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BIOTIC AND ABIOTIC DRIVERS OF ACYCLIC SNOWSHOE HARE POPULATION DYNAMICS IN A SPATIOTEMPORALLY COMPLEX SYSTEM

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Biotic and abiotic drivers of acyclic snowshoe hare population dynamics in a spatiotemporally complex system

Chairperson: Dr. L. Scott Mills

Although periodic fluctuations in species abundance have long fascinated society (e.g. lemming mass migrations and locust plagues in Egypt), it was not until 1924 that Charles Elton brought cycles to the attention of the scientific community. Following his work, cycle dynamics have remained an enigmatic area of ecology with many cyclic species exhibiting dampened and even acyclic dynamics across space (i.e. portions of their range) or time. One such species, snowshoe hares, exhibit drastic population fluctuations in the northern boreal, but are thought to exhibit dampened cyclic or acyclic population dynamics in the southern portion of their range with quantification hampered by lack of data. For my dissertation, I contrasted multiple biotic and abiotic drivers of hare population dynamics and quantified the cyclic nature of hare population fluctuations in Montana using a novel 21 year dataset and a rigorous modeling framework. I first directly estimated hare densities over space and time with a spatially-explicit capture-mark-recapture model. I then removed the measurement error component to focus on drivers of process variance in hare densities using a Bayesian state space model. I found support for hare population dynamics driven by landscapes with more open areas, greater generalist predation and warmer temperatures. Consistent with other studies, I found that increasing camouflage mismatch resulting from shorter snow duration lowers hare density. I also found that less frequent cold winter days increase density while hotter summers lower density with the future negative effect of warming summers likely overwhelming the future positive effect of reductions of cold winter days. Both increased generalist predation and more open landscapes were associated with lower hare densities supporting the generalist predation and landscape structure hypotheses. Finally, using four different cyclicity metrics, I concluded that Montana hares are acyclic. Thus, multiple drivers act simultaneously to produce acyclic dynamics emphasizing the need to apply a unified modeling framework which considers multiple drivers to other cyclic systems in order to better elucidate cycle dynamics.

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Chapter 1: Introduction to the dissertation: Cyclicity and population dynamics of hares in their southern range

Background

From the biblical references of the plagues of locust in Egypt, to the purported lemming mass migrations in Scandinavia possibly providing inspiration for the myth of the pied piper, cyclic populations have pervaded our culture for millennia (Green and Evans 1940, Barraquand et al. 2017). However, Charles Elton's seminal work in 1924 is widely credited with bringing cycles to the attention of the scientific community (Elton 1924). Following his work, cycle dynamics have remained an enigmatic and often controversial area of ecology (Chitty 1996, Turchin 2003, Lambin et al. 2006).

In addition to fascinating basic ecologists, population cycles also have direct connections to applied science. Population peaks of some species can have detrimental effects on ecosystems. For example, during population peaks, gypsy moths defoliated millions of hectares of forest (Liebhold et al. 2000), voles in Finland destroyed almost 5 million seedlings (Huitu et al. 2009) and snowshoe hares in the US had substantial effects on tree plantations (Aldous and Aldous 1944).

Conservation implications also abound with cyclic species. Not only are some cyclic species threatened (e.g. Canada lynx; Ruggiero et al. 2000), but other cyclic species threaten biodiversity such as the crown-of-thorns starfish, a leading factor in the decline of the Great Barrier Reef (De'ath et al. 2012). Finally, cyclic species may have higher risks of extinction due to their spatial synchrony (Heino et al. 1997).

A common feature exhibited by many cyclic species is diminishing and even vanishing cycles (Stenseth et al. 1996, Klemola et al. 2002, Newey et al. 2007). Leading explanations for weakening cycles over space include a decreased ratio of specialist to generalist predators (Hanski et al. 1991, 2001, Klemola et al. 2002) and increasing habitat fragmentation (Wolff 1980, Sievert and Keith 1985, Griffin and Mills 2009). The fragmentation could occur naturally (e.g. high elevation boreal habitat separated by low elevation temperate forest; Howell 1923, Sievert and Keith 1985) or anthropogenically (e.g. timber harvesting; Vitense et al. 2016). Alternatively, cycles can collapse through time with changes in winter severity identified as a possible driver of the collapse (Ims et al. 2008, Kausrud et al. 2008, Cornulier et al. 2013). However, these studies generally examine only one or two drivers of cycle dampening in relative isolation. The next step is to consider multiple biotic and abiotic drivers simultaneously in one unified modeling framework.

To take the next step of considering multiple biotic and abiotic drivers simultaneously in one unified modeling framework, I employed a novel, two decade-long time series from rigorous field-based density estimates (Mills et al. 2005, Mills unpublished data). This dataset is spatially extensive, (14 trapping grids in two different areas in western Montana separated by ~175 km), temporally intensive (approximately 20 years for all grids) and rigorous (live trapping yielding mark recapture data).

Study System

An iconic cyclic species, the snowshoe hare, is famed for their drastic 25-fold population fluctuations in the northern boreal of North America (Hodges 2000a, Krebs et al. 2018, Myers 2018). Snowshoe hares, *Lepus americanus*, are a strongly interacting boreal species that provide a vital food resource for a diverse guild of carnivores including the federally threatened Canada lynx (Boutin et al. 1995, Squires and Ruggiero 2007). In addition, hares, along with 20 other species globally, have become well known as models for climate change adaptation due to their seasonal coat color molts serving as camouflage against seasonal snow cover (Mills et al. 2018, Zimova et al. 2018). However, a lesser known element of hare biology is that their cycles are thought to be diminished or nonexistent in the southern portion of their range (Howell 1923, Keith 1990, Hodges 2000b). Rigorous quantification of the cyclic nature of hares in their southern range is hampered by the lack of long-term population monitoring studies of hares in the lower latitudes as none have exceeded four years in duration (Keith 1990, Murray 2000, Griffin and Mills 2009).

Overview of Dissertation

For my dissertation, I contrasted multiple biotic and abiotic drivers of hare population dynamics and quantified the cyclic nature of hare population fluctuation in Montana, a region where anecdotal evidence suggests that snowshoe hare cycles are ether dampened (Hodges 2000b) or nonexistent (Howell 1923, Keith 1990). In short, I ask whether hare cycles are diminished or nonexistent in the southern portion of their range, and why?

To answer these questions, I used a rigorous state space modeling framework based on a 21-year mark recapture hare dataset. Importantly, this modeling framework improves upon the analytical methods usually used to study cyclic populations. Typically, researchers have relied on highly uncertain indices of population abundance (Barraquand et al. 2017). Instead of indexing population abundance, I directly estimated hare density using a spatially-explicit capture-mark-recapture framework (Efford 2004). Further, I incorporated these density estimates and their associated uncertainty into a state space modeling framework that models the biotic and abiotic drivers of cycles directly on the biological process with the measurement error component removed.

Chapter 2 of my dissertation centers on two key abiotic drivers of dampened cycle dynamics: temperature and snow. I examined several mechanisms whereby these abiotic conditions might influence hare density. Consistent with other studies that linked increased mismatch to lowered hare survival (Zimova et al. 2016, Wilson et al. 2018), I found that increasing mismatch resulting from shorter snow duration was associated with lower hare density. I also found that less frequent cold winter days (daily minimum below -5^{o} C) was associated with increased density possibly by reducing hare susceptibility to predation. Finally, I found that warmer summers were associated with lower hare density by potentially lowering juvenile survival possibly due to malnutrition. I then projected the temperature changes observed in this study forward to examine some of the positive and negative benefits of a warming climate on hare densities. I found that for hares, the positive effect of reductions of cold winter days overwhelms the negative effect of warming summer temperatures.

Chapter 3 focuses on the two main purported biotic drivers of dampened hare cycle dynamics, increased generalist predation relative to specialist predation and landscapes with more open areas. In addition, in this chapter I considered other metrics of predation and habitat structure in a framework that accounts for both direct (survival) and indirect (e.g. stress related) costs of predation. To do so, I estimated site specific yearly survival for hares with a Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) using 4,037 captures of 2,939 unique hares. I found support for both the generalist predation and landscape structure hypotheses as well as evidence for indirect predation risk influencing habitat specific densities.

In the final chapter, I synthesized the findings of the previous two chapters to answer the question, are hare cycles diminished or collapsed in the southern portion of their range, and why? By examining four different metrics of cyclicity, I conclude that hares in Montana are acyclic. I then combined the results of the first two chapters into another state space model and found support for hare population dynamics in Montana driven by increased habitat heterogeneity, greater generalist predation and warmer temperatures.

Concluding Thoughts

Throughout the dissertation, I examined the diminishing hare cycles in Montana as a spatial phenomenon in comparison to the cyclic populations in the northern boreal. However, cycles can collapse through time as well as space (Ims et al. 2008, Kausrud et al. 2008, Cornulier et al. 2013). This begs the question if the lack of cycles in Montana is a recent phenomenon, possibly anthropogenically driven, or is acyclicity inherent to the area due to latitudinal differences compared to the northern boreal. Although my dissertation does not contain the data to answer this question, I share the belief of many that some inherent latitudinal differences have always caused dampened or nonexistent cycles in the southern portion of the snowshoe hare range (Howell 1923, Wolff 1980, Sievert and Keith 1985, Griffin and Mills 2009). Nonetheless, I also believe that increased fragmentation due to timber harvest and land use change may have recently exacerbated the dampening. The near ubiquity of dampening cyclic dynamics over a latitudinal gradient (Stenseth et al. 1996, Klemola et al. 2002, Newey et al. 2007) points to inherent latitudinal differences. However, the significance of the landscape structure covariate, which is partially driven by timber harvest, suggests an additional role of some forest management practices in dampening cycles.

Likewise, the drivers identified in my dissertation can be used to potentially guide conservation and management of other cyclic species. For example, if the goal was to reduce detrimental outbreaks of a cyclic species (e.g. the crown-of-thorns starfish threatening the viability of the Great Barrier Reef or gypsy moth devastating large tracts of forest), we can apply these mechanistic drivers of dampened hare dynamics to possibly dampen the population fluctuations. Additionally, these concepts may be applied in reverse to help cyclic species avoid the low phase, which is when they would be most at risk of extinction. For example, limiting winter warming, possibly through reduced greenhouse gas emissions, might increase densities of lemmings (Kausrud et al. 2008). Thus, although my dissertation strictly focuses on dampened cyclic dynamics of snowshoe hares, I am hopeful that my findings can be used to inform conservation and management of other cyclic species.

As this research, which constitutes my dissertation, reflects the work of many (see Acknowledgements section), I use the collective “we” throughout the dissertation.

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Chapter 2: Effects of temperature and snow on snowshoe hare densities under a changing climate

Abstract

Local snow and temperature can affect the phenology, predation rate and physiology of many species. However, considerable uncertainty exists in first identifying the appropriate climate metrics that affect individual species and then projecting species responses to these metrics under climate change. Using an extensive 21 year, live-trapping dataset of snowshoe hares we identified biologically informed climate covariates that influenced snowshoe hare densities. We found that shorter snow duration increased mismatched white hares on snowless backgrounds and was associated with lower hare density. We also found temperature had conflicting effects on hare density depending on the season. Less frequent cold winter days were associated with increased hare density, perhaps by reducing hare susceptibility to predation. By contrast, warmer summers were associated with lower density. Using models from the Coupled Model Intercomparison Project Phase 5 (CMIP5), we found that the negative effect of future warming summer temperatures overwhelmed the positive effect of future reductions of cold winter days and yielded projected population declines. Thus, warming temperature serves as an example of the opposing ways climate change can affect species and exemplifies the need to consider the multiple effects of climate change in a unified data-driven framework.

Introduction

Climate change is manifested through a multitude of abiotic factors, including increased temperatures particularly in boreal and Arctic zones (Screen and Simmonds 2010, Bintanja and Linden 2013, Williams et al. 2015) and strong reductions in northern hemisphere snow cover (Pederson et al. 2011, Kunkel et al. 2016, Zhu et al. 2019). In turn, both snow and temperature can affect biota by influencing phenology, predation and physiology. Snow affects hibernation (e.g. ground squirrels; Sheriff et al. 2011, Lane et al. 2012), seasonal migration (e.g. elk; Rickbeil et al. 2019), camouflage (e.g. hares and weasels; Mills et al. 2018, Davis et al. 2019) and clutch initiation advancement (e.g. arctic shorebirds and passerines; Liebezeit et al. 2014). Snow also influences locomotion to the benefit of both predators (e.g. wolves predating ungulates; Huggard 1993) and prey (e.g. snowshoe hares evading lynx and coyotes; Murray and Boutin 1991, Stenseth et al. 2004). Temperature can trigger needle growth and senescence in deciduous trees (e.g. western larch; Rosenthal and Camm 1996), affect antipredator behaviors (e.g. bank voles; Sipari et al. 2016) and alter development time (e.g. tropical songbirds; Ton and Martin 2017). Finally, temperature can interact with snow to increase mortality. For example, mild temperatures encrust snow with ice compromising the forage and thermal benefits of the subnivium (e.g. voles and lemmings; Aars and Ims 2002, Kausrud et al. 2008). However, the multifaceted ways in which snow and temperature can influence fauna are still being elucidated, even in well-known systems.

To unravel connections between multiple climate metrics on wild animal population dynamics, we focus on a species whose phenology, survival and physiology are profoundly shaped by snow and temperature. Snowshoe hares, *Lepus americanus*, are a strongly interacting boreal species (Boonstra et al. 2016) that provide a crucial food resource for a diverse array of carnivores (Boutin et al. 1995, Squires and Ruggiero 2007) including the federally threatened Canada lynx (Ruggiero et al. 2000). Snowshoe hares, along with 20 other species globally, undergo seasonal coat color molts as camouflage against transient snow cover (Mills et al. 2018), and snow presence influences the rate of these molts (Kumar et al. In Press). In addition, hares possess lower foot-loading than their main predators (Murray and Boutin 1991, Buskirk et al. 2000) likely conferring an advantage in deep, soft snow. Finally, lower temperatures may increase energy demands (Speakman 1996) possibly eliciting riskier foraging in hares (Griffin and Mills 2009) which ultimately increases predation risk (Hodges and Sinclair 2005).

Snow presence, depth and compaction may affect hare survival and ultimately density. Reductions in snow cover duration result in white hares mismatched with snowless backgrounds (Mills et al. 2013), decreasing hare survival (Zimova et al. 2016, Wilson et al. 2018). Snow conditions may influence snowshoe hare predator effectiveness. In particular, coyotes select for areas with shallow more supportive snow (Murray and Boutin 1991, Kolbe et al. 2007) as hunting success decreases in deep snow (Wells and Bekoff 1982). Meanwhile, lynx select for intermediate snow depth (Holbrook et al. 2017a), possibly because their superior foot-loading provides a competitive advantage but may be ineffective in deep snow.

Temperature can also affect hare vital rates and consequently hare density. Generally, temperatures outside the thermoneutral zone (-5 °C to 38° C for hares; Hart et al. 1965) lead to greater resting energy demand (Speakman 1996, 1999) possibly resulting in riskier foraging. Indeed, lower daily minimum temperatures have been associated with lower hare survival, body mass and bone marrow fat (Meslow and Keith 1971, Hodges et al. 2006). In turn, hares with decreased marrow fat may have a higher risk of predation (Keith et al. 1984, Sievert and Keith 1985, Hodges et al. 2006; but see Murray 2002, Wirsing et al. 2002a). Although, hares tolerate warm temperatures well through evaporative cooling via respiration (Hart et al. 1965), the costs of engaging in increased evaporative cooling may lower foraging efficiency, decreasing body condition and ultimately reducing survival (as shown in arid birds; Du Plessis et al. 2012, Gardner et al. 2016). Additionally, extreme summer weather may also affect juvenile hares. For example, approximately one-third of leverets died from exposure to snow and rain in southwestern Yukon with the majority of these deaths occurring during the first five days of life (Krebs et al. 2002). Furthermore, severe heat could affect juveniles if hot temperatures limit female milk production, as was found in mouse experiments (Krol et al. 2007) and with dairy cattle (Rhoads et al. 2009). Therefore, increasing spring precipitation and higher summer temperatures may reduce hare survival and subsequently decrease hare densities.

These potential effects of snow and temperature on hare density can be distilled into the following *a priori* list of covariates: camouflage mismatch, snow compaction, snow depth, number of days with minimum temperature below -5° C (lower critical temperature for hares; Hart et al. 1965), minimum winter temperature, spring precipitation, maximum summer temperature and number of days with maximum above 38° C (upper critical temperature for hares; Hart et al. 1965).

