

Risky behavior and its effect on survival: snowshoe hare behavior under varying moonlight conditions

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Abstract

Predation and predation risk can exert strong influences on the behavior of prey species. However, risk avoidance behaviors may vary among populations of the same species. We studied a population of snowshoe hares (*Lepus americanus*) near the southern edge of their range, in Pennsylvania. This population occupies different habitat types, experiences different environmental conditions, and are exposed to different predator species and densities than northern hare populations; therefore, they might exhibit differences in risk avoidance behaviors. We analyzed hare survival, movement rates, and habitat use under different levels of predation risk, as indexed by moonlight. Similar to previous work, we found snowshoe hare survival decreased with increased moon illumination during the winter, but we found differences in behavioral responses to increased predation risk. We found that snowshoe hares did not reduce movement rates during high-risk nights, but instead found that hares selected areas with denser canopy cover, compared to low-risk nights. We suggest that behavioral plasticity in response to predation risk allows populations of the same species to respond to localized conditions.

Introduction

Predators influence the dynamics of prey populations, through both direct predation and non-consumptive effects. Increased predation risk, as a result of higher predator densities or improved hunting conditions for predators, can result in increased direct predation as well as non-consumptive effects such as changes in habitat use (Creel *et al.*, 2005; Thaker *et al.*, 2011), behavior (Suraci *et al.*, 2016), morphology (Relyea, 2001), and physiology of prey (Boonstra *et al.*, 1998). In turn, these non-consumptive effects can alter reproductive rates (Sheriff, Krebs & Boonstra, 2009a; Zanette *et al.*, 2011), and have the potential to alter community structures (Suraci *et al.*, 2016). Prey must balance the risk of encountering a predator with the need to forage and obtain the necessary energy to carry out life processes (McNamara & Houston, 1987; Brown, 1988, 1999; Lima & Dill, 1990).

For nocturnal and crepuscular species, changes in lunar illumination (i.e. moon phase) have the potential to cause variation in predation risk. To reduce predation risk, prey can decrease movement rates to reduce the probability of being ambushed by a predator, or select for areas that offer visual protection from predators. Studies of several prey taxa found reductions in nightly movement rates during full moon phases (Kotler, 1984; Julien-Laferrière, 1997; Kramer & Birney, 2001). Other studies have reported greater use of dense

vegetation, which reduces the probability of detection by predators (Kotler, Brown & Mitchell, 1993; Orrock, Danielson & Brinkerhoff, 2004). Responses to predation risk also have been found to differ within taxa (Maestri & Marinho, 2014; Prugh & Golden, 2014). For example, some rodent species decrease movement during times of high illumination (Hughes, Ward & Perrin, 1994; Kramer & Birney, 2001), whereas other species increase movement rates during full moon periods (Longland & Price, 1991; Prugh & Brashares, 2010). Within geographically distinct populations of the same species, differences in predator abundance and species, habitat quality, and resource availability could lead to differences in both predation risk and behavioral responses to predation (Lima & Dill, 1990). Thus, investigating differences in behavioral responses to predation risk among populations can offer insight into population-level plasticity of risk avoidance mechanisms.

We studied behavioral responses to predation risk in a snowshoe hare population in Pennsylvania. Research on the responses of snowshoe hares to predation risk in other populations has suggested differences in predation avoidance behaviors. During full moon phases in the winter when predation risk is highest, snowshoe hares in Montana experience lower survival and decrease movement rates, but do not alter habitat use patterns (Griffin *et al.*, 2005). Conversely, Gilbert & Boutin (1991) found that snowshoe hares in the Yukon used open habitats less on nights near the full moon, and Wolff (1980)

found that hares in Alaska used dense spruce and willow thickets during periods of high predator densities, suggesting that shifts in habitat use might be a means of reducing predation risk. In addition, hares in fenced predator exclosures forage to maintain body condition rather than balancing foraging behaviors with anti-predator behaviors (Hik, 1995) and have lower movement rates in the summer than hares in unfenced control areas (Hodges, 1999), suggesting that adjusting movement rates also might be a predator avoidance tactic. Hares in Pennsylvania are near the southern edge of their range and occupy habitats with a mixture of hardwood and conifer species, as compared to the conifer-dominated boreal forests associated with northern hare populations. Southern hare populations also are exposed to different predator species and densities. In addition, hares in this populations exhibit different adaptations to winter conditions than in other areas of their range (Gigliotti, Diefenbach & Sheriff, 2017). This variation in environmental conditions, coupled with evidence that adaptations vary geographically in snowshoe hares, suggests that hares in Pennsylvania might have different behavioral adaptations to predation risk than populations in other parts of their range.

