

Geographic variation in winter adaptations of snowshoe hares (*Lepus americanus*)

L.C. Gigliotti, D.R. Diefenbach, and M.J. Sheriff

Abstract: Understanding adaptations of nonhibernating northern endotherms to cope with extreme cold is important because climate-induced changes in winter temperatures and snow cover are predicted to impact these species the most. We compared winter pelage characteristics and heat production of snowshoe hares (*Lepus americanus* Erxleben, 1777) on the southern edge of their range, in Pennsylvania (USA), to a northern population, in the Yukon (Canada), to investigate how hares might respond to changing environmental conditions. We also investigated how hares in Pennsylvania altered movement rates and resting spot selection to cope with variable winter temperatures. Hares from Pennsylvania had shorter, less dense, and less white winter coats than their northern counterparts, suggesting lower coat insulation. Hares in the southern population had lower pelage temperatures, indicating that they produced less heat than those in the northern population. In addition, hares in Pennsylvania did not select for resting spots that offered thermal advantages, but selected locations offering visual obstruction from predators. Movement rates were associated with ambient temperature, with the smallest movements occurring at the lower and upper range of observed ambient temperatures. Our results indicate that snowshoe hares may be able to adapt to future climate conditions via changes in pelage characteristics, metabolism, and behavior.

Key words: *Lepus americanus*, snowshoe hare, pelage, winter acclimatization, movement, resource selection.

Résumé : La compréhension des adaptations d'endothermes septentrionaux non hibernants pour composer avec le froid extrême est importante parce qu'il est prédit que ce sont ces espèces qui subiront les impacts les plus importants des variations des températures hivernales et de la couverture nivale induites par le climat. Nous avons comparé les caractéristiques du pelage hivernal et la production de chaleur de lièvres d'Amérique (*Lepus americanus* Erxleben, 1777) à la limite méridionale de leur aire de répartition, en Pennsylvanie (États-Unis), à celles d'une population septentrionale, au Yukon (Canada), pour voir comment les lièvres pourraient réagir aux conditions ambiantes changeantes. Nous avons également examiné comment les lièvres en Pennsylvanie modifient la vitesse de leurs déplacements et la sélection de leurs lieux de repos pour composer avec des températures hivernales variables. Les lièvres de Pennsylvanie présentaient un pelage hivernal plus court, moins dense et moins blanc que celui des individus septentrionaux, ce qui indiquerait une moins grande capacité isolante du pelage. Les lièvres dans la population méridionale présentaient de plus faibles températures du pelage, ce qui indique qu'ils produisaient moins de chaleur que ceux de la population septentrionale. De plus, les lièvres en Pennsylvanie ne choisissaient pas des lieux de repos offrant des avantages thermiques, mais plutôt des lieux offrant des obstacles visuels à la détection par les prédateurs. Les vitesses de déplacement étaient associées à la température ambiante, les déplacements plus courts se produisant dans les fourchettes inférieure et supérieure de températures ambiantes observées. Nos résultats indiquent que les lièvres d'Amérique pourraient être en mesure de s'adapter aux conditions climatiques futures grâce à la modification de caractéristiques de leur pelage, de leur métabolisme et de leur comportement. [Traduit par la Rédaction]

Mots-clés : *Lepus americanus*, lièvre d'Amérique, pelage, acclimatation hivernale, déplacement sélection des ressources.

Introduction

Global climate change is altering winter conditions via changes in temperature and snow cover, and these changes are predicted to become more pronounced in the future (IPCC 2014). Changes in temperature and snow cover have the potential to affect animals by disrupting energy balances (Humphries et al. 2002), phenology (Both et al. 2009; Sheriff et al. 2013), morphology (Høye et al. 2009), the stress axis (Boonstra 2004), reproductive fitness (Ozgul et al. 2010), and population and community dynamics (Both and Visser 2005; Helm et al. 2013). Animals living in the Arctic and Boreal

regions, especially those adapted to survive harsh, cold winters, are particularly vulnerable because these regions are experiencing the greatest changes in winter conditions (Post et al. 2009; IPCC 2014). Understanding variability in responses to winter temperature across a species' range could offer insight into the ability of species to respond to future changes in winter conditions.

During winter in cold climates, nonhibernating endotherms account for heat losses by undergoing changes in their physical condition, physiology, and behavior (Hafez 1965). For example, animals may increase their insulation (Hart 1956; Stokkan 1992;

Received 7 July 2016. Accepted 14 April 2017.

L.C. Gigliotti.* Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, University Park, PA 16802, USA.

D.R. Diefenbach. U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, University Park, PA 16802, USA.

M.J. Sheriff. Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA 16802, USA.

Corresponding author: L.C. Gigliotti (email: lcgigli@clemson.edu).

*Present address: Department of Forestry and Environmental Conservation, 261 Lehotsky Hall, Clemson University, Clemson, SC 29634, USA.

This work is free of all copyright and may be freely built upon, enhanced, and reused for any lawful purpose without restriction under copyright or database law. The work is made available under the [Creative Commons CC0 1.0 Universal Public Domain Dedication](https://creativecommons.org/licenses/by/4.0/) (CC0 1.0).

Langman et al. 2015), reduce their overall winter energy expenditure (Humphries et al. 2005; Sheriff et al. 2009b), and increase their metabolic rate as winter temperatures decrease (Anderson and Jetz 2005). Furthermore, many animals may use behavioral modifications as a means of coping with cold winter temperatures, including reducing activity (Loe et al. 2007) and selecting thermally advantageous microhabitats (Chappell 1980; Litvaitis et al. 1985).

Changing winter conditions may have consequences for animals living in cold northern environments because adaptations that allow animals to endure low winter temperatures may become detrimental (Williams et al. 2014a). Snowshoe hares (*Lepus americanus* Erxleben, 1777) are an excellent species to investigate the potential for species to alter winter adaptations in response to climate change because unlike other small mammals that hibernate, group huddle, or use nests as means of coping with cold temperatures (Pauls 1978; Merritt 1986; Prestrud 1991; Humphries et al. 2005), snowshoe hares remain active on the surface throughout winter and are active at night when temperatures are typically the lowest (Keith 1964; Feierabend and Kielland 2014). Thus, they experience the coldest of winter temperatures. Snowshoe hares also have well-documented morphological and physiological adaptations to cope with winter, such as an increase in pelage density (in addition to their coat color change), and a downregulation of their metabolic rate (Sheriff et al. 2009a, 2009b). Lastly, hares have a very broad geographic range which permits exploration and comparison of winter adaptations from populations that experience very different winter conditions.