To quantify effects of snow and temperature on snowshoe hare density we analyzed a time series spanning two decades across 14 grids and based on rigorous capture-mark-recapture data of approximately 2,000 hares. Specifically, we evaluated four non-mutually exclusive hypotheses by which snow and/or temperature could impact snowshoe hare densities: a) if longer durations of mismatched hares (hares whose coat color does not match their background) lower adult survival, then longer periods of putative mismatch will be associated with lower hare density, b) if compact, shallow snow decreases hare survival by facilitating terrestrial mammalian predator locomotion, then compact, shallow snow will be associated with lower hare density, c) if less extreme winter temperatures increase adult survival by decreasing hare predation risk, then years with fewer cold winter days will be associated with increased hare density and d) if increased summer severity (warmer temperatures and/or wetter springs) reduces adult or leveret survival, then warmer summers and/or wetter springs will be associated with lower adult hare density the subsequent year. Finally, using the modeled relationship between the climate covariates and hare density, we projected how a changing climate would likely affect snowshoe hare densities in the future.

Methods

Study Areas

We collected snowshoe hare summer density data from 1998-2018 at 14 trapping grids in two areas (Seeley Lake and Tally Lake) in western Montana, USA (Figure 1; for site descriptions see Mills et al. 2005). All sites were managed by the Forest Service (USFS) with a history of multiple use including timber production. Seeley Lake (Lat. = 47.2°, Long. = -113.4°) and Tally Lake (Lat. = 48.5°, Long. = -114.8°) are approximately 175 km apart and span similar elevations (approximately 1500-1900 m.a.s.l.). Both areas are dominated by moist, coniferous forests of Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and Ponderosa pine (*Pinus ponderosa*) with a herbaceous understory.

Capture/Handling

Snowshoe hares were trapped during the summer (May-August) using live-traps (51x18x18 cm, Tomahawk Live Trap Company, Tomahawk, WI) baited with alfalfa cubes and apples, spaced approximately 50m apart (Mills et al. 2005). Each of the seven Seeley Lake hare trapping grids consisted of approximately 50 traps, while the seven Tally Lake trapping grids had approximately 80 traps each. Each grid was trapped for 3-5 days each summer, ensuring population closure. We marked all hares >500g with a unique numbered ear tag. We weighed all hares, determined sex, measured right hind foot length and determined breeding status (lactating or pregnant, testes abdominal or testes scrotal). All capture and handling procedures were approved by the University of Montana Animal Care and Use Committee (various permits over 21 years).

Climate Data Sources

We derived temperature data from Daymet which provides daily weather parameters at 1 km resolution based on modeling and interpolating meteorological station data (Thornton et al. 2018a). In a cross-validation of Daymet predictions, mean absolute error for single day predictions for 2010 maximum temperature was less than 1^{o}C for western Montana (Thornton et al. 2018b). Specific temperature derived covariates included: number of days with minimum below -5^{o} C, minimum winter temperature and the maximum summer temperature. No days had temperatures with maximum temperatures above 38^{o} C so that covariate was omitted. We also considered the total precipitation from May 15 to June 15 to represent the period (0-5 days old; O'Donoghue 1994) when leverets were most likely to succumb to exposure as determined by live-trapping weights and growth curves (Keith et al. 1968). Since we hypothesized this covariate only affected juveniles, we only considered an effect on adult hare density the following year when juveniles reached adulthood (e.g. spring 2010 precipitation affects summer 2011 adult hare density). Finally, we used Daymet temperature data to quantify snow compaction using a field validated temperature fluctuation index (Kausrud et al. 2008) calculated as follows:

$$\overline{T_t} = \begin{cases} \Sigma_i \, T_{i,t}^{max,d} - T_{i,t}^{min,d} & \text{if } T_{i,t}^{min,d} < -3, \; T_{i,t}^{max,d} > 0 \\ \Sigma_i \, \theta_1 & \text{if } T_{i,t}^{min,d} > -3, \; T_{i,t}^{max,d} > 0 \\ \Sigma_i \, \theta_2 & \text{if } \quad T_{i,t}^{max,d} < 0 \end{cases}$$

where T_t = temperature fluctuation, $T_{i,t}^{max,d}$ = daily temperature maximum, $T_{i,t}^{min,d}$ = daily temperature minimum, θ_1 = 1 and θ_2 = 4.3. θ_1 and θ_2 are constants representing the daily contribution to snow hardness.

We derived snow data from the NOAA National Weather Service's National Operational Hydrologic Remote Sensing Center (NOHRSC) Snow Data Assimilation System (SNODAS) (Barrett 2003). SNODAS provides estimates of snow cover and associated parameters at 1 km resolution using modeling and data assimilation from 2003-2018 (Barrett 2003). SNODAS accurately predicts snow depth in the Rocky Mountains (Clow et al. 2012), and has been used to approximate western Montana snow depth (Holbrook et al. 2017b, 2017a). We used SNODAS to quantify two grid specific snow depth covariates: maximum yearly snow depth (Hodges et al. 2006) and mean yearly snow depth throughout the snow season (November through May). We also defined snow presence as snow water equivalent > 0 to approximate daily snow cover.

Finally, we used climate variables projected under different greenhouse gas concentration scenarios to examine how future changes in important climate covariates might influence hare densities. Climate variables were calculated using climate grids from the Rocky Mountain Research Station, USDA Forest Service (Crookston and Rehfeldt 2008) that considered an ensemble of 17 different climate models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) under two representative concentration pathways (RCPs) including medium-low (RCP4.5) and high (RCP8.5) greenhouse gas concentration scenarios.

Hare Molt Phenology and Camouflage Mismatch

Our trapping data were all in the summer, so we could not directly attribute molt phenology to our time series density estimates. Therefore, we used six years (2009-2014) of hare molt phenology data within 60 <km of our Seeley Lake sites and at similar elevations (Mills et al. 2013, Kumar et al. In Press) to estimate the average molt phenology of the hares during our 21 year study (see Appendix A). These six years of molt phenology data include the year with the highest maximum snow depth and the year with the third lowest maximum snow depth across the 21 year time series. Furthermore, the years with molt phenology data spanned the range of snowpack variation from the recent past (1970-1999; Mills et al. 2013).

Camouflage mismatch occurs when the hare color molt contrasts with their background (Mills et al. 2013), and so depends on both local snow cover and the snowshoe hare molt phenology. We used the daily estimates of snow cover in combination with daily expected hare coat color (Appendix A) to approximate number of days hares were mismatched each year. We defined white hare mismatch as hares ≥ 50% white and snow absent. Similarly, brown hare mismatch was defined as hares < 50% white and snow present. Total mismatch was the total number of days of either brown or white hare mismatch. Note, our definition of white mismatch contrasts slightly with Mills et al. 2013 that defined mismatch as ≥60% white hares on snowless background. We used a 50% threshold so that we could symmetrically include both white hares on snowless backgrounds and brown hares on snowy backgrounds. Our use of 50% for the mismatch threshold causes only 0-3 days difference compared to the 60% threshold. Furthermore, our definition minimizes the plasticity in molt timing as the date hares become 50% white is less variable than the start and end dates of the molt (Appendix A, Table S1).

The effect of mismatch on survival is likely non-linear. Hare survival decreases with increasing contrast (the absolute difference between percent of the hare that is white and percent of the ground covered with snow) (Zimova et al. 2016). As the number of mismatch days increase beyond when hares first contrast their background by 50%, their changing coat color increases their contrast against their background (up to 100%). Due to the likely non-linear effect of increasing contrast on survival, we included quadratic terms in the model (total mismatch squared, white mismatch squared and brown mismatch squared).

Statistical Analysis

Density

We performed a spatially-explicit capture-mark-recapture (SECR) analysis using the Package SECR (Efford 2004, Borchers and Efford 2008, Efford and Fewster 2013) in Program R (version 3.5.3, R Development Core Team 2019) to estimate adult hare densities. We considered traps that caught nontarget species or were otherwise unable to capture a hare inoperable for that night. We varied models for g0, the probability of detection given the individual's activity center is at the detector, to include: a constant detection probability, a behavioral effect where detection probability changes after first capture, a sex effect where detection probability differs between sexes and a two-class finite mixture allowing for heterogeneity in detection probability. The behavioral effect accounts for individual responses to being trapped such as avoiding traps (i.e. trap shyness) or seeking them out (i.e. trap happiness), while individual heterogeneity may affect hare abundance estimation (Boulanger and Krebs 1994, 1996). We ran all combinations of the above models for g0 while holding sigma, the spatial scale over which the detection probability declines, constant. We fit models with the conditional likelihood, half-normal detection function and the Nelder-Mead maximization algorithm. We ranked models using AICc and used AICc differences (ΔAICc) and Akaike weights to evaluate model support. Once we identified the best model for g0, we used it for g0 and varied sigma to include all combinations of: a constant sigma, a sex effect where sigma differs between sexes and a two-class finite mixture allowing for heterogeneity in sigma. A sex effect on sigma could result from males having larger home ranges and movement rates (Hodges 1999). We again used AICc to determine the best overall model.

Because we had 21 years of data across up to 14 sites per year for 242 grid-years of sampling, we could pool data to estimate g0 and sigma, ultimately allowing us to estimate density for years when trapping yielded no individuals (~3% of all grid-year combinations). For the five grids where no individuals were caught for one or more years, we estimated density for trapping years with no captures by modeling g0 and sigma as constant and using the full as opposed to the conditional likelihood.

Snow and Temperature Effects on Density

We used a state space model based on the framework developed by Rotella et al (2009) to determine the effects of snow and temperature on summer hare density. State space models consist of both an observation model and a process model, and can separate measurement error from process noise (Dennis et al. 2006, Rotella et al. 2009). In this context, we use measurement error to refer to variability in the data that arises purely as a result of the sampling process and process noise to refer to fluctuations caused by environmental variability (Humbert et al. 2009).

The observation model used hare density estimates and the associated measurement error to approximate the unknown true hare density. The process model then estimated process variance and covariates on density with measurement error removed. Our observation model linked estimated density to true density with the following relationship: $\widehat{D}_t \sim \mathrm{N}(D_t, se_t^2)$, where $\widehat{D}_t$ is the time specific density estimates obtained from the SECR model, D_t is the true density and se_t^2 is the squared estimate of measurement error obtained from the SECR model. Our process model was as follows: $\log(D_t) = \mu + y_t$ with μ being the equilibrium value of the logarithm of true density and $y_t \sim \mathrm{N}(\alpha_t, \sigma_{pr}^2)$ where σ_{pr}^2 is process variation. Finally, $\alpha_t = \beta_1(cov1) + \beta_2(cov2) + \beta_3(cov3) \ldots$ where β represented the coefficient relating the covariate to α_t. We assumed that process variation and measurement errors were independent.

We implemented the model in a Bayesian framework (Rotella et al. 2009) to accommodate years when we did not trap (~18% of all grid-year combinations). We considered the following covariates: number of days with minimum temperature below -5° C, minimum winter temperature, maximum summer temperature, total precipitation from May 15 to June 15, snow compaction, maximum yearly snow depth, mean yearly snow depth, white hare mismatch, brown hare mismatch, total hare mismatch, white hare mismatch squared, brown hare mismatch squared and total hare mismatch squared. All covariates required a lag of four to fourteen months between when the covariate was measured and when it affected hare density so that we could consider the effects of previous springs, winters or summers on current summer hare densities. We standardized all covariates to have a mean of 0 and a standard deviation (SD) of 1 to ease interpretation and expedite convergence. If two covariates were strongly correlated ($\rho > 0.6$), we used indicator variable selection, a process that informs how important each of the two correlated covariates are to the model, to determine which covariate best fit the model (Hooten and Hobbs

2015). Doing so allowed us to include both covariates in the model but each iteration only included one of the two correlated covariates ensuring that the two correlated covariates were never included in the model at the same time. Once we determined which covariate fit best, we used that covariate in the full model and omitted the other correlated covariate. If indicator variable selection revealed approximately equal support for both correlated covariates, then we chose one covariate to include based on biological knowledge. Because SNODAS derived covariates (snow depth and mismatch) were only available from 2004 onwards we ran two models. The first model considered all covariates but only used data from 2004-2018. After removing correlated covariates (Appendix B, Table S2) this model contained the following covariates: days below -5° C, maximum temperature, minimum temperature, spring precipitation, white mismatch squared and brown mismatch squared. The second model only considered Daymet derived covariates but used all years of data; no covariates were correlated.

We fit models with Markov Chain Monte Carlo (MCMC) in JAGS using the R package jagsUI with uninformative priors except in the case of indicator variables where we used the "slab and spike" prior to alleviate computational problems and improve mixing (Hooten and Hobbs 2015). Specifically, we used a gamma distribution as a prior for σ_{pr}^2 with both hyperparameters set to 0.001. We specified the prior for μ as a normal distribution with a mean of 0 and a precision (1/variance) of 0.01. We used a normal distribution with a mean of 0 and a precision of 0.01 as a prior for all the betas, except when they were used with indicator variable selection. In such cases, we specified the slab and spike prior with a normal distribution with a mean of 0 + (ω * mean of beta) and a precision of 0.01 + (ω * 10) with ω being the binary indicator variable and the mean of the beta coefficient being determined in a previous model run. These priors represent a stationary distribution of 1 hare/ha and no effects of any covariate on density. We ran all models with five chains of at least 110,000 iterations discarding the first 10,000 as burn-in. We assessed convergence by visually examining the trace and density plots for the beta coefficients and with the Gelman-Rubin statistic ($\hat{R} < 1.1$). We used the 95% credible intervals as well as the probability that the beta coefficient does not equal 0 to determine the importance of the covariates.

Effects of Changing Climate

In order to examine the effects of climate change, we used future climate covariate values estimated for our study area under two greenhouse gas concentration scenarios (RCP4.5 and RCP 8.5). Specifically, we used the future mean maximum temperature in the warmest month (mmax) and mean minimum temperature in the coldest month (mmin) for each grid in 2060 and 2090. We first calculated current values for mmax and mmin using the Daymet data. Specifically, we calculated grid and year specific values for mmax and mmin from 1995-2018 and averaged them to represent the average value of mmax and mmin that the hares experienced. We then calculated the future proportional change in both mmax and mmin using the current and projected values. Finally, we applied those proportional changes in mmax and mmin to our modeled summer and winter climate covariates, respectively, yielding future estimates of our climate covariates of interest. We then used the beta coefficients from the state space model, the future covariate values and the estimated equilibrium value of the logarithm of true density, μ, to quantify future climate effects on density and ultimately inform the importance of the climate covariates to hares in the future.

Results

Density

From 1998-2018, we captured 1,940 individual adult hares 4,625 times from 14 locations that span ~175 km in western Montana. The best density model included the effects of sex and heterogeneity on g0 and heterogeneity on sigma (Tables 1 & 2). Male hares had a lower estimate of g0 than females (Appendix C, Table S3). Mean density across all years and sites was 0.42 hares/ha with site-specific high densities of 1.27 hares/ha in 2014 and low densities of 0.03 hares/ha in 2017.

Snow and Temperature Effects on Density

Using data from the years with snow data (2004-2018), we found support for four covariates influencing hare density (probability > 0.90 that beta coefficient ≠ 0) (Table 3). The number of cold days (below -5° C), maximum summer temperature and the number of days of white mismatch squared were all correlated with lower hare densities while the number of days of brown mismatch squared was correlated with higher hare densities (Table 3).

Using the full dataset (1998-2018), lower hare densities were correlated with both the number of cold days (β = -0.166, 95% credible interval of -0.307 to -0.026) and the maximum summer temperature (β = -0.277, 95% credible interval of -0.405 to -0.149) (Figures 2 & 3, Table 4). All other covariates were either correlated with a more supported covariate (Appendix B, Table S2), as indicated with indicator variable selection, or did not have significant effects on hare density. The equilibrium value of the logarithm of true density (measurement error removed) for hares from 1998-2018 was estimated to be 0.29 hares per hectare (95% credible interval of 0.26 to 0.33).

Effects of Changing Climate

Both RCP scenarios (RCP 4.5 and RCP 8.5) showed an increase in maximum temperatures and a decrease in minimum temperatures at our study area. Specifically, mean maximum temperature in the warmest month (mmax) increased by 7% or 12% by 2060 and by 9% or 23% by 2090 under RCP 4.5 or RCP 8.5, respectively. Meanwhile, mean minimum temperature in the coldest month (mmin) increased by 6% or 11% by 2060 and by 10% or 31% by 2090 under RCP 4.5 or RCP 8.5, respectively. Assuming these proportional changes in our covariates of interest, the isolated effect of a reduction in the number of cold days predicted an increased hare density of 110% (2060: RCP 4.5 and RCP 8.5; 2090: RCP 4.5) or 140% (2090: RCP 8.5). The isolated effect of increased maximum summer temperatures predicted a decreased hare density of 130% or 160% in 2060 and 140% or 250% in 2090 under RCP 4.5 or RCP 8.5, respectively.

