
SSE<15$_M$ + ΔSSE>15	3	110.61	11.41	0.00
SSE<15$_M$ + SEXP<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP	8	110.73	11.52	0.00
SSE<15$_M$ + SEXP<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP + ΔSSE>15	9	110.96	11.76	0.00
ΔSSE<15 + SEXP<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP + ΔSSE>15	9	111.50	12.30	0.00
ΔSSE<15 + WTEXP	3	111.63	12.43	0.00
ΔSSE<15 + ΔSSE>15	3	112.06	12.86	0.00
SSE<15$_M$ + SEXP>15 + ΔSSE>15	4	112.17	12.97	0.00
ΔSSE<15 + WTEXP + ΔWTSE	4	113.05	13.85	0.00
ΔSSE<15 + WTEXP + ΔSSE>15	4	113.23	14.03	0.00
ΔSSE<15 + WTEXP + WTSE$_M$	4	113.24	14.04	0.00
SSE<15$_M$	2	113.24	14.04	0.00
SSE<15$_M$ + SEXP>15 + WTSE$_M$ + ΔSSE>15	5	113.46	14.26	0.00
ΔSSE<15 + SEXP>15 + WTEXP	4	113.63	14.42	0.00
SSE<15$_M$ + SEXP>15 + ΔWTSE + ΔSSE>15	5	113.90	14.70	0.00
ΔSSE<15 + WTEXP + WTSE$_M$ + ΔSSE>15	5	114.68	15.47	0.00
ΔSSE<15 + WTEXP + WTSE$_M$ + ΔWTSE	5	114.79	15.59	0.00
ΔSSE<15 + WTEXP + ΔWTSE + ΔSSE>15	5	114.83	15.62	0.00
SSE<15$_M$ + SEXP>15	3	114.85	15.65	0.00
ΔSSE<15 + SEXP>15 + ΔWTSE + WTEXP	5	115.05	15.85	0.00
Null	1	115.07	15.87	0.00
ΔSSE<15 + SEXP>15 + WTEXP + ΔSSE>15	5	115.11	15.91	0.00
ΔSSE<15 + SEXP>15 + WTSE$_M$ + WTEXP	5	115.24	16.04	0.00
SSE<15$_M$ + SEXP>15 + WTSE$_M$ + ΔWTSE + ΔSSE>15	6	115.42	16.22	0.00
SSE<15$_M$ + SEXP>15 + ΔWTSE	4	115.43	16.23	0.00
ΔSSE>15	2	115.77	16.57	0.00
SSE>15$_M$	2	115.99	16.79	0.00
ΔSSE<15 + WTEXP + WTSE$_M$ + ΔWTSE + ΔSSE>15	6	116.45	17.24	0.00
ΔSSE<15 + SEXP>15 + WTSE$_M$ + WTEXP + ΔSSE>15	6	116.53	17.32	0.00
ΔSSE>15 + WTEXP	3	116.67	17.46	0.00
ΔSSE<15 + SEXP>15 + ΔWTSE + WTEXP + ΔSSE>15	6	116.74	17.53	0.00
SSE<15$_M$ + SEXP>15 + WTSE$_M$	4	116.77	17.57	0.00
ΔSSE<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + WTEXP	6	116.80	17.60	0.00
ΔWTSE	2	116.85	17.65	0.00
SEXP>15	2	116.97	17.76	0.00
WTSE$_M$	2	117.09	17.88	0.00
SSE>15M + SEXP>15	3	117.14	17.94	0.00
SSE<15$_M$ + SEXP>15 + WTSE$_M$ + ΔWTSE	5	117.44	18.23	0.00
FEXP + OEXP	3	118.06	18.86	0.00
ΔSSE<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + WTEXP + ΔSSE>15	7	118.33	19.13	0.00
ΔSSE>15 + WTEXP + ΔWTSE	4	118.41	19.21	0.00
ΔSSE>15 + WTEXP + WTSE$_M$	4	118.53	19.33	0.00

