LETTER

An experimental translocation identifies habitat features that buffer camouflage mismatch in snowshoe hares

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Funding Information
National Institute of Food and Agriculture, Grant/Award Numbers: Hatch Project 1003605, Hatch Project 1006604

Abstract
Conservation for species impacted by climate change often occurs at scales impractical for local land managers. Snowshoe hares (Lepus americanus) are one of the most well-documented species declining from climate change—specifically a reduction in snowcover—yet clear management strategies have yet to emerge. To test whether camouflage mismatch is reducing hare survival we translocated 96 hares to a site recently extirpated of snowshoe hares, and monitored coat color change, mismatch with snow, habitat use, and weekly survival in winter-spring of 2017. Hare survival was low during periods of camouflage mismatch, and mismatched hares were 3.2 × less likely to survive, but this pattern varied by habitat. We found that aspen-alder stands >5 hectares negated the mortality costs of mismatch. We provide experimental evidence that mismatch is driving the range contraction of snowshoe hares, and identify specific habitats to buffer the consequences of climate change on this declining winter specialist.

Keywords
alder, aspen, coat color, molt, phenology, range shift, reintroduction, varying hare

1 INTRODUCTION

Climate change has altered the distribution of many species (Parmesan, 2006), with nearly 90% of mammals and >95% of amphibians predicted to experience range contractions by the end of the century (Lawler, Shafer, Bancroft, & Blaustein, 2010; Schloss, Nuñez, & Lawler, 2012). The majority of these contractions will involve poleward shifts, currently occurring at a median rate of 16.9 km/decade (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). Although mechanisms behind some range shifts have been identified (Yang & Rudolph, 2010), most remain unknown (Cahill et al., 2013). This lack of a mechanistic understanding has placed conservation managers, particularly those operating at local scales (i.e., individual reserves, parks, or private properties), in challenging positions as they possess limited options for on-the-ground efforts to reduce climate-driven extirpations (Mawdsley, O’Malley, & Ojima, 2009).

One strategy in climate change conservation involves reintroductions to reestablish species to portions of their historic range, as well as regions where future climatic conditions are expected to be suitable (Seddon, 2010). However, reintroductions are often economically and logistically impractical (Seddon, Armstrong, & Maloney, 2007), and in isolation, do not address the causes of population decline (Seddon, 2010). Conservation biologists have also explored identifying areas that could serve as refugia for vulnerable species until climatic conditions return to historic norms and species can recolonize former parts of their range (Hannah et al., 2014). However, there are problems in
identifying static refugia for species (Ashcroft, 2010) during a time of rapid climate change (Keppel et al., 2012). The limited options available to local land managers present challenges (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010), not only for managing individual species, but for conservation of ecological communities (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013). This is particularly important at northern latitudes where dramatic shifts in species ranges and communities are occurring at rates unprecedented in modern times (Myers, Lundrigan, Hoffman, Haraminac, & Seto, 2009).

Snowshoe hares (Lepus americanus) are central in food webs across northern forests of North America (Krebs, 2011) and in our understanding of population dynamics and predator–prey interactions (Keith & Windberg, 1978). The direct (Krebs, Boonstra, & Boutin, 2018) and indirect effects of predation (MacLeod, Krebs, Boonstra, & Sheriff, 2018) predominately drive snowshoe hare population fluctuations. A key strategy in their overwinter survival is camouflage as predator-avoidance (Mills et al., 2013). Hares are among 21 vertebrate species that change coat or plumage color to match snow conditions (Zimova et al., 2018). Timing of coat color change is dependent on photoperiod, and periods of camouflage mismatch occur when molting is misaligned with the duration of snow cover (Mills et al., 2013)—resulting in white hares contrasting conspicuously against a brown vegetative background. Given that snowshoe hares lack avoidant behavioral responses to predators in the face of mismatch (Zimova et al., 2018), periods of mismatch are associated with increased predation and decreased survival among hares (Zimova, Mills, & Nowak, 2016). Under future climate change scenarios periods of camouflage mismatch are predicted to increase up to 8× over the next century (Mills et al., 2013). Although polymorphisms for winter coat color in snowshoe hare exist in regions with historically shorter and more variable snow duration, they are absent across the majority of the range distribution, leaving little prospect of evolutionary adaptability in these regions (Mills et al., 2018).