Thus, when changes in maximum temperatures and the number of cold days are considered simultaneously (and separately from other potential drivers of hare population dynamics), hare density is predicted to decrease 120% or 140% in 2060 to an equilibrium value of the logarithm of true density of 0.24 or 0.20 hares/ha under RCP 4.5 or RCP 8.5, respectively. These declines worsen by 2090 as hare density is predicted to decrease 130% or 180% to an equilibrium value of the logarithm of true density of 0.23 or 0.17 hares/ha under RCP 4.5 or RCP 8.5, respectively.

Discussion

Despite rapid changes in climate, ecologists know precious little about how specific climate variables interact to affect densities of wild species. We used a 21-year time series and a unified data-driven modeling framework to understand how climate affects densities of snowshoe hares, a species whose life history and behaviors are directly shaped by climate. We found that the effects of snow and temperature on phenology, predation rate and physiology lead to subsequent changes in density. Furthermore, the effects of temperature were dependent on season with warmer winters associated with increased density while warmer summers were associated with decreased density. Future projections reveal that the negative effect of warmer summers will likely overwhelm the positive effect of fewer cold days. Although this projection only considers two of the myriad effects of climate change, it underscores the value of considering simultaneous and potentially opposing effects on vital rates when considering climate change outcomes on population dynamics.

In addition to insights on abiotic factors affecting hare densities, our extensive live-trapping hare dataset also provided insights into factors affecting hare density estimation. Our dataset of 4,625 captures of 1,940 individual hares, is the largest snowshoe hare dataset we are aware of to use capture probability models (sensu Otis et al. 1978) in a spatially-explicit capture-mark-recapture framework (Efford 2004). We tested for a behavioral response where detection probability changes after first capture, a sex effect and heterogeneity in detection probability. The best model considered both sex and heterogeneity in detection probability with males having lowering detection probability. The lower detection probability of males could be due to their lower survival (Chapter 3) or behavioral differences during the mating season. The best model for sigma, which relates to movement, only contained heterogeneity. We expected support for a sex effect on sigma as male hares move more during the summer breeding season likely to find mates while females restrict movement to care for young (Hodges 1999). However, our results imply that sex specific movement rates in summer do not vary strongly.

Other studies that estimated hare density with spatially-explicit capture-mark-recapture methods found the most support for using the null model on detection probability (Cheng et al. 2017, Kumar et al. 2018). These studies had an order of magnitude smaller sample sizes than ours, possibly implying that individual variation is present but data limitations may prevent AIC from selecting this biologically relevant model. Our results underscore the importance of considering heterogeneity in closed population models to approximate the biological process of individual variation present in most systems.

We now return to the main objective of our study: determining the effects of snow and temperature on hare density. We found strong evidence that both snow and temperature can affect hare densities. Specifically, we found support for three hypotheses: a) longer durations of mismatched hares lowers adult survival, b) less extreme winter temperatures increases adult survival and c) increased summer severity reduces leveret survival. We did not find support for the hypothesis that compact, shallow snow decreases hare survival.

Temperatures below -5° C may lower hare densities indirectly by increasing hare predation, which accounts for >90% of hare mortality (Hodges 2000, Wirsing et al. 2002b). Keith et al. (1984) found that as minimum winter temperatures decreased from -25° C to -37° C predator kills of radio-collared hares increased threefold. Lower temperatures lead to greater resting energy demand (Speakman 1996) and temperatures below the thermal neutral zone (-5° C in hares) increase metabolism (Williams et al. 2015). The increased energy demands of cold temperatures may encourage hares to forage in more risky places (Hodges and Sinclair 2005) increasing their predation risk (Griffin and Mills 2009).

Increased maximum summer temperatures were associated with lower hare densities is the subsequent summer, which could be driven by changes in adult survival. Although none of the summer maximum temperatures were above the thermoneutral threshold for hares (38^{o} C; Hart et al. 1965), hot temperatures may still lower body condition due to the costs of increased evaporative cooling lowering foraging efficiency (e.g. arid birds; Du Plessis et al. 2012, Gardner et al. 2016). As a poor body condition has been associated with increased predation in snowshoe hares (Keith et al. 1984, Sievert and Keith 1985, Hodges et al. 2006), temperature driven reductions in body condition could then lower hare survival over the course of the year and ultimately lower density in the subsequent summer. However, Montana hares are likely warm adapted and thus better able to cope with warm temperatures than cold adapted individuals (Lemoine 2017). For example, hares in Pennsylvania produce less heat than hares in the Yukon (Gigliotti et al. 2017).

Alternatively, or in addition, increased maximum summer temperatures may reduce juvenile survival (e.g. arid birds; Cunningham et al. 2013) and ultimately lower hare densities. The effect of summer temperature on adult density occurred with a one-year lag, consistent with hot summers lowering juvenile survival and the number of juveniles that recruit to be sampled as adults the subsequent year. Extreme heat may reduce the quantity of milk that females produce leading to malnourished leverets susceptible to predation. For example, shaved mice increase milk production because of their increased ability to dissipate the additional heat produced by lactation (Krol et al. 2007), and reduced milk production due to heat stress has been described for other mammals including dairy cattle (Rhoads et al. 2009) and anecdotally in white-tailed deer (Chitwood et al. 2015) and African wild dogs (Woodroffe et al. 2017). Another possibility is increased leveret mortality due to heat exposure. We find this possibility unlikely as leverets tend to be found under cover and are not directly exposed to the sun in the heat of the day.

Putative coat color mismatch had opposing effects on density depending on the type of mismatch. As predicted, increasing durations of white hares mismatched on snowless ground were associated with lower densities in the subsequent summer. White hare mismatch has been shown to reduce hare survival in both Montana (Zimova et al. 2016) and Wisconsin (Wilson et al. 2018). Surprisingly, increasing durations of brown hares mismatched on snowy ground was associated with higher summer densities, contrasting our prediction that mismatch in either direction (white on brown or brown on white) would decrease hare densities. We propose two possible explanations to the association between higher densities and brown mismatch. First, we may have overestimated actual brown hare mismatch on snow by not accounting for snow-driven plasticity, mediated by snow presence (Kumar et al. In Press). Second, brown hare mismatch was strongly correlated with mean snow depth ($\rho = 0.83$; Appendix B, Table S2), which was nearly as predictive a variable as brown hare mismatch (43% of model iterations; indicator variable selection). Thus, some of the positive effect of brown hare mismatch on density may actually be due to the associated deeper mean snow depth, which is known to inhibit hare predators (Murray and Boutin 1991, Kolbe et al. 2007, Holbrook et al. 2017a) and decrease hunting success (Wells and Bekoff 1982, Stenseth et al. 2004).

We did not consider the costs of mismatch in our projections of future hare densities for several reasons. Snow data was only available for 15 of the 21-year dataset (2004-2018), reducing data available to model climate effects on hares. Additionally, we made the following simplifying assumptions to estimate putative mismatch to apply to our summer density estimates: no year to year plasticity, identical phenologies over a large spatial scale and application of a population average to a process with high individual variation (Zimova et al. 2014). Previous studies avoided these assumptions by tracking the same individuals throughout their molts (e.g.

Mills et al. 2013, Zimova et al. 2014, Kumar et al. In Press), leading to robust projections of hare populations in the future under climate change (Zimova et al. 2016). These previous findings are consistent with ours in that climate induced reductions in snow cover duration should increase white hare mismatch, decrease brown hare mismatch and potentially reduce future hare densities in the absence of an adaptive response. However, these studies did not account for the effects that temperature may have on hares. Although we found a positive effect of fewer days below -5° C in the future on hare density, it was overwhelmed by the negative effect of future increased maximum summer temperatures in the future. Thus, the cumulative negative effect of warming temperatures may compound the negative effect of increased pelage mismatch. New methods of quantifying molt phenology from camera traps (Zimova et al. 2019, 2020) combined with field-based climate measurements could further elucidate how future changes in temperature and snow affect hares.

Our projections tested the future relative effects of warmer summers versus warmer winters (ignoring color mismatch for reasons stated above). In order to accurately predict future hare densities under climate change, in addition to linking temperature to hare density, all relevant effects of climate change (e.g. snow cover) need to be considered simultaneously. Thus, we were unable to include all necessary covariates to predict future hare densities. Instead, our projections demonstrate how future temperature changes may influence hare density and serve as an example of the opposing ways climate change can affect species.

Our finding that the negative effect of warming summers overwhelms the positive effect of warming winters could be due to either disproportionately stronger effects of summer temperatures on hare densities or disproportionately stronger summer warming. Past and projected Arctic winters warm at a much faster rate than summers (Screen and Simmonds 2010, Bintanja and Linden 2013) and this pattern also extends to temperate latitudes such as the Northeast United States (Thibeault and Seth 2014). Consistent with this pattern, we found the mean minimum temperature in the coldest month (mmin) increased by 31% in 2090 (RCP 8.5) while the mean maximum temperature in the warmest month (mmax) increased by 23% in 2090 (RCP 8.5). Thus, our observed stronger effect of summer densities is more likely to be driven by disproportionately stronger effects of summer versus winter warming on hare densities and not due to disproportionately stronger summer warming.

The issue of magnitude of change versus effect of change also applies to the stage-based changes in vital rates that we believe connect our climate variables to density. Survival of leverets and adults have been shown to have the highest elasticity values in snowshoe hares (Haydon et al. 1999), implying that infinitesimal changes in these vital rates will have the highest infinitesimal effects on changes in density from year to year. However, large changes in vital rates with low elasticities can affect population growth more than small changes in high elasticity vital rates (Mills et al. 1999, Wisdom et al. 2000). Therefore, without information on process variation in component vital rates we cannot identify which stage-specific mortalities due to predation are most important in determining hare densities.

Overall, we found strong support for both snow and temperature influencing hare densities. Consistent with previous findings, longer periods of hare mismatch were associated with lower hare densities. Additionally, the effects of a warming climate had contrasting, but unequal, effects depending on the season. The positive effect of fewer cold winter days was overwhelmed by the negative effect of warmer summer temperatures on hare density. This projection exemplifies the importance of considering the many and possibly opposing effects of climate in a unified framework to predict the cumulative population outcome for wild species in a changing climate.

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Tables

Table 1 - Support for various models of hare density in western Montana from 1998-2018. Models varied g0, the probability of detection given the individual's activity center is at the detector while holding sigma, the spatial scale over which the detection probability declines, constant. Behavioral accounts for a change in detection probability after first capture. Heterogeneity uses a two-class finite mixture to account for individual differences. Density was estimated using the Package SECR in Program R. K indicates the number of parameters in the model.

Model	K	AICc	ΔAICc
g0 ~ sex + heterogeneity, sigma ~ 1	5	37280.33	0.00
g0 ~ sex + heterogeneity + behavior, sigma ~ 1	6	37282.49	2.16
g0 ~ heterogeneity, sigma ~ 1	4	37461.65	181.33
g0 ~ heterogeneity + behavior, sigma ~ 1	5	37469.94	189.61
g0 ~ sex, sigma ~ 1	3	37512.51	232.18
g0 ~ sex + behavior, sigma ~ 1	4	37512.95	232.62
g0 ~ 1, sigma ~ 1	2	37761.58	481.25
g0 ~ behavior, sigma ~ 1	3	37762.41	482.09

Table 2 - Support for various models of hare density in western Montana from 1998-2018. Models varied sigma, the spatial scale over which the detection probability declines, while using the best supported model for g0, the probability of detection given the individual's activity center is at the detector (Table S3). Heterogeneity uses a two-class finite mixture to account for individual differences. Density was estimated using the Package SECR in Program R. K indicates the number of parameters in the model.

Model	K	AICc	ΔAICc
g0 ~ sex + heterogeneity, sigma ~ heterogeneity	6	37181.87	0.00
g0 ~ sex + heterogeneity, sigma ~ sex + heterogeneity	7	37218.94	37.07
g0 ~ sex + heterogeneity, sigma ~ sex	6	37272.45	90.58
g0 ~ sex + heterogeneity, sigma ~ 1	5	37280.33	98.45

Table 3 - Support for covariates on density estimates for snowshoe hares in western Montana from 2004-2018. Density estimates were obtained using a spatially-explicit capture-mark-recapture framework. Covariates were placed on true density using a state space model implemented in a Bayesian framework. Maximum and minimum temperatures are yearly maximum and minimum temperatures, respectively from the previous winter or summer. Spring precipitation is the total precipitation from May 15 to June 15 of the previous year. White mismatch squared is the square of the number of days white hares were on snowless ground in the previous year. Brown mismatch squared is the square of the number of days brown hares were on snowy ground in the year.

Covariate	Mean	95% CI	Probability $\beta \neq 0$
Days Below -5° C	-0.124	(-0.256, 0.006)	0.970*
Maximum Temperature	-0.095	(-0.239, 0.049)	0.902*
Minimum Temperature	0.049	(-0.071, 0.168)	0.789
Spring Precipitation	-0.025	(-0.157, 0.106)	0.648
White Mismatch Squared	-0.128	(-0.282, 0.009)	0.965*
Brown Mismatch Squared	0.238	(0.099, 0.379)	1.000*

* Covariate with high probability that their beta coefficient does not equal 0.

Table 4 - Support for covariates on density estimates for snowshoe hares in western Montana from 1998-2018. Density estimates were obtained using a spatially-explicit capture-mark-recapture framework. Covariates were placed on true density using a state space model implemented in a Bayesian framework. Snow compaction was indexed using temperature fluctuations (Kausrud et al. 2008). Maximum and minimum temperatures are yearly maximum and minimum temperatures, respectively from the previous winter or summer. Spring precipitation is the total precipitation from May 15 to June 15 of the previous year.

Covariate	Mean	95% CI	Probability $\beta \neq 0$
Snow Compaction	0.085	(-0.054, 0.224)	0.884
Days Below -5° C	-0.166	(-0.307, -0.026)	0.989*
Maximum Temperature	-0.277	(-0.405, -0.149)	1.000*
Minimum Temperature	-0.003	(-0.109, 0.103)	0.520
Spring Precipitation	-0.031	(-0.141, 0.080)	0.707

* Covariate with high probability that their beta coefficient does not equal 0.

Figures

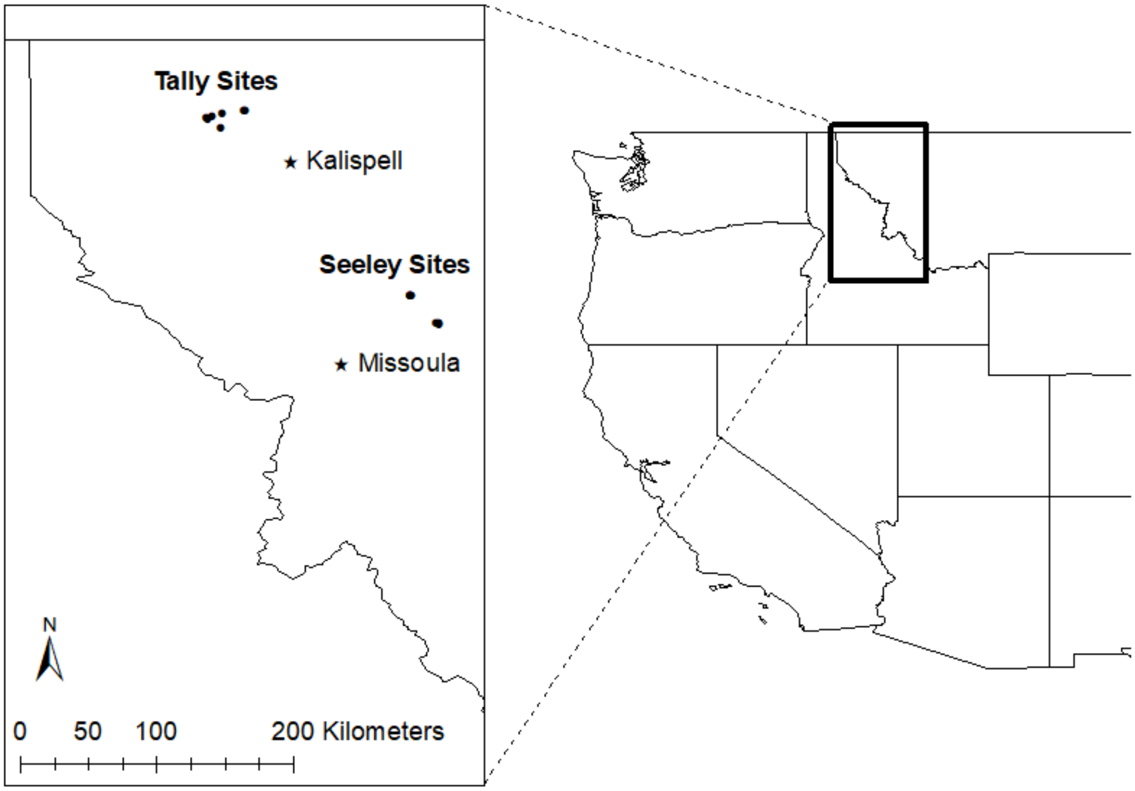

Figure 1 - Snowshoe hare study areas in western Montana from 1998-2018, with locations of the 7 Tally trapping grids and 7 Seeley trapping grids. In some cases, multiple sites are close enough to each other to appear as one dot.