In this study, we tested the hypothesis that the winter adaptations of snowshoe hares differ across their range. Comparing a southern population of snowshoe hares in Pennsylvania, USA, near the southern edge of their range, with a northern population in the Yukon, Canada, we predicted that (i) southern hares would have shorter and less dense winter pelage than northern hares, (ii) southern hares would have lower winter heat production than northern hares, as indicated by their pelage temperature, (iii) snowshoe hares would select for resting locations that offer a thermal advantage during winter to cope with low winter temperatures, and (iv) snowshoe hares would decrease their movement rates at extreme low and high temperatures.

Materials and methods

Study area

The study area in Pennsylvania encompassed approximately 4050 ha near Long Pond, Pennsylvania (41°02'N, 75°25'W). The majority of the study area was dominated by xeric oak stands; however, historical changes in fire regimes also resulted in areas with a mosaic of mesic till barrens dominated by mature scrub oak (*Quercus ilicifolia* Wangenh.) >2 m tall and pitch pine (*Pinus rigida* Mill.). Dominant understory species included blueberry (species of the genus *Vaccinium*L.), rhodora (*Rhododendron canadense* (L.) Torr.), eastern teaberry (*Gaultheria procumbens* L.), and sheep laurel (*Kalmia angustifolia* L.). Planted stands of mature Norway spruce (*Picea abies* (L.) Karst.), red pine (*Pinus resinosa* Aiton), and European larch (*Larix decidua* Mill.) made up a small portion of the study area. From January to March of 2014 and 2015, temperatures fluctuated from a mean daily minimum of -11.8 °C to a mean daily maximum of 0.8 °C.

The study area in the Yukon was conducted in the southwestern part of the Kluane region (60°57'N, 138°12'W). The Yukon study area was a boreal forest dominated by white spruce (*Picea glauca* (Moench) Voss) and understory species including gray willow (*Salix glauca* L.), bog birch (*Betula glandulosa* Michx.), soapberry (*Shepherdia canadensis* (L.) Nutt.), and herbaceous plants. From January to March of 2007, the temperature ranges from a mean daily minimum of -26.7 °C to a mean daily maximum of -2.3 °C.

Capture and handling

We trapped in Pennsylvania from January to August 2014 and from January to June 2015 using Tomahawk live traps (Tomahawk Live Trap Company, Hazelhurst, Wisconsin, USA) baited with apples and alfalfa cubes. Upon capture, we recorded sex, body mass, right hind-foot length (RHF), and coat color. We uniquely marked newly caught hares using passive integrated transponder (PIT) tags (Biomark, Inc., Boise, Idaho, USA) inserted under the skin near the right shoulder blade and with numbered Monel ear tags placed on the right ear (National Tag and Band Co., Newport, Kentucky, USA). We fitted hares >900 g in body mass with a VHF transmitter (model M1555, Advanced Telemetry Systems, Isanti, Minnesota, USA), or a GPS collar equipped with a VHF transmitter (model UltraLITE G10, Advanced Telemetry Systems, Isanti, Minnesota, USA; model 150mAh SnapTraX Pathfinder, Skorpa Telemetry, Aberfeldy, Scotland), set to record locations every 20 min. Animal protocols were approved by The Pennsylvania State University Institutional Animal Care and Use Committee (protocol No. 43476), and after the completion of the study, we removed collars whenever we were able to recapture a hare. We also trapped snowshoe hares in the Yukon in March 2007, but these hares were not collared (for details see Sheriff et al. 2009a, 2009b).

Pelt characteristics

To estimate differences in pelt characteristics between southern and northern populations, we measured hair length and density, as well as the amount of visible white coloration in coats, of a sample of hares in winter prior to the spring molt. We cut pelts approximately 12 cm × 12 cm in size from the dorsal portion of hares in Pennsylvania during winter (January–March) and mounted them on wooden boards ($n = 7$). We used pelts in good condition and from hares deceased <24 h prior to collection. We removed 12 guard and 12 downy hairs from each pelt at the skin's surface and measured their length under a dissecting scope. We then shaved the hairs on the pelt to 0.5 mm and measured density (number of hairs/cm²) of guard and downy hairs in a 1 cm² area under a dissecting scope. The same data were collected from the winter pelts of six snowshoe hares at the Yukon site in March 2007. To illustrate differences in seasonal coat characteristics, we used autumn pelage data from the Yukon site in October 2007.

To determine the proportion of white hairs in the winter pelage of snowshoe hares, we photographed 3 cm² areas on the preserved pelts from both southern and northern populations using a 12.1 megapixel Canon PowerShot SX130 camera. We converted the pelage photos to binary pixels and calculated the percentage of visible white using program ImageJ (Rasband 1997–2016).

Pelage temperature

To investigate geographic differences in heat flux of snowshoe hares, we measured the temperature of the pelage surface (T_p) by attaching iButton® temperature sensors (model DS1921G-F5, Maxim Integrated Products Inc., San Jose, California, USA) to the GPS collars of eight snowshoe hares from the Pennsylvania population and six hares from the Yukon population. The sensors were placed on 4 cm tabs that rested directly on the pelage between the shoulder blades of the hare. The sensors recorded temperature every hour and represent an indirect measure of heat production because the sensors were influenced by heat produced by the hares, the pelage insulative values, and the ambient temperature (T_a). Given that T_p was compared at the same T_a between the two sites, T_p is only influenced by the heat produced by the hare and pelage insulative value. This method has been used previously in a variety of taxa (Dausmann 2005; Langer and Fietz 2014) and by ourselves (Sheriff et al. 2009b). We calibrated the iButtons prior to deployment by comparing measurements to known temperature conditions.

Temperatures of the pelage surface (T_p) data were collected during January–March 2015 in Pennsylvania ($n = 8$) and March 2007 in

the Yukon ($n = 6$). To compare differences in T_p between Pennsylvania and Yukon populations, we binned T_a by 5 °C increments and calculated the mean T_p for each range. We only compared T_p between populations for shared temperature categories.