We investigated the effects of predation risk on survival, movement, and habitat use of snowshoe hares in Pennsylvania to investigate potential plasticity in risk avoidance behaviors across populations of the same species. We predicted that (1) snowshoe hares would have lower survival rates with increased illumination, (2) snowshoe hares would decrease movement rates as moon illumination increases, and (3) snowshoe hares would select for areas of denser vegetation during periods of high predation risk compared to periods of low predation risk.

Materials and methods

Study Area

The study area encompassed approximately 4050 ha near Long Pond, PA (41°02'N, 75°25'W). The majority of the study area contained 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*) >2 m tall, and pitch pine (*Pinus rigida*). Dominant understory species included blueberry (*Vaccinium spp.*), rhodora (*Rhododendron canadense*), teaberry (*Gaultheria procumbens*) and sheep laurel (*Kalmia angustifolia*). Planted stands of mature Norway spruce (*Picea abies*), red pine (*Pinus resinosa*) and European larch (*Larix decidua*) made up a small portion of the study area.

Capture and Handling

We trapped hares from January to August 2014 and January to June 2015 using Tomahawk live traps (Tomahawk Live Trap Company, Hazelhurst, WI). We marked newly caught hares using passive integrated transponder (PIT) tags (Biomark, Inc., Boise, ID), and with numbered Monel ear tags placed on the right ear (National Tag and Band Co., Newport, KY). We fit hares >900 g in body mass with a VHF transmitter (model

M1555, Advanced Telemetry Systems, Isanti, MN), or a GPS collar equipped with a VHF transmitter (model UltraLITE G10, Advanced Telemetry Systems, Isanti, MN; model 150mAH SnapTraX Pathfinder, Skorpa Telemetry, Aberfeldy, Scotland), set to record locations every 20 min. We only used hares collared with GPS collars for our habitat use and movement analyses, and included VHF and GPS-collared hares in our survival analysis. Capture and handling protocols were approved by The Pennsylvania State University Institutional Animal Care and Use Committee (Protocol #43476).

Survival

To estimate survival based on predation risk, we monitored the daily survival of collared hares. When a mortality was suspected we located the collar as soon as possible. If a carcass was recovered, we attempted to determine cause of death by examining the mortality location for tracks, scat or damage to the collar. When the cause of death was not visibly apparent and the carcass was intact, it was necropsied at the Animal Diagnostic Laboratory, Pennsylvania State University. Because we were only interested in predation for the purpose of this study, we censored hares from survival analysis if transmitter failure occurred or the hare died as a result of non-predation causes. Because we monitored survival on a daily basis, we considered scavenging rates to be negligible and assumed all apparent predation events to be a result of direct predation (Murray, Cary & Keith, 1997; Feierabend & Kielland, 2015). Although we could not determine the time of death for most hares, snowshoe hares are most active at night (Keith, 1964; Feierabend & Kielland, 2014) and in our study area had movement rates that were 64.7% higher at night than during the day. Therefore, we felt justified in focusing on moonlight as a proxy for predation risk.

We analyzed survival in relation to moon illumination and snow cover. Rather than treat moon phase as a categorical variable, we calculated a moonlight risk index (MRI) as the proportion of moon illuminated (MOON) multiplied by the proportion of the night that the moon was above the horizon (HORIZON), and multiplied by the proportion of sky not covered by clouds (1 – CLOUDS) during the time that the moon was above the horizon:

$$\text{MRI}_i = \text{MOON}_i \times \text{HORIZON}_i \times (1 - \text{CLOUDS})_i$$

, where i indexes the date.

We calculated moon illumination for each night using the package *LUNAR* (Lazaridis, 2014) in Program R (R Core Team, 2014). We calculated the proportion of time that the moon was above the horizon when the sun was below the horizon using sunrise and sunset times from the R package *RATmosphere* (Teets, 2003) and moonrise and moonset times from the U.S. Naval Oceanography Portal (<http://www.usno.navy.gov>). We determined the proportion of cloud cover each night using the *NCEP.gather* function in package *RNCEP* (Kemp *et al.*, 2012). Snow cover was represented by two categories: snow present and snow absent. We determined snow cover based on visual observations in the field, in which snow present was defined

as more than 80% of the study area covered in snow. Because of sample size limitations, we analyzed survival on a weekly basis; therefore, we averaged nightly moonlight risk index values for each week.

To identify factors potentially important in modeling weekly snowshoe hare survival, we created seven known-fate models in program MARK (White & Burnham, 1999). Models included effects of MRI, snow cover, and week of the year, additive models of survival based on MRI and snow cover ($S[MRI + \text{snow cover}]$), and MRI and week ($S[MRI + \text{week}]$), and a multiplicative model ($S[MRI \times \text{snow cover}]$) which allowed for differences in survival based on MRI under both snow conditions. We compared models using Akaike's Information Criterion adjusted for sample size (AIC_c ; Burnham & Anderson, 2002).