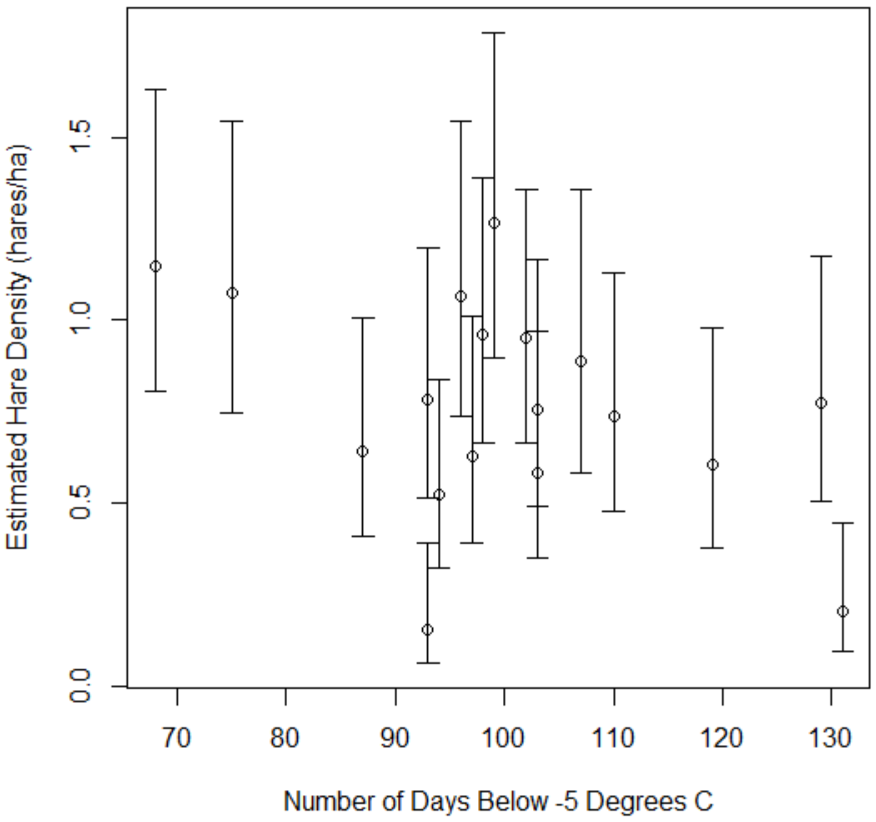

Figure 2 - Summer hare density compared to the number of days below 5°C of the previous winter at one grid (Pigskin) in western Montana. Density estimates were obtained using a spatially-explicit capture-mark-recapture framework. Temperature data was derived from Daymet.

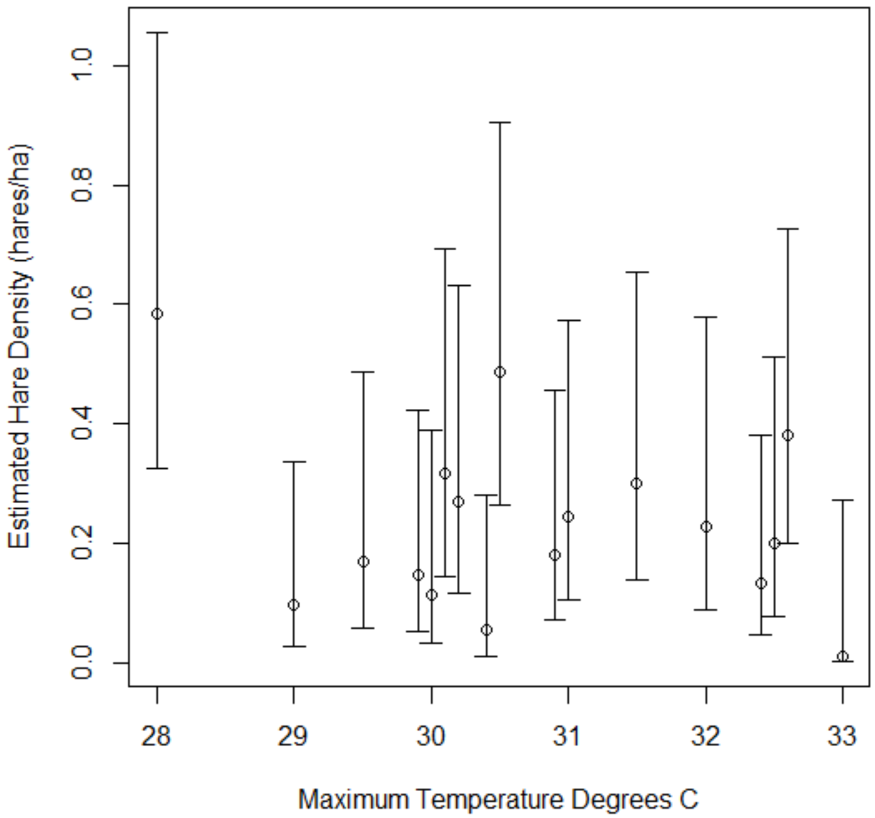

Figure 3 - Summer hare density compared to the maximum temperature of the previous summer at one grid (SCCO) in western Montana. Density estimates were obtained using a spatially-explicit capture-mark-recapture framework. Temperature data was derived from Daymet.

Appendix A

Hare Molt Phenology

We have rigorously quantified the hare molt for four years from two sites near the Seeley Lake study area (Mills et al. 2013, Kumar at al. In Press) (Table S1). At these sites (Morrell Creek and Marcum Mt.), the molt lasted 40-50 days (Mills et al. 2013, Kumar at al. In Press). Both of these sites are located within 60 <km of our Seeley Lake study area at similar elevations. As the variation between Marcum Mt. and Morrell Creek in molt phenology is low (Table S1), we assumed that the hare molt of these sites is representative of the hare molt at the Seeley Lake study area.

Next, we used the raw molt phenology data from Mills et al. 2013 and Kumar at al. In Press to estimate daily hare coat color (white or brown). First, we found the average date that hare population became 50% white during their spring and fall molts for each of the four years of molt phenology data (Table S1). We then used the average date of those four years to approximate the date when hares reach the 50% white threshold in the fall and spring (Table S1). Using these two dates, we then determined daily hare coat color (white or brown) from 2004-2018. This approach assumes a fixed date that hares become 50% white. However, hares display some plasticity in the initiation (Kumar et al. In Press) and substantial plasticity in the completion of their molts (Mills et al. 2013, Zimova et al. 2014) allowing them to partially track snow cover. Nevertheless, the dates that the molt reaches 50% are less variable than the molt start and end dates and differ by just four days in the fall and 12 days in the spring (Table S1). Thus, plasticity influences the start and end dates of the molt more than the date that the molt reaches 50%. Finally, no molt phenology data exist from the Tally Lake study area so we assumed the same molt phenology as Seeley Lake. Hares exhibit a low degree of genetic differentiation at regional levels (Burton et al. 2002) and hares from Tally Lake and Seeley Lake from one genetic group (Cheng et al. 2014).

Table S1. Estimates of snowshoe hare molt phenology from two study sites in western Montana. From Mills et al. 2013 and Kumar at al. In Press.

Location	Molt Start	50% White (Fall)	50% White (Spring)	Molt End
Morrell Creek	10/13/2009	10/27/2009	4/21/2010	5/10/2010
Morrell Creek	10/8/2010	10/25/2010	5/1/2011	5/26/2011
Morrell Creek	10/7/2011	10/29/2011	4/22/2012	5/18/2012
Marcum Mt.	10/13/2013	10/28/2013	5/3/2014	5/26/2014
Average	*10/10*	*10/27*	*4/27*	*5/20*
Range (days)	*6*	*4*	*12*	*16*

Appendix B

Correlation Between Covariates

Table S2 - Correlation between all covariates. We considered covariates strongly correlated when $\rho > 0.6$.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
1	1.00	-0.33	0.50	0.95	-0.42	0.43	-0.58	-0.55	0.02	-0.20	0.28	-0.05	-0.24
2	-0.33	1.00	0.62	-0.42	0.94	0.64	0.78	0.66	0.16	0.47	-0.56	-0.18	0.13
3	0.50	0.62	1.00	0.40	0.54	0.97	0.23	0.17	0.15	0.33	-0.33	-0.22	-0.06
4	0.95	-0.42	0.40	1.00	-0.52	0.37	-0.67	-0.62	-0.02	-0.21	0.33	-0.05	-0.21
5	-0.42	0.94	0.54	-0.52	1.00	0.60	0.83	0.72	0.19	0.54	-0.58	-0.15	0.14
6	0.43	0.64	0.97	0.37	0.60	1.00	0.27	0.20	0.18	0.39	-0.31	-0.21	-0.05
7	-0.58	0.78	0.23	-0.67	0.83	0.27	1.00	0.96	0.06	0.37	-0.40	-0.06	0.21
8	-0.55	0.66	0.17	-0.62	0.72	0.20	0.96	1.00	-0.03	0.30	-0.35	-0.03	0.21
9	0.02	0.16	0.15	-0.02	0.19	0.18	0.06	-0.03	1.00	0.62	0.22	-0.15	-0.03
10	-0.20	0.47	0.33	-0.21	0.54	0.39	0.37	0.30	0.62	1.00	-0.27	-0.15	0.29
11	0.28	-0.56	-0.33	0.33	-0.58	-0.31	-0.40	-0.35	0.22	-0.27	1.00	-0.04	-0.45
12	-0.05	-0.18	-0.22	-0.05	-0.15	-0.21	-0.06	-0.03	-0.15	-0.15	-0.04	1.00	0.27
13	-0.24	0.13	-0.06	-0.21	0.14	-0.05	0.21	0.21	-0.03	0.29	-0.45	0.27	1.00

1 = white hare mismatch squared, 2 = brown hare mismatch squared, 3 = total hare mismatch squared, 4 = white hare mismatch, 5 = brown hare mismatch, 6 = total hare mismatch, 7= mean yearly snow depth, 8 = maximum yearly snow depth, 9 = snow compaction, 10 = number of days with minimum temperature below -5° C, 11 = maximum summer temperature, 12 = minimum winter temperature and 13 = total precipitation from May 15 to June 15.

Appendix C

Sex Effects on Detection Probability

Table S3 - Estimates of g0, the probability of detection given the individual's activity center is at the detector, for all combinations of sex and group. The parameter g0 was used to estimate hare density in western Montana from 1998-2018. Group refers to the two classes used in the mixture model used to represent heterogeneity.

Sex	Group	Estimate	95% CI
Male	H1	0.13	0.11 - 0.15
Male	H2	0.01	0.01 - 0.02
Female	H1	0.26	0.23 - 0.30
Female	H2	0.03	0.02 - 0.04

Chapter 3: Landscape structure and generalist predation drive hare densities in the southern portion of their range

Abstract

Periodic fluctuations in abundance commonly occur in diverse taxa and these cycles frequently dampen in portions of species' ranges. Although numerous explanations have been proposed to explain cycle dampening, high generalist predation is generally the most supported explanation in many systems. Additionally, landscapes with more open areas could exacerbate the effects of generalist predation further dampening cycles. Therefore, we tested the joint effects of landscape structure and generalist predation using an extensive 21 year time series of snowshoe hare density estimates from 14 sites in western Montana, an area with dampened hare cycles. We found strong support for the effects of both predation and landscape structure on hare densities. Increased open areas surrounding trapping grids were associated with lower hare densities, supporting the landscape structure hypothesis. In addition, greater numbers of hare predator species, detected via trail cameras, and higher direct predation rates determined via a survival analysis, were associated with lower hare densities. Furthermore, we detected more generalist predator species in our area of dampened cycles than occur in areas where hares cycle, consistent with the generalist predation hypothesis. Both landscape structure and generalist predation may combine to dampen population dynamics in other systems where only the generalist predation hypothesis has been considered.

Introduction

Cyclic species are an enigmatic topic in ecology (Chitty 1996, Turchin 2003, Lambin et al. 2006, Barraquand et al. 2017, Myers 2018) dating back to the work of Charles Elton (Elton 1924). As many as 30% of all animal species undergo cyclic dynamics (Kendall et al. 1998) and cyclic animal species present special management challenges at high densities (e.g. reducing timber production: Liebhold et al. 2000, Huitu et al. 2009; threatening the Great Barrier Reef: De'ath et al. 2012).

Dampened and even non-existent cycles altogether are a common feature exhibited by many cyclic species in portions of their range (Stenseth et al. 1996, Klemola et al. 2002, Newey et al. 2007). Notable examples include dampening towards southern latitudes in Fennoscandian lemmings, voles and moths (Bjørnstad et al. 1995, Klemola et al. 2002), dampening towards westward longitudes in Japanese voles (Stenseth et al. 1996) and dampening towards northern latitudes in Central European voles (Tkadlec and Stenseth 2001). Other species exhibit dampened cyclic dynamics throughout much of their range with no clear gradient or pattern (e.g. mountain hare; Newey et al. 2007).

The geographic and taxonomic diversity of dampened cyclic dynamics has led to numerous proposed explanations including latitude and snow cover (Hansson and Henttonen 1985). However, a leading explanation of cycle dampening over space is a decreased ratio of specialist to generalist predators as generalists respond rapidly to changing prey numbers (Hanski et al. 1991, 2001, Klemola et al. 2002). Increasing generalist predation is either considered to be the primary driver (Hanski et al. 1991, 2001, Klemola et al. 2002) or in combination with a more open landscape structure (Sievert and Keith 1985, Griffin and Mills 2009, Vitense et al. 2016). Herein, we quantify how both of these purported drivers of cycle dampening: generalist predation and landscape structure, affect the density of snowshoe hares, *Lepus americanus*.

Snowshoe hares are famed for their drastic population fluctuations in the northern boreal forests of North America (Hodges 2000a, Krebs et al. 2018, Myers 2018). Conversely, hare cycles are thought to be dampened or nonexistent in the southern portion of their range (Howell 1923, Keith 1990, Hodges 2000b), a region roughly corresponding to the continental USA (Hodges 2000b). However, few researchers have conducted data-based analyses of hare population dynamics in these lower latitudes (Keith 1990, Murray 2000, Griffin and Mills 2009), and none have exceeded four years in duration.

Landscape structure has long been hypothesized to drive dampened cyclic or acyclic southern hare population dynamics (Howell 1923, Lewis et al. 2011) Mechanistically, landscapes with more open areas are thought to increase predation rates on hares that move through the open areas (Dolbeer and Clark 1975, Sievert and Keith 1985), and thereby create source-sink dynamics sufficient to dampen cycle peaks across the landscape (Griffin and Mills 2009). This proposed mechanism implies that high direct predation of hares in open areas ultimately drives the negative effects of the patchy landscape on hare densities. Indirect effects may also interact with direct mortality to affect densities in populations across heterogeneous landscapes (Brown et al. 1999, Creel and Christianson 2008). In snowshoe hares, an increase in stress due to increased exposure to predators can lower reproductive output of both the females that experienced increased predator exposure and their offspring (Sheriff et al. 2009, Krebs et al. 2018, MacLeod et al. 2018), thereby prolonging the low phase characteristic of cyclic northern hares (Oli et al. 2020).

As landscapes with more open areas are thought to lead to increased predation, an increase in generalist predation is usually proposed with the landscape structure hypothesis (also referred to as the landscape fragmentation hypothesis; Keith et al. 1993, Vitense et al. 2016) as generalists can better exploit edge and early successional habitat (e.g. coyotes; Buskirk et al. 2000). In addition to lynx and coyotes which inhabit northern boreal forests, southern hares face predation from generalist predators such as bobcats and cougars (Major and Sherburne 1987, Elbroch and Wittmer 2013). Generalist predators stabilize densities and dampen cycles by maintaining sustained numerical responses even as prey numbers change (Andersson and Erlinge 1977, Hanski et al. 1991, Klemola et al. 2002, Mills 2013). Theoretical models of hare dynamics support both generalist predation and landscape structure dampening cycles; jointly they produce the most severe dampening (Vitense et al. 2016). However, the generalist predation and landscape structure hypotheses have not been explicitly tested with snowshoe hare field data from the southern portion of their range.

To jointly quantify the roles of landscape structure and generalist predation on hare densities we used the most extensive set of capture-recapture data on snowshoe hares in the southern part of their range (Mills, unpublished data). This dataset spans two decades and includes live captures of almost 2,000 individuals from 14 different grids in western Montana. We also included predator detections from trail cameras at 280 different locations within the grid areas.