Snowshoe hares have experienced a recent northward range-shift along much of their trailing range boundary (Burt, Roloff, & Etter, 2016; Sultaire et al., 2016a). Repeated track surveys over a 70-year period in Wisconsin have documented an 8.7 km/decade range contraction since 1980 (Buehler & Keith, 1982; Leopold, 1945; Sultaire et al., 2016a). This research has linked snowshoe hare range contractions with decreased snowpack duration (Sultaire et al., 2016a), but has also shown that land use change (Buehler & Keith, 1982), especially the amount of forest cover, was important to historical range contractions (Sultaire, Pauli, Martin, Meyer, & Zuckerberg, 2016b). Snowshoe hares strongly select for forests featuring dense understory (Litvaitis, Sherburne, & Bissonette, 1985), and experience reduced predation (Sievert & Keith, 1985) as well as greater population stability (Griffin & Mills, 2009) within those habitats. Habitat loss and climate change can synergistically increase the probability of extinction (Mantyka-Pringle, Martin, & Rhodes, 2012). However, the relative contributions and potential interplay of camouflage mismatch and habitat in driving the extirpation of snowshoe hare populations along the southern range boundary is unknown.

To disentangle the relative influence of camouflage mismatch and habitat we took an experimental approach to temporarily resurrect a snowshoe hare population that now falls outside of their current distributional range. Specifically, we translocated snowshoe hares from a source population located within the species’ current distribution to a site formerly occupied by hares but now functionally extirpated (Keith, Bloomer, & Willebrand, 1993), and documented the processes causing extirpation. We hypothesized that camouflage mismatch due to decreased snow duration would be the ultimate cause of snowshoe hare extirpation and predicted that hares would experience extended periods of mismatch, wherein mismatched hares would be vulnerable to predation. We also predicted that the availability of high-quality habitat (i.e., high understory cover) would dampen the effect of mismatch. By documenting the causes of past and potential future population extirpation, and identifying those environmental features that interact with climate change to shape the range boundary of this species, we aimed to provide conservation managers with actionable information to slow the pace of range contraction under rapidly changing conditions.

2 | METHODS

2.1 | Data collection

We captured snowshoe hares for translocation from a population in the Chequamegon National Forest (45.293° N, 90.505° W) from 14 January to 15 February 2017. We then translocated hares 137 km to Sandhill Wildlife Area (44.307° N, 90.129° W; hereafter Sandhill; Figure 1). Traps (Type 204, Tomahawk Live Trap, Tomahawk, WI) were baited with alfalfa cubes, apples, and rabbit feed. We weighed hares, determined sex, and then outfitted each hare with a VHF radio-collar equipped with a mortality sensor (M1575, Advanced Telemetry Systems, Isanti, MN). Hares were transported to Sandhill in pet carriers and housed in one of three 9 m² chain-link enclosures (Figure 1) enriched with food and cover to provide a “soft release” after 2 days. We monitored survival of released hares daily via radiotelemetry and surveyed mortality sites to determine cause of mortality and identify predator species. All protocols conformed with the American Society of Mammalogists guidelines for use of wild mammals in research (Sikes et al., 2011).
Beginning 27 February 2017, we randomly selected 25 translocated hares to assess the timing of coat color change in relation to snow cover. Each week we visually observed each hare and recorded the percent of the hare’s coat that was white, as well as the percent of ground covered by snow within a 10 m radius of the hare (Mills et al., 2013), both in bins of 10% increments (e.g., 0–10%). Additionally, we recorded the GPS location and photographed the hare and surrounding ground to validate recorded values. Color contrast is defined hereafter as the absolute value obtained by subtracting percent snow cover by the percent of a hare’s coat color that was white, whereby a fully matched hare was scored as 5% and a fully mismatched hare was 95%, and an individual is considered “mismatched” when color contrast was ≥60% (Mills et al., 2013, Supplementary Methods). As hares within the original sample of 25 individuals were lost to mortality, we randomly added new individuals to maintain a minimum sample size of 20 individuals observed each week.

### 2.2 Data analysis

We quantified vegetation within Sandhill using five habitat classes: “aspen-alder,” “mature forest,” “clear-cut,” “open,” and “other” (Supplementary Methods). We used hare relocations recorded during the measurement of mismatch to assess relationships between habitat composition and configuration and hare survival. Each relocation was buffered by a 180 m radius circle representing the mean nightly movement distance of hares under snow-free conditions (Griffin, Griffin, Waroquiers, & Mills, 2005), and all relocations were merged into a single feature for each individual hare to reduce pseudo-replication where multiple buffers overlapped. We used FRAGSTATS (McGarigal, Cushman, & Ene, 2012) to calculate class-level mean estimates of percent cover for all covertypes and patch size and contiguity index for aspen-alder and mature forest within buffers.