Movement Rates

To investigate effects of moonlight on snowshoe hare movement rates, we calculated the distance (m) that individual hares moved between successive locations. We summed the distance moved per hour ($m\ h^{-1}$) and excluded any time periods with missing locations. We limited the analysis to nighttime movements, which we defined as occurring after sunset and before sunrise. For each hour of movement, we assigned the MRI and snow cover as described above. We created five multiple regression models to describe snowshoe hare movements which included effects of snow cover and MRI, as well as an interaction between the two. To account for individual differences in movement rates, we treated individual hares as a random effect. We compared models using Akaike's Information Criterion adjusted for sample size (AIC_c ; Burnham & Anderson, 2002).

Fine-Scale Habitat Use

To investigate the effect of moonlight on fine-scale habitat use, we used a third-order (habitat selection within the extent of a home range; Johnson, 1980) resource selection function. We collected fine-scale vegetation data on a 50 m \times 50 m grid within the boundaries of the study area, for a total of 378 sampled squares (i.e. plots). We sampled plots only when leaves were absent (January–April), and restricted our analysis to this time period.

From the center point of each plot, we measured horizontal understory density in 0.5 m increments in height ≤ 2 m using a vegetation profile board positioned 10 m from the center point in each cardinal direction (Nudds, 1977). We grouped densities into three density classes based on coverage of the board (Low = 0–20%, Medium = 21–80% and High = 81–100%) based on a normal distribution, with the Low and High classes representing the highest and lowest 20% of understory density, and we calculated total understory density by averaging the sum of the four density measurements (0–2 m high). We measured canopy cover by taking a hemispherical photo 1 m above the center point and analyzing the photos using Gap Light Analyzer Version 2.0 (Institute of Ecosystem Studies, Millbrook, NY, USA).

We placed non-overlapping circular units with 25-m radii (Nielson & Sawyer, 2013) within our vegetation sampling grid, with the center point of each unit centered on the vegetation sampling grid cells. We summarized our vegetation measurements for each unit. Our covariates included percent canopy cover and total percent understory cover. We treated understory cover as a categorical variable with medium vegetation density (21–80% coverage) as our reference group. For each hare we defined the analysis extent by calculating a 95% kernel density estimate (KDE) with reference bandwidth selection (href) using all locations in R with the package *adehabitat* (Calenge, 2006). We used all sampling units falling within the boundaries of these extents for our analysis.

We modeled habitat use via a negative binomial resource selection function (NB RSF). The NB RSF estimates intensity of use while addressing issues of temporally correlated locations associated with a frequent GPS collection schedule (Nielson & Sawyer, 2013). The response variable was the number of locations within our defined sampling units. To account for differences in moonlight risk, we separated all locations into low-risk periods (MRI < 0.5) and high-risk periods (MRI > 0.5).

We calculated the NB RSF using the R package *MASS* (Venables & Ripley, 2002). In all models we included an offset term of the natural log of total locations per hare to model frequency of use rather than the count of locations within each habitat unit. We treated the individual hare, rather than each location, as the experimental unit because of the large number of relocations per hare and to include individual variation in the models. To obtain population-level models, we averaged parameter estimates and standard errors across individual animals for each model (Millsbaugh *et al.*, 2006; Thomas & Taylor, 2006; Sawyer, Kauffman & Nielson, 2009) and weighted parameter estimates and standard errors based on the number of locations of each individual hare. For each parameter estimate we calculated the 85% confidence interval (Arnold, 2010). We compared the models by summing AIC_c values for each hare for a given model and selecting the model with the lowest summed AIC_c values across hares (Glenn, Hansen & Anthony, 2004; Zielinski *et al.*, 2004). To compare habitat selection by MRI, we compared parameter estimates for individual hares between high moonlight risk and low moonlight risk using a paired *t*-test.

Results

Survival

We monitored 69 snowshoe hares for survival over the duration of the study. We censored 30 hares due to collar failure, capture myopathy or non-predation deaths and included the remaining 39 hares in the survival analysis. For predation deaths ($n = 22$), 59% were associated with mammalian predators, 14% from avian predation and 27% from an unknown predator. The nightly MRI ranged from 0 to 1 with an average MRI of 0.19 ($SE = 0.01$). When considered on a weekly basis, MRI ranged from 0.01 to 0.51 ($SE = 0.02$).