Our primary objective was to test the effects of landscape structure and generalist predation on southern hare density estimates over time. We predicted that higher generalist predation and landscapes with more open areas would lower hare densities. To test the generalist predation hypothesis we first determined if there was evidence that predation influences hare density by testing for an effect of the following covariates on hare densities: various predation metrics derived from trail camera predator detections, direct predation rate and the probability of lynx use of the grid (Holbrook et al. 2017a). We approximated direct predation rate with mortality rate (Murray 2002) which we calculated with a survival model since nearly all hares die by predation (Hodges 2000b, Wirsing et al. 2002, Abele et al. 2013). Including direct predation rate also enabled us to test for the role of indirect predation because if predictors are significant after accounting for the effects of direct predation, their significance may be driven in part through indirect predation. We then examined the role of generalist predators on hare densities by quantifying the number of generalist predator species detected and the effect of increased numbers of predator species on hare density. Finally, in addition to landscape structure, we accounted for other effects of local vegetation structure on hare densities, by considering canopy closure (Pietz and Tester 1983, Holbrook et al. 2017b, Gigliotti and Diefenbach 2018), horizontal cover (Pietz and Tester 1983, Lewis et al. 2011, Holbrook et al. 2017b) and sapling density (Fuller et al. 2007, Lewis et al. 2011, Ivan and Shenk 2016).

Methods

Study Areas

We collected snowshoe hare summer density data from 1998-2018 at 14 trapping grids in two areas (Seeley Lake and Tally Lake) in western Montana, USA (Figure 1; for site descriptions see Mills et al. 2005). All sites were managed by the Forest Service (USFS) with a history of multiple use including timber production. Seeley Lake (Lat. = 47.2°, Long. = -113.4°) and Tally Lake (Lat. = 48.5°, Long. = -114.8°) are approximately 175 km apart and span similar elevations (approximately 1500-1900 m.a.s.l.). Both areas are dominated by moist, coniferous forests of

Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and Ponderosa pine (*Pinus ponderosa*) with a herbaceous understory.

Capture/Handling

Snowshoe hares were trapped during the summer (May-August) using live-traps (51x18x18 cm, Tomahawk Live Trap Company, Tomahawk, WI) baited with alfalfa cubes and apples, spaced approximately 50m apart (Mills et al. 2005). Each of the seven Seeley Lake hare trapping grids consisted of approximately 50 traps, while the seven Tally Lake trapping grids had approximately 80 traps each. Each grid was trapped for 3-5 days each summer, ensuring population closure. We marked all hares >500g with a unique numbered ear tag. We weighed all hares, determined sex, measured right hind foot length and determined breeding status (lactating or pregnant, testes abdominal or testes scrotal). Hares were considered juveniles if they weighed < 700 grams or if their right hind foot length was < 10 cm. All other hares were considered adults. All capture and handling procedures were approved by the University of Montana Animal Care and Use Committee (various permits over 21 years).

Landscape Structure

We estimated landscape structure as percent open-structured area buffering each grid each year (Lewis et al. 2011). We classified the area in a 300 m buffer around each hare trapping grid as closed canopy moist deciduous forest or open-structured area (Lewis et al. 2011) using satellite imagery during the leaf-on season (June-September) from Google Earth. We divided the buffer area into eight sections and visually approximated the percent of the section that was open canopy in 25% increments. Then we estimated the percent open canopy of the entire buffer by averaging the eight sections weighted by their area. As the vegetation structure likely changed during the approximately 20-year study duration, we analyzed all available images taken during the study duration (1998-2018). We extrapolated values for years with missing images (n = 14) by averaging the two estimates that spanned the missing year when possible; otherwise we applied the nearest estimate to the missing year.

Vegetation Structure

We measured vegetation characteristics twice, once at the beginning of the study (1998-2001) and once at the end (2019) using 6-10 plots (5m radius or three 2m radius subplots) per grid. We considered the following vegetation attributes: sapling density, basal area, horizontal cover and canopy cover (Lewis et al. 2011, Kumar et al. 2018). We estimated sapling density using complete counts of all stems greater than 0.5m tall and less than 8 cm diameter at breast height (DBH). Initially, we estimated basal area of trees with variable radii, using a Relaskop (Speigel, Germany) while at the end of the study we estimated basal area by measuring DBH of all stems greater than 8 cm DBH. The results of these two methods should not differ by more than a few percent (West 2015). We estimated horizontal cover initially using visual observation of a coverboard (100 cm x 50 cm) divided into two 50 cm tall sections at 3-4 locations per plot at 7 of the 14 grids. In 2019, we used a similar technique but rather than quantifying cover with visual observation, we estimated horizontal cover and canopy closure using photographs analyzed in Adobe Photoshop (Kumar et al. 2018). Horizontal cover was estimated by photographing a coverboard (100 cm x 50 cm) and counting the number of unobstructed coverboard pixels in Adobe Photoshop. This number was then divided by the total number of pixels comprising the coverboard to yield an estimate of the proportion of the coverboard unobstructed by vegetation. We estimated horizontal cover at three different compass azimuths, the first chosen randomly and the last two 120° apart from the first. Similarly, we estimated canopy closure at the center of each plot using a fisheye lens mounted to a camera. We again used Adobe Photoshop to divide the number of pixels unobstructed by cover by the total number of pixels and subtracted that number from one to estimate canopy closure.

We did not measure canopy closure at the beginning of the study. However, we did measure basal area which is correlated with canopy closure (Mitchell and Popovich 1997). Indeed, canopy closure and basal area, both measured at the end of the study, were correlated ($\rho = 0.65$) so we used basal area as a proxy for canopy closure. We then fit grid-specific linear models using the years we measured vegetation and used the model to extrapolate values for years that we did not measure vegetation. Thus, we obtained grid and year specific estimates of sapling density, canopy closure (indexed by basal area) and horizontal cover.

Quantifying Hare Predation

We quantified hare predation using a survival analysis (see below), predator detections via trail cameras and a lynx resource selection function (Holbrook et al. 2017a). We recorded predator detections from trail cameras set on each hare grid during the summers of 2017 and 2018, simultaneously with hare trapping to approximate predator use of the grid. Ten cameras were set on each grid for approximately 15-20 days and then moved to a new location on the same grid for the same duration. This setup yielded 20 locations and 300-400 camera days per grid per year, a sampling intensity that should be sufficient to detect most common species (Rowcliffe et al. 2008, Tobler et al. 2008). Predator detections were considered independent if they were on different cameras or greater than one hour apart (Tobler et al. 2008, Brodie and Giordano 2012, Burton et al. 2015).

Since predation data from trail cameras were only available from 2017-2018, we tested for a difference between years using a paired t-test for each grid. None of the 14 grids had significant differences in predator detections between the two years. Therefore, we averaged the detections for the two years yielding grid specific trail camera predation metrics that we then used for the full study duration (1998-2018). This approach assumes that two years of trail camera data are representative of the full study duration. To further test this assumption, we examined the relative effects of grid versus year in the hare survival model (below). We also standardized all predictors resulting from trail camera images to reflect the number of detections per 1000 camera days.

Generalist Predation

We indexed generalist predation pressure as the total number of all hare predator species detected. In the northern boreal forest, the following three predator species function as hare specialists: lynx, coyotes and great horned owls (Tyson et al. 2010, Krebs et al. 2018); the following remaining predators are generalists: red squirrels, ground squirrels, red foxes, wolves and weasels along with three species of *Accipitriformes* (O'Donoghue 1994, Boonstra et al. 2016, Krebs et al. 2018). Of particular note, both ground and red squirrels were the main source of mortality for newborn hares (O'Donoghue 1994). In addition to all the boreal predators, southern hares face predation from bobcats (Major and Sherburne 1987), cougars (Spalding and Lesowski 1971, Elbroch and Wittmer 2013), black bears (Raine and Kansas 1990), grizzly bears (Mace and Jonkel 1986) and barred owls (Hamer et al. 2001). Some of these predators (i.e bears) have relatively low average hare consumption, but we included them because plasticity in diet for many carnivores (Theberge and Wedeles 1989), including individual specialization (Elbroch and Wittmer 2013), could lead to higher localized kill rates for these species. Excluding the northern boreal specialists, all the aforementioned predator species can be considered hare generalists in Montana. As for northern specialists, we did not detect great horned owls on any grid (although they are known to occur in the region) and coyotes do not appear to specialize on hares in Montana with hares comprising just 12% of food items in coyote scat (Kolbe et al. 2007). However, lynx are not generalists in Montana as their diet was comprised of 96% snowshoe hare by biomass (Squires and Ruggiero 2007). Nonetheless, partially due to difficulties distinguishing lynx from bobcats, we considered total number of all hare predator species detected to index generalist predation pressure.

We also considered four additional grid level predictors related to general predation: cumulative predation index, squirrel detections, avian detections and primary predator detections. The cumulative predation index was calculated by weighting each independent species detection (excluding squirrels and birds) by the portion of their diet comprised of hares (Table 1) and summing for all species detected on each grid. We excluded red squirrels because we did not want to overwhelm our index with the disproportionately high red squirrel detections. We also excluded avian predators and ground squirrels due to difficulty with species level identification using remote cameras. However, both groups were included as separate predictors: avian detections (the number of independent detections of avian predators) and squirrel detections (the number of independent detections of red squirrels and ground squirrels). Primary predator detections is the number of independent detections of predators with a weight of three or four in Table 1. Detections only identifiable to the genus level (*Canis* & *Lynx*) were included in the primary predators predictor.

Lynx Predation

Because we had so few lynx detections (Figure 2) we also accounted for local and landscape level lynx predation using two additional predictors. Local grid specific probability of lynx use was obtained from a map predicting lynx probability of use throughout western Montana at 30m resolution integrating second and third order resource selection functions (Holbrook et al. 2017a). Landscape level grid specific probability of lynx use was approximated using the same map and a 4 km buffer around each grid (approximate radius of a Montana lynx home range; Holbrook et al. 2018).

Statistical Analysis

Hare Survival

We used a Cormack-Jolly-Seber survival model (Cormack 1964, Jolly 1965, Seber 1965) to approximate hare direct predation rate since nearly all hares die by predation (Hodges 2000b, Wirsing et al. 2002, Abele et al. 2013). We used the package RMark (Laake 2013) to construct models for program MARK (White and Burnham 1999) in Program R (version 3.5.3, R Development Core Team 2019).

We combined multiple detections of the same individual in the same year to estimate yearly survival and capture probability. We considered the following categorical predictors on survival: region (Seeley or Tally), grid, age (juvenile or adult), sex (male or female) and year. We first ran models with only one categorical predictor at a time. Because grid is nested within region, we first evaluated the effects of each of these two location predictors separately. We then compared the best of the nested predictors (determined by AICc) to year. We did not consider year and location predictors in the same model due to insufficient data.

Next, we accounted for differences in body condition (mass/hind foot length) as it has been related to hare survival (Murray 2002) by testing for grid level differences in body condition. We accounted for effort by including an effort predictor on detection probability corresponding to the number of days trapped. Finally, we also included null (intercept only) models for both survival and detection probability.

We deemed predictors significant if the beta coefficient did not overlap zero. We ranked models with significant predictors using Akaike information criterion corrected for small sample size (AICc) and we used AICc differences (ΔAICc) to evaluate model support. We considered models with ΔAICc ≤2 to be indistinguishable from each other and models with ΔAICc >7 to have little support (Burnham et al. 2011).

Hare Density

We estimated adult snowshoe hare density with a spatially-explicit capture-mark-recapture (SECR) model using the Package SECR (Efford 2004, Borchers and Efford 2008, Efford and Fewster 2013) in Program R (version 3.5.3, R Development Core Team 2019) (see Chapter 2 for details). In brief, we built models varying g0, the probability of detection given the individual's activity center is at the detector and sigma, the spatial scale over which the detection probability declines. We ranked models using AICc and used AICc differences (ΔAICc) and Akaike weights (wi) to evaluate model support. The best model included the effects of sex and heterogeneity on g0 and heterogeneity on sigma (Chapter 2).

The SECR density estimates assume that the area immediately surrounding the grid has the same hare density as the trapping grid. This assumption may be violated if a large portion of that area was open structured as this is poor hare habitat (Griffin and Mills 2009). To verify this assumption, we calculated the percent open structured area of the trappable area which we defined as the area used by approximately 95% of the hares available for capture (trap grid plus buffer of 2*sigma = 160 m). We found that open structured area accounted for less than 5% on average of the total trappable area supporting the assumption that the area immediately surrounding the grid has the same density as the trapping grid. However, it is important to note that our landscape covariate which buffers the trapping grid by 300 m really only provides landscape inference for the 140 m immediately buffering the trappable area. We considered this 140 m buffer size large enough to represent the landscape available to hares as the total buffer area was approximately five times the home range size of hares in this area (Kumar et al. In Press).

Vegetation Structure and Predation Effects on Density

We used a state space model (Rotella et al. 2009) to determine the effects of local and landscape level vegetation structure and predation predictors on hare density. In addition to the aforementioned predictors, we tested for the effects of the following predictors on hare density: region (Seeley vs Tally), individual trapping grid and year. State space models consist of both observation and process components to separate measurement error from process noise (Dennis et al. 2006, Rotella et al. 2009). In this context, we use measurement error to refer to variability in the data that arises purely as a result of the sampling process and process noise to refer to fluctuations caused by environmental variability (Humbert et al. 2009). The observation model used hare density estimates and the associated measurement error from the SECR model to approximate the unknown true hare density with the following relationship: $\widehat{D}_t \sim \mathrm{N}(D_{t\,,}\; se_t^2)$, where $\widehat{D}_t$ is the time specific density estimates, D_t is the true density and se_t^2 is the squared estimate of measurement error. The process model then estimated process variance and the effects of predictors on true density as follows: $\log(D_t) = \mu + y_t$ with μ being the equilibrium value of the logarithm of true density and $y_t \sim \mathrm{N}(\alpha_{t\,,}\, \sigma_{pr}^2)$ where σ_{pr}^2 is process variation. Finally, $\alpha_t = \beta_1(cov1) + \beta_2(cov2) + \beta_3(cov3)$ ... where β represented the coefficient relating the predictor to α_t. We assumed that process variation and measurement errors were independent.

We implemented the model in a Bayesian framework (Rotella et al. 2009) to accommodate grid-years when we did not trap (~18% of all grid-year combinations). We standardized all predation and vegetation structure predictors to have a mean of 0 and a standard deviation (SD) of 1 to ease interpretation and expedite convergence. If two predictors were strongly correlated ($\rho > 0.6$), we used indicator variable selection, a process that informs how important each of the two correlated predictors are to the model, to determine which predictor best fit the model (Hooten and Hobbs 2015). Doing so allowed us to include both predictors in the model but each iteration only included one of the two correlated predictors ensuring that the two correlated predictors were never included in the model at the same time. Once we determined which predictor fit best, we used that predictor in the full model and omitted the other correlated predictor. If indicator variable selection revealed approximately equal support for both correlated predictors, then we chose one predictor to include based on *a priori* biological knowledge. Using this process, squirrel detections (correlated with basal area), primary predator detections (correlated with generalist predation pressure) and landscape level lynx probability of use (correlated with grid level lynx probability of use) were removed from the final model.

We fit models with Markov Chain Monte Carlo (MCMC) in JAGS using the R package jagsUI with uninformative priors except in the case of indicator variables where we used the "slab and spike" prior to alleviate computational problems and improve mixing (Hooten and Hobbs 2015). Specifically, we used a gamma distribution as a prior for σ_{pr}^2 with both hyperparameters set to 0.001. We specified the prior for μ as a normal distribution with a mean of 0 and a precision (1/variance) of 0.01. We used a normal distribution with a mean of 0 and a precision of 0.01 as a prior for all the betas, except when they were used with indicator variable selection. In such cases, we specified the slab and spike prior with a normal distribution with a mean of 0 + (ω * mean of beta) and a precision of 0.01 + (ω * 10) with ω being the binary indicator variable and the mean of the beta coefficient being determined in a previous model run. These priors represent a stationary distribution of 1 hare/ha and no effects of any predictor on density. We ran all models with five chains of at least 110,000 iterations discarding the first 10,000 as burn-in. We assessed convergence by visually examining the trace and density plots for the beta coefficients and with the Gelman-Rubin statistic ($\hat{R} < 1.1$). We used the 95% credible intervals as well as the probability that the beta coefficient does not equal 0 to determine the importance of the predictors.

Results

Predator Detections

We recorded 1,585 independent predator detections representing a minimum of 12 different hare predators (Figure 2) from 9,866 camera days ($\bar{n}$ = 18 camera days per location).

Red squirrels were by far the most common hare predator detected (n = 1,231), followed by black bears (n = 204; Figure 2). On each grid we detected between 6 and 12 hare predator species per 1000 camera days.

