The Journal of Wildlife Management 82(2):435–444; 2018; DOI: 10.1002/jwmg.21375

Research Article

Snowshoe Hare Multi-Level Habitat Use in a Fire-Adapted Ecosystem

LAURA C. GIGLIOTTI,[1,2] *Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, 435 Forest Resources Building, University Park, PA 16802, USA*

BENJAMIN C. JONES, *Pennsylvania Game Commission, Harrisburg, PA, USA*

MATTHEW J. LOVALLO, *Pennsylvania Game Commission, Harrisburg, PA, USA*

DUANE R. DIEFENBACH, *U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, 404 Forest Resources Building, University Park, PA 16802, USA*

ABSTRACT Prescribed burning has the potential to improve habitat for species that depend on pyric ecosystems or other early successional vegetation types. For species that occupy diverse plant communities over the extent of their range, response to disturbances such as fire might vary based on post-disturbance vegetation dynamics among plant communities. Although responses of snowshoe hares (*Lepus americanus*) to fire have been studied in conifer-dominated forests in northern parts of the species' range, there is a lack of information on snowshoe hare habitat use in fire-dependent communities in southern parts of their range. We used global positioning system (GPS) and very high frequency (VHF) radio-collars to monitor the habitat use of 32 snowshoe hares in a scrub-oak (*Quercus ilicifolia*)-pitch pine (*Pinus rigida*) barrens complex in northeastern Pennsylvania where prescribed fire has been used for habitat restoration. The area contained stands that underwent prescribed burning 1–6 years prior to our study. Also, we investigated fine-scale determinants of habitat use within stands. We found that regardless of season, hares did not select for areas that had been burned within 6 years prior. Hares primarily used stands of older scrub oak, conifer, or hardwoods, which contained dense understory vegetation and canopy cover. Hare habitat use also was positively associated with stand edges. Our results suggest that hares do not respond to prescribed burning of scrub oak in the short-term. In addition, by focusing on structural determinants of habitat use, rather than broad-scale characteristics such as stand type, management strategies for snowshoe hares can be adapted over the extent of their range despite the multitude of different land cover types across which the species occurs.

KEY WORDS conifer, habitat use, *Lepus americanus*, Pennsylvania, prescribed fire, scrub oak, snowshoe hare.

Historically, fire has been used for habitat management purposes, although prescribed burning is only starting to be widely used again after decades of fire suppression regulations (Ryan et al. 2013, Brose 2014). As managers are beginning to incorporate more prescribed burning into management plans, a better understanding of the effects of fire on wildlife is important. Fires, both natural and prescribed, can positively affect wildlife species by creating early successional habitat and increasing or improving the quality of forage and browse (Brose and Van Lear 1998, Lashley et al. 2011). However, fire also has the potential to negatively affect wildlife by limiting available habitat in the short term (Joly et al. 2003, Fisher and Wilkinson 2005). Prescribed burns often create patchy and diverse vegetation, leading to fine-scale differences in vegetation structure (Larson and Churchill 2012). Different forest types require different burn frequencies and vary in their regeneration rates (Fryer and Luensmann 2012); thus, understanding the responses of wildlife to prescribed burns in different forest types is important.

Snowshoe hares (*Lepus americanus*) are found throughout Canada and the northern United States, but the ecology of populations near the southern extent of their range is not well-understood and these populations are more vulnerable to changes in habitat availability and climate (Burt 2014, Diefenbach et al. 2016, Sultaire et al. 2016*a*). Throughout their range, hares are associated with areas of dense understory vegetation and canopies (Litvaitis et al. 1985, Griffin and Mills 2009, Ivan et al. 2014), but dominant vegetation types differ greatly over the extent of their range, leading to differences in vegetative regeneration patterns following disturbance or management. Therefore, to best manage habitat for snowshoe hares throughout the extent of their range, it is important to develop an understanding of how hares respond to management of diverse vegetation communities.

Received: 30 May 2016; Accepted: 17 August 2017

[1]*E-mail: lcgigli@clemson.edu*
[2]*Present Address: Department of Forestry and Environmental Conservation, Clemson University, 261 Lehotsky Hall, Clemson, SC 29634, USA*

Hares in northern forests frequently avoid newly cleared or burned areas (Ferron et al. 1998, de Bellefeuille et al. 2001). Hares have been found to eventually recolonize burned areas, although previous research indicates variability in the timing of this process. An occupancy study following a fire in Alberta indicated hares began using burned areas 2 years post-burn (Keith and Surrendi 1971). In lodgepole pine (*Pinus contorta*) stands in Glacier National Park, Montana, stands 17–19 years post-burn supported more hares than stands 11–13 years post-burn and unburned stands (Cheng et al. 2015). In Quebec, Canada, peak snowshoe hare browsing was found to occur 40–60 years post-fire (Hodson et al. 2011, Allard-Duchêne et al. 2014). Snowshoe hares in Alaska, USA, are also associated with the dense vegetation and patchy habitats resulting from burning and typically occupy these areas 15–30 years post-fire (Paragi et al. 1997, Nelson et al. 2008).

However, these studies have all been conducted in northern, conifer-dominated habitats and the effects of fire on southern populations of hares, where conifers are often interspersed with deciduous (i.e., oak [*Quercus* spp.]) forests are not well understood. Although following disturbance northern coniferous forests may be dominated by early succession deciduous species such as willow (*Salix* spp.), aspen (*Populus* spp.), or birch (*Betula* spp.; Bergeron 2000), differences in regeneration rates and vegetation structure may lead to differences in hare habitat use compared to oak forests. In the eastern United States, oak forests were historically maintained by fire (Abrams 1992). One particular type of oak forest is the scrub oak (*Quercus ilicifolia*) barren, which is found throughout the northeastern United States. In the absence of fire, these barrens succeed to closed canopy oak forests (Jordan et al. 2003). These areas need to be burned every 5–50 years to maintain the barrens (Fryer and Luensmann 2012), so understanding the responses of hares to fire at a shorter time scale than previous research in other vegetation types is important.