Resting spot selection

To assess whether snowshoe hares selected resting spots based on structural or thermal characteristics, we identified clusters of GPS locations from the Pennsylvania population where individual hares rested, i.e., successive GPS locations that spanned ≥ 1 h and were ≤ 10 m apart. Because the location error of the GPS collars is approximately 10 m in all habitat types (Feierabend and Kielland 2014; L.C. Gigliotti, unpublished data), our selected distance of 10 m is the shortest distance that we could identify as a cluster with the available technology. We analyzed GPS locations and extracted cluster locations using the Space Time Permutation Scan Statistic (STPSS) in the program SaTScan (Kulldorff et al. 2005). To account for potential temporal differences in resting spot selection, we used identified resting spots from both night ($n = 42$) and day ($n = 53$). We did not conduct this analysis on the Yukon population.

To characterize the thermal characteristics of resting spots versus random locations, we randomly selected 24 resting spots and 28 random locations and deployed iButton® temperature sensors programmed to measure temperature every 2 h. The iButtons® were placed in unsealed plastic bags and suspended approximately 25 cm above the ground. Although hares will often hide under logs or in low vegetation (Hodges and Sinclair 2005), we felt that this distance still offered an accurate measurement of the resting spot temperature. We used a Student's t test ($\alpha = 0.05$) to identify differences in daily minimum, maximum, and mean temperatures between identified resting and random locations.

To characterize the vegetation characteristics of resting spots versus random locations, we selected 95 snowshoe hare resting spots and 378 randomly selected locations. Ten metres from the sampling location, we measured horizontal understory density using a vegetation profile board in each cardinal direction (Nudds 1977). We categorized understory density into three classes based on coverage of the board (low = 0%–20%; medium = 21%–80%; high = 81%–100%) and estimated total understory density by averaging the density measurements of all four directions. We estimated canopy cover using Gap Light Analyzer version 2.0 (Institute of Ecosystem Studies, Millbrook, New York, USA) from a hemispherical photo taken directly overhead of the center point.

To identify structural characteristics for Pennsylvania snowshoe hare resting locations, we developed a logistic regression resource selection function in which we compared the characteristics of used resting locations with the characteristics of a random sample of available locations. We developed models that included canopy cover and total understory cover as covariates. We compared models using Akaike's information criterion (AIC; Burnham and Anderson 2002) and models within 2 AIC of the top model were considered to be competitive. We chose to conduct this analysis separate of our resting location temperature analysis because vegetation remains relatively fixed over the course of a season, whereas temperature fluctuates regularly. Because resting locations were determined retroactively, we were not able to collect a temperature measurement at the same time the hare used the resting location.

Movement rates

To investigate the potential for snowshoe hares to alter behavior based on thermal factors, we calculated the distance that individual hares in Pennsylvania moved between successive locations. We did not conduct this analysis on the Yukon population. We summed the distance moved per hour and excluded any time periods with missing locations. For each distance, we deter-

mined the T_a , hourly precipitation, and wind speed using data from a weather station approximately 5 km from the study area.

Consistent with other studies (Hodges 1999; Feierabend and Kielland 2014), movement rates based on time of day indicated that snowshoe hares were nocturnal with minimal movement between the hours of 0600 and 1600. Therefore, we used nighttime movements that were defined as occurring after sunset and before sunrise. Because environmental factors such as precipitation and wind speed alter the movement patterns of mammals (Vickery and Bider 1981; Beier and McCullough 1990), we excluded data when wind speed was ≥ 7 miles/h (≥ 11.26 km/h) and no precipitation was recorded. We chose 7 miles/h (11.26 km/h) as our cut-off point because this represented the top 20% of observed wind speeds and based on the Beaufort wind scale excludes any wind above a light breeze. Contrary to other studies (Gilbert and Boutin 1991; Griffin et al. 2005), moon phase did not affect snowshoe hare movement rates (L.C. Gigliotti, unpublished data), and all moon phases were included in the movement analysis.

We specified four models that could explain the relationship between temperature and movement based on energetic principles for Pennsylvania hares. The models we considered were an intercept-only model, a linear model, a quadratic temperature model, a third-order temperature model, and a fourth-order temperature model. We compared models using AIC (Burnham and Anderson 2002) and models within 2 AIC of the top model were considered to be competitive.

Results

Pelt characteristics

Winter pelage characteristics differed between hares from Pennsylvania and Yukon (Figs. 1a–1d). Guard hairs were 32% less dense in Pennsylvania hares (95.42 ± 13.45 hairs/cm²; mean \pm SE) than Yukon hares (141.50 ± 21.41 hairs/cm²; $t_{[11]} = 1.88$, $P = 0.087$) and 20% shorter in Pennsylvania hares (34.57 ± 1.35 mm) than Yukon hares (43.19 ± 0.69 mm; $t_{[11]} = 5.4$, $P < 0.001$). Similarly, downy hairs were 58% less dense in Pennsylvania hares (3295.14 ± 95.73 hairs/cm²) than Yukon hares (7788.83 ± 266.63 hairs/cm²; $t_{[11]} = 16.88$, $P < 0.001$) and 23% shorter in Pennsylvania hares (19.76 ± 0.76 mm) than Yukon hares (25.64 ± 0.38 mm; $t_{[11]} = 6.51$, $P < 0.0001$). In addition, pelage samples from Pennsylvania hares ($n = 7$) were, on average, $83.05\% \pm 3.88\%$ white compared with samples from Yukon hares ($n = 4$) that were, on average, $99.09\% \pm 0.50\%$ white ($t_{[9]} = -3.05$, $P = 0.014$).