Hare Survival

From 1998-2018, we captured 2,939 unique hares 4,037 times. The best survival model included the additive effects of hare age and grid on survival and effort on capture probability (Table 2). Adult annual survival, 0.34 (95% CI = 0.31-0.36) was significantly higher than juvenile annual survival, 0.13 (95% CI = 0.10-0.16). Two grids had significantly higher survival than the other twelve grids (Figure 3). Grid was better supported than year (Table 2; see Appendix A Figure S1 for yearly survival estimates). Although sex had a marginally significant effect on survival (Table 2, Appendix A Table S1), the effect size was small relative to that of age or grid, ΔAICc was > 30 (Table 2) and other studies have found little to no effect of sex on survival (Sievert and Keith 1985, Griffin and Mills 2009, Abele et al. 2013). Therefore, we excluded sex from our best model to avoid overparameterization. Pairwise comparisons of body condition among grids were not significant so body condition was left out of the best model. Yearly capture probability using a constant detection probability and including the effects of age and grid on survival was 0.69 (95% CI = 0.65-0.73).

Vegetation Structure and Predation Effects on Density

We found support for eight predictors influencing hare density. Direct predation rate and lynx probability of use had the strongest support with probabilities of 1.00 that their beta coefficients do not equal 0 (Table 3). Direct predation rate had a negative correlation with hare density while lynx probability of use had a positive correlation. The following six additional predictors had probabilities > 0.90 that their beta coefficients do not equal 0: horizontal cover, sapling density, landscape structure, generalist predation pressure, cumulative predation index and avian detections (Table 3). Both landscape structure and generalist predation pressure had negative correlations with hare density. The remaining four predictors had positive correlations with hare density. No other predictor had significant effects on hare density.

Discussion

High generalist predation is usually the primary explanation to the dampened cyclic dynamics that commonly occur in diverse taxa. Additionally, landscape structure has also been thought to have the potential to exacerbate the cycle dampening effects of generalist predation. Using 242 grid and year specific density estimates from the largest live-trapping dataset of snowshoe hares in the southern portion of their range, we found strong support for joint effects of landscape structure and predation. As predicted by the landscape structure hypothesis, increasing open areas surrounding trapping grids were associated with lower hare densities. In addition, greater numbers of hare predator species on the trapping grid and increasing direct predation rates were associated with lower hare densities. Furthermore, we found significant effects of various vegetation structure predictors after accounting for the direct effects of predation.

Landscape structure has long been hypothesized to influence southern hare population dynamics (Dolbeer and Clark 1975, Buehler and Keith 1982, Keith et al. 1993) primarily via a source-sink dynamic of increased predation on dispersers moving through open areas (Dolbeer and Clark 1975, Sievert and Keith 1985, Griffin and Mills 2009). Consistent with this mechanism, we found lower hare densities in grids surrounded by more open areas. Our findings agree with Lewis et al. (2011) who found that sites surrounded by more open areas had lower hare pellet densities and with a simulation study in which synchronous landscape scale conversion of closed to open canopy forests, led to overall decreased hare abundance (Griffin and Mills 2004). In addition to causing disperser mortality in the surrounding landscape, the open area around the grid may also increase predator accessibility to the grid itself (Buskirk et al. 2000), thereby increasing direct predation on the grid. However, direct predation rate was uncorrelated with landscape openness ($\rho < 0.1$) implying direct predation does not increase in grids surrounded by more open areas. In addition, none of the predation metrics were positively related to landscape openness ($\rho < 0.1$), suggesting that more open landscapes did not increase predator accessibility to the grid. Thus, our findings are consistent with the landscape structure hypothesis which posits that more open areas promote increased predation on dispersers moving through the surrounding open landscape.

We also found evidence that predation strongly influences southern hare density. Unsurprisingly, direct predation rate had a strong negative association with hare density, indicating that adult survival may influence hare population dynamics. Indeed, changes in adult hare survival tracked density changes in the northern boreal forests (Keith and Windberg 1978, Oli et al. 2020). Also, lynx probability of use had a strong positive association with hare density. As lynx diet consists of a high proportion of hares, (Roth et al. 2007, Squires and Ruggiero 2007, Ivan and Shenk 2016) they are likely attracted to areas that have high hare densities. Higher hare densities attracting predators likely also explains the positive associations of cumulative predation index and avian detections with hare density.

Increasing generalist predation, in particular, is thought to combine with landscape structure to lower southern hare densities (Buehler and Keith 1982, Vitense et al. 2016). We detected four to eight different hare predators on each grid, cumulatively representing at least 12 different predators (10 excluding avian generalists). In contrast, northern hares are thought to have just eight total predators excluding avian generalists (three main specialist predators: lynx, coyotes and great horned owls and five generalists: red squirrels, ground squirrels, red foxes, wolves and weasels; Tyson et al. 2010, Boonstra et al. 2016, Krebs et al. 2018). All 12 predator species we detected (except lynx) can be considered generalists in Montana. Furthermore, as we detected lynx on just three of the fourteen grids, lynx detections should have a minimal effect on our generalist predation pressure index. Beyond the predators found in the northern boreal forests, we cumulatively detected at least five additional generalist hare predators, with as many as four of these species detected on single grids. However, despite detecting numerous generalist predators, we do not know how much of their diets are comprised of hares. Nonetheless, we detected more generalist predator species than occur in the northern boreal forests and our index of generalist predation pressure was correlated with lower hare densities, findings consistent with the generalist predation hypothesis.

We did not find that all generalist predators on hares influenced hare density. In some cases we did not detect hare predators known to occur in the study region: red fox (Halpin and Bissonette 1988, Theberge and Wedeles 1989), marten (Raine 1987, Cumberland et al. 2001) and fisher (Raine 1987). In the case of red squirrels, we found that they comprised the vast majority of our predator detections, but did not affect hare density. This came as somewhat of a surprise given that both ground and red squirrels can be primary sources of mortality on preweaning hares (O'Donoghue 1994), and preweaning survival follows adult and post-weaning survival in its elasticity on population growth rate (Haydon et al. 1999). However, population growth rate changes depend not only on elasticity of vital rates but also on their magnitude of change (Mills et al. 1999, Wisdom et al. 2000), so we presume that squirrels in our region do not impose as strong a kill rate on newborn hares as in the northern boreal.

We made numerous simplifying assumptions in formulating our predation metrics. Since our direct predation metric was derived from a Cormack-Jolly-Seber survival model, we conflated death and permanent emigration. However, using data from radio-collared hares from 1999-2002 at our study site (Griffin and Mills 2009), we found that under 4% of hare movement was longer than the radius of trappable area (grid plus buffer of three times sigma from the SECR model). Additionally, home range estimates from these radio-collared hares indicate that that the trappable area is six to eight times larger than the average hare home range (Kumar et al In Press). Therefore, we believe the probability of permanent emigration is low.

We assumed that two years of trail camera data capture predator composition across the 21-year study duration. Although we found no significant differences in predator detections between the two years from any of the 14 grids, the two years of camera data may not be representative of the full study duration. However, it is encouraging that in our survival analysis, which approximates direct predation rate, spatial variability overwhelmed temporal variability, with grid varying survival estimates better supported than time varying survival estimates.

We likely underestimated our total count of hare predators by assuming all avian detections represented one species, as we detected barred owls and likely multiple species of hawks. However, as our trail cameras were not designed to capture birds, we had very low avian detections and felt it was more appropriate to combine them into one metric. Also, our camera metrics approximate predation pressure by quantifying predator use of the grid. Ideally, we would instead quantify total predation rate as a function of both the numerical and functional responses of predators (Mills 2013). Finally, we could not assess stage-specific predation rates of hares by different predator species, which can affect how predation would affect prey densities (Mills 2013). Instead, we compromised fine scale, detailed predation quantification in order to achieve our extensive spatial and temporal scale providing large scale support for our predation predictors correlating with hare density.

Increases in horizontal cover and sapling density were also associated with higher hare densities. These findings are consistent with previous studies (horizontal cover: Pietz and Tester 1983, Lewis et al. 2011, Holbrook et al. 2017b; sapling density: Fuller et al. 2007, Lewis et al. 2011, Ivan and Shenk 2016). These structural features enhance hare evasion from predators (Mowat et al. 2000, Fuller et al. 2007, Ivan and Shenk 2016). However, horizontal cover and sapling density were significant after including the effects of direct predation rate in the model. Therefore, in addition to direct predation rate, these vegetation features may influence other factors such as forage availability. However, hare body condition (mass/hind foot length) did not differ between grids suggesting forage differences are not strongly influencing hare density. Instead, indirect predation effects might play a role (Brown et al. 1999, Creel and Christianson 2008), possibly lowering hare reproductive output (Sheriff et al. 2009, Krebs et al. 2018, MacLeod et al. 2018).

We did not find a strong effect of canopy closure on hare density. Although we indexed canopy closure from basal area, they were correlated ($\rho = 0.65$). Canopy closure has been positively related to hare density (Pietz and Tester 1983) and habitat use (Holbrook et al. 2017b, Gigliotti and Diefenbach 2018) but it has also been uncorrelated with hare density (Lewis et al.

2011). Therefore, canopy closure *per se* appears to play a less significant role driving hare densities compared to horizontal cover or stem densities.

In short, we find both landscape structure and generalist predation combine to drive hare density in an area where cycles are thought to be dampened or nonexistent. Although these mechanisms have long been hypothesized to drive spatial gradients in cyclicity (Howell 1923, Wolff 1980, Hanski et al. 1991), we provide novel support to these hypotheses using long-term field data from a southern hare population. Both landscape structure and generalist predation might also drive spatial gradients in cycles of other species such as voles and moths, where the generalist predation hypothesis has generally been considered in isolation (Klemola et al. 2002).

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Tables

Table 1 - Species considered hare predators in western Montana and the relative frequency with which they consume hares. Relative frequencies are defined as: 4 = hares are almost always the most important food source; 3 = hares can be but are not always the most important food source; 2 = hares are not the most important food source but are regularly consumed; 1 = hares only rarely consumed

Species	Common Name	Weight	Source(s)
Lynx canadensis	Canada Lynx	4	(Squires and Ruggiero 2007)
Canis latrans	Coyote	3	(O'Donoghue et al. 1998, Arjo et al. 2002, Kolbe et al. 2007)
Lynx rufus	Bobcat	3	(Major and Sherburne 1987)
Vulpes vulpes	Red Fox*	3	(Halpin and Bissonette 1988, Theberge and Wedeles 1989)
Martes americana	American Marten*	3	(Raine 1987, Cumberland et al. 2001)
Pekania pennanti	Fisher*	3	(Raine 1987)
Mustela frentata	Long-tailed Weasel	2	(Hodges 2000b)
Tamiasciurus hudsonicus	American Red Squirrel	2	(O'Donoghue 1994)
Puma concolor	Mountain Lion	2	(Spalding and Lesowski 1971, Elbroch and Wittmer 2013)
Canis lupus	Gray Wolf	2	(Cowan 1947, Arjo et al. 2002)
Ursus americanus	American Black Bear	1	(Raine and Kansas 1990)
Ursus arctos	Grizzly Bear	1	(Mace and Jonkel 1986)

* indicates species not detected by trail cameras.

Table 2 - Model support for predictors on annual survival estimates for snowshoe hares in western Montana from 1998-2018. Estimates were obtained by analyzing yearly live trapping data with a Cormack-Jolly-Seber model implemented in RMark. Survival was modeled to vary only by one predictor at a time and detection probability was modeled to be constant. K indicates the number of parameters in the model.

Predictor	K	AICc	ΔAICc
Grid*	15	3685.81	0.00
Age*	3	3687.57	1.76
Region*	3	3693.79	7.98
Year*	21	3703.29	17.48
Sex*	3	3720.24	34.43

* indicates significant beta coefficient.

Table 3 - Support for predictors on density estimates for snowshoe hares in western Montana from 1998-2018. Density estimates were obtained using a spatially-explicit capture-mark-recapture framework. Predictors were placed on true density using a state space model implemented in a Bayesian framework.

Predictor	Mean	95% CI	Probability $\beta \neq 0$
Canopy Closure	0.021	(-0.111, 0.154)	0.621
Horizontal Cover	0.149	(0.036, 0.264)	0.995*
Sapling Density	0.183	(0.055, 0.317)	0.997*
Landscape Structure	-0.138	(-0.291, 0.009)	0.967*
Direct Predation Rate	-0.355	(-0.455, -0.255)	1.000*
Generalist Predation Pressure	-0.109	(-0.256, 0.038)	0.927*
Cumulative Predation Index	0.202	(0.047, 0.361)	0.995*
Avian Detections	0.117	(-0.013, 0.250)	0.961*
Lynx Probability of Use	0.320	(0.183, 0.460)	1.000*

* Predictor with high probability that their beta coefficient does not equal 0.

Figures

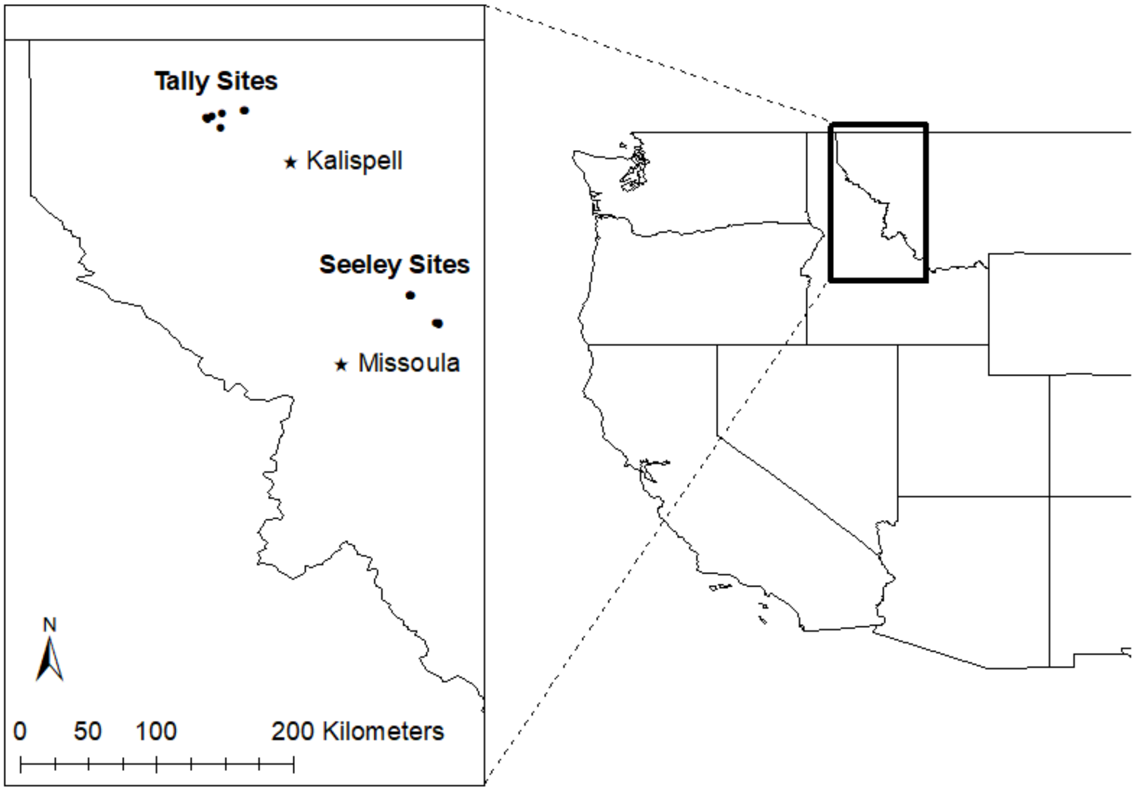


Figure 1 - Snowshoe hare study areas in western Montana from 1998-2018, with locations of the 7 Tally trapping grids and 7 Seeley trapping grids. In some cases, multiple sites are close enough to each other to appear as one dot.