Additionally, differences in the ecology of hares throughout their range may lead to differences in habitat use patterns with regard to recently burned areas. Snowshoe hares in Pennsylvania, USA, have larger winter body masses than those at northern latitudes (Gigliotti 2016). Because of this size difference, hares in Pennsylvania would likely need to consume more calories than populations in other areas of their range (Robbins 1983). Recently burned vegetation, including scrub oak, has high nutritional value (Woodwell et al. 1975, Hallisey and Wood 1976) and therefore represents a potentially important food source for hares. Although these stands might not be as structurally complex as older forest stands, all prey species experience a trade-off between predation avoidance and caloric intake (Brown 1988, Lima and Dill 1990). As a result, hares with larger body masses, such as those in Pennsylvania, might have more motivation to use recently burned stands than hares in more northern populations and might use recently burned areas sooner and to a greater extent than previous research has reported.

In addition, most previous research has used presence or abundance of tracks (Paragi et al. 1997, Hodson et al. 2010, Sultaire et al. 2016*a*) or pellets (Litvaitis et al. 1985, Fuller and Harrison 2013, Ewacha et al. 2014) as a proxy for habitat use and did not use hare location data. By using frequent global positioning system (GPS) locations of snowshoe hares and fine-scale vegetation data, we assessed fine-scale snowshoe hare habitat use patterns within a managed landscape near the southern extent of this species' range. Our objectives for this study were to investigate seasonal stand-level resource selection of snowshoe hares in a managed habitat in Pennsylvania, and investigate fine-scale influences of snowshoe hare habitat use. We predicted that hares would prefer stands of mature scrub oak or conifers and that fine-scale habitat use would be positively associated with canopy cover and understory cover.

STUDY AREA

The study area encompassed approximately 4,050 ha in Tunkhannock and Jackson townships in Monroe County, Pennsylvania (Fig. 1). The study site was relatively flat, with an average elevation of 575 m. The average annual temperature was 7.5°C and mean monthly temperatures range from a low of −5.6°C in January to a high of 19.8°C in July. The average annual precipitation was approximately 127 cm. Common mammalian species in the study area included black bear (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), eastern cottontail (*Sylvilagus floridanus*), and red

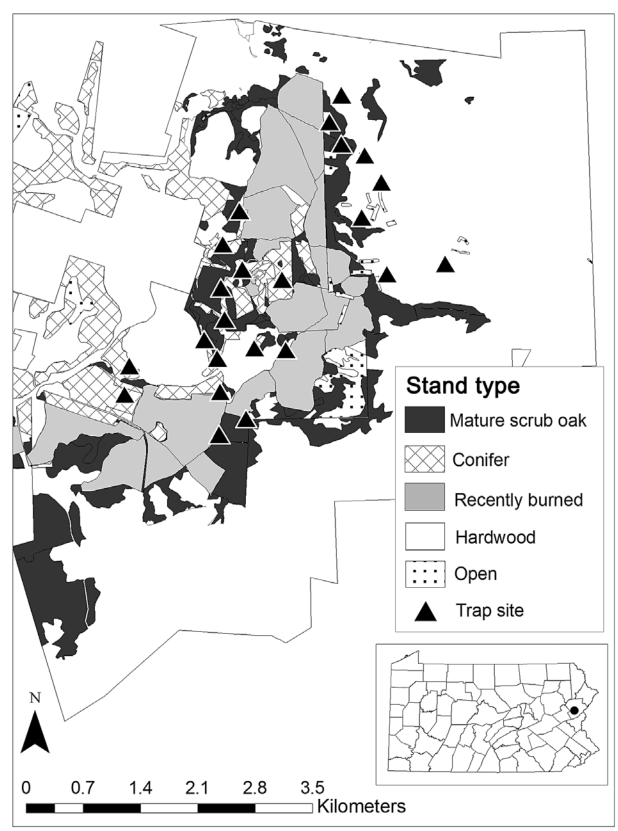

Figure 1. Dominant stand types within the snowshoe hare study area, Long Pond, Pennsylvania, USA, 2014–2015.

squirrel (*Tamiasciurus hudsonicus*). This area was dominated by scrub oak (*Quercus ilicifolia*)-pitch pine (*Pinus rigida*) barrens, which occur on glacial mesic till soils rather than the xeric sandy soils commonly associated with barrens communities (Latham et al. 1996, Eberhardt and Latham 2000). The vegetative community of this area pre-dates European settlement in Pennsylvania and has historically relied on high-severity fires to maintain the vegetation structure (Latham et al. 1996).

Changes in fire regimes have changed the structure of the vegetation in the barrens of this area. In the late 1950s forest fire suppression programs in Pennsylvania reduced wildfires and >70% of the barrens succeeded into oak or red maple (*Acer rubrum*) forests with limited mid-level vegetation (Maurice et al. 2004). In an effort to restore and maintain scrub oak-pitch pine stands, portions of the study area were part of a prescribed burn program that began in 2007 using low to moderate severity fires. The majority of the burning occurred in the summers of 2012, 2013, and 2014 with burn area consisting of 190 ha, 241 ha, and 162 ha, respectively. At the time of this study, the burned patches were 1–6 years old and were dominated by low scrub oak <1 m tall, blueberry (*Vaccinium* spp.), and bracken fern (*Pteridium aquilinum*) and contained very few trees >5 m tall.

The remainder of the study area consisted of older stands of scrub oak, conifer, and hardwood containing natural and manmade openings. Older scrub oak stands covered 23% of the study area and consisted of scrub oak >2 m tall with interspersed pitch pine. These stands were burned historically, resulting in dense scrub oak along with dominant understory species of blueberry, rhodora (*Rhododendron canadense*), teaberry (*Gaultheria procumbens*), and sheep laurel (*Kalmia angustifolia*). The average size of older scrub oak stands was 11.2 ha.

Conifer stands made up 26% of the study area and contained planted and natural stands. Planted stands were composed of mature Norway spruce (*Picea abies*), red pine (*Pinus resinosa*), and European larch (*Larix decidua*). These stands were planted between 1940 and 1960 and had an average patch size of 5.27 ha. Natural conifer stands made up a small portion (4%) of the conifer stands and had canopies of red spruce (*Picea rubens*). All conifer stands had very low understory vegetation density.