SEXP>15 + ΔWTSE	3	118.55	19.35	0.00
ΔSSE>15 + SEXP>15 + WTEXP	4	118.56	19.36	0.00
ΔSSE<15 + WTEXP + WTSE$_M$ + ΔWTSE + FEXP + OEXP	7	118.73	19.53	0.00
WTSE$_M$ + ΔWTSE	3	118.85	19.64	0.00
SEXP>15 + WTSE$_M$	3	118.98	19.78	0.00
SSE>15$_M$ + SEXP>15 + ΔWTSE	4	119.11	19.90	0.00
SSE>15$_M$ + SEXP>15 + WTSE$_M$	4	119.12	19.91	0.00
SSE<15$_M$ + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP + ΔSSE>15	8	119.46	20.26	0.00
ΔSSE<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP	7	119.55	20.34	0.00
ΔSSE>15 + SEXP>15 + ΔWTSE + WTEXP	5	120.32	21.12	0.00
ΔSSE>15 + WTEXP + WTSE$_M$ + ΔWTSE	5	120.37	21.17	0.00
ΔSSE<15 + WTEXP + WTSE$_M$ + ΔWTSE + FEXP + OEXP + ΔSSE>15	8	120.39	21.19	0.00
ΔSSE>15 + SEXP>15 + WTSE$_M$ + WTEXP	5	120.41	21.21	0.00
SEXP>15 + WTSE$_M$ + ΔWTSE	4	120.56	21.36	0.00
SSE<15$_M$ + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP	7	121.04	21.84	0.00
SSE>15$_M$ + SEXP>15 + WTSE$_M$ + ΔWTSE	5	121.12	21.91	0.00
ΔSSE<15 + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP + ΔSSE>15	8	121.56	22.35	0.00
ΔSSE>15 + SEXP>15 + WTSE$_M$ + ΔWTSE + WTEXP	6	122.28	23.08	0.00
ΔSSE>15 + WTEXP + WTSE$_M$ + ΔWTSE + FEXP + OEXP	7	123.56	24.35	0.00
SSE>15$_M$ + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP	7	124.25	25.05	0.00
ΔSSE>15 + SEXP>15 + WTSE$_M$ + ΔWTSE + FEXP + OEXP	7	124.72	25.52	0.00

Table S4. Predictors influencing Ruffed Grouse over-winter survival. Predictors in the model were: $SSE>15_M$ = mean probability of selection between 15 cm and the population-level maximum available snow depth (i.e. personality in selection of deep snow; obtained from a step-selection function) and SEXP<15 = the median snow depth at an individual’s used roost sites for snow depths < 15 cm. β = beta estimate, SE = standard error, 95% CI = 95% Confidence Interval.

Predictors	β	SE	95% CI
Intercept	1.77	0.57	0.66, 2.89
$SSE>15_M$	0.70	0.43	-0.14, 1.54
SEXP<15	-1.99	0.62	-3.21, -0.77

Table S5. Candidate models evaluating Ruffed Grouse over-winter survival used in an analysis exploring sensitivity to uncertainty in estimation of random slopes. Plasticity (i.e., change in probability of selection) and personality (i.e., mean probability of selection) covariates for each individual were derived from a step-selection function using a Bayesian approach. Random slopes were drawn from the 0.4 quantile (low), 0.5 quantile (median), and 0.6 quantile (high) of each individual's posterior distribution of the random slope for each covariate. Exposure covariates are the median values across all roost sites used by an individual, and were not derived from random slopes. Models included in the low, median, and high rounds of the sensitivity analysis were candidate models evaluated in the survival analysis with a $\Delta AIC_c < 4$ (Table S2). ΔSSE>15 = change in probability of selection between 15 cm and the maximum snow depth available to each individual. ΔSSE<15 = change in probability of selection between the minimum snow depth available to each individual and 14.9 cm. $SSE>15_M$ = mean probability of selection between 15 cm and the population-level maximum available snow depth. $SSE<15_M$ = mean probability of selection between the population-level minimum available snow depth and 14.9 cm. SEXP<15 = the median snow depth at an individual's used roost sites for snow depths < 15 cm. SEXP>15 = the median snow depth at an individual's used roost sites for snow depths ≥ 15 cm. ΔWTSE = change in probability of selection across winter minimum temperature conditions available to each individual. $WTSE_M$ = mean probability of selection across the range of winter minimum temperature conditions available to the population in a given year. WTEXP = the median winter minimum temperature at an individual's used roost sites. k = number of parameters in the model, AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = change in AIC_c from the top model, w_i = Akaike weight.