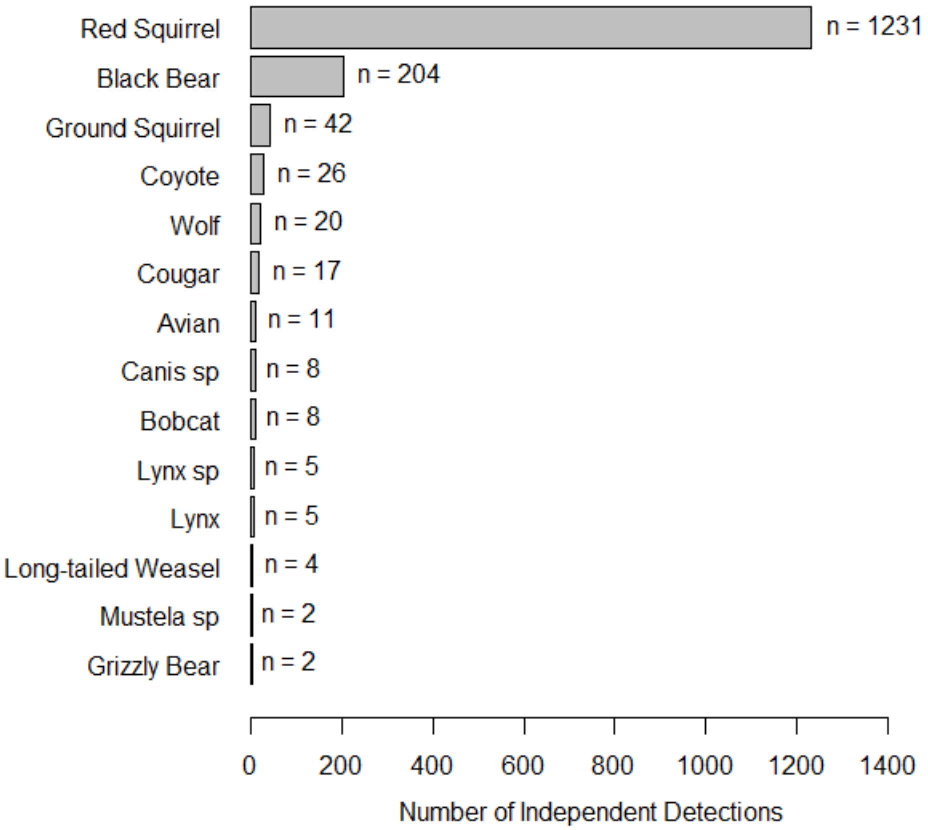
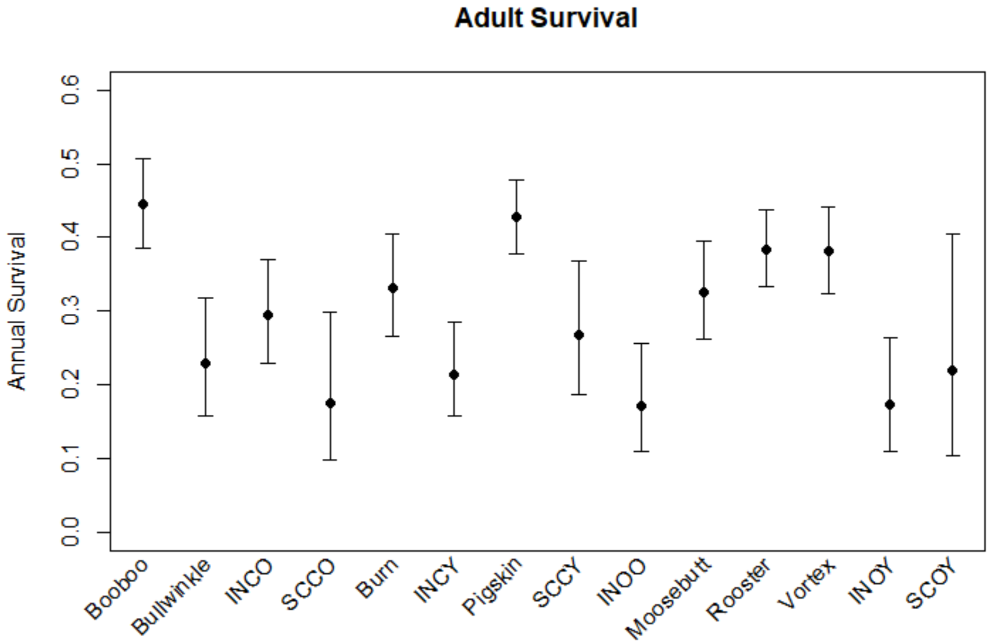


Figure 2 - Predator detections from 280 unbaited locations in western Montana during the summer of 2017 and 2018. Detections were considered independent if they were on different cameras or are greater than one hour apart. Avian represents detections or birds of prey such as owls and hawks. Canis sp represents an unidentified canid (either a wolf or a coyote). Lynx sp represents an unidentified felid (either a lynx or a bobcat). Mustela sp represents an unidentified mustelid (either a long-tailed or a short-tailed weasel).



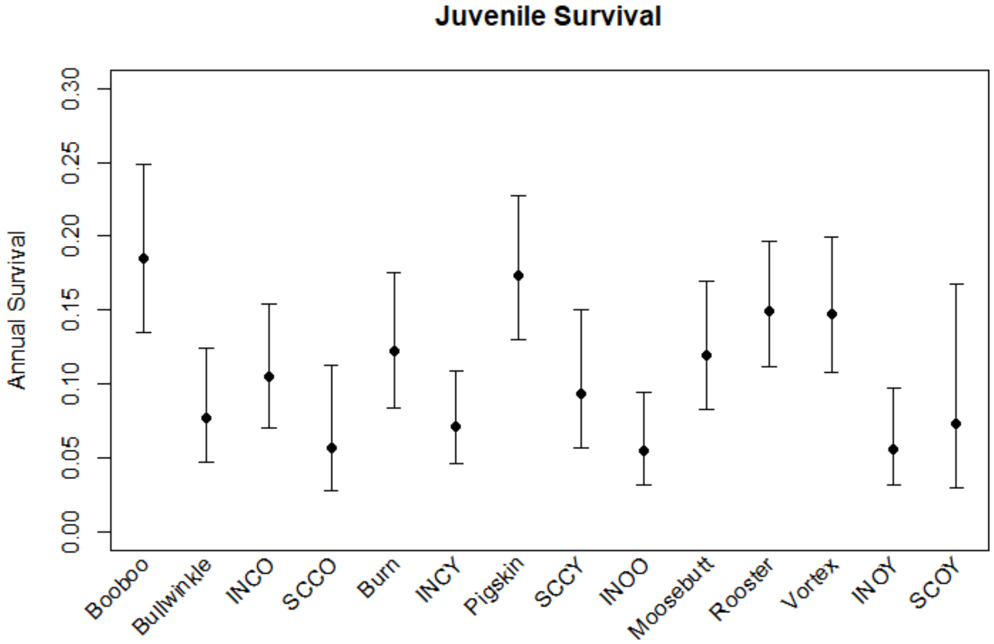


Figure 3 - Grid specific survival estimates for snowshoe hares in western Montana from 1998-2018. Estimates were obtained by analyzing yearly live-trapping data with a Cormack-Jolly-Seber model implemented in RMark. Survival was modeled to vary only by grid and age and detection probability was modeled to vary by effort (number of days trapped).

Appendix A

Table S1 - Sex specific survival estimates for snowshoe hares in western Montana from 1998-2018. Estimates were obtained by analyzing yearly live-trapping data with a Cormack Jolly Seber model implemented in RMark. Survival was modeled to vary only by sex and detection probability was modeled to vary by effort (number of days trapped).

Parameter	Estimate	Standard Error	95% Confidence Interval
Annual Survival - Male	0.29	0.01	0.27 to 0.32
Annual Survival - Female	0.34	0.01	0.31 to 0.36
Beta coefficient for Male Survival	-0.20	0.09	-0.37 to -0.04

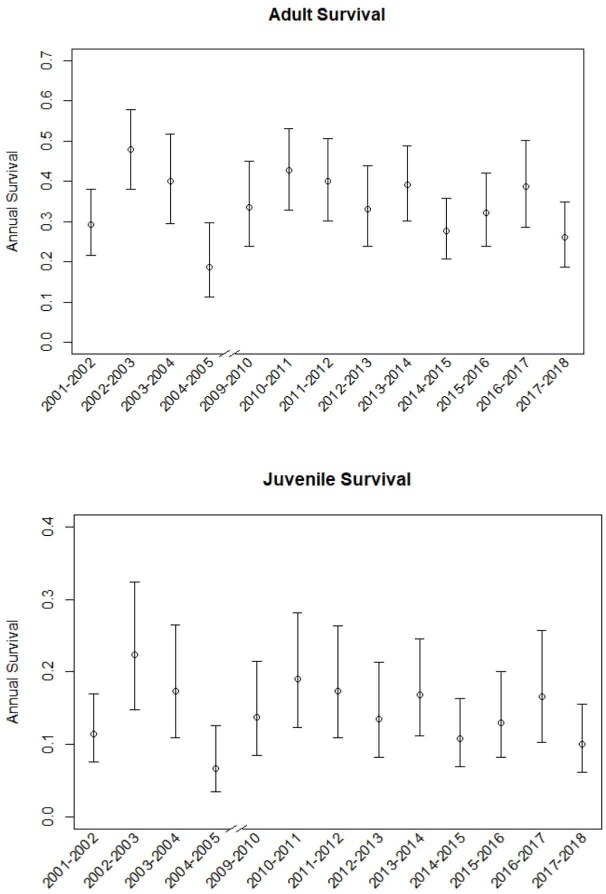


Figure S1 - Yearly survival estimates for snowshoe hares in western Montana from 1998-2018. Only years where at least 10 out of the 14 grids were trapped are shown. Estimates were obtained by analyzing yearly live-trapping data with a Cormack-Jolly-Seber model implemented in RMark. Survival was modeled to vary only by year and age and detection probability was modeled to vary by effort (number of days trapped).

Chapter 4: Biotic and abiotic factors drive acyclic population dynamics of snowshoe hares in their southern range

Abstract

As many as 30% of all animal species cycle, including species of conservation concern and species that threaten biodiversity. Many of these cyclic species exhibit cycle dampening in time or space. Snowshoe hares, famed for their drastic population fluctuations in the northern boreal forests of North America, are thought to exhibit dampened cyclic or acyclic population dynamics in the southern portion of their range. However, no long-term field data has been available to quantify the status of population cycles in southern hares. Using the longest snowshoe hare live-trapping dataset from the southern part of their range (1998-2018) and a Bayesian state space model, we quantified the cyclic nature of hares in Montana and examined the factors associated with their population dynamics. Overall, we found evidence of acyclic population dynamics in Montana associated with greater generalist predation, a landscape that has more open areas and warmer temperatures. Thus, multiple factors act simultaneously to produce acyclic dynamics. Our results emphasize the need to apply a unified modeling framework which considers multiple factors to other cyclic systems that exhibit cycle dampening in order to better elucidate this phenomenon.

Introduction

Periodic fluctuations, or cycles, in species abundance have long fascinated ecologists (Elton 1924, Green and Evans 1940, Myers 2018) and may occur in 30% of all animal species (Kendall et al. 1998). However, cycles are not fixed or permanent over time or space. Cycles that become dampened (cyclic dynamics present but with reduced amplitude) or collapsed (cyclic dynamics no longer present, i.e. acyclic) commonly occur (Stenseth et al. 1996, Klemola et al. 2002, Ims et al. 2008).

In several cases these dampened cyclic or acyclic dynamics have occurred recently (Ims et al. 2008, Ecke et al. 2010, Cornulier et al. 2013). Climate change, particularly changes in winter severity, has been linked to collapsing cycles in several systems (e.g. voles; Hornfeldt et al. 2005, Bierman et al. 2006, Ims et al. 2008, Cornulier et al. 2013, lemmings; Hornfeldt et al. 2005, Kausrud et al. 2008, insects; Ims et al. 2008 and grouse; Ims et al. 2008). However, the reemergence of some cycles (e.g. voles in Finland; Brommer et al. 2010) and the influential role of summer conditions driving cycles of Finnish voles (Korpela et al. 2013, 2014) suggest that other factors, in addition to changes in winter severity, contribute to cyclic collapse.

In addition to dampening over time, cycles can dampen over space. Latitudinal gradients in cycles have primarily been attributed to changes in predator species composition; specifically, a decreased ratio of specialist to generalist predators (Hanski et al. 1991, 2001, Klemola et al. 2002). However, other factors have been proposed to induce these latitudinal gradients. Landscapes with more open areas are thought to dampen cycles possibly by increasing predation on dispersers moving through open areas with less cover (Sievert and Keith 1985, Strann et al. 2002, Griffin and Mills 2009). Finally, in addition to contributing to cyclic collapse through time, winter climate covariates such as snow cover have also been proposed to influence latitudinal gradients in cyclicity (Hansson and Henttonen 1985, Strann et al. 2002, Pomara and Zuckerberg 2017).

Given the complexities of interacting drivers of population dynamics, unraveling the mechanisms that lead to population cycling requires both multi-factor analyses and time series data that allow rigorous estimation of densities instead of relying on highly uncertain indices of abundance (Yoccoz et al. 2001, Barraquand et al. 2017). Additionally, these density estimates should ideally account for both process and sample variance (Buonaccorsi et al. 2001). What is required is a unified modeling framework including multiple biotic and abiotic cyclic drivers (e.g. predation, landscape structure and climate) and based on rigorous density estimates while accounting for measurement error.

Linear autoregressive (AR) models are commonly used to model population cycles by using time lagged density estimates to predict current density (Moran 1953, Kendall et al. 1999, Williams et al. 2004). The coefficients of AR models provide information on the relative strengths of direct and delayed density dependence, with cycles collapsing as direct density dependence strengthens and/or delayed density dependence weakens (Bjørnstad et al. 1995, Williams et al. 2004). Increasing direct density dependence leads to cyclic collapse via period shortening while decreasing delayed density dependence leads to cyclic collapse via period lengthening (Williams et al. 2004). For example, Williams et al. (2004) found that North American grouse exhibited period increases from north to south, leading to cyclig collapse via period lengthening.

Snowshoe hares (*Lepus americanus*) are iconic cyclic species across the northern boreal forests of North America (Keith and Windberg 1978, Cary and Keith 1979, Krebs et al. 1995, 2018, Oli et al. 2020). Hares are a strongly interacting species that provide a vital food resource for a diverse guild of carnivores (Boutin et al. 1995). However, an unresolved question centers on whether hares exhibit dampened cyclic or acyclic population dynamics in the southern portion of their range (Howell 1923, Keith 1990, Hodges 2000). In these lower latitudes, roughly corresponding to the continental USA (Hodges 2000), analyses of cycle dynamics have been limited by study duration (<5 years for rigorous time series based on capture-mark-recapture estimates; Keith 1990, Murray 2000, Griffin and Mills 2009).

Purported explanations for dampened hare cycles in the southern portion of their range include landscape structure (Dolbeer and Clark 1975, Buehler and Keith 1982, Keith et al. 1993, Griffin and Mills 2009) and an increase in generalist predation (Buehler and Keith 1982, Roth et al. 2007, Vitense et al. 2016). Landscapes with more open areas increase predation on individuals moving through these open areas (Dolbeer and Clark 1975, Sievert and Keith 1985, Griffin and Mills 2009). Furthermore, a greater diversity of generalist predators occurs in the southern portion of the hare's range potentially increasing generalist predation (Chapter 3, Hodges 2000b). Additionally, effects of both generalist predation and landscape structure could co-occur; indeed, theoretical models show that their joint effects produce the most severe dampening (Vitense et al. 2016).

Dampened hare cycles have not been linked to winter severity explicitly, unlike other cyclic systems (e.g voles; Aars and Ims 2002, lemmings; Kausrud et al. 2008, and grouse; Pomara and Zuckerberg 2017). Changes in temperature and snow cover may influence hare survival by multiple routes including inducing camouflage mismatch between seasonal white coat color and a snowless background (Zimova et al. 2018, Kumar et al. In Press) and by affecting predator locomotion (Murray and Boutin 1991, Stenseth et al. 2004). In addition, temperature could affect hare physiology (Meslow and Keith 1971, Hodges et al. 2006), with warmer winter temperatures associated with increased hare densities (Chapter 2). Therefore, winter severity manifested through snow or temperature may also contribute to dampened hare cycles.

Here, we quantified the biotic and abiotic factors associated with hare density in their southern range using a 21 year capture-mark-recapture time series containing almost 2,000 individual hares across 14 sites. We also compared our southern range dataset to a 40 year time series of hare densities from a cyclic hare population in Yukon, Canada (Krebs et al. 2018). Yukon hares display strongly cyclic dynamics with a period (time from one population peak to the next) of approximately 10 years and amplitude (range of density values) fluctuations of ≥ 100 fold (Krebs et al. 2018). We compared cycle metrics calculated from both datasets using a uniform methodology to determine the differences in cyclic behavior between the two areas and the mechanism of cycle collapse (period shortening or period lengthening).

Our two main objectives were to determine if southern hares exhibit a dampened cycle and to identify the main biotic and abiotic factors influencing southern hare population dynamics. Specifically, we used four different metrics to characterize hare population dynamics as cyclic or acyclic. We then quantified the relative effects of landscape structure, generalist predation and winter severity on snowshoe hare cycle dynamics using a rigorous state space modeling framework that accounts for both measurement error and process variance separately. We also accounted for other measures of vegetative structure and predation thought to influence hare density (Chapter 3). Finally, following Williams et al. (2004), we used autoregressive models to quantify the mechanism of cycle collapse (period shortening or period lengthening).

Methods

Study Areas

We collected snowshoe hare summer density data from 1998-2018 at 14 trapping grids in two areas (Seeley Lake and Tally Lake) in western Montana, USA (Figure 1; for site descriptions see Mills et al. 2005). All sites were managed by the Forest Service (USFS) with a history of multiple use including timber production. Seeley Lake (Lat. = 47.2°, Long. = -113.4°) and Tally Lake (Lat. = 48.5°, Long. = -114.8°) are approximately 175 km apart and span similar elevations (approximately 1500-1900 m.a.s.l.). Both areas are dominated by moist, coniferous forests of Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and Ponderosa pine (*Pinus ponderosa*) with a herbaceous understory.