Hardwood stands comprised approximately 33% of the study area and were dominated by scarlet oak (*Quercus coccinea*) or white oak (*Quercus alba*) and contained moderate levels of understory vegetation including rhodora and blueberry. These stands were an average of 18.3 ha and were an average of 60 years old. These stands all had similar fire histories and structural characteristics (Latham et al. 1996, Maurice et al. 2004) so we did not further differentiate between specific hardwood types. A very small percentage (1.5%) of the study area was composed of natural and manmade open areas. These areas were planted and natural fields, and openings and did not contain any trees or mid-story vegetation. Because deciduous species made up a large portion of the study area, vegetation structure differed based on season, with leaf-off periods corresponding with late fall and winter, and leaf-on periods corresponding with late spring and summer.

METHODS

Capture and Measurements

We trapped hares from January–August 2014 and January–June 2015 using Tomahawk live traps (Tomahawk Live Trap Company, Hazelhurst, WI, USA) baited with apples and alfalfa cubes. We placed traps throughout the study area in clusters of 5–10 traps and kept them open for 5–6 days a week. For each captured hare, we recorded sex, body mass, right hind foot length (RHF), and coat color. We uniquely marked newly captured hares using passive integrated transponder (PIT) tags (Biomark, Boise, ID, USA) inserted under the skin near the right shoulder blade and with numbered Monel ear tags placed on the right ear (National Band and Tag, Newport, KY, USA). We fit hares >900 g in body mass with a very high frequency (VHF) transmitter (model M1555, Advanced Telemetry Systems, Isanti, MN, USA), or a GPS collar equipped with a VHF transmitter (model UltraLITE G10, Advanced Telemetry Systems, Isanti, MN, USA; model 150mAH SnapTraX Pathfinder, Skorpa Telemetry, Aberfeldy, Scotland). We programmed the GPS collars to record a location every 20 minutes. Animal capture and handling protocols were approved by The Pennsylvania State University Institutional Animal Care and Use Committee (protocol no. 43476).

Vegetation Data

We analyzed snowshoe hare resource selection at the stand-level, in which we considered stand types and arrangement, and at a fine-scale, in which we examined within-stand measurements of vegetation structure. For our stand-level snowshoe hare resource selection analysis, we used existing shapefiles created by the Pennsylvania Game Commission through a combination of aerial photography and ground-truthing. In the Pocono landscape, boundaries among older forest, young forest, scrub oak barrens, and evergreen stands are very easy to distinguish from heads-up imagery interpretation and we ground-truthed stand boundaries with a GPS unit to account for more-subtle changes in forest type. Therefore, we considered any error in these shapefiles to be negligible. We created 30-m × 30-m raster cells based on the dominant vegetation type using these shapefiles. We grouped stand types into 5 categories: scrub oak (excluding recently burned scrub oak stands), conifer, recently burned (including stands 1–6 years post-burn), hardwood, and open as described in our study area description. We included natural and planted conifers in the conifer category because they were structurally similar. Although the recently burned stands and open areas were structurally similar, we chose to separate them into 2 separate categories to investigate the effects of recent prescribed burning on snowshoe hare habitat use. Also, we used the stand shapefile to create 1-m × 1-m raster cells of distance to edge using the Euclidean distance tool in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA, USA).

To study the fine-scale habitat associations of snowshoe hares, we measured vegetation characteristics in a subsection of the study area that contained areas of use and non-use by hares. We placed a 50-m × 50-m grid randomly within the boundaries of the study area using ArcMap 10.1 and used the center point of each grid cell as vegetation sampling plot centers. We sampled plots only when leaves were absent (Jan–Apr).

From the center point of each grid cell, 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 3 density classes based on coverage of the board (low = 0–20%, medium = 21–80%, high = 81–100%) and we calculated total understory density by averaging the sum of all density measurements (0–2 m high) in each direction. We measured canopy cover by taking a hemispherical photo 1 m directly overhead the center point and analyzing the photos using Gap Light Analyzer Version 2.0 (Institute of Ecosystem Studies, Millbrook, NY, USA). Within a 10-m radius of the plot center, we counted all trees >2 m in height to estimate the number of trees per hectare.

Stand-Level Resource Selection

We estimated snowshoe hare resource selection at the stand level using a second-order (placement of home ranges within available habitat; Johnson 1980) negative binomial resource selection function (NB RSF). Unlike the approach of comparing used locations to available locations (Manly et al. 2002), the NB RSF accounts for the frequency of locations within specified sampling units (Nielson and Sawyer 2013). This analysis estimates intensity of use as a continuous response, rather than a binary response (used vs. unused). In addition, it addresses issues of temporally correlated locations because the response variable is the count of locations within a sampling unit over an extended time, instead of individual locations that have a timestamp associated with them (Nielson and Sawyer 2013).

We defined the stand-level seasonal analysis extent by calculating a 95% kernel density estimate (KDE) with reference bandwidth selection (href) using all locations from all hares in either winter or summer in R with the package adehabitat (Calenge 2006). Also, we excluded areas with very low probability of use such as large bodies of water or urbanized habitats. We did not find any shifts in home range or changes in movement rates during the breeding seasons; therefore, we conducted stand-level analyses in leaf-off (winter; Jan–Apr) and leaf-on (summer; May–Aug) seasons.

Over the analysis extent we systematically placed a grid of non-overlapping circular habitat units with 25-m radii and we counted the number of locations per hare within each unit. We selected this radius size to capture the spatial variability of habitats within the study area, while still including a large enough area to include multiple hare locations within each unit. The radius of the sampling units was greater than the estimated GPS location error (10 m; Feierabend and Kielland 2014, Gigliotti 2016), so we ignored this type of error.

For each habitat unit, we summarized the stand-level raster files by determining the dominant stand type based on the stand type with the highest percentage of raster cells by area. We chose to treat stand type as a categorical variable, rather than a continuous variable based on percentages of specific stand types within the habitat units to eliminate problems associated with correlations of percentages (Aebischer et al. 1993). We selected mature scrub oak as our reference category because we hypothesized that it would have high relative use based on its structure, and because it offered a contrast to the recently burned category that we were interested in. Also, we calculated the average distance of each habitat unit to the nearest stand edge using the distance raster. To facilitate the numerical optimization routine used to estimate the parameters of the NB RSF, we normalized the distance to edge covariate. To be able to use habitat units with centers near the analysis extent, we included a buffer of raster cells beyond the analysis extent. For summer and winter we considered *a priori* models: stand type, distance to stand edge, stand type and distance to edge, and an intercept only model.

Fine-Scale Resource Selection

To investigate fine-scale vegetation characteristics influencing patterns of winter snowshoe hare habitat use, we used a second-order (placement of home ranges within available habitat; Johnson 1980) and third-order (habitat selection within the extent of a home range; Johnson 1980) NB RSF. This allowed us to identify areas important to the general location of hare home ranges and important characteristics within home ranges of individual hares.

We placed a grid of non-overlapping 378 circular sampling units with 25-m radii within our vegetation sampling grid, with the center point of each sampling unit centered on the vegetation sampling grid cells. We created 50-m × 50-m raster cells from measurements taken in our vegetation grid and summarized these values for each sampling unit. Our covariates of interest included percent canopy cover, percent understory cover, and trees/ha. We estimated correlation between all covariates using a Pearson product-moment correlation statistic to determine if any should be excluded from analysis ($|r| > 0.75$).

Similar to our stand-level second order analysis, we defined analysis extent for our fine-scale second-order analysis by calculating a 95% KDE with reference bandwidth selection (href) using all locations from all hares in winter in R with the package adehabitat (Calenge 2006). For all fine-scale analyses, we used only individual hares that occupied the extent of the vegetation grid. We conducted second-order analysis using a zero-inflated negative binomial resource selection function (ZINB RSF) because of the large number of zero response values, whereas we used an NB RSF for the third-order analysis.

Analysis

For both scales of analysis, we estimated the ZINB RSF using program R (R Core Team 2014) using the zeroinfl function within package pscl (Zeileis et al. 2008), and the NB RSF using the R package MASS (Venables and 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. For our stand-level analysis, the presented estimates and confidence intervals for stand types are in relation to mature scrub oak, which was our reference category. Similarly, in our fine-scale analysis our understory density results are presented in relation to medium understory density (21–80% dense).

For both the stand-level analysis and the fine-scale analysis, 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 (Millspaugh et al. 2006, Thomas and Taylor 2006, Sawyer et al. 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) and defined variables of importance as variables with confidence intervals that did not overlap zero. We compared the models by summing the individual animal model Akaike's Information Criterion (AIC) values for a given model and selecting the model with the lowest total AIC value (Glenn et al. 2004, Zielinski et al. 2004). We calculated Akaike model weights and log-likelihoods for all models (Burnham and Anderson 2002). For all analyses we report the ranking of all candidate models and present the parameter estimates from the top models. For the fine-scale analysis, we used the best-fit population-level model to create a predictive surface across all habitat units. Using the values of relative use, we classified habitat units into 3 equal categories of high, medium, and low probability of use. We calculated average vegetative characteristics in each of the 3 categories and used the high use category as a reference for assessing snowshoe hare preferences (Sawyer et al. 2009).

RESULTS

Stand-Level Resource Selection

For winter stand-level analysis, we used locations from 30 GPS-collared hares. The number of locations per hare ranged from 118 to 3,663 ($\bar{x} = 1,166 \pm 917$ [SD]). The summer stand-level analysis included locations from 8 GPS-collared hares with the number of locations per hare ranging from 355 to 4,309 ($\bar{x} = 1,779 \pm 1,281$). Zero counts comprised 94.7% of winter habitat units and 94.3% of summer habitat units, indicating that a zero-inflated model was appropriate for analysis in both seasons. No covariates were correlated, so we included all covariates of interest.

During both winter and summer, stand-level snowshoe hare habitat use was best described by stand type and distance to stand edge (Table 1). Individual variation in habitat selection was present, but on the population level during the winter, areas of mature scrub oak had high intensity of use, whereas recently burned and open areas were avoided by hares (Table 2). Hares continued to use areas of mature scrub oak in the summer, and there was no difference in the intensity of use between mature scrub oak and either conifer or hardwood stands. Similar to winter, and hares did not select for recently burned or open areas in the summer (Table 2). The distance to stand edge was a positive predictor for snowshoe hare habitat use in winter, with hares selecting areas located near stand edges, with relatively no use occurring in areas >80 m away from a stand edge (Fig. 2). There was no effect of distance to edge during summer (Table 2).

Fine-Scale Resource Selection

We conducted fine-scale second-order and third-order winter habitat selection analysis using locations from 24 hares. The number of locations per hare ranged from 116 to 2,529 ($\bar{x} = 857 \pm 701$). Zero counts comprised 87.3% of the habitat units at the second order and 18.5% of habitat units at the third order. The extent of analysis contained canopy cover ranging from 5.8% to 92.9% and a mixture of low-, medium-, and high-density understory vegetation.

Fine-scale predictors of habitat use varied based on the scale of analysis. Second-order resource selection analysis indicated during winter snowshoe hare habitat use was best described by canopy cover, understory density, and tree density (Table 3). In particular, understory cover was an important variable for describing snowshoe hare winter habitat use, with hares selecting areas with low understory density (<20% visual obstruction) approximately 95% less than areas with medium understory density (21–80% visual obstruction), and 96% less than areas with high understory density (>81% visual obstruction; Table 4). Areas classified as high use had an average canopy cover of 57.1%

Table 1. Model selection results for winter and summer stand-level snowshoe hare resource selection models, Long Pond, Pennsylvania, USA, 2014–2015.

Season	Model	ΔAIC[a]	$-2 \times \ln(L)$[b]	Model likelihood	w_i[c]	K[d]
Winter	Distance to edge + stand type	0.0	27,698.4	1.0	1.0	7
	Stand type	272.0	27,972.4	0.0	0.0	6
	Distance to edge	1,336.0	29,040.4	0.0	0.0	4
	Intercept only	1,621.1	29,327.5	0.0	0.0	3
Summer	Distance to edge + stand type	0.0	8,781.0	1.0	1.0	7
	Stand type	67.4	8,850.4	0.0	0.0	6
	Distance to edge	759.4	9,546.4	0.0	0.0	4
	Intercept only	864.7	9,653.7	0.0	0.0	3

[a] Akaike's Information Criterion.
[b] Log-likelihood.
[c] Akaike model weight.
[d] Number of model parameters.

Table 2. Parameter estimates and associated 85% confidence intervals from the top winter and summer stand-level zero-inflated negative binomial resource selection models averaged from individual models of snowshoe hares in Long Pond, Pennsylvania, USA, 2014–2015. Mature scrub oak is the reference level and is included in the intercept term.

Season	Covariate	Estimate	SE	85% CI
Winter	Intercept	−7.95	0.81	−9.14 to −6.76
	Conifer	−1.35	1.14	−3.03 to 0.34
	Recently burned	−9.84	1.40	−11.91 to −7.76
	Hardwood	−1.34	0.97	−2.78 to 0.09
	Open	−9.34	1.48	−11.53 to −7.15
	Distance to edge	−0.89	0.15	−1.11 to −0.67
Summer	Intercept	−9.00	2.33	−12.75 to −5.24
	Conifer	−1.69	1.15	−3.56 to 0.16
	Recently burned	−10.87	3.87	−17.13 to −4.61
	Hardwood	−1.82	3.08	−6.80 to 3.16
	Open	−11.30	2.84	−15.89 to −6.72
	Distance to edge	−0.53	0.44	−1.24 to 0.17

(SE = 1.6%) and an average of 257 (SE = 14) trees/ha. Understory density distribution in high use areas was 45% high density, 55% medium density, and 0% low density. However, when we conducted the same analysis at the third order (within the home range of individual hares), canopy cover alone best described snowshoe hare habitat use (Table 5).

DISCUSSION

Studying the habitat preference of snowshoe hares in Pennsylvania offered insight into habitat relationships in fire-associated forests near the southern edge of this species' range. Regardless of season, hares in Pennsylvania did not select for recently burned areas (Table 2), likely because these areas did not offer sufficient concealment cover to hares. Although hares in Pennsylvania likely require more calories than hares at northern latitudes because of their larger body size (Gigliotti 2016), hares did not use recently burned stands, despite the high nutritional value of scrub oak post-fire (Woodwell et al. 1975, Hallisey and Wood 1976). This habitat use pattern suggests that predator avoidance outweighs the benefits of foraging in the newly burned areas. Previous research suggests that snowshoe hare predation rates are higher in areas with low tree and shrub cover compared to areas with higher vegetation density (Sievert and Keith 1985, Rohner and Krebs 1996). Although the burned areas offer substantial forage, the reduced cover in these areas compared to older forest stands likely was important in shaping the habitat use patterns of hares in our study area. The importance of vegetation structure is highlighted by the fact that the only important covariate associated with winter habitat use in our fine-scale analysis at the second order was understory cover, with hares avoiding areas with <20% visual obstruction (Table 4).

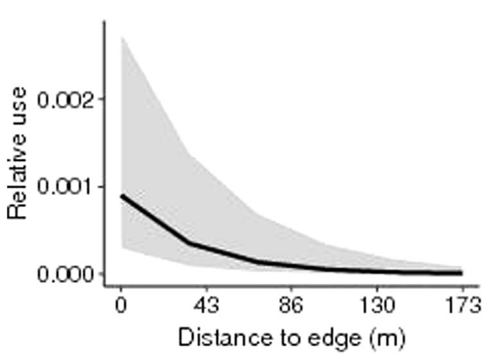

Figure 2. Relative winter habitat use by snowshoe hares ($n = 30$) as a function of distance to stand edges (shaded region represents 85% CI), Long Pond, Pennsylvania, USA, 2014–2015.

Previous research on snowshoe hare habitat use or occupancy in burned stands has mostly focused on long-term responses to burning (6–28 years post-fire, Paragi et al. 1997; 17–265 years post-fire, Hodson et al. 2011; 20–200 years post fire, Allard-Duchêne et al. 2014; 11–40 years post-fire, Cheng et al. 2015). Although these studies have been beneficial in determining the re-occupation rates of hares post-fire, examining post-burn habitat use at such a long time scale is not suitable in vegetation types that require more frequent burning, such as scrub oak barrens. Scrub oak barrens need to be burned 5–50 years to prevent growth into a closed canopy oak forest (Fryer and Luensmann 2012). Because we found that hares do not use burned stands for a minimum of 12–100% of the recommended burn interval for scrub oak, managers should attempt to intersperse prescribed burning into a larger matrix of older forest to ensure that hares have optimal vegetation to use in the years immediately post-burn. The practice of retaining vegetation refuges for hares has proven beneficial in other habitat management practices (de Bellefeuille et al. 2001, Potvin et al. 2005) and could be implemented into prescribed burn plans.

Snowshoe hares in Pennsylvania selected for areas of conifers, mature scrub oak, and hardwoods near the edge of stands. Previous research has not found scrub oak to be an important determinant of snowshoe hare habitat use, but scrub oak is not found throughout the majority of their range. However, in other parts of the hare's range, plant species with similar vegetative form, such as Gamble oak (*Quercus gambelii*), willow saplings, and speckled alder (*Alnus incana* subsp. *rugosa*), are understory species that are associated with snowshoe hare habitat use (Pietz and Tester 1983, Ewacha et al. 2014). Thus, it appears that structure rather than species affects snowshoe hare habitat use throughout their range.

Similar to the findings of this study, hares have been reported to be associated with conifer-dominated forests in Wyoming (Berg et al. 2012), Wisconsin (Buehler and Keith 1982), Colorado (Dolbeer and Clark 1975, Ivan et al. 2014), Utah (Dolbeer and Clark 1975), Alaska (Feierabend and Kielland 2014), Washington (Lewis et al. 2011), Maine (Litvaitis et al. 1985), and Minnesota (Pietz and Tester 1983), USA, and the Yukon (Strong and Jung 2012) and Nova Scotia, Canada (Orr and Dodds 1982). In general, conifer stands offer dense canopy cover to help hares avoid avian predators. In Alaska, hares trapped in black spruce (*Picea mariana*) stands were reported to have higher survival than hares trapped in deciduous stands (Feierabend and Kielland 2015). In this study, the conifer cover used by hares was mainly provided by planted pines and spruce. These plantations may be a surrogate for pine regeneration that

Table 3. Model selection results for second-order winter fine-scale snowshoe hare resource selection models, Long Pond, Pennsylvania, USA, 2014–2015.

Model	ΔAIC[a]	$-2 \times \ln(L)$[b]	Model likelihood	w_i[c]	K[d]
Trees/ha + canopy cover + understory density	0.0	14,066.5	1.0	1.0	8
Trees/ha + canopy cover	12.5	14,085.0	0.0	0.0	5
Canopy cover + understory density	16.7	14,085.2	0.0	0.0	7
Canopy cover	42.6	14,117.2	0.0	0.0	4
Understory density	48.8	14,119.3	0.0	0.0	6
Intercept only	53.5	14,130.0	0.0	0.0	3
Trees/ha	55.1	14,129.6	0.0	0.0	4

[a] Akaike's Information Criterion.
[b] Log-likelihood.
[c] Akaike model weight.
[d] Number of model parameters.

would have occurred naturally following major historical fire disturbances. As restoration efforts of the barrens continue, the natural interspersion of pitch pine, scrub oak, and planted conifers may create beneficial conditions for hares by creating a matrix of food and cover.

There was no difference between relative use of older scrub oak stands and hardwood stands in either winter or summer. Hares have been reported to use hardwood stands in other areas of their range (Litvaitis et al. 1985, Scott and Yahner 1989, Sultaire et al. 2016*b*), but these stands usually contain high densities of regenerating saplings, which provide food and cover. In our study area, dry oak hardwood stands represented the next successional state for the scrub oak barrens in the absence of fire (Latham et al. 1996, Maurice et al. 2004). Although these stands offered moderate amounts of understory vegetation, the understory of these stands was not as complex as scrub oak stands (Hallisey and Wood 1976). If fire continues to be excluded from this area, the resulting vegetation structure might not be as beneficial to hares than dense scrub oak stands resulting from burning.

We found that hares frequently used >1 stand type, which is consistent with research on hare habitat use in Alaska (Feierabend and Kielland 2014). By selecting home ranges that include >1 stand type, hares are potentially able to maximize the advantages provided by each stand type. In a habitat matrix that contains mature scrub oak and conifers, hares are able to benefit from the forage and understory cover of scrub oak and the dense canopies of conifer stands. When creating habitat management plans with regards to snowshoe hares, it is important to take the arrangement of stands in the landscape and the plant species that are present, into consideration.

We found edge use to be an important influence on snowshoe hare habitat use in winter (Fig. 2). Edges might be important for hares in the winter by offering an interspersion of optimal forage and dense cover for predator cover (Conroy et al. 1979, Wolff 1980). High dispersion between predation refuges and foraging habitats, as indicated by high edge densities, has been proposed as a mechanism of moderating snowshoe hare population dynamics (Liu et al. 2014). However, other studies reported a positive relationship between hare occupancy and distance to stand edges (Berg et al. 2012). The specific type of edge might be important to understanding snowshoe hare habitat preferences. For example, an edge of an open area might act as a barrier for movement, but animals might use areas in dense vegetation directly adjacent to an open area. In Quebec, Canada, hares were reported to forage on vegetation within forest gaps that were located near the edge of forested areas (Hodson et al. 2010). On the other hand, an edge between a conifer stand and a mature scrub oak stand might offer connectivity between 2 beneficial stand types. Because hares preferred multiple stand types within their home ranges, these stand intersections function as providing contiguous optimal habitat within these areas of high use. However, the strong preference for hares to use areas near stand edges might be confounded by the study area, which was comprised of many small stands and therefore most areas available to the hares were near a stand edge. The average distance from a stand edge was 35.0 ± 0.2 m and only 10% of the study area was located >80 m from a stand edge. Although our study area had a high edge density, if we considered only habitat preference at a small scale to account for edge density (e.g., only from 0 m to 35 m from edges), we would still see a negative relationship between distance and relative use. We also saw that distance to edge was significant only in winter. If the negative relationship between distance to edge and relative use was solely influenced by the high edge density, we would expect results to be similar in both summer and winter.

Table 4. Parameter estimates and associated 85% confidence intervals from the top winter second-order fine-scale zero-inflated negative binomial resource selection models averaged from individual models of snowshoe hares ($n = 24$) in Long Pond, Pennsylvania, USA, 2014–2015. Medium understory density is the reference category and is included in the intercept term.

Covariate	Estimate	SE	85% CI
Intercept	−5.96	0.38	−6.53 to −5.39
Canopy cover	0.01	0.01	0.00 to 0.02
Trees/ha	−0.001	0.00	−0.002 to 0.00
Low understory density (<20% dense)	−2.92	1.09	−4.55 to −1.29
High understory density (>81% dense)	0.25	0.24	−0.11 to 0.60

Table 5. Model selection results for third-order winter fine-scale snowshoe hare resource selection models, Long Pond, Pennsylvania, USA, 2014–2015.

Model	ΔAIC[a]	$-2 \times \ln(L)$[b]	Model likelihood	w_i[c]	K[d]
Canopy cover	0.0	7,340.9	1.0	0.9	4
Trees/ha + canopy cover + understory density	5.4	7,338.4	0.1	0.1	8
Canopy cover + understory density	5.9	7,340.8	0.1	0.0	7
Intercept only	5.7	7,348.8	0.1	0.0	3
Trees/ha	12.8	7,353.8	0.0	0.0	4
Understory density	13.1	7,350.1	0.0	0.0	6
Trees/ha + canopy cover	24.1	7,363.1	0.0	0.0	5

[a] Akaike's Information Criterion.
[b] Log-likelihood.
[c] Akaike model weight.
[d] Number of model parameters.

Even though snowshoe hares occupy areas with different dominant species of vegetation and exhibit different population dynamics based on their geographic location (Hodges 2000), hares usually select areas with dense vegetation cover (Litvaitis et al. 1985, Griffin and Mills 2009, Berg et al. 2012, Ivan et al. 2014), indicating the range-wide importance of this habitat feature, rather than plant species composition. By concentrating on structural determinants of optimal hare habitats rather than general forest type or dominant species, management strategies can be developed for the diversity of forests types over the extent of the hare's range to create and maintain habitat for this species. In addition, snowshoe hare range contraction has been more strongly associated with climate change than changes in forest structure (Burt 2014, Diefenbach et al. 2016, Sultaire et al. 2016*a*). Therefore, to potentially mitigate the effects of climate change, active habitat management might be essential for retaining the current distribution of this species.

MANAGEMENT IMPLICATIONS

Throughout their range snowshoe hares use habitats containing fire-adapted vegetation, but the number of years after burning before hares begin using these habitats is highly variable. In our study, snowshoe hares did not use areas of scrub oak 1–6 years post-burn, suggesting that the value of this vegetation community for hares may need to be considered on a longer time scale. Maintaining nearby areas of older, dense vegetation may allow for hare populations to persist until burned stands are used by hares. Within stands, hares selected for areas of dense understory vegetation and canopy cover, and areas <80 m from stand edges, so these characteristics should be created or maintained in managed habitats. In the absence of fire, mature scrub oak stands will revert to hardwood stands, which do not offer structural characteristics that are as beneficial to hares. Fire should be maintained in areas with fire-adapted vegetation, to ensure the continued availability of preferred snowshoe hare habitat.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank D. C. O'Leary, B. D. Smith, R. J. Ritson, and R. E. Scavotto who helped with the data collection for this research, and 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 D.S. Jachowski and 4 anonymous reviewers for providing comments that improved the manuscript.

LITERATURE CITED

Abrams, M. D. 1992. Fire and the development of oak forests. BioScience 42:346–353.

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Composition analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Allard-Duchêne, A., D. Pothier, A. Dupuch, and D. Fortin. 2014. Temporal changes in habitat use by snowshoe hares and red squirrels during post-fire and post-logging forest succession. Forest Ecology and Management 313:17–25.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Berg, N. D., E. M. Gese, J. R. Squires, and L. M. Aubry. 2012. Influence of forest structure on the abundance of snowshoe hares in western Wyoming. Journal of Wildlife Management 76:1480–1488.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81:1500–1516.

Brose, P. H. 2014. Development of prescribed fire as a silvicultural tool for the upland oak forests of the eastern United States. Journal of Forestry 112:525–533.

Brose, P. H., and D. H. Van Lear. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Canadian Journal of Forest Research 28:331–339.

Brown, J. S. 1988. Patch use as an indication of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Buehler, D. A., and L. B. Keith. 1982. Snowshoe hare distribution and habitat use in Wisconsin. Canadian Field-Naturalist 96:19–29.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media. New York, New York, USA.

Burt, D. M. 2014. Factors influencing snowshoe hare (*Lepus americanus*) in Michigan. Thesis, Michigan State University, East Lansing, USA.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Cheng, E., K. E. Hodges, and L. S. Mills. 2015. Impacts of fire on snowshoe hares in Glacier National Park, Montana, USA. Fire Ecology 11:119–136.

Conroy, M. J., L. W. Gysel, and G. R. Dudderar. 1979. Habitat components of clear-cut areas for snowshoe hares in Michigan. Journal of Wildlife Management 43:680–690.

de Bellefeuille, S. L. Bélanger, J. Huot, and A. Cimon. 2001. Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare. Canadian Journal of Forest Research 31:41–51.

Diefenbach, D. R., S. L. Rathbun, J. K. Vreeland, D. Grove, and W. J. Kanapaux. 2016. Evidence for range contraction of snowshoe hare in Pennsylvania. Northeastern Naturalist 23:229–248.

Dolbeer, R. A., and W. R. Clark. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. Journal of Wildlife Management 39:535–549.

Eberhardt, R. W., and R. E. Latham. 2000. Relationships among vegetation, surficial geology and soil water content at the Pocono mesic till barrens. Journal of the Torrey Botanical Society. 127:115–124.

Ewacha, M. V. A., J. D. Roth, and R. K. Brook. 2014. Vegetation structure and composition determine snowshoe hare (*Lepus americanus*) activity at arctic tree line. Canadian Journal of Zoology 92:789–794.

Feierabend, D., and K. Kielland. 2014. Movements, activity patterns, and habitat use of snowshoe hares (*Lepus americanus*) in interior Alaska. Journal of Mammalogy 95:525–533.

Feierabend, D., and K. Kielland. 2015. Seasonal effects of habitat on sources and rates of snowshoe hare predation in Alaskan boreal forests. PLoS ONE 10:e0143543.

Ferron, J., F. Potvin, and C. Dussault. 1998. Short-term effects of logging on snowshoe hares in the boreal forest. Canadian Journal of Forest Research 28:1335–1343.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35:51–81.

Fryer, J. L., and P. S. Luensmann. 2012. Fire regimes of the conterminous United States. Fire Effects Information System (FEIS). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana, USA.

Fuller, A. K., and D. J. Harrison. 2013. Modeling the influence of forest structure on microsite habitat use by snowshoe hares. International Journal of Forestry Research 2013:1–7.

Gigliotti, L. C. 2016. Ecology, habitat use, and winter thermal dynamics of snowshoe hares in Pennsylvania. Thesis, The Pennsylvania State University, State College, USA.

Glenn, E. M., M. C. Hansen, and R. G. Anthony. 2004. Spotted owl home-range and habitat use in young forests of western Oregon. Journal of Wildlife Management 68:33–50.

Griffin, P. C., and L. S. Mills. 2009. Sinks without borders: snowshoe hare dynamics in a complex landscape. Oikos 118:1487–1498.

Hallisey, D. M., and G. W. Wood. 1976. Prescribed fire in scrub oak habitat in central Pennsylvania. Journal of Wildlife Management 40:507–516.

Hodges, K. E. 2000. Ecology of snowshoe hares in southern boreal and montane forests. Pages 163–206 *in* L. Ruggiero, L. M. Aubry, S. Buskirk, G. M. Koehler, C. J. Krebs, K. Mckelvey, and J. R. Squires, editors . Ecology and conservation of lynx in the United States. University Press of Colorado, Denver, USA.

Hodson, J., D. Fortin, and L. Bélanger. 2010. Fine-scale disturbances shape space-use patterns of a boreal forest herbivore. Journal of Mammalogy 91:607–619.

Hodson, J., D. Fortin, and L. Bélanger. 2011. Changes in relative abundance of snowshoe hares (*Lepus americanus*) across a 265-year gradient of boreal forest succession. Canadian Journal of Zoology 89:908–920.

Ivan, J. S., G. C. White, and T. M. Shenk. 2014. Density and demography of snowshoe hares in central Colorado. Journal of Wildlife Management 78:580–594.

Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Joly, K., B. W. Dale, W. B. Collins, and L. G. Adams. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. Canadian Journal of Zoology 81:1192–1201.

Jordan, M. J., W. A. Patterson, and A. G. Windisch. 2003. Conceptual ecological models for the Long Island pitch pine barrens: Implications for managing rare plant communities. Forest Ecology and Management 185:151–168.

Keith, L. B., and D. C. Surrendi. 1971. Effects of fire on a snowshoe hare population. Journal of Wildlife Management 35:16–26.

Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267:74–92.

Lashley, M. A., C. A. Harper, G. E. Bates, and P. D. Keyser. 2011. Forage availability for white-tailed deer following silvicultural treatments in hardwood forests. Journal of Wildlife Management 75:1467–1476.

Latham, R. E., J. E. Thompson, S. A. Riley, and A. W. Wibiralske. 1996. The Pocono till barrens: shrub savanna persisting on soils favoring forest. Bulletin of the Torrey Botanical Club 123:330–349.

Lewis, C. W., K. E. Hodges, G. M. Koehler, and L. S. Mills. 2011. Influence of stand and landscape features on snowshoe hare abundance in fragmented forests. Journal of Mammalogy 92:561–567.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1985. Influences of understory characteristic on snowshoe hare habitat use and density. Journal of Wildlife Management 49:866–873.

Liu, R., D. L. DeAngelis, and J. P. Bryant. 2014. Dynamics of herbivores and resources on a landscape with interspersed resources and refuges. Theoretical Ecology 7:195–208.

Manly, B., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Maurice, K. R., J. M. Welch, C. P. Brown, and R. E. Latham. 2004. Pocono mesic till barrens in retreat: topography, fire and forest contagion effects. Landscape Ecology 19:603–620.

Millspaugh, J. J., R. M. Nielson, L. McDonald, M. John, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.

Nelson, J. L., E. S. Zavaleta, and F. S. Chapin. 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. Ecosystems 11:156–171.

Nielson, R. M., and H. Sawyer. 2013. Estimating resource selection with count data. Ecology and evolution 3:2233–2240.

Orr, C. D., and D. G. Dodds. 1982. Snowshoe hare habitat preferences in Nova Scotia spruce-fir forests. Wildlife Society Bulletin 10:147–150.

Paragi, T. F., W. N. Johnson, D. D. Katnik, and A. J. Magoun. 1997. Selection of post-fire seres by lynx and snowshoe hares in the Alaskan taiga. Northwestern Naturalist 78:77–86.

Pietz, P. J., and J. R. Tester. 1983. Habitat selection by snowshoe hares in north central Minnesota. Journal of Wildlife Management 47:686–696.

Potvin, F., N. Bertrand, and J. Ferron. 2005. Attributes of forest strips used by snowshoe hare in winter within clear-cut boreal landscapes. Canadian Journal of Forest Research 35:2521–2527.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robbins, C. 1983. Wildlife feeding and nutrition. Academic Press, New York.

Rohner, C., and C. Krebs. 1996. Owl predation on snowshoe hares: consequences of antipredator behaviour. Oecologia 108:303–310.

Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Frontiers in Ecology and the Environment 11:e15–e24.

Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.

Scott, D. P., and R. H. Yahner. 1989. Winter habitat and browse use by snowshoe hares, *Lepus americanus*, in a marginal habitat in Pennsylvania. Canadian Field-Naturalist 103:560–563.

Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management 49:854–866.

Strong, W. L., and T. S. Jung. 2012. Stand-level attributes of snowshoe hare (*Lepus americanus*) habitat in a post-fire trembling aspen (*Populus tremuloides*) chronosequence in Central Yukon. Canadian Field-Naturalist 126:295–305.

Sultaire, S. M., J. N. Pauli, K. J. Martin, M. W. Meyer, M. Notaro, and B. Zuckerberg. 2016*a*. Climate change surpasses land-use change in the contracting range boundary of a winter-adapted mammal. Proceedings of the Royal Society B 283:1–9.

Sultaire, S. M., J. N. Pauli, K. J. Martin, M. W. Meyer, and B. Zuckerberg. 2016*b*. Extensive forests and persistent snow cover promote snowshoe hare occupancy in Wisconsin. Journal of Wildlife Management 80:894–905.
Thomas, D., and E. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.
Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA.
Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecological Monographs 50:111–130.
Woodwell, G. M., R. H. Whittaker, and R. A. Houghton. 1975. Nutrient concentrations in plants in the Brookhaven oak pine forest. Ecology 56:318–332.
Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression models for count data in R. Journal of Statistical Software 27:8.
Zielinski, W. J., R. L. Truex, G. A. Schmidt, F. V. Schlexer, K. N. Schmidt, and R. H. Barrett. 2004. Resting habitat selection by fishers in California. Journal of Wildlife Management 68:475–492.

Associate Editor: Jamie Sanderlin.