Table 1 Model selection results for known-fate models of snowshoe hare survival using a moonlight risk index (MRI) based on week of the year, moon phase, proportion of night the moon was above the horizon, and cloud cover (see Methods) and a categorical measure of snow cover (1 = >80% snow cover; 0 otherwise), Long Pond, Pennsylvania, 2014–2015

Model	ΔAIC_c	$-2 \times \ln(L)^a$	Model Likelihood	w^b	k^c
S(snow × MRI)	0.00	205.45	1.00	0.35	4
S(.)	0.34	211.83	0.84	0.29	1
S(MRI)	1.28	210.75	0.53	0.18	2
S(snow)	2.32	211.79	0.31	0.11	2
S(snow + MRI)	3.26	210.73	0.20	0.07	3
S(week)	91.45	153.94	<0.01	<0.01	71
S(MRI + week)	93.72	153.94	<0.01	<0.01	72

^aLog likelihood.

^bAkaike model weight.

^cNumber of model parameters.

Snowshoe hare survival was best described by an interactive effect of MRI and snow cover (Table 1). However, the constant survival model (S[.]) and the survival model based on only moonlight risk (S[MRI]) were both competitive models and were within two AIC_c units of the top model. There was no effect of MRI on survival during snow-free phases, but weekly survival decreased with increasing MRI during periods with snow (Fig. 1).

Movement

Nightly movement rates ($m\ h^{-1}$) were best described by a model including an interactive effect between MRI and snow cover (Table 2). Hares had higher hourly movement rates when snow was present compared to when snow was absent (Fig. 2; $t = 4.42$, d.f. = 575, $P < 0.001$). Across all levels of moonlight risk, hares moved an average of $80.8\ m\ h^{-1}$ (SE = 5.2) more on nights when snow was present than nights

without snow. During both snow phases, moonlight risk did not have a strong effect on movement rates of hares ($t = 1.47$, d.f. = 572, $P = 0.14$).

Habitat Use

Canopy cover ranged from 0 to 92.9% with an average of 53.5% (SE = 1.0). Our sampled plots were comprised of 5% low understory cover, 79% medium understory cover and 16% high understory cover. Winter habitat use within the home ranges of hares differed between high-risk and low-risk periods. During both high-risk periods and low-risk periods, canopy cover best described relative habitat use with hares more likely to use areas with denser canopies (Table 3, Fig. 3). Individual hares had higher relative use in areas with denser canopy cover during high-risk nights compared to low-risk nights ($t = 2.38$, d.f. = 13, $P = 0.03$).

Discussion

Snowshoe hares in Pennsylvania exhibited different anti-predator behaviors than hares in other parts of their range (Gilbert & Boutin, 1991; Hodges, 1999; Griffin *et al.*, 2005), suggesting plasticity in risk-avoidance behaviors based on local conditions. We found that hares had lower survival during high-risk periods and potentially minimized this risk by selecting habitats with characteristics to reduce the probability of detection by predators, rather than reducing movement rates. Animals have a variety of tactics that can be used to balance the costs associated with anti-predator behavior with the benefits of foraging (Lima & Dill, 1990; Brown & Kotler, 2004) and we suggest that geographic plasticity in anti-predator behaviors exists as a result of local conditions.

Movement

We found that hares had higher movement rates when snow was present, but moonlight did not influence nightly movement rates of hares. In our study area, altering movement rates might not be a beneficial predator avoidance strategy. During winter, the benefits of thermoregulation and maximizing forage

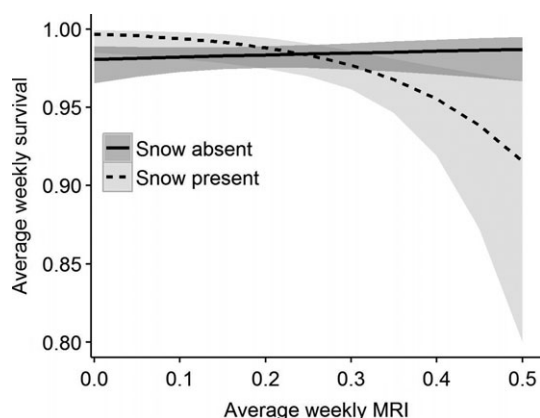


Figure 1 Estimated snowshoe hare ($n = 39$) weekly survival in relation to a moonlight risk index (MRI) based on moon phase, proportion of night the moon was above the horizon, and cloud cover (see Methods) and a categorical measure of snow cover (1 = >80% snow cover; 0 otherwise), Long Pond Pennsylvania, 2014–2015. Shaded regions indicate the 85% confidence interval.