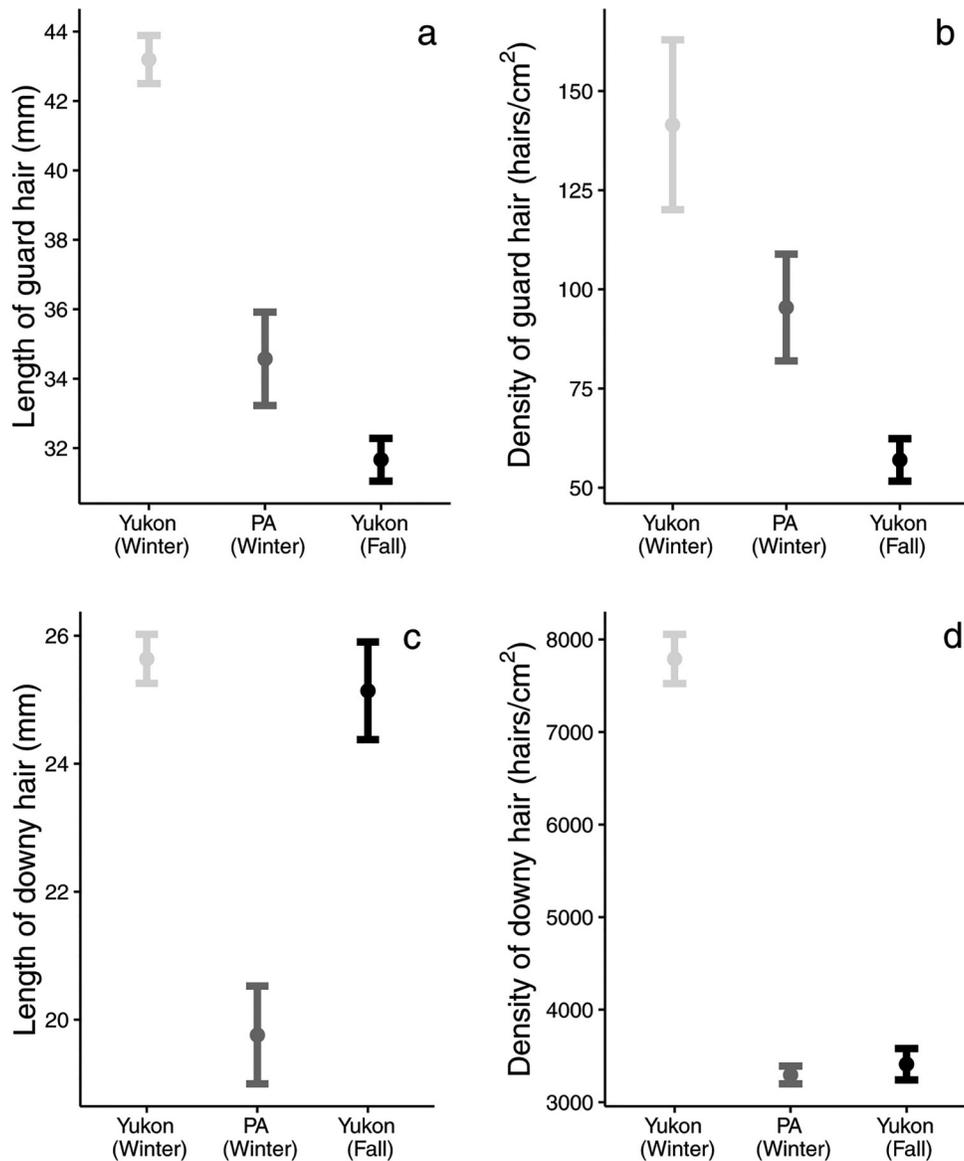
Pelage temperature

Pelage temperature differed between hares from Pennsylvania and the Yukon (Fig. 2). The T_p of Pennsylvania hares averaged 9.33 ± 0.07 °C (mean \pm SE) warmer than T_a , whereas the T_p of Yukon hares averaged 18.4 ± 0.2 °C warmer than T_a . Interestingly, changes in T_p of the Pennsylvania population were not proportional to changes in T_a , and for every 5 °C decrease in T_a , T_p decreased 3.5 °C. In contrast, in Yukon hares, T_p changed relatively proportional to changes in T_a , maintaining an approximate 18 °C difference until T_a dropped below -20 °C, at which point there was an upward acceleration of $T_p - T_a$ differentials such that T_p rarely dropped below -10 °C even though $T_a < -28$ °C was not uncommon.

Resting spot selection

Snowshoe hares did not select resting locations based on thermal characteristics. Resting spots had mean (\pm SE) daily maximum temperatures of 0.92 ± 0.13 °C, whereas random locations had mean (\pm SE) daily maximum temperatures of 0.76 ± 0.13 °C ($t_{[7124]} = 0.41$, $P = 0.68$). Resting spots had mean (\pm SE) daily minimum temperatures of -11.95 ± 0.15 °C, whereas random locations had mean (\pm SE) daily minimum temperatures of -11.61 ± 0.14 °C ($t_{[7124]} = 1.08$, $P = 0.28$). Finally, resting spots had daily mean (\pm SE) temperatures of -5.94 ± 0.12 °C, whereas random locations had daily mean (\pm SE) temperatures of -5.86 ± 0.11 °C ($t_{[7124]} = 0.08$, $P = 0.94$).

Fig. 1. Pelage characteristics of snowshoe hares (*Lepus americanus*) from Yukon, Canada, in winter ($n = 6$) and autumn ($n = 6$) and from Long Pond, Pennsylvania (PA), USA, in winter ($n = 7$): guard hair length (a), guard hair density (b), downy hair length (c), and downy hair density (d). Values are means \pm SE.



Snowshoe hares selected resting locations based on canopy cover and understory density (Table 1). Resting spots had a mean (\pm SE) canopy cover of $64.19\% \pm 1.73\%$, whereas random locations had a mean (\pm SE) canopy cover of $53.51\% \pm 1.04\%$ ($t_{[472]} = 5.29$, $P < 0.001$). Resting spots were 1.6 times more likely to occur in high understory density (>81% coverage) compared with medium understory density (21%–80% coverage) and hares did not rest in areas of low understory density (<20% coverage; $t_{[472]} = 4.42$, $P < 0.001$).

Movement rates

Although there was variability in movement rates, the nighttime winter movement rates of snowshoe hares in Pennsylvania were related to T_a and were best described by a fourth-order interaction with temperature ($n = 1797$; Fig. 3, Table 2). Across all temperatures, the mean (\pm SE) hourly distance moved was 191.3 ± 3.2 m, although movement changed with temperature. Movement rates remained relatively constant below -10 °C and averaged 160.1 ± 4.8 m/h (mean \pm SE). Rates increased linearly between -10 and 3 °C by 6.9 ± 1.1 m/h for every 1 °C increase in T_a to a maximum rate of

264.8 ± 51.7 m/h at 3 °C. Rates decreased above 3 °C by 17.3 ± 10.7 m/h for every 1 °C increase in T_a to a minimum of 102.7 ± 20.1 m/h at 8 °C.