#### 2.2.1 Hare survival

To test hypotheses about the survival of hares along the current southern range boundary, we constructed known-fate models in Program MARK (White & Burnham, 1999), at two different scales. First, to compare survival between periods of hares being mismatched as well as matched with their environments, we estimated survival of all hares released during the translocation, excluding 10 individuals right-censored due to collar failure, between January 14 and May 31 when daily mortality checks ceased (hereafter, the whole population analysis). Because a subset of hares were tracked for mismatch and habitat use, we used population-level covariates in this analysis (i.e., all individuals had the same time-varying covariate values). We included the mean color contrast for all hares monitored during each sampling period (1 week) as a time-varying covariate. We included mean percent whiteness of coat color and snow cover as time-varying covariates. Inclusion of coat color and snow cover allowed us to test alternative hypotheses as to the potential effects of seasonal change or coat color change independent of the other. We included release site (Figure 1) as a grouping covariate, and tested for additive and interaction effects between site and mismatch, coat color, and snow cover. Additionally, we included a group-level effect for sex within our candidate model set.

Next, we constructed known-fate models using encounter histories of only those hares that we visually sampled weekly for estimates of color contrast (hereafter, the observed
3 | RESULTS

We captured and translocated 96 snowshoe hares to Sandhill: 29 at Site 1, 28 at Site 2, and 39 at Site 3. We detected 70 mortalities between initiation of releases and May 31. Sixty-five mortalities were from predation (26 terrestrial predators, 6 avian predators, and 33 unknown), and five were due to unknown causes. We monitored coat color change of 42 hares. Loss of snow cover began during the 6th week after release (February 21 to February 27); initiation of coat color change among hares was not observed until the 7th week (February 28 to March 6) (Figure 2). We observed the completion of coat color change of all monitored hares by the 15th week (April 17 to April 23).

We found a strong negative relationship between hare weekly survival and contrast that interacted with release site (Table 1). Mean weekly survival was lower at Site 1 ($\hat{S} = 0.86; 95\% \text{ CI} = 0.78, 0.91$) compared to Sites 2 ($\hat{S} = 0.94; 95\% \text{ CI} = 0.89, 0.97$), and 3 ($\hat{S} = 0.96; 95\% \text{ CI} = 0.93, 0.98$) during pre- and post-mismatch periods (Figure 3a). Similarly, survival across the entire 20-week period was consistently lower at Site 1 ($\hat{S} = 0.09; 95\% \text{ CI} = 0.03, 0.23$) than Sites 2 ($\hat{S} = 0.24; 95\% \text{ CI} = 0.11, 0.47$) or 3 ($\hat{S} = 0.18; 95\% \text{ CI} = 0.09, 0.32$). However, survival at Site 3 exhibited a strong negative relationship with degree of contrast ($\hat{\beta}_3 = -0.03; 95\% \text{ CI} = -0.04, -0.02$), whereas sites 1 and 2 showed a neutral relationship with contrast ($\hat{\beta}_1 = 0.02; 95\% \text{ CI} = -0.003, 0.04; \hat{\beta}_2 = -0.01; 95\% \text{ CI} = -0.03, 0.01$; Figure 3b). Once mismatch began, predation occurred at high rates at Site 3 (Figure 2), and weekly survival fell considerably ($\hat{S} = 0.70; 95\% \text{ CI} = 0.55, 0.82$) during the 8th week of monitoring, which coincided with the highest mean value of contrast in the population (82%) (Figure 3a).

Focusing on the observed cohort, we found that mismatch alone had the most support with no competing models (Table S2B). Appearance of mismatch among hares was negatively related to survival ($\hat{\beta}_{\text{Mismatch}} = -1.18; \text{ SE} = 0.44$); and mismatched hares were 3.2 x less likely to survive a week compared to a matched hare (Odds Ratio [OR] = 0.31; 95\% CI = 0.74, 0.13). When considering habitat features in the second phase of model selection, those models that accounted for patch size of aspen-alder and a contiguity index for aspen-alder emerged as competitive (Table 1). No other cover type was relevant (Table S2C). Although we tested for interaction effects between mismatch and these habitat covariates, they were equivalent in support to the top model and in all cases the 95\% confidence interval for interaction
TABLE 1  Ranking of known-fate models for the effects of phenology and survival on the (A) whole population and (B) observed cohort of snowshoe hares (*Lepus americanus*) by AICc (Akaike's Information Criterion corrected for small sample size), ΔAICc (the difference between a model and the top-ranked model in the candidate set), *w* (model weight), and *k* (number of parameters). Variables shown below include site (release site), contrast (mean difference between percent white of coat color and ground cover), mismatch (color contrast ≥ 60% for an individual), sex, patch size aspen-alder (mean patch size of aspen-alder within buffer), contiguity aspen-alder (mean contiguity index values of aspen-alder within buffer), and percent aspen-alder (proportion of aspen-alder within buffer).

| (A) Survival-Whole population | AICc  | ΔAICc | *w* | *k* |
|-------------------------------|-------|-------|-----|-----|
| Site*Contrast                 | 422.53| 0.00  | 0.64| 6   |
| Site*Contrast+Sex             | 423.82| 1.28  | 0.34| 7   |
| .                             | 438.40| 15.8  | 0   | 1   |

| (B) Survival-Observed Cohort  | AICc  | ΔAICc | *w* | *k* |
|-------------------------------|-------|-------|-----|-----|
| Mismatch+Patch Size aspen-alder+Contiguity aspen-alder | 129.47| 0.00  | 0.27| 4   |
| Mismatch*Contiguity aspen-alder+Patch Size aspen-alder  | 130.60| 1.13  | 0.15| 5   |
| Mismatch*Patch Size aspen-alder+Contiguity aspen-alder  | 131.08| 1.61  | 0.12| 5   |
| Mismatch+Patch Size aspen-alder+Contiguity aspen-alder+Percent aspen-alder | 131.36| 1.89  | 0.11| 5   |
| Mismatch+Patch Size aspen-alder                                     | 131.37| 1.90  | 0.10| 3   |
| .                             | 149.40| 19.9  | 0   | 1   |

terms overlapped zero. Weekly survival rates from the top survival–hare mismatch model with aspen-alder patch size and contiguity – varied from \( S = 0.87 \) (95\% CI = 0.75, 0.94) in week 2, when mismatch was highest, to \( S = 0.95 \) (95\% CI = 0.89, 0.98) in weeks 7, 8, and 9 when mismatch was low (Figure 4a). Although hares occupying landscapes with larger patches of aspen-alder had higher survival (\( \beta_{\text{Patch Size Aspen-Alder}} = 0.249; 95\% \text{ CI} = 0.06, 0.43; \) Figure 4b), the contiguity index of aspen-alder had no effect (\( \beta_{\text{Contiguity Aspen-Alder}} = -4.38; 95\% \text{ CI} = -9.1, 0.34). The relationship of aspen-alder patch size with survival (\( \text{OR} = 1.28; 95\% \text{ CI} = 1.06, 1.55) indicated that mismatched hares with 4.7 hectares of aspen-alder available had equivalent weekly survival to matched hares with no aspen-alder available (Figure 4b).

4 | DISCUSSION

Our findings provide a causal link between the multi-decade regional range contraction of snowshoe hares (Buehler & Keith, 1982; Sultaire et al., 2016a) and snow cover loss. Specifically, we provide experimental evidence that amplified predation during extended periods of camouflage mismatch is the likely mechanism behind range contraction for snowshoe hares in the Great Lakes Region. The negative effect of camouflage mismatch on hare survival was supported by analyses of both the whole translocated population and the fine-scale observed cohort, and we propose that prolonged camouflage mismatch from declining snow cover duration is the likely cause of the southern range contraction across the snowshoe hare’s distribution.

**Figure 4**  Survival analysis for an observed cohort of snowshoe hares (*Lepus americanus*) experiencing camouflage mismatch in Sandhill Wildlife Area during the winter of 2017. (a) Weekly survival estimates from the top-ranked model including phenology and habitat covariates. (b) Fitted values from the top-ranked model of the phenology and habitat survival models, with patch size of aspen-alder ranging from minimum to maximum observations (0–20 hectares) and contiguity index of aspen-alder was constant at mean observed values (0.81). Standard errors are shown for both.

Our translocation suggests that snowshoe hare populations previously extant south of the current range boundary were subject to high mortality due to camouflage mismatch and experienced increased duration of mismatch, which in concert
likely led to extirpation. In the western United States, mismatched snowshoe hares experienced a severe 7% reduction in weekly survival compared to matched hares (Zimova et al., 2016); in Wisconsin, we observed a 12% reduction in weekly survival for mismatched hares, confirming that the negative fitness consequences of mismatch are concordant geographically. The duration of mismatch (3 weeks where more than half of hares were mismatched) is similar to predictions for the duration of mismatch for high emission scenarios in the midcentury (17 days) (Mills et al., 2013). Although translocation itself is a well-known stressor and can contribute to mortality (Letty et al., 2007), given the amount of time that elapsed between the cessation of translocations and mortality associated with mismatch, we are confident that the high mortality rate during this period was primarily due to mismatch. We suggest that the degree of camouflage mismatch governs much of the current southern range boundary of snowshoe hares, which we predict will likely move farther north as future snow cover is projected to decline in both duration and extent across this region (Notaro, Lorenz, Hoving, & Schummer, 2014; Sultaire et al., 2016a).

Weekly survival varied across sites, and as a function of mean patch size of aspen-alder. In particular, mismatched hares occupying patches of aspen-alder >5 hectares had equivalent survival rates to matched hares. Patch size of aspen-alder stands has been previously associated with increased survival of snowshoe hare within our study system (Keith et al., 1993), and elsewhere (Thornton, Wirsing, Roth, & Murray, 2013). Aspen-alder stands possess high stem-density that provides refuge from predators (Litvaitis et al., 1985). It is likely that the buffering effect of aspen-alder is translatable to other habitats that provide dense cover, including conifer forests that are common in northern parts of the snowshoe hare’s range. Maintaining high-quality forest patches of appropriate size will likely benefit hare populations north of the current range boundary in places where populations have not yet begun to decline. Current policies and initiatives, like the Young Forest Initiative (https://youngforest.org), are promoting heterogeneous landscapes by incentivizing private landowners to manage for mixed age-classed forests. Although the financial benefit for managing early successional stands for many forest types exists, this program also incentivizes the shearing of alder, a noncommercial cover type, to the benefit early successional species, including hares. In Wisconsin, these efforts have been restricted to northern parts of the state; expansion of such policies further south could benefit a number of species along their southern range boundary.

By understanding the effects of habitat quality and camouflage mismatch on snowshoe hare survival, land managers can begin to prioritize actions to conserve species dependent on young forest habitat (e.g., ruffed grouse [Bonasa umbellus; Dessecker & McAuley, 2001]) or subject to camouflage mismatch (e.g., least weasel [Mustela nivalis; Atmeh, Andruszkiewicz, & Zub, 2018]). For example, conservation or restoration of high-quality habitat patches >5 hectares within the snowshoe hare’s range will buffer the effects of mismatch and promote persistence. Delaying extirpation in these regions may allow for adaptation, if there are polymorphisms related to coat color change within the population (although these are uncommon in Great Lakes populations; Mills et al., 2018). Furthermore, by including sufficiently sized patches of young aspen or alder with criteria for identifying or managing climate refugia, the effectiveness of such sites can be greatly enhanced.

The conservation of species threatened by climate change is a global challenge, yet local management is critical to prevent extinction (Lawler, 2009). Effectively combating local extirpations, range shifts, and extinction can only occur if conservationists have information to identify and regulate the mechanisms affected by climate change. We have shown that high-quality habitat (young aspen, alder, or regional analogues) can improve survival of mismatched snowshoe hares. Management of sufficiently sized aspen, alder, and conifer forest patches for snowshoe hares is an accomplishable management action. We offer this regional management tool to complement national adaptive management plans, and as a way to engage local land managers in the mitigation of climate change to conserve sensitive species of wildlife.

ACKNOWLEDGMENTS

This work was supported by the National Institute of Food and Agriculture, United States Department of Agriculture, Hatch Projects 1006604 & 1003605. Data collection was assisted by C. Lane and J. Steketee. Wisconsin Department of Natural Resources provided logistical support, and particular thanks to S. Hull, R. Paisley, W. Hall, C. Milestone, R. Brathal, R. Greene and the Department of Forest and Wildlife Ecology.

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Additional supporting information may be found online in the
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**How to cite this article:** Wilson EC, Shipley AA, Zuckerberg B, Zachariah Peery M, Pauli JN. An experimental translocation identifies habitat features that buffer camouflage mismatch in snowshoe hares. *Conservation Letters*. 2019;12:e12614. https://doi.org/10.1111/conl.12614