Table 2 Model selection results for mixed-effects models of snowshoe hare nightly movement rates (m h^{-1}) using a moonlight risk index (MRI) based on moon phase, proportion of night the moon was above the horizon, and cloud cover (see Methods) and a categorical measure of snow cover (1 = >80% snow cover; 0 otherwise), Long Pond, Pennsylvania, 2014–2015

Model	ΔAIC_c	$-2 \times \ln(L)^a$	Model Likelihood	w^b	k^c
Snow \times MRI	0.00	7,054.96	1.00	0.99	4
Snow + MRI	9.08	7,066.04	0.01	0.01	3
Snow	15.15	7,074.10	<0.01	<0.01	2
MRI	38.38	7,097.34	<0.01	<0.01	2
Intercept only	44.31	7,105.27	<0.01	<0.01	1

^aLog likelihood.

^bAkaike model weight.

^cNumber of model parameters.

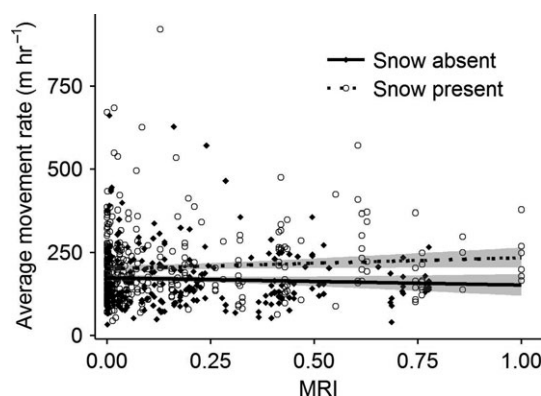


Figure 2 Hourly movement rates (mean \pm 85% CI) of snowshoe hares ($n = 32$) using a moonlight risk index (MRI) based on moon phase, proportion of night the moon was above the horizon, and cloud cover (see Methods) and a categorical measure of snow cover (1 = >80% snow cover; 0 otherwise), Long Pond, Pennsylvania, 2014–2015. Shaded regions indicate the 85% confidence interval.

intake might outweigh the risk of predation. Snowshoe hares in Pennsylvania potentially vary movement rates as a means of responding to variable winter temperatures, rather than coping

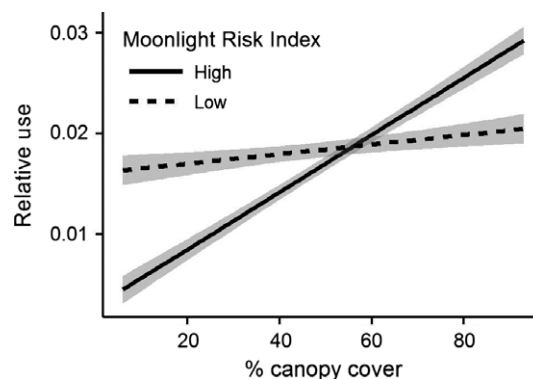


Figure 3 Relative habitat use by snowshoe hares ($n = 14$) as a function of canopy cover during periods of high (> 0.5; greater moonlight illumination) predation risk (solid line) and low (<0.5; lesser moonlight illumination) predation risk (dashed line) phases; Long Pond Pennsylvania, 2014–2015. Shaded regions indicate the 85% confidence interval.

with low winter temperatures through metabolic or physical adaptations (Gigliotti *et al.*, 2017); therefore altering movement rates as an anti-predator behavior might be especially costly. In addition, the available browse during winter has low caloric content and hares need to constantly feed to consume the calories needed to carrying out biological processes (Pease, Vowles & Keith, 1979; Bryant & Kuropat, 1980; Wirsing & Murray, 2002). Similarly, the cost of foregoing foraging activities for predator avoidance behaviors for a variety of desert rodents has been found to be higher in winter when colder temperatures increase the metabolic needs of the rodents (Brown, Kotler & Valone, 1994). Thus, altering movement rates as a response to predation risk might have a negative effect on the fitness of the hares.

The suggestion that movement rates in our study are primarily driven by metabolic or nutritional needs rather than predation risk is reflected in the observed difference in movement rates between snow-present and snow-free periods in our study. The snow-free periods generally corresponded to warmer temperatures and greater food availability, meaning that hares

Table 3 Model selection results for snowshoe hare fine-scale habitat use under high (MRI >0.5) and low (MRI <0.5) moonlight risk conditions using a moonlight risk index (MRI) based on moon phase, proportion of night the moon was above the horizon, and cloud cover (see Methods) and a categorical measure of snow cover (1 = >80% snow cover; 0 otherwise), Long Pond, Pennsylvania, 2014–2015

Risk Level	Model	ΔAIC_c	$-2 \times \ln(L)^a$	Model Likelihood	w^b	k^c
High	Canopy cover	0.00	2300.46	1.00	1.00	4
	Canopy cover + understory density	12.06	2306.51	0.00	0.00	7
	Understory density	25.34	2321.80	0.00	0.00	6
	Intercept only	28.02	2330.47	0.00	0.00	3
Low	Canopy cover	0.00	5763.53	1.00	0.86	4
	Canopy cover + understory density	3.68	5761.22	0.16	0.14	7
	Understory density	36.84	5796.37	0.00	0.00	6
	Intercept only	40.43	5805.96	0.00	0.00	3

^aLog likelihood.

^bAkaike model weight.

^cNumber of model parameters.

would not need to move as far to find forage. Even with movement being less important for survival during the snow-free periods, we still did not see moonlight affecting hare movement rates, likely because we did not find survival to be strongly influenced by moonlight risk during these periods. Similarly, Hodges (1999) found that hares in predator exclosures had greater nightly movement rates than those in unfenced controls, but only during summer. The availability of forage and higher temperatures might have allowed hares to increase movement rates as a predator avoidance strategy if risk of predation was actually greater than in the winter.

In populations of hares that rely on other means of coping with cold temperatures, or in species that occur in temperate areas, altering movement rates might not be as costly to fitness. For example, snowshoe hares in Montana reduce movement rates during periods of high moonlight in the winter (Griffin *et al.*, 2005). Hares in northern latitudes primarily cope with cold winter temperatures by altering metabolic rates and increasing insulation (Sheriff *et al.*, 2009b,c). The hares in the Montana study potentially had different adaptations to the cold than the hares in our study, which would allow them to reduce movement rates in the winter without incurring major fitness costs. Similarly, several studies of rodents also have indicated a reduction in movements during nights with high moon illumination (Kotler, 1984; Kramer & Birney, 2001; Orrock *et al.*, 2004). However, several of these studies were conducted in spring or summer months when the energetic demands might be less, or under laboratory conditions. In addition, rodents use burrows (Brown *et al.*, 1988) and cache seeds (Bouskila, 1995), which might reduce thermoregulatory demands during periods of low temperatures and allow them to reduce movements during risky nights.

Habitat Use

We found that regardless of moonlight, hares selected areas within their home ranges with dense canopy cover, and that individual hares preferred areas with the densest canopy cover during high-risk nights compared to low-risk nights when snow was present. This pattern of habitat selection is consistent with observations of hares in the Yukon (Gilbert & Boutin, 1991) and Alaska (Wolff, 1980), but differs from research conducted on hares in Montana, which found that hares did not alter their habitat use in relation to increased predation risk (Griffin *et al.*, 2005). Collectively, this suggests that shifting habitat use as a predator avoidance strategy might only be beneficial to a species under certain conditions.

For snowshoe hares in our study area, shifting habitat use into areas with denser canopies might be the most beneficial predator avoidance strategy. The time when snow is present in Pennsylvania corresponds to periods when hardwood trees lack leaves. Therefore, hardwood stands likely pose a greater risk of predation than conifer stands because there is less obstruction in the canopy to restrict moonlight reaching the forest floor. Some species of predators have been found to have higher activity rates during periods of high moon illumination. For example, coyotes are more active under brighter moonlight conditions (Kenaga, Krebs & Clapham, 2013), and bobcats

have higher nightly movement rates during the full moon (Rockhill, DePerno & Powell, 2013). By using areas with dense canopy cover during risky nights, hares can use areas with less moonlight reaching the forest floor and thus minimize risk of predation.

By altering habitat use but not reducing movement rates, hares in Pennsylvania are likely still able to forage. In our study area, scrub oak was the dominant understory vegetation and provided forage for the hares, even under dense tree canopies. In addition, most of the areas with the densest canopies were stands of Norway spruce and red spruce (*Picea rubens*), and hares have been found to consume needles and twigs of spruce in other parts of their range (Wolff, 1978). This availability of winter browse would allow hares to continue to forage even in habitats that offer them better visual protection from predators. Altering habitat use patterns as an anti-predator tactic might be not the optimal predator avoidance strategy in other habitat types. The Montana study consisted of conifer stands of varying stem densities, meaning that hares could still access overstory cover under individual trees, even if the overall stand was relatively open. A shift to only using areas within the densest stands might also limit forage availability. In Alaska, hares use dense thickets of willow and alder for predation refuges during periods of high predation risk, but these refuges still offer forage for hares (Wolff, 1980). However, Hodges & Sinclair (2005) found that hares do not alter foraging behaviors in response to predation risk, but instead select for areas primarily based on the distribution of browse. As a result, hares in Montana and Pennsylvania might exhibit differences in habitat selection based on risk because habitat characteristics associated with the highest forage availability might differ.