Discussion

Snowshoe hares exhibited variability in winter adaptations in different areas of their range, suggesting the potential to respond to future changing winter conditions. Hares near the southern edge of their range exhibited shorter and less dense winter pelage, were more variable in color, and produced less heat than hares from a northern population. Also, we found that hares did not select resting spots that offered thermal advantages, but preferred those that provided visual cover. Finally, we found that snowshoe hare movement rates were related to T_a .

Physical characteristics

Hares in Pennsylvania had shorter and less dense winter pelage compared with hares from the Yukon (Figs. 1a–1d), reducing their

Fig. 2. Pelage temperature (T_p) as a function of ambient temperature (T_a) for snowshoe hares (*Lepus americanus*) from Yukon, Canada, ($n = 6$) and from Long Pond, Pennsylvania, USA, ($n = 8$). Values are means \pm SE.

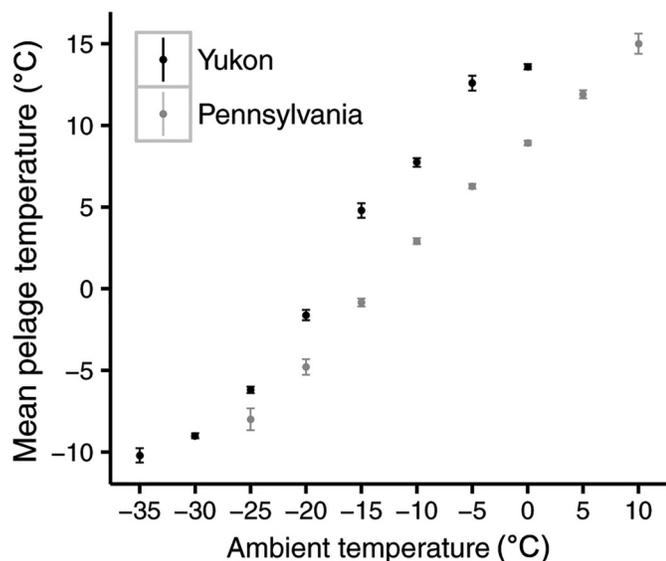


Table 1. Model selection results for characteristics of snowshoe hare (*Lepus americanus*) winter resting spots in Long Pond, Pennsylvania, USA.

Model	Δ AIC	$-2 \times \ln(L)^a$	Model likelihood	w^b	k^c
Canopy cover + understory density	0.00	440.04	1.00	0.95	5
Canopy cover	5.87	451.91	0.05	0.05	2
Understory density	19.20	461.24	<0.01	<0.01	4
Intercept only	26.45	474.49	<0.01	<0.01	1

^aLog-likelihood.

^bAkaike model weight.

^cNumber of model parameters.

insulation (Hart et al. 1965) with higher winter temperatures near the southern edge of their range. In addition to warmer overall winter temperatures, southern hares also face greater potential to have long warm periods throughout winter, and reduced insulation is likely beneficial because it reduces the potential for heat stress. However, even with their reduced insulation, during warm periods (≥ 3 °C), hares greatly reduced their movement (Fig. 3). Although we did not directly measure the potential for hares to overheat during the winter, heat stress has been measured in other cold-acclimatized mammals such as arctic reindeer (*Rangifer tarandus* (L., 1758)) (Blix et al. 2011) and pygmy rabbits (*Brachylagus idahoensis* (Merriam, 1891)) (Katzner et al. 1997). Arctic reindeer, which have well-insulated winter coats, increase their respiration and carotid blood flow during periods of high T_a (Blix et al. 2011). We suggest that a decrease in winter pelage density may be one way that snowshoe hares can adapt to climate-induced increases in winter temperatures.

We found that Pennsylvania hares exhibited greater variability in winter coat coloration than Yukon hares. This may be caused by two nonexclusive adaptations. First, southern hares may not completely molt into their winter coats. During January 2014 and 2015, we trapped three snowshoe hares in Pennsylvania that exhibited complete brown winter coat coloration, with the exception of white coloration on their ears, feet, and around their noses, suggesting neuro-endocrine pathways that control the fall molt have been disrupted so that the hares remained in their brown summer coat (Gigliotti 2016). We were not able to measure pelage characteristics of brown-morph winter hares to determine if they had

similar characteristics as white winter hares or were more similar to summer hares. Second, the shift to a brown phenotype at southern latitudes may be in response to predation risk in an environment with variable snow cover. Being mismatched with the environment, such as a pure white hare on a brown substrate, may increase the likelihood of death, thus driving selection for a mottled pelage. Zimova et al. (2016) found that hares experiencing coat mismatch with their surroundings had weekly survival rates 4%–7% lower than non-mismatched hares. Other populations of snowshoe hares in the Cascade Mountains exhibit polymorphic winter coloration, which is thought to be beneficial for crypsis due to the lack of snow cover during most winters (Dalquest 1942; Nagorsen 1983). Further research is needed to understand the influence of both increasing winter temperatures and predation risk on coat coloration.

Physiological characteristics

The T_p of Pennsylvania snowshoe hares was much lower than that of Yukon hares for any given T_a (Fig. 2), combined with the fact that Pennsylvania hares had lower insulative values of their pelage suggests that southern hares produced less heat. Although we did not directly measure metabolic rate, heat production is known to be correlated with metabolic rate (Bakken 1976); thus, we suggest that southern hares also have a lower winter metabolic rate than their northern counterparts. A lower metabolic rate may be advantageous because it would reduce the potential for heat stress in warmer southern winters, which are regularly above 0 °C, and would decrease energy expenditure during the food-limited winter. Pennsylvania hares also respond by increasing their heat production to decreasing winter temperatures much earlier than their northern counterparts (Sheriff et al. 2009b). We found that $T_p - T_a$ differentials of Pennsylvania hares increased from 8.9 °C at a T_a of 0 °C to 17.0 °C at a T_a of -25 °C, whereas Yukon hares do not begin to increase their $T_p - T_a$ differentials until T_a decreases below -20 °C (Fig. 2). Thus, we suggest that hares facultatively exhibit differences in physiological adaptations to deal with different winter conditions across their range.

Behavioral characteristics

Resting spot selection

Snowshoe hares did not select thermally advantageous resting locations as predicted, but rather selected locations based on structural cover. The greater canopy and understory cover at resting spots may have provided a number of advantages other than thermal refugia. First, areas of dense cover offer visual protection from avian and mammalian predators, and it has been shown that hares in these areas have higher survival rates (Sievert and Keith 1985). Predation is the major source of hare mortality (Krebs et al. 1995), and as such, protection from predators is critical. Second, high understory density likely provides greater food resources for hares. During winter, hares need to constantly feed due to the low caloric content of woody browse (Pease et al. 1979; Bryant and Kuropat 1980; Sinclair et al. 1982). Third, the selected resting spots may also offer protection from other environmental stressors such as wind and precipitation, which can increase energy loss because of their effect on the insulative ability of their coat. Given that hares did not select areas with higher T_a suggests that temperature is not the driving factor in microhabitat selection, and at least in southern populations, protection from predators and increased food availability may be more important.

Movement rates

We found that nighttime mean (\pm SE) hourly movement rates were 191.3 ± 3.2 m/h (Fig. 3). Because hares must consume approximately 300 g of forage per 24 h during winter (Pease et al. 1979), we suggest that movement rates are associated primarily with feeding. However, the patterns we observed with winter movement rates suggest that hares responded to changing T_a (Fig. 3). At

Fig. 3. Snowshoe hare (*Lepus americanus*) winter hourly movement rates across various winter ambient temperatures (T_a) based on the best-fit (fourth-order) model in Long Pond, Pennsylvania, USA. Shaded area represents 85% confidence interval around the best-fit model.

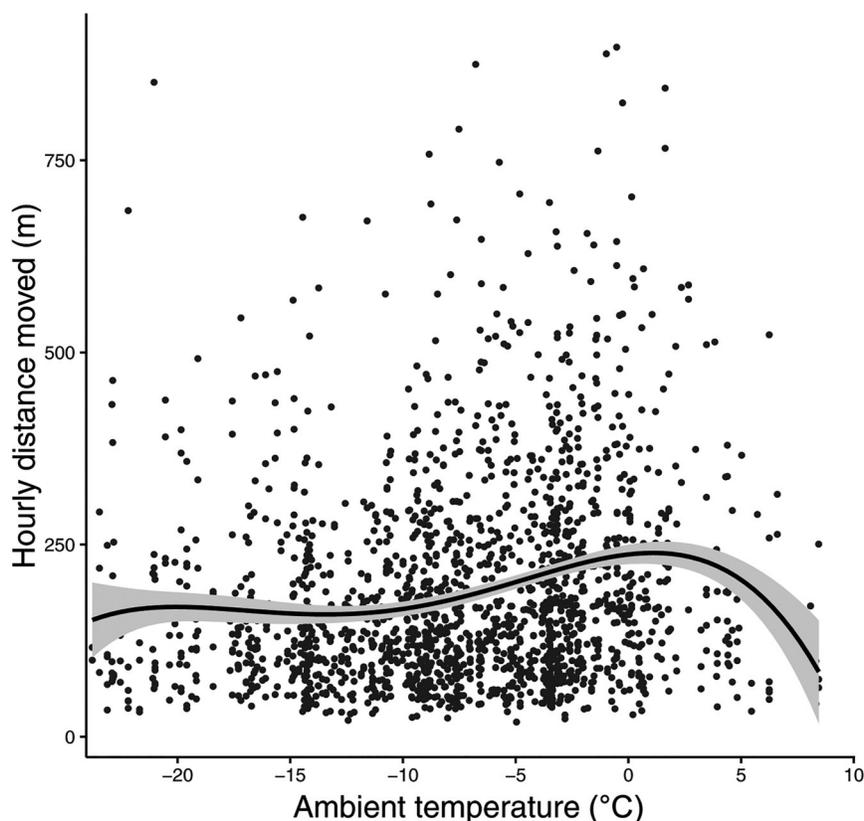


Table 2. Model selection results for modelling the influence of winter ambient temperature on snowshoe hare (*Lepus americanus*) hourly movement rates in Long Pond, Pennsylvania, USA.

Model	ΔAIC	$-2 \times \ln(L)^a$	Model likelihood	w^b	k^c
Fourth-order temperature	0.00	22676	1.00	0.99	5
Third-order temperature	9.00	22687	0.01	0.01	4
Linear temperature	28.00	22710	<0.01	<0.01	2
Quadratic temperature	29.00	22709	<0.01	<0.01	3
Intercept only	73.00	22757	<0.01	<0.01	1

^aLog-likelihood.

^bAkaike model weight.

^cNumber of model parameters.

$T_a > -10$ °C, hares had low movement rates (160.1 ± 4.8 m/h), possibly caused by the need to forage despite the loss of thermal protection. During the winter, hares only have enough fat and protein reserves to last approximately 4 days, so foraging is critical regardless of the temperature (Whittaker and Thomas 1983). Below -25 °C, hares appeared to reduce movement rates, although our data are not sufficient to statistically test this; possibly at this very low T_a , the loss of thermal microhabitat outweighs the benefits of feeding. As T_a increased from -10 to 3 °C, hare movement rates also increased linearly to a maximum rate of 264.8 ± 51.7 m/h, but sharply decreased thereafter to a minimum of 102.7 ± 20.1 m/h at 8 °C (the warmest measured nightly temperature). At these extremely warm temperatures (>3 °C), hares may need to forage little and may reduce movements to minimize their exposure to predators. Additionally, hares may become heat stressed above 3 °C and may reduce movement to decrease heat production. Red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)) reduce their activity at low T_a (Humphries et al. 2005), whereas arctic ground squirrels (*Urocyon parryi* (Richardson, 1825)) reduce their

activity at both extremely low and high T_a (Williams et al. 2014b). In a variable winter climate, altering activity patterns and movement rates may provide a flexible adaptation to temperature regulation.

Conclusions

The physical and physiological characteristics of snowshoe hares differ greatly across their range and our study offers insight into potential coping mechanisms as winter temperatures warm. A reduction in pelage insulation and heat production provides a coping mechanism for warmer and more variable winter temperatures, particularly extended warm periods. Additionally, behavioral plasticity may be a means for hares to cope with variable winter T_a and may be useful as a flexible means of temperature regulation. Although, we recognize that our two-population comparison limits our ability to draw concrete conclusions about the driving forces behind our observed differences in winter adaptations, we suggest that hares have a suite of mechanisms that may allow them to cope with changing winter temperatures. A better understanding of the plasticity of these mechanisms is critical and future range-wide studies could provide additional insight.

Acknowledgements

We thank D. O'Leary, B. Smith, R. Ritson, R. Scavotto, and D. Snyder who helped with the data collection for this research, as well as numerous individuals from the Pennsylvania Game Commission, Bethlehem Water Authority, and The Nature Conservancy who were involved with the implementation and support of this research. We also thank R. Boonstra for providing comments that improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Anderson, K.J., and Jetz, W. 2005. The broad-scale ecology of energy expenditure of endotherms. *Ecol. Lett.* **8**(3): 310–318. doi:10.1111/j.1461-0248.2005.00723.x
- Bakken, G.S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* **60**(2): 337–384. doi:10.1016/0022-5193(76)90063-1. PMID:957719.
- Beier, P., and McCullough, D.R. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildl. Monogr.* **109**: 3–51. Available from <http://www.jstor.org/stable/3830629>.
- Blix, A.S., Walloe, L., and Folkow, L.P. 2011. Regulation of brain temperature in winter-acclimatized reindeer under heat stress. *J. Exp. Biol.* **214**: 3850–3856. doi:10.1242/jeb.057455. PMID:22031750.
- Boonstra, R. 2004. Coping with changing northern environments: the role of the stress axis in birds and mammals. *Integr. Comp. Biol.* **44**(2): 95–108. doi:10.1093/icb/44.2.95. PMID:21680490.
- Both, C., and Visser, M.E. 2005. The effect of climate change on the correlation between avian life-history traits. *Global Change Biol.* **11**(10): 1606–1613. doi:10.1111/j.1365-2486.2005.01038.x.
- Both, C., van Asch, M., Bijlsma, R.G., van den Burg, A.B., and Visser, M.E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim. Ecol.* **78**(1): 73–83. doi:10.1111/j.1365-2656.2008.01458.x. PMID:18771506.
- Bryant, J.P., and Kuropat, P.J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annu. Rev. Ecol. Syst.* **11**(1): 261–285. doi:10.1146/annurev.es.11.110180.001401.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media. Available from <https://books.google.com/books?hl=en&lr=&id=fT1lu-h6E-oC&pgis=1> [accessed 29 April 2015].
- Chappell, M.A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. *J. Mammal.* **61**(2): 278–291. doi:10.2307/1380049.
- Dalquest, W.W. 1942. Geographic variation in northwestern snowshoe hares. *J. Mammal.* **23**(2): 166–183. doi:10.2307/1375069.
- Dausmann, K.H. 2005. Measuring body temperature in the field — evaluation of external vs. implanted transmitters in a small mammal. *J. Therm. Biol.* **30**(3): 195–202. doi:10.1016/j.jtherbio.2004.11.003.
- Feierabend, D., and Kielland, K. 2014. Movements, activity patterns, and habitat use of snowshoe hares (*Lepus americanus*) in interior Alaska. *J. Mammal.* **95**(3): 525–533. doi:10.1644/13-MAMM-A-199.
- Gigliotti, L.C. 2016. Ecology, habitat use, and winter thermal dynamics of snowshoe hares in Pennsylvania. M.S. thesis, The Pennsylvania State University, University Park.
- Gilbert, B.S., and Boutin, S. 1991. Effect of moonlight on winter activity of snowshoe hares. *Arct. Antarct. Alp. Res.* **23**(1): 61–65. doi:10.2307/1551438.
- Griffin, P.C., Griffin, S.C., Waroquiers, C., and Mills, L.S. 2005. Mortality by moonlight: predation risk and the snowshoe hare. *Behav. Ecol.* **16**(5): 938–944. doi:10.1093/beheco/ari074.
- Hafez, E.S.E. 1965. Behavioral thermoregulation in mammals and birds. *Int. J. Biometeorol.* **7**(3): 231–240. doi:10.1007/BF02187455.
- Hart, J.S. 1956. Seasonal changes in insulation of the fur. *Can. J. Zool.* **34**(1): 53–57. doi:10.1139/z56-007.
- Hart, J.S., Pohl, H., and Tener, J.S. 1965. Seasonal acclimatization in varying hare (*Lepus americanus*). *Can. J. Zool.* **43**(5): 731–744. doi:10.1139/z65-077. PMID:5829174.
- Helm, B., Ben-Shlomo, R., Sheriff, M.J., Hut, R.A., Foster, R., Barnes, B.M., and Dominoni, D. 2013. Annual rhythms that underlie phenology: biological time-keeping meets environmental change. *Proc. R. Soc. B Biol. Sci.* **280**: 20130016. doi:10.1098/rspb.2013.0016.
- Hodges, K.E. 1999. Proximate factors affecting snowshoe hare movements during a cyclic population low phase. *Ecoscience*, **6**(4): 487–496. doi:10.1080/11956860.1999.11682558.
- Hodges, K.E., and Sinclair, A.R.E. 2005. Browse site selection by snowshoe hares: effects of food supply and predation risk. *Can. J. Zool.* **83**(2): 280–292. doi:10.1139/z05-015.
- Høye, T.T., Hammel, J.U., Fuchs, T., and Toft, S. 2009. Climate change and sexual size dimorphism in an Arctic spider. *Biol. Lett.* **5**: 542–544. doi:10.1098/rsbl.2009.0169. PMID:19435831.
- Humphries, M.M., Thomas, D.W., and Speakman, J.R. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature*, **418**(6895): 313–316. doi:10.1038/nature00828. PMID:12124621.
- Humphries, M.M., Boutin, S., Thomas, D.W., Ryan, J.D., Selman, C., McAdam, A.G., Berteaux, D., and Speakman, J.R. 2005. Expenditure freeze: the metabolic response of small mammals to cold environments. *Ecol. Lett.* **8**(12): 1326–1333. doi:10.1111/j.1461-0248.2005.00839.x.
- Intergovernmental Panel on Climate Change (IPCC). 2014. Climate change 2014: impacts, adaptation, and vulnerability. Cambridge University Press, Cambridge, UK, and New York, N.Y., USA. Available from <http://www.ipcc.ch/report/ar5/wg2/>.