We also analyzed the published 40 year time series (1977-2016) of Yukon hare densities (Krebs et al. 2018) for comparison with our Montana time series. Yukon hare densities were calculated using a spatially-explicit capture-mark-recapture framework and averaged across nine trapping grids (Krebs et al. 2018). See Boonstra et al. (2016) for Yukon study area description.

Capture/Handling

Snowshoe hares were trapped during the summer (May-August) using live-traps (51x18x18 cm, Tomahawk Live Trap Company, Tomahawk, WI) baited with alfalfa cubes and apples, spaced approximately 50m apart (Mills et al. 2005). Each of the seven Seeley Lake hare trapping grids consisted of approximately 50 traps, while the seven Tally Lake trapping grids had approximately 80 traps each. Each grid was trapped for 3-5 days each summer, ensuring population closure. We marked all hares >500g with a unique numbered ear tag. We weighed all hares, determined sex, measured right hind foot length and determined breeding status (lactating or pregnant, testes abdominal or testes scrotal). All capture and handling procedures were approved by the University of Montana Animal Care and Use Committee (various permits over 21 years).

Statistical Analysis

Hare Density

We estimated adult snowshoe hare density with a spatially-explicit capture-mark-recapture (SECR) model using the Package SECR (Efford 2004, Borchers and Efford 2008, Efford and Fewster 2013) in Program R (version 3.5.3, R Development Core Team 2019) (see Chapter 2 for details). In brief, we built models varying g0, the probability of detection given the individual's activity center is at the detector and sigma, the spatial scale over which the detection probability declines. We ranked models using AICc and used AICc differences (ΔAICc) and Akaike weights (wi) to evaluate model support. The best model included the effects of sex and heterogeneity on g0 and heterogeneity on sigma (Chapter 2).

Cycle Metrics

Metrics to quantify cycles typically assume true density is known. However, this is rarely the case and most cycle analyses rely on indices of abundance (Yoccoz et al. 2001, Barraquand et al. 2017). Even in cases when abundance is statistically estimated, measurement error is usually not accounted for (Buonaccorsi et al. 2001). Using a state space model (Rotella et al. 2009) we accounted for measurement error and estimated, D_t, time specific true density, which we used in our cyclic metrics.

We used four different metrics to quantify cycles for Montana (14 trapping sites) and Yukon hares. Cycles occur when density fluctuates with a regular period and high amplitude. The S-index (see below) quantifies exclusively the amplitude component, while the other three metrics additionally quantify periodicity. Because the Yukon time series was averaged across trapping sites we also compared it to a Montana time series averaged across all sites. In addition, because cycle metrics can be influenced by time series length, we also analyzed the portion of Yukon data (1996-2016) that best corresponded to the duration and timeframe of the Montana time series (1998-2018). All cycle metrics were calculated in Program R (version 3.5.3, R Development Core Team 2019) using the log transformation of estimated true density. The first metric estimated beta coefficients of an autoregressive-moving average process [ARMA (2,1)] using hare densities and their one and two-year lags (Williams et al. 2004).

$$D_t = \beta_0 + \beta_1 D_{t-1} + \beta_2 D_{t-2} + \varepsilon_t + \theta\varepsilon_{t-1} \qquad \text{ARMA (2,1)}$$

where D_t = hare density at time t, ε = error term and β and θ represent the coefficients of the autoregressive and moving average components of the ARMA model, respectively. Cycles occur when ${\beta_1}^2 + 4\beta_2 < 0$ (Williams et al. 2004). The second metric was the S-index (standard deviation of density estimates) (Hansson and Henttonen 1985, Krebs 1996, Stenseth 1999, Turchin 2003). Values of the S-index <0.2 indicate low amplitude oscillations (acyclic), values between 0.2-0.4 indicate mild amplitude oscillations (weakly cyclic) and values >0.4 indicate high amplitude oscillations (cyclic). The third metric was the autocorrelation function (ACF) (Turchin 2003). Autocorrelation can be thought of as the similarity between density estimates dependent on the lag time between them. Cycles are present when the ACF value at the length of the period is > $2/\sqrt{n}$ (n = the number of data points), weak evidence of cycles occurs when the ACF value at half the length of the period is < $-2/\sqrt{n}$ and acyclicity occurs when the ACF is not significantly different than 0 (Turchin 2003). The final metric was the periodogram maximum based on the null hypothesis of an Ornstein-Uhlenbeck state space (OUSS) process (Louca and Doebeli 2015). This metric is similar to the ACF as periodograms are the Fourier transformation of the autocovariance function, a close relative of the ACF (Turchin 2003). However, this metric was based on the null hypothesis of an OUSS process as opposed to a null hypothesis of white noise typically assumed for an ACF (Louca and Doebeli 2015). A statistically significant periodogram maximum indicates cycles (Louca and Doebeli 2015).

Biotic and Abiotic Factors Influencing Density

We used a state space model to incorporate important vegetation structure, predation and climate covariates expected to influence hare density (Chapters 2 and 3). Vegetation structure covariates included horizontal cover, sapling density and landscape structure to test the hypothesis that landscapes with more open areas dampen hare cycles (see Chapter 3 for more details). Horizontal cover and sapling density were estimated at the beginning and end of the study using 6-10 random points established within each grid. Landscape structure was estimated for a 300 m buffer around each hare trapping grid by classifying vegetative structure as closed canopy moist deciduous forest or open-structured area using satellite imagery from Google Earth.

Predation covariates included direct predation risk, generalist predation pressure, cumulative predation index, avian detections and lynx probability of use (see Chapter 3 for more details). Direct predation risk was estimated from a hare survival model (Chapter 3, Murray

2002) since nearly all hares die by predation (Hodges 2000, Wirsing et al. 2002, Abele et al. 2013). We detected predators using camera traps placed at 20 locations per grid. Generalist predation pressure was included to test the hypothesis that increased generalist predation dampens hare cycles and was defined as the total number of hare predator species detected on a grid as all these predators (with the exception of lynx) can be considered generalists in Montana (Chapter 3). The cumulative predation index was calculated by multiplying each independent species detection (excluding squirrels and avian predators) by a weight approximating the importance of hares in their diet (Chapter 3). Avian detections is the number of independent detections of avian predators. Finally, lynx probability of use was obtained from a map predicting lynx probability of use throughout western Montana at 30m resolution integrating second and third order resource selection functions (Holbrook et al. 2017a).

Climate covariates included the number of days with a minimum temperature below -5° C (lower critical temperature for hares; Hart et al. 1965) and the maximum summer temperature of the previous year (see Chapter 2 for more details). We specifically included the number of days with minimums below -5° C to test the hypothesis that increased winter severity dampens hare cycles perhaps by increasing hare susceptibility to predation. Climate data was derived from Daymet (Thornton et al. 2018).

We developed the state space model based on the framework developed by Rotella et al (2009). State space models consist of both an observation model and a process model, and can separate measurement error from process noise (Dennis et al. 2006, Rotella et al. 2009). In this context, we use measurement error to refer to variability in the data that arises purely as a result of the sampling process and process noise to refer to fluctuations caused by environmental variability (Humbert et al. 2009). The observation model used hare density estimates and the associated measurement error to approximate the unknown true hare density. The process model then estimated process variance and the effects of factors on density with measurement error removed. Our observation model linked estimated density to true density with the following relationship: $\widehat{D}_t \sim \mathrm{N}(D_{t\,,}\ se_t^2)$, where $\widehat{D}_t$ is the time specific density estimates obtained from the SECR model, D_t is the true density and se_t^2 is the squared estimate of measurement error obtained from the SECR model. Our process model was: $\log(D_t) = \mu + y_t$ with μ being the equilibrium value of the logarithm of true density and $y_t \sim \mathrm{N}(\alpha_{t\,,}\ \sigma_{pr}^2)$ where σ_{pr}^2 is process variation. Finally, $\alpha_t = \beta_1(cov1) + \beta_2(cov2) + \beta_3(cov3)$ ... where β represented the coefficient relating the covariate to α_t. We assumed that process variation and measurement errors were independent.

We implemented the model in a Bayesian framework (Rotella et al. 2009) to accommodate years when we did not trap (~18% of all grid year combinations). We standardized all covariates to have a mean of 0 and a standard deviation (SD) of 1 to ease interpretation and expedite convergence and only included uncorrelated covariates ($\rho < 0.6$). We fit models with Markov Chain Monte Carlo (MCMC) in JAGS using the R package jagsUI with uninformative priors. Specifically, we used a gamma distribution as a prior for σ_{pr}^2 with both hyperparameters set to 0.001. We specified the prior for μ as a normal distribution with a mean of 0 and a precision (1/variance) of 0.01. We used a normal distribution with a mean of 0 and a precision of 0.01 as a prior for all the betas. These priors represent a stationary distribution of 1 hare/ha and no effects of any covariate on density. We ran all models with five chains of at least 110,000 iterations discarding the first 10,000 as burn-in. We assessed convergence by visually examining the trace and density plots for the beta coefficients and with the Gelman-Rubin statistic ($\hat{R} <$

1.1). We used the 95% credible intervals as well as the probability that the beta coefficient does not equal 0 to determine the importance of the covariates.

Mechanism of Cycle Collapse

The ARMA(2,1) model provides insights into the mechanism of the collapse of cycles (cyclic dynamics change to acyclic) using the values of the beta coefficients for time lagged densities (Williams et al. 2004). β_1 represents the effect of direct density dependence, while β_2 represents the effect of delayed density dependence. The effects of density dependence grow stronger as the beta coefficients become more negative. Mathematically, if values of β_1 are negative, cycles collapse via period shortening (Williams et al. 2004). Conversely, positive values of β_1 suggest period lengthening. Therefore, we compared beta coefficients from ARMA (2,1) models using Montana density estimates (both site specific and averaged across all sites) to those from the Yukon density estimates to infer the process leading to cycle collapse.

Results

Cycle Metrics

Overall, the 14 sampled Montana hare populations appear to be acyclic (Table 1). For two of the three metrics that account for both components of cycles (amplitude and period), the OUSS metric suggested acyclicity for 13 of the 14 sites and the ACF suggested acyclicity for 9 of the 14 sites (5 sites were weakly cyclic; Table 1). For the third metric accounting for both amplitude and period, the ARMA (2,1) model suggested acyclicity for 6 sites and cyclic dynamics for 8 sites. The S-index, which only considers the amplitude, suggested that 6 sites were weakly cyclic and 8 sites were cyclic. Only three sites were weakly cyclic or cyclic in at least three of the four cycle metrics (Table 1, Figure 2). In contrast, the other 11 sites displayed acyclicity in at least two of the four metrics and also showed no visible evidence of cycles in their time series plots (Figure 3).

In contrast, the 40 year Yukon time series was cyclic according to all four cycle metrics and the 21 year subset of the Yukon data was cyclic in three out of the four metrics (Table 1). In contrast with the Yukon results, applying the cycle metrics to the average densities across all Montana sites yielded acyclicity according to the three metrics that account for both periodicity and amplitude (Table 1). Comparing the average Montana density with that of Yukon shows that Montana hares tend to exist at densities intermediate to the cyclic peaks and lows of Yukon hares (Figure 4).

Biotic and Abiotic Factors Influencing Density

Density estimates from the state space model with measurement error removed had increased precision compared with the estimates from the SECR model (Figure 5). In addition, state space model mean densities were less variable, slightly reducing the amplitude of mean density fluctuations when compared to the SECR model (Figure 5).

We found support for all ten covariates influencing hare density as they all had probabilities > 0.90 that their beta coefficients do not equal 0 (Table 2), consistent with analyses that considered the biotic and abiotic factors separately (Chapter 2, Chapter 3). Specifically, hare density decreased as landscape structure became more open and as horizontal cover and sapling density decreased. Increased direct predation risk and generalist predation pressure had negative associations with hare density while cumulative predation index, avian detections and lynx probability of use all had positive associations with hare density. Less frequent colder days in winter had a positive association with hare density, while higher maximum temperatures in the preceding summer had a negative association with hare density.

Mechanism of Cycle Collapse

All fourteen sites, as well as the time series resulting from their average densities, had higher estimates for β_2 compared with Yukon suggesting decreased strength of delayed density dependence in Montana (Figure 6). Similarly, all but two Montana sites had lower estimates for β_1 compared with Yukon suggesting increased strength of direct density dependence in Montana (Figure 6). Twelve of the fourteen Montana sites had positive values of β_1 possibly implying a role of period lengthening. However, the value of β_1 for the time series of the average Montana hare density was negative, indicative of period shortening.

Discussion

Using rigorous modeling and a 21 year dataset spanning 14 sites, we found southern hare populations to be acyclic, resolving almost a century of speculation on the extent of cycle dampening in the southern hare range (Howell 1923, Keith 1990, Hodges 2000). Furthermore, we found support for multiple biotic and abiotic factors influencing southern hare population dynamics, including summer and winter temperatures, landscape structure and generalist predation. Finally, we found evidence that both decreased delayed density dependence and increased direct density dependence contributed to the observed acyclic dynamics.

We considered four cyclicity metrics: OUSS, ACF, ARMA and S-index, each with differing strengths and weaknesses. The OUSS and ACF metrics are particularly well suited to our analysis of hare cycles. The OUSS process is more appropriate than the null hypothesis of uncorrelated fluctuations (i.e. white noise) for ecological dynamics because it can account for the temporal correlations between fluctuations around an equilibrium. As such, the OUSS process falsely identifies cyclicity far less often than white noise (Louca and Doebeli 2015). Meanwhile, the ACF metric is particularly robust to shorter time series, as in our case (Turchin 2003). In contrast, the ARMA metric may provide biased estimates of β_1 and β_2 for shorter time series (e.g. 50 year lek counts were considered shorter than desired; Williams et al. 2004). Finally, the S-index does not address the periodic component of cycles and therefore only indicates the magnitude of population fluctuations (Stenseth 1999).

The vast majority of Montana sites were acyclic according to the two most appropriate metrics: OUSS and ACF. The ARMA metric showed somewhat contrasting results with acyclicity in just six of the fourteen sites. However, since it may be biased by short time series (Williams et al. 2004), some caution is warranted in interpreting results from this metric. The final metric we considered, the S-index, provided evidence that Montana hare populations fluctuated, but did not address the periodic nature of those fluctuations. Finally, analysis of the average Montana and Yukon time series suggested cycles in Yukon and acyclicity in Montana. Therefore, cumulatively, our results suggest that Montana hare populations are acyclic.

Three of the 14 sites exhibited at least weak evidence of cycles in the majority of the cycle metrics. These sites had similar period lengths to Yukon data subset but S-indices of less than half that of Yukon suggestive of dampened dynamics. Also, peaks and troughs were out of phase with the cycles of Yukon (Figure 2). The first peak lagged by four to five years while the second peak lagged by seven to eight years. Lagged peaks may suggest lagged synchronous dynamics induced by a traveling wave (Ranta and Kaitala 1997, Lambin et al. 1998, Moss et al. 2000) possibly originating with northern hares. However, lag times under a traveling wave should be consistent and it is unclear why the wave would only affect three of the 14 sites. Historically, population peaks of lynx in the continental US were synchronous but lagged behind those of Canada by two to four years (McKelvey 2000). Conversely, a comprehensive examination of synchrony in hares revealed that while northern populations (Alaska and Canada) were significantly synchronized at distances up to several thousand kilometers, southern populations were not significantly synchronized at any distance (Cheng 2010). This lack of synchrony in southern hare populations provides further evidence of acyclic dynamics in southern hares. The potential cyclic behavior of these three sites is, thus, more likely due to chance than an underlying biological mechanism.

As previously mentioned, although this dataset is 21 years long, it may be shorter than optimal to quantify hare cycles, although there is little guidance as to the length of meaningful time series (Newey et al. 2007). One recommendation for optimal time series length for the ACF is 20-30 years so as to span three periods (Turchin 2003). Our 21-year time series only spans two of the suggested three period lengths but includes three population peaks (Krebs et al. 2018). A longer time series is optimal for the OUSS metric (simulations examined 40 and 100 years; Louca and Doebeli 2015) and the ARMA models (e.g. 50 + years; Williams et al. 2004) and might clarify the dynamics of the three sites that displayed some evidence of cycles. However, almost all longer time series rely on highly uncertain indices of abundance (Yoccoz et al. 2001, Barraquand et al. 2017). Thus, we tradeoff some time series length in order to rigorously estimate density using the longest-running live-trapping dataset of southern snowshoe hares.

Predation appears to strongly influence southern hares, consistent with northern hares (Krebs et al. 2018, Oli et al. 2020). Increased direct predation risk had a strong negative association with hare density (Chapter 3). Other metrics of predation including cumulative predation index, avian detections and lynx probability all had positive associations with hare density, consistent with higher hare densities attracting predators (Chapter 3). