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Climate Factors Related to Localized Changes in Snowshoe Hare (*Lepus americanus*) Occupancy

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Abstract

Information on climate that influences snowshoe hares (*Lepus americanus* Erxleben, 1777) can inform adaptation strategies. We identified climate factors correlated with localized changes in occupancy of snowshoe hares in Michigan, USA. A change in occupancy occurred if a site (approximately 7.5 ha) knowingly occupied by hares sometime in the past became unoccupied. We used local ecological knowledge to map sites where hares historically occurred and to assign a year of last known occupancy. At 134 historically occupied sites, we conducted snow track surveys in 2013 to determine current occupancy status. We identified climate variables having relevance to hare population demographics and modeled the likelihood that those variables influenced current occupancy status. The top-ranking model included maximum temperature from May 15 – January 19; as maximum temperature increased the likelihood of a site becoming unoccupied increased. The second ranked model included total number of days with measurable snow on the ground; as days with snow on the ground decreased, the likelihood of a site becoming unoccupied increased. Our data indicated that site occupancy status of hares can be described by climate variables and that the southern edge of snowshoe hare distribution in Michigan shifted northward by ~45 km over the last 20 years.

Key Words

Climate change, *Lepus americanus*, occupancy, snowshoe hare, southern range boundary

Introduction

The Great Lakes Region of the United States is projected to get warmer with more precipitation in the 21st century (Hayhoe et al. 2010). Warmer temperatures and snow that does not persist will likely have negative affects on species that are uniquely adapted to snowy or cold environments like snowshoe hares (*Lepus americanus* Erxleben 1777; Mills et al. 2013). Michigan is at the southernmost range boundary of hares in the Great Lakes Region of North America. Buehler and Keith (1982) noted that hare populations in this region will likely shift northward in response to a warming climate because of reduced duration of snow cover and depth. The processes of localized changes in occupancy status can be precursors to longer-term range contraction or expansion. For winter-adapted species, localized extinction caused by warming or drying climates can be difficult to document because the effects are potentially confounded by other stressors like changes in food abundance, competitors, or mismatched timing with host species (Cahill et al. 2013).

The population-level mechanisms causing range shifts in snowshoe hares are not well understood. Plausible hypotheses relate to direct effects on population vital rates and indirect effects on individual life history strategies (Bardsen et al. 2011). For example, some have suggested that hare productivity is lower during years with warmer summers, falls, and winters (Meslow and Keith 1971; Kielland et al. 2010); others have indicated that survival is lower during winters with more snow-free days (Kielland et al. 2010; Mills et al. 2013). Most support to date exists for the survival hypothesis as it relates to higher predation rates (Hone et al. 2011; Zimova et al. 2016).

During various phases of the 10-year population cycle at southern latitudes, mortality of snowshoe hares from predation can be >90% (Hodges 2000). Concealment is recognized as a

leading evolutionary force that influences pelage coloration among mammals (Caro 2005); molting at the proper time is critical to the survival of individual hares (Mills et al. 2013; Zimova et al. 2016). Molt initiation dates for hares in Maine and Montana (USA) began in late September and early April, and research to date indicates that onset of the fall molt exhibits low plasticity (Severaid 1945; Mills et al. 2013; Zimova et al. 2014). Climate data suggest that the number of days with snow on the ground throughout much of the southern distribution of hare range has decreased by up to 25 days from 1972-2004 (Choi et al. 2010). By the end of the 21st century, duration of snow cover throughout the entire range of snowshoe hares is expected to significantly decrease (Brown and Mote 2009).

Long-term data sets suitable for documenting shifts in species distribution have historically relied on museum records (Newbold 2010). More recently, traditional or local ecological knowledge (TEK or LEK, respectively) has been identified as an accurate source of information about wildlife (Gilchrist et al. 2005; Charnley et al. 2007; Jacqmain et al. 2007; Jordan et al. 2012; Polfus et al. 2014). Traditional or local ecological knowledge is based on individual experiences or familiarity with local history. The utility of TEK or LEK depends on the complexity of the information sought (e.g., species occurrence is more reliable than counts) and the type of experience (e.g., hunting is more reliable than casual observation; Anadón et al. 2009; Cook et al. 2014). Here, we relied on LEK to portray the historical distribution of snowshoe hares in Michigan.

Hunter trend data (Frawley 2015), persistent stakeholder concerns about hares disappearing from the Michigan landscape, and results from biologist and hunter surveys all suggested a long-term decline in hares, leading us to hypothesize that factors other than the

population cycle were negatively affecting hares. We identified and described the relationships between climate factors and localized changes in hare occupancy status, focusing on sites that were historically occupied. Our study occurred near the southern boundary of hares, where climate effects should be most pronounced. Our results have relevance to recently published vulnerability assessments on hare (e.g., Hoving et al. 2013), and suggest potential population-level mechanisms causing localized changes in occupancy status. Additionally, our results can inform climate adaptation strategies, like providing dense cover in areas experiencing reduced snowfall.

Materials and Methods

Study Area

We conducted our study in the Upper and northern Lower Peninsulas of Michigan on publically owned lands during the winter of 2013. This spatial extent corresponds to the known historic distribution of snowshoe hares in Michigan (Fig. 1). Primary vegetation types varied by ecoregion but included northern hardwoods, aspen (*Populus* spp.), upland conifers (white pine (*Pinus strobus* L.), red pine (*P. resinosa* Aiton), jack pine (*P. banksiana* Lamb.)), hardwood-conifer and conifer swamps, and wet meadows (Albert 1995). The western Upper Peninsula experiences the most extreme winters and shortest growing seasons (Albert 1995). Monthly average temperatures ranged from -10°C to 17°C, with average annual precipitation of 90 cm, including 435 cm of snowfall (NOAA, 2012). In the eastern Upper Peninsula, monthly average temperatures varied from -10°C to 18°C with average annual precipitation of 80 cm, including 194 cm of snowfall (NOAA 2012). The climate of coastal areas in the northern Lower Peninsula is moderated by Lakes Huron and Michigan resulting in warmer and cooler temperatures in

winter and summer, respectively. Monthly average temperatures ranged from -8°C in January to 20°C in July, with average annual precipitation of 90 cm, including 169 cm of snowfall (NOAA 2012).

Site Selection

We interviewed 45 individuals that had reliable local knowledge of historical snowshoe hare locations in Michigan. Interviewees included Michigan Department of Natural Resources employees, hare hunters, and tribal members and biologists. Each interviewee was asked to map locations that, based on their experiences, were unequivocally occupied by snowshoe hares sometime in the past. Unequivocal evidence included tracks, harvested hares, or observed hares. Each interviewee was asked to estimate the year of last confirmed occupancy within 5 yrs. We compiled potential study sites from the locations provided by interviews and selected a subset of locations that encompassed broad spatial (throughout hare range in Michigan; Fig. 1) and temporal (1955-2010; Fig. 2) domains. Study sites selected for sampling were separated by >1.6 km (mean = 10.2 km, SE = 0.7). Our interview protocol was reviewed and approved by the Human Research Protection Program, Institutional Review Board, at Michigan State University (IRB# x11-805).

Field Sampling

Winter track counts along transects are commonly used to document snowshoe hare occupancy and habitat use (Brocke 1975; Conroy et al. 1979; Thompson et al. 1989). We used 9 transects that were each 125 m long and spaced 75 m apart. We previously demonstrated that hare occupancy at sites could reliably ($>90\%$ probability) be estimated using this configuration, even at low hare densities (Burt et al. 2016). Our transect configuration encompassed

approximately 7.5 ha, roughly corresponding to the size of snowshoe hare home ranges documented in the literature (summarized in Wolff 1980). Sampling for snowshoe hares occurred on a single day from December to March in 2013 and was completed 12-72 hours after fresh snowfall to allow for track accumulation. If a track was detected on ≥ 1 transect at a site, then the site was designated as occupied; sites without tracks were deemed unoccupied.

Climate Covariates

We conducted a review of scientific publications that evaluated how climate influenced snowshoe hare population demographics. We identified 4 precipitation and 3 temperature variables (Table 1). The precipitation variables included mean snow depth (SD) in an annual snow season (approximately November through April), total number of days with measurable snow on the ground (DSoG) during the snow season, total number of days with a snowfall event (DSE), and total spring precipitation from March 20 – June 20 (spring precipitation; Table 1). Temperature variables included mean minimum temperature from February 4 – April 24 (minimum winter temperature), mean maximum temperature from May 15 – January 19 (maximum temperature), and mean winter temperature from December 21 to March 19 (mean winter temperature; Table 1).

We compiled climate covariates for each snowshoe hare survey site from the closest National Oceanic and Atmospheric Administration (NOAA) weather station that had archived data for all 7 variables dating back to the year of last known hare occupancy (<http://www.ncdc.noaa.gov/>). We used 35 weather stations and calculated average annual values from the year of last known occupancy to 2012. Although climate data from some sites came from the same weather station, times of last known occupancy often varied among those

sites so the average climate conditions tended to differ. Additionally we accounted for the potential effects of weather station redundancy in our logistic regression model.

Data Analysis

We analyzed all combinations of climate covariates for collinearity using Pearson's correlation coefficient (Sokal and Rohlf 2011); covariates were considered correlated if $r \geq |0.15|$ and $p \leq 0.05$. Correlated covariates were not used in the same candidate model. We modeled the likelihood that a site (approximately 7.5 ha) became unoccupied from year of last known occupancy using logistic regression. We included a random effect for each weather station to account for autocorrelation among sites that used the same weather station data. We created a candidate set of models ($n=9$; Table 2) from all possible combinations (additive terms) of uncorrelated climate variables. We ranked models based on Akaike Information Criteria (AIC) and parameter estimates were deemed significant if the 95% confidence intervals did not overlap 0 (Burnham and Anderson 2002; Nakagawa and Cuthill 2007). We subsequently used our top-ranking models with significant parameter estimates to predict the climate values that would result in >90% probability that a site would become unoccupied given a warming climate. We assumed that a warming climate corresponded to higher summer temperatures, fewer days with snow on the ground, and reduced snow depths (Mortsch and Quinn 1996; Hayhoe et al. 2010).

Results

Our interviews resulted in 386 potential study sites with year of last known hare occupancy ranging from 1955 to 2010 (Fig. 2); climate data were compiled for 134 of those sites. Most climate variables were correlated except for spring precipitation and DSoG and spring

precipitation and SD. Regardless of the climate variable, we documented a broad range of minimum and maximum values and considerable variation in measurements across sites (Table 3). These results typify the temperature and precipitation variation often found at small scales in Michigan; caused by a combination of lake effect, topography, and prevailing direction of weather fronts.

Statewide, we found that 52 of 134 sites (39%) became unoccupied. In the Lower Peninsula 36 of 74 sites (~49%) were unoccupied. Only 16 out of 60 (~27%) sites were unoccupied in the Upper Peninsula. Our results indicated almost a two-fold increase in unoccupied sites in the southern versus the northern Peninsulas of Michigan.

All candidate models for describing change in occupancy of snowshoe hares received some support (i.e., $\omega_i \geq 0.01$), but our top-ranking model included maximum temperature between May 15 and January 19 and accounted for 53% weight of evidence (Table 2). As maximum temperature increased the likelihood of a site becoming unoccupied significantly increased ($\beta = 0.043$, 95% CI = 0.013 – 0.087; Table 2). The second ranked model included DSoG and accounted for 15% weight of evidence (Table 2). The model indicated that as the number of days with snow on the ground decreased, the likelihood of a site becoming unoccupied significantly increased ($\beta = -0.026$, 95% CI = -0.054 – -0.004). All other models received minimal support (i.e., $\omega_i \leq 0.10$) and only one additional significant covariate was identified (SD). As SD decreased, the likelihood of a site becoming unoccupied extinction increased ($\beta = -0.004$, 95% CI = -0.0091 - -0.0004).

Mean maximum temperature since time of last known hare occupancy ranged from 13 to 17°C across our study sites, corresponding to a 3-fold increase in the likelihood of a site

becoming unoccupied on warmer sites (Fig. 3a). Model projections indicated >0.90 probability of a site becoming unoccupied if mean average maximum temperatures exceed 21.2°C. Average days with snow on the ground in our study ranged from 60 to 140; sites with fewer days were >3 times more likely to become unoccupied (Fig. 3b). Model projections indicated that sites with <3 days with snow on the ground would have a >0.90% probability of becoming unoccupied. Average snow depths in our study ranged from 100 to 600mm; sites with lower snow depth were ~1.5 times more likely to become unoccupied (Fig. 3c). Model projections indicated that even with low average snow depths (1 mm), the probability of a site becoming unoccupied was still <0.60. Because these three climate covariates were correlated and significant in our models, our results suggest that maximum temperature, days with snow on the ground, and snow depth have an integrated effect on the likelihood of sites becoming unoccupied by snowshoe hares.

Discussion

We sampled a broad spatial and temporal domain throughout the range of snowshoe hares in Michigan and found that climate variables were significantly correlated to local changes in occupancy status. Our findings substantiate assessments that hares are vulnerable to climate change (Hoving et al. 2013; Mills et al. 2013; Diefenbach et al. 2016; Saultaire et al. 2016). We demonstrated a greater percentage of unoccupied sites closer to the southern range periphery, but also found unoccupied sites throughout the Upper Peninsula suggesting that factors other than climate were affecting localized hare populations. Sites with warmer temperatures from summer to early winter, fewer days with snow on the ground, and shallower snow depths were more likely to become unoccupied by hares. Population mechanisms potentially linked to

unoccupied sites include reduced litter sizes from higher temperatures (Meslow and Keith 1971), increased predation from fewer days with snow on the ground (Kielland et al. 2010; Mills et al. 2013; Zimova et al. 2016), and less food availability during periods of low snow depths (Bider 1961; Meslow and Keith 1971; Conroy et al. 1979).

The probability for localized occurrence of hares is likely the result of interacting demographic processes, including fluctuating rates of adult and juvenile survival, and births (Meslow and Keith 1968). The effects of individual climate variables (e.g., maximum temperatures from summer to early winter) are undoubtedly correlated across these demographic responses. For example, we found that maximum temperatures from summer to early winter were negatively correlated with the number of days with snow on the ground and snow depth. Although Meslow and Keith (1971) found that summer to early winter temperatures were correlated with reduced fecundity in hares, another potential interpretation is that this climate covariate encompassed a suite of environmental conditions that affect hare fecundity and survival across the year. These responses for the genus *Lepus* may include reduced survival from pelage-environmental mismatch (Zimova et al. 2016) and reduced reproduction caused by predation stress (Boonstra et al. 2014), increased fitness from climate-related improvements in habitat quality and quantity (Schrama et al. 2015; Tape et al. 2016), reduced survival from climate induced changes in ectoparasites or intestinal flora (Posautz et al. 2015), and reduced survival from increases in spring rains (Rodel and Dekker 2012).

Our results are consistent with studies that have explored climate-related mechanisms associated with population declines for other species. Average temperature and sum of precipitation in June were the strongest predictors of the numbers of brown hare (*L. europaeus*

Pallas, 1778) during fall and winter in Hungary (Beukovic et al. 2013). Lee et al. (2000) found that warmer weather and wetter winters resulted in fewer reindeer (*Rangifer tarandus* Linnaeus, 1758) calves in northern Finland and Norway. Higher total rainfall in spring was correlated with a smaller proportion of breeding in wild pig (*Sus scrofa scrofa* Linnaeus, 1758) females the following season (Sabrina et al. 2009). While deep snows impose higher energetic costs to hares (Hodges et al. 2006), similar to findings observed for Alpine red deer (*Cervus elaphus* sp. Linnaeus, 1758; Schmidt 1993; Rivrud et al. 2010) and moose (*Alces alces* Linnaeus, 1758; Dussault et al. 2005), our results indicated that deeper snows benefit snowshoe hares. We speculate that our study sites with deeper winter snows corresponded to areas with lower deer (*Odocoileus virginianus* Zimmermann, 1780) browse pressure, thereby increasing the structural complexity of understory vegetation and amount of browse available to hares during the winter (Bider 1961; Meslow and Keith 1971; Conroy et al. 1979).

Although our results suggest that multiple climate factors influence snowshoe hare occupancy status, these factors likely interact with predator-prey relationships, vegetation structure, spatial arrangement of habitats, and food availability. Indeed, Burt (2014) found evidence for a significant vegetation structure effect in this study, and some minimal support for a predator effect. Predators are the primary cause of mortality for snowshoe hares and early winter is a time of increased predation from mammalian predators (Hodges 2000). With a changing climate that results in fewer days with snow on the ground, coupled with a relatively fixed timing of the fall molt in hares (Mills et al. 2013), the camouflage advantages of white pelage are negated (Zimova et al. 2016). Increased predation pressure resulting from compromised camouflage can also have negative indirect effects on hare body condition and

fecundity (Hodges et al. 1999; Boonstra et al. 2014). Increased predation pressure, indirect effects of predation on fitness, and decreased litter sizes associated with warmer maximum temperatures likely interact to result in sites unoccupied by hares.

Most of the Upper Peninsula of Michigan is estimated as poor to marginal snowshoe hare habitat (Linden et al. 2010). Snowshoe hare populations tend to thrive in continuously forested areas with dense understories (>60% visual obstruction) that provide food, safety from predators, and thermal cover (Litvaitis et al. 1985). Hare survival rates are lower in areas with sparse horizontal cover (Litvaitis et al. 1985). Sparse understory cover exacerbates higher predation pressures already caused by fewer days with snow on the ground. Additionally, lower mean snow depths can restrict access to forage during critical winter months (Bider 1961; Meslow and Keith 1971; Conroy et al. 1979). Although food availability does not appear to limit hares during winter (Conroy et al. 1979; Carreker 1985), low levels of understory cover coupled with decreased snow depths potentially concentrates hares and restricts access to high quality forage. The effective browse height for snowshoe hares is about 46 cm and browsing efficiency is maximized when snow depths increase throughout the winter making new browse available (Bider 1961).

Based on future climate projections indicating warming and wetter conditions in the Great Lakes Region (Hayhoe et al. 2010), our results suggest that the southern edge of snowshoe hare range will continue to move northward. This result is consistent with patterns of hare distribution observed in other states of this region (e.g., Pennsylvania, Diefenbach et al. 2016; Wisconsin, Saultaire et al. 2016). Abundant and diverse predators and poor habitat conditions will likely exacerbate this change. In Michigan, we found that the current

distribution of snowshoe hares at the southern edge of the range shifted northward by ~45 km over the last 20 years. An important unanswered question is whether management focused on reducing predator numbers or improving hare habitat quality and connectivity can help reduce the negative impacts of climate change. The loss of snowshoe hares from Michigan would have important ecological and cultural ramifications and hence developing and testing strategies for conserving this species during periods of rapid climate change are needed.

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Table 1. Climate covariates identified from the literature review, citation, and observed or inferred relationship to snowshoe hare (*Lepus americanus* Erxleben, 1777) population demographics.

Variable	Citation(s)	Importance to hares
Mean snow depth (SD)	Bider 1961, Meslow and Keith 1971, Conroy 1979, Hodges et al. 2006, Kielland et al. 2010	Increased snow depth creates different browse availability and increased energetic costs
Total number of days with measureable snow on the ground (DSoG)	Kielland et al. 2010, Mills et al. 2013	Incorrect pelage coloration for crypsis with lack of snow on the ground during winter months
Total number of days with a snowfall event	Kielland et al. 2010, Meslow and Keith 1971	Decreased juvenile and adult survival with more snowfall
Total spring precipitation (March 20 – June 20)	Kielland et al. 2010	Duration of decline phase associated with increased spring precipitation
Mean minimum temperature (February 4 – April 24)	Meslow and Keith 1971	Warmer minimum temperatures during this time period, the greater the adult survival
Mean maximum temperature (May 15 – January 19)	Meslow and Keith 1971	Colder temperatures during this period were associated with larger litter sizes in subsequent breeding seasons
Mean winter temperature (December 21 – March 19)	Kielland et al. 2010	Warmer temperatures during this time period associated with the decline phase of the snowshoe hare cycle

Table 2. Candidate model set for estimating the likelihood of a site (~7.5 ha site) becoming unoccupied by snowshoe hares (*Lepus americanus* Erxleben, 1777) in Michigan. LL = log-likelihood, AICc = Akaike Information Criteria adjusted for small sample sizes, k = model parameters, ω_i = Akaike weight of evidence, β = beta coefficients for model variables.

Candidate Model ^a	LL	AICc	K	ω_i	β (SE)
Maximum temperature	-85.23	176.65	3	0.53	0.043 (0.018)
Days snow on ground (DSOG)	-86.51	179.21	3	0.15	-0.026 (0.012)
DSOG + Spring precipitation	-85.80	179.90	4	0.10	-0.023 (0.010), 0.001 (0.0005)
Snow Depth (SD)	-87.04	180.27	3	0.09	-0.004 (0.002)
SD + Spring precipitation	-86.59	181.50	4	0.05	-0.020 (0.011), 0.001 (0.0005)
Days snowfall event (DSE)	-88.10	182.39	3	0.03	-0.018 (0.012)
Mean winter temperature	-88.34	182.86	3	0.02	0.017 (0.012)
Spring precipitation	-88.42	183.03	3	0.02	0.001 (0.0005)
Minimum winter temperature	-89.10	184.38	3	0.01	0.010 (0.012)

^a Maximum temperature = mean maximum temperature between May 15 and January 19; Days snow on ground = Total number of days with measurable snow on the ground in an annual snow season (approximately November through April); Spring precipitation = total spring precipitation from March 20 thru June 20; Snow depth = Mean snow depth in an annual snow season; Days snowfall event = Total number of days with a snowfall event in an annual snow season; Mean winter temperature = Mean winter temperature from December 21 thru March 19; Minimum winter temperature = Mean minimum temperature from February 4 thru April 24.

Table 3. Means (SE) and ranges of climate covariates used for estimating the likelihood of a site becoming unoccupied by snowshoe hares (*Lepus americanus* Erxleben, 1777) in Michigan. Climate data were compiled from 35 weather stations that occurred throughout the study area (NOAA 2012).

Variable	Mean	SE	Range
Mean snow depth (SD; mm)	234.40	9.55	107 - 562
Total number of days with measureable snow on the ground (DSoG)	108.26	1.59	61 - 145
Total number of days with a snowfall event	49.81	1.52	20 - 90
Total spring precipitation (March 20 – June 20; mm)	221.80	29.69	150.1 - 310.3
Mean minimum temperature (February 4 – April 24; °C)	-6.24	0.14	-9.8 - -2.7
Mean maximum temperature (May 15 – January 19; °C)	14.96	0.12	12.6 – 17.6
Mean winter temperature (December 21 – March 19; °C)	-5.52	0.14	-9.2 - -1.4

Figure Captions

FIGURE 1. Location and occupancy status of snowshoe hare (*Lepus americanus* Erxleben, 1777) survey sites throughout the northern Lower and Upper Peninsulas of Michigan, USA, winter 2013. The geographic range of snowshoe hares and Michigan are portrayed in the map inset. The geographic range was derived from the International Union for Conservation of Nature (www.iucnredlist.org/technical-documents/spatial-data#mammals).

FIGURE 2. Number of study sites and year (5-year groupings through 2010) of last confirmed snowshoe hare (*Lepus americanus* Erxleben, 1777) occupancy in the northern Lower and Upper Peninsulas of Michigan, USA. Study sites were compiled from local ecological knowledge.

FIGURE 3. The probability of a localized site (~7.5 ha) becoming unoccupied by snowshoe hares (*Lepus americanus* Erxleben, 1777) and (A) mean maximum temperature during May 15 – January 19, (B) number of days with snow on the ground, and (C) mean snow depth in Michigan, USA.

Location and occupancy status of snowshoe hare (*Lepus americanus* Erxleben, 1777) survey sites throughout the northern Lower and Upper Peninsulas of Michigan, USA, winter 2013. The geographic range of snowshoe hares and Michigan are portrayed in the map inset. The geographic range was derived from the International Union for Conservation of Nature (www.iucnredlist.org/technical-documents/spatial-data#mammals).

Fig. 1
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