Conclusions

Understanding differences in anti-predator behavior among populations of the same species can offer insight into the benefits and trade-offs of balancing predation avoidance with other behaviors, such as foraging. Our results suggest plasticity in predation risk avoidance behaviors based on local conditions. In particular, we suggest that individuals use anti-predator behaviors that allow them to best maximize fitness. Because predation risk and local conditions can vary greatly, it is beneficial for behaviorally mediated predator avoidance to be flexible.

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References

- Arnold, T.W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* **74**, 1175–1178.
- Boonstra, R., Hik, D., Singleton, G.R. & Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecol. Monogr.* **68**, 371–394.
- Bouskila, A. (1995). Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* **76**, 165–178.
- Brown, J.S. (1988). Patch use as an indication of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47.
- Brown, J.S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.* **1**, 49–71.
- Brown, J.S. & Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* **7**, 999–1014.
- Brown, J.S., Kotler, B.P., Smith, R.J. & Wirtz, W.O. (1988). The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* **76**, 408–415.
- Brown, J.S., Kotler, B.P. & Valone, T.J. (1994). Foraging under predation: a comparison of energetic and predation costs in rodent communities of the Negev and Sonoran deserts. *Aust. J. Zool.* **42**, 405–433.
- Bryant, J.P. & Kuropat, P.J. (1980). Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annu. Rev. Ecol. Syst.* **11**, 261–285.
- Burnham, K.P. and Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer Science & Business Media.
- Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**, 516–519.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**, 3387–3397.
- Feierabend, D. & Kielland, K. (2014). Movements, activity patterns, and habitat use of snowshoe hares (*Lepus americanus*) in interior Alaska. *J. Mammal.* **95**, 525–533.
- Feierabend, D. & Kielland, K. (2015). Seasonal effects of habitat on sources and rates of snowshoe hare predation in Alaskan boreal forests. *PLoS One* **10**, e0143543.
- Gigliotti, L.C., Diefenbach, D.R. & Sheriff, M.J. (2017). Geographic variation in winter adaptations of snowshoe hares (*Lepus americanus*). *Can. J. Zool.* **95**, 539–545.
- Gilbert, B.S. & Boutin, S. (1991). Effect of moonlight on winter activity of snowshoe hares. *Arct. Antarct. Alp. Res.* **23**, 61–65.
- Glenn, E.M., Hansen, M.C. & Anthony, R.G. (2004). Spotted owl home-range and habitat use in young forests of western Oregon. *J. Wildl. Manage.* **68**, 33–50.
- Griffin, P.C., Griffin, S.C., Waroquiers, C. & Mills, L.S. (2005). Mortality by moonlight: predation risk and the snowshoe hare. *Behav. Ecol.* **16**, 938–944.
- Hik, D.S. (1995). Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. *Wildl. Res.* **22**, 115–129.
- Hodges, K.E. (1999). Proximate factors affecting snowshoe hare movements during a cyclic population low phase. *Ecoscience* **6**, 487–496.
- Hodges, K.E. & Sinclair, A.R.E. (2005). Browse site selection by snowshoe hares: effects of food supply and predation risk. *Can. J. Zool.* **83**, 280–292.
- Hughes, J.J., Ward, D. & Perrin, M.R. (1994). Predation risk and competition affect habitat selection and activity of namib desert gerbils. *Ecology* **75**, 137–140.
- Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.
- Julien-Laferrrière, D. (1997). The influence of moonlight on activity of woolly opossums (*Caluromys philander*). *J. Mammal.* **78**, 251–255.
- Keith, L.B. (1964). Daily activity pattern of snowshoe hares. *J. Mammal.* **45**, 626–627.
- Kemp, M.U., Emiel van Loon, E., Shamoun-Baranes, J. & Bouten, W. (2012). RNCEP: global weather and climate data at your fingertips. *Methods Ecol. Evol.* **3**, 65–70.
- Kenaga, B.A., Krebs, R.A. & Clapham, W.B.J. (2013). Coyote land use inside and outside urban parks. *Am. Midl. Nat.* **170**, 298–310.
- Kotler, B.P. (1984). Effects of illumination on the rate of resource harvesting in a community of desert rodents. *Am. Midl. Nat.* **111**, 383–389.
- Kotler, B.P., Brown, J.S. & Mitchell, W.A. (1993). Environmental factors affecting patch use in two species of gerbilline rodents. *J. Mammal.* **74**, 614–620.
- Kramer, K.M. & Birney, E.C. (2001). Effect of light intensity on activity patterns of patagonian leaf eared mice, *Phyllotis xanthopygus*. *J. Mammal.* **82**, 535–544.
- Lazaridis, E. (2014). LUNAR: Lunar Phase & Distance, Seasons and Other Environmental Factors. <http://statics.lazaridis.eu>
- Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.
- Longland, W.S. & Price, M.V. (1991). Direct observations of owls and heteromyid rodents - can predation risk explain microhabitat use? *Ecology* **72**, 2261–2273.
- Maestri, R. & Marinho, J.R. (2014). Singing in the rain. Rainfall and moonlight affect daily activity patterns of rodents in a Neotropical forest. *Acta Theriol. (Warsz)* **59**, 427–433.
- McNamara, J.M. & Houston, A.I. (1987). Starvation and predation as factors limiting population size. *Ecology* **68**, 1515–1519.
- Millspaugh, J.J., Nielson, R.M., McDonald, L., John, M., Gitzen, R.A., Rittenhouse, C.D., Hubbard, M.W. & Sheriff, S.L. (2006). Analysis of resource selection using utilization distributions. *J. Wildl. Manage.* **70**, 384–395.
- Murray, D.L., Cary, J.R. & Keith, L.B. (1997). Interactive effects of sublethal nematodes and nutritional status on

- snowshoe hare vulnerability to predation. *J. Anim. Ecol.* **66**, 250–264.
- Nielson, R.M. & Sawyer, H. (2013). Estimating resource selection with count data. *Ecol. Evol.* **3**, 2233–2240.
- Nudds, T.D. (1977). Quantifying the vegetative structure of wildlife cover. *Wildl. Soc. Bull.* **5**, 113–117.
- Orrock, J.L., Danielson, B.J. & Brinkerhoff, R.J. (2004). Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behav. Ecol.* **15**, 433–437.
- Pease, J.L., Vowles, R.H. & Keith, L.B. (1979). Interaction of snowshoe hares and woody vegetation. *J. Wildl. Manage.* **43**, 43–60.
- Prugh, L. & Brashares, J. (2010). Basking in the moonlight? Effect of illumination on capture success of the endangered giant kangaroo rat. *J. Mammal.* **91**, 1205–1212.
- Prugh, L.R. & Golden, C.D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J. Anim. Ecol.* **83**, 504–514.
- R Core Team. (2014). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Relyea, R.A. (2001). Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* **82**, 523–540.
- Rockhill, A.P., DePerno, C.S. & Powell, R.A. (2013). The effect of illumination and time of day on movements of bobcats (*Lynx rufus*). *PLoS ONE* **8**: 40–42.
- Sawyer, H., Kauffman, M.J. & Nielson, R.M. (2009). Influence of well pad activity on winter habitat selection patterns of mule deer. *J. Wildl. Manage.* **73**, 1052–1061.
- Sheriff, M.J., Krebs, C.J. & Boonstra, R. (2009a). The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *J. Anim. Ecol.* **78**, 1249–1258.
- Sheriff, M.J., Kuchel, L., Humphries, M.M. & Boutin, S. (2009b). Seasonal metabolic acclimatization in a northern population of free-ranging snowshoe hares, *Lepus americanus*. *J. Mammal.* **90**, 761–767.
- Sheriff, M.J., Speakman, J.R., Kuchel, L., Boutin, S. & Humphries, M.M. (2009c). The cold shoulder: free-ranging snowshoe hares maintain a low cost of living in cold climates. *Can. J. Zool.* **87**, 956–964.
- Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. (2016). Fear of large carnivores causes a trophic cascade. *Nat. Commun.* **7**, 10698.
- Teets, D.A. (2003). Predicting sunrise and sunset times. *Coll. Math. J.* **34**, 317–321.
- Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* **92**, 398–407.
- Thomas, D. & Taylor, E. (2006). Study designs and tests for comparing resource use and availability II. *J. Wildl. Manage.* **70**, 324–336.
- Venables, W.N. & Ripley, B.D. (2002). *Modern applied statistics with S*. 4th edn. New York: Springer.
- White, G.C. and Burnham, K.P. (1999). Program MARK: survival estimation from from populations of marked animals. *Bird Study*. **46**, S120–S139.
- Wirsing, A.J. & Murray, D.L. (2002). Patterns in consumption of woody plants by snowshoe hares in the northwestern United States. *Ecoscience* **9**, 440–449.
- Wolff, J.O. (1978). Food habits of snowshoe hares in interior Alaska. *J. Wildl. Manage.* **42**, 148–153.
- Wolff, J.O. (1980). The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecol. Monogr.* **50**, 111–130.
- Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M. (2011). Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* **334**, 1398–1401.
- Zielinski, W.J., Truex, R.L., Schmidt, G.A., Schlexer, F.V., Schmidt, K.N. & Barrett, R.H. (2004). Resting habitat selection by fishers in California. *J. Wildl. Manage.* **68**, 475–492.