Round	Model	k	AIC_c	ΔAIC_c	w_i
Low	**$SSE>15_M$ + SEXP<15**	**3**	**99.42**	**0.00**	**0.20**
Low	SEXP<15	2	100.02	0.60	0.15
Low	$SSE<15_M$ + SEXP<15 + ΔSSE>15	4	100.27	0.85	0.13
Low	$SSE>15_M$ + SEXP<15 + SEXP>15	4	101.22	1.80	0.08
Low	ΔSSE>15 + SEXP<15 + WTEXP	4	101.32	1.90	0.08
Low	$SSE>15_M$ + SEXP<15 + $WTSE_M$	4	101.41	1.99	0.07
Low	$SSE>15_M$ + SEXP<15 + ΔWTSE	4	101.42	2.00	0.07
Low	SEXP<15 + SEXP>15	3	101.71	2.29	0.06
Low	$SSE<15_M$ + SEXP<15	3	101.95	2.53	0.06
Low	ΔSSE<15 + SEXP<15 + WTEXP	4	102.29	2.87	0.05
Low	$SSE>15_M$ + SEXP<15 + SEXP>15 + ΔWTSE	5	103.24	3.82	0.03
Low	$SSE>15_M$ + SEXP<15 + SEXP>15 + $WTSE_M$	5	103.24	3.82	0.03
Low	$SSE<15_M$ + SEXP<15 + SEXP>15 + $WTSE_M$	5	105.42	6.01	0.01

Low	Null	1	115.07	15.65	0.00
Median	**SSE>15$_{M}$ + SEXP<15**	**3**	**99.17**	**0.00**	**0.23**
Median	SEXP<15	2	100.02	0.84	0.15
Median	SSE>15$_{M}$ + SEXP<15 + SEXP>15	4	101.00	1.80	0.10
Median	SSE>15$_{M}$ + SEXP<15 + WTSE$_{M}$	4	101.20	1.99	0.09
Median	SSE>15$_{M}$ + SEXP<15 + ΔWTSE	4	101.20	2.00	0.09
Median	SEXP<15 + SEXP>15	3	101.71	2.53	0.07
Median	SSE<15$_{M}$ + SEXP<15 + ΔSSE>15	4	102.00	2.78	0.06
Median	SSE<15$_{M}$ + SEXP<15	3	102.00	2.82	0.06
Median	ΔSSE<15 + SEXP<15 + WTEXP	4	102.30	3.12	0.05
Median	ΔSSE>15 + SEXP<15 + WTEXP	4	102.60	3.38	0.04
Median	SSE>15$_{M}$ + SEXP<15 + SEXP>15 + ΔWTSE	5	103.00	3.83	0.03
Median	SSE>15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$	5	103.00	3.83	0.03
Median	SSE<15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$	5	105.50	6.33	0.01
Median	Null	1	115.01	15.90	0.00
High	**SSE>15$_{M}$ + SEXP<15**	**3**	**99.30**	**0.00**	**0.24**
High	SEXP<15	2	100.10	0.76	0.16
High	SSE>15$_{M}$ + SEXP<15 + SEXP>15	4	101.13	1.88	0.09
High	SSE>15$_{M}$ + SEXP<15 + WTSE$_{M}$	4	101.30	2.01	0.09
High	SSE>15$_{M}$ + SEXP<15 + ΔWTSE	4	101.30	2.02	0.09
High	SEXP<15 + SEXP>15	3	101.71	2.45	0.07
High	SSE<15$_{M}$ + SEXP<15	3	102.10	2.76	0.06
High	ΔSSE<15 + SEXP<15 + WTEXP	4	102.30	3.04	0.05
High	SSE>15$_{M}$ + SEXP<15 + SEXP>15 + ΔWTSE	5	103.16	3.90	0.03
High	SSE>15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$	5	103.16	3.90	0.03
High	ΔSSE>15 + SEXP<15 + WTEXP	4	103.22	3.96	0.03
High	SSE<15$_{M}$ + SEXP<15 + ΔSSE>15	4	103.40	4.14	0.03
High	SSE<15$_{M}$ + SEXP<15 + SEXP>15 + WTSE$_{M}$	5	105.60	6.32	0.01
High	Null	1	115.10	15.82	0.00

Table S6. Predictors influencing Ruffed Grouse over-winter survival. Predictors shown are from the top models from three rounds (low, median, and high) of a sensitivity analysis to explore the effects of uncertainty in random slope estimation (Table S4). Predictors in all three top models were: SSE>15_M = mean probability of selection between 15 cm and the population-level maximum available snow depth (i.e., personality in selection of deep snow; obtained from a step-selection function) and SEXP<15 = the median snow depth at an individual's used roost sites for snow depths < 15 cm. β = beta estimate, SE = standard error, 95% CI = 95% Confidence Interval.

Round	Predictors	β	SE	95% CI
Low	Intercept	1.76	0.57	0.64, 2.88
	SSE>15_M	0.66	0.42	-0.17, 1.49
	SEXP<15	-1.98	0.62	-3.21, -0.76
Median	Intercept	1.78	0.57	0.66, 2.90
	SSE>15_M	0.70	0.43	-0.14, 1.55
	SEXP<15	-1.99	0.62	-3.21, -0.77
High	Intercept	1.80	0.57	0.67, 2.93
	SSE>15_M	0.71	0.44	-0.15, 1.56
	SEXP<15	-2.01	0.67	-3.23, -0.78

Dissertation Epilogue

Animal species in temperate regions employ a variety of strategies to survive the winter, including seasonal migration, lowering metabolic rates, and increasing fat stores. Some species seek out ephemeral winter microrefugia, and the behavioral flexibility to find areas that can buffer them from temperature extremes and conceal them from predators may be particularly important in dynamic landscapes with fluctuating environmental conditions. The overarching goal of this dissertation was to explore the role of behavioral flexibility in a winter-adapted species, provide insight into the environmental conditions that facilitate flexibility, and determine whether flexibility in the use of ephemeral winter microrefugia confers physiological or demographic benefits to the individuals that use them.

We found compelling evidence that snow conditions influence the use of winter microrefugia (e.g., snow burrows) in ruffed grouse (*Bonasa umbellus*), a winter-adapted bird, and that land cover can influence the relationship between snow conditions and use of microrefugia. Importantly, grouse experienced reduced physiological stress at cold temperatures when in snow burrows, and when snow was deep. Snow conditions also played an important role in habitat selection, and individual flexibility to seek out deep snow and use snow burrows promoted over-winter survival. However, the relationships between snow cover, use of microrefugia, habitat selection, and overwinter survival were complex and non-linear, and there was considerable variation in individual use of deep snow. Additionally, we found several lines of evidence indicating that microrefugia can provide a buffer from thermoregulatory stress and protection from predators, but there are tipping points where snow can be hazardous at shallow depths, but confer physiological and demographic benefits when snow is deep.

We found non-linear relationships between use of microrefugia and snow conditions. Grouse were more likely to use snow burrows when snow was deep and powdery, but the likelihood of using snow burrows only increased when snow depths were greater than 15-20 cm, and when snow was very powdery (Chapter 1). Grouse experienced physiological benefits from using microrefugia. We found a strong relationship between ambient temperature and physiological stress: grouse were more stressed when temperatures were cold. However, when grouse used snow burrows, grouse were buffered from cold temperatures, and stress levels were not influenced by ambient temperature. We also found a non-linear relationship between stress and snow depth. When snow depths surpassed about 15-20 cm, stress rapidly decreased (Chapter 2). Further, we found that grouse were more stressed in open areas (Chapter 3), and grouse generally avoided open areas (Chapter 4). Because we did not find a relationship between temperature and open areas, increased stress in open areas may be due to increased perceived risk of predation (Chapter 3). As stress may represent the combined effects of increased thermoregulatory demands (Chapters 2 and 3) and increased perceived risk of predation (Chapter 3), mapping the landscape of stress, or “stress-scape” may function as a unique visual tool that represents how land cover and dynamic weather conditions influence thermoregulatory demands and risk of predation across the landscape (Chapter 3).

Behavioral flexibility in the use of microrefugia also conferred fitness benefits, but the relationship between habitat selection and snow depth was non-linear, and there was considerable individual variation in the selection of deep snow, which was associated with survival. All individuals were very likely to select habitat with very shallow snow or no snow, but as snow approached 15-20 cm, grouse increasingly avoided deeper snow. When snow depths surpassed 15-20 cm, and snow burrowing behavior became more probable, some individuals flipped their behavior and increasingly selected for deeper snow and were more likely to use snow burrows, while other individuals continued to avoid deeper snow (Chapter 4). The individuals that were more flexible and switched their behavior to seek out deep snow instead of avoiding it were more likely to survive the winter (Chapter 4).

Behavioral flexibility and the use of microrefugia serves to buffer individuals from thermoregulatory stress (Chapter 2) and function as a refuge from predators. We found several lines of evidence that indicate snow burrows protect individuals from predation. Most compellingly, individuals that sought out deep snow and were more likely to use snow burrows were also more likely to survive the winter than individuals that avoided deep snow and did not use snow burrows (Chapter 4). Because almost all mortality was attributed to predation, we conclude that use of microrefugia promotes concealment from predators. Additionally, temperature did not influence the likelihood that grouse would use snow burrows (Chapter 1), indicating that microrefugia may have other functions beyond buffering animals from cold temperatures, such as predator avoidance. Further, grouse were more likely to use snow burrows in open habitats in shallower snow (Chapter 1), and were more stressed in open areas (likely due to an increased perceived risk of predation, Chapter 3), potentially indicating an increased importance of using snow burrows for protection from predators in open habitats where grouse would be more visible when not using snow burrows.

Importantly, we found that tipping points in environmental conditions may exist that alter the ability of overwintering species to use microrefugia, and that influence the relative benefits associated with the use of microrefugia. We found that 15-20 cm of snow depth was an important tipping point for wintering ruffed grouse. As snow depth increased past 15-20 cm, grouse were more likely to use snow burrows (Chapter 1), stress rapidly decreased (Chapter 2), and the individuals that completely flipped their behavior from avoiding deeper snow up to 15 cm, and preferred deeper snow beyond 15 cm, were more likely to survive the winter (Chapter 4). Exposure to deeper snow that approached 15 cm was associated with increased risk of mortality, and individuals uniformly avoided deeper snow that approached 15 cm. These moderate snow depths that are too shallow for burrowing may pose a distinct hazard for wintering grouse and may make them more visible to predators and hinder an escape from an attack (Chapter 4). Thus, deeper snow below 15-20 cm represents a hazard, but once the tipping point is reached, deeper snow becomes an important refuge. Other overwintering species may have their own tipping points, based on factors such as body size, physiology, or predator-prey relationships, which may influence the availability and importance of winter microrefugia. While the availability and use of microrefugia are clearly important for overwintering species, such as the ruffed grouse, and are associated with reduced stress and increased overwinter survival, the loss of snow cover due to anthropogenic climate change may severely limit the use of behavioral flexibility for overwintering species.