- Katzner, T.E., Parker, K.L., and Harlow, H.H. 1997. Metabolism and thermal response in winter-acclimatized pygmy rabbits (*Brachylagus idahoensis*). *J. Mammal.* **78**(4): 1053–1062. doi:10.2307/1383048.
- Keith, L.B. 1964. Daily activity pattern of snowshoe hares. *J. Mammal.* **45**(4): 626–627. doi:10.2307/1377333.
- Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K., and Turkington, R. 1995. Impact of food and predation on the snowshoe hare cycle. *Science*, **269**: 1112–1115. doi:10.1126/science.269.5227.1112.
- Kulldorff, M., Heffernan, R., Hartman, J., Assunção, R., and Mostashari, F. 2005. A space-time permutation scan statistic for disease outbreak detection. *PLoS Med.* **2**(3): 216–224. doi:10.1371/journal.pmed.0020059. PMID:15719066.
- Langer, F., and Fietz, J. 2014. Ways to measure body temperature in the field. *J. Therm. Biol.* **42**(1): 46–51. doi:10.1016/j.jtherbio.2014.03.002. PMID:24802148.
- Langman, V.A., Langman, S.L., and Ellifrit, N. 2015. Seasonal acclimatization determined by non-invasive measurements of coat insulation. *Zool Biol.* **34**(4): 368–373. doi:10.1002/zoo.21219. PMID:26087320.
- Litvaitis, J.A., Sherburne, J.A., and Bissonette, J.A. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. *J. Wildl. Manage.* **49**(4): 866–873. doi:10.2307/3801359.
- Loe, L.E., Bonenfant, C., Mysterud, A., Severinsen, T., Oritsland, N.A., Langvatn, R., Stien, A., Irvine, R.J., and Stensth, N.C. 2007. Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm. *Oecologia*, **152**(4): 617–624. doi:10.1007/s00442-007-0681-7. PMID:17370092.
- Merritt, J.F. 1986. Winter survival adaptations of the short-tailed shrew (*Blarina brevicauda*) in an Appalachian montane forest. *J. Mammal.* **67**(3): 450–464. doi:10.2307/1381276.
- Nagorsen, D.W. 1983. Winter pelage colour in snowshoe hares (*Lepus americanus*) from the Pacific Northwest. *Can. J. Zool.* **61**(10): 2313–2318. doi:10.1139/z83-305.
- Nudds, T.D. 1977. Quantifying the vegetation structure of wildlife cover. *Wildl. Soc. Bull.* **5**: 113–117.
- Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E., Tuljapurkar, S., and Coulson, T. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, **466**(7305): 482–485. doi:10.1038/nature09210. PMID:20651690.
- Pauls, R.W. 1978. Behavioural strategies relevant to energy economy of the red squirrel (*Tamiasciurus hudsonicus*). *Can. J. Zool.* **56**: 1519–1525. doi:10.1139/z78-210.
- Pease, J.L., Vowles, R.H., and Keith, L.B. 1979. Interaction of snowshoe hares and woody vegetation. *J. Wildl. Manage.* **43**(1): 43–60. doi:10.2307/3800634.
- Post, E., Forchhammer, M.C., Bret-Harte, D.S., Callaghan, T.V., Christiansen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., and Aastrup, P. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science*, **325**: 1355–1358. doi:10.1126/science.1173113.
- Prestrud, P. 1991. Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. *Arctic*, **44**(2): 132–138. doi:10.2307/40511073.
- Rasband, W.S. 1997–2016. ImageJ. U.S. National Institutes of Health, Bethesda, Md. Available from <https://imagej.nih.gov/ij/>.
- Sheriff, M.J., Kuchel, L., Humphries, M.M., and Boutin, S. 2009a. Seasonal metabolic acclimatization in a northern population of free-ranging snowshoe hares, *Lepus americanus*. *J. Mammal.* **90**(3): 761–767. doi:10.1644/08-MAMM-A-247R.1.
- Sheriff, M.J., Speakman, J.R., Kuchel, L., Boutin, S., and Humphries, M.M. 2009b. The cold shadow: free-ranging snowshoe hares maintain a low cost of living in cold climates. *Can. J. Zool.* **87**(10): 956–964. doi:10.1139/Z09-087.
- Sheriff, M.J., Richter, M.M., Buck, C.L., and Barnes, B.M. 2013. Changing seasonality and phenological responses of free-living male arctic ground squirrels: the importance of sex. *Philos. Trans. R. Soc. B Biol. Sci.* **368**: 20120480. doi:10.1098/rstb.2012.0480.
- Sievert, P.R., and Keith, L.B. 1985. Survival of snowshoe hares at a geographic range boundary. *J. Wildl. Manage.* **49**(4): 854–866. doi:10.2307/3801358.
- Sinclair, A.R.E., Krebs, C.J., and Smith, J.N.M. 1982. Diet quality and food limitation in herbivores: the case of the snowshoe hare. *Can. J. Zool.* **60**(5): 889–897. doi:10.1139/z82-121.
- Stokkan, K.A. 1992. Energetics and adaptations to cold in ptarmigan in winter. *Ornis Scand.* **23**(3): 366–370. doi:10.2307/3676662.
- Vickery, W.L., and Bider, J.R. 1981. The influence of weather on rodent activity. *J. Mammal.* **62**(1): 140–145. doi:10.2307/1380484.
- Whittaker, M.E., and Thomas, V.G. 1983. Seasonal levels of fat and protein reserves of snowshoe hares in Ontario. *Can. J. Zool.* **61**(6): 1339–1345. doi:10.1139/z83-180.
- Williams, C.M., Henry, H.A.L., and Sinclair, B.J. 2014a. Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biol. Rev. Camb. Philos. Soc.* **90**: 214–235. doi:10.1111/brv.12105. PMID:24720862.
- Williams, C.T., Wilsterman, K., Kelley, A.D., Breton, A.R., Stark, H., Humphries, M.M., McAdam, A.G., Barnes, B.M., Boutin, S., and Buck, C.L. 2014b. Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents. *J. Mammal.* **95**(6): 1230–1239. doi:10.1644/14-MAMM-A-062.
- Zimova, M., Mills, L.S., and Nowak, J.J. 2016. High fitness costs of climate change-induced camouflage mismatch. *Ecol. Lett.* **19**: 299–307. doi:10.1111/ele.12568. PMID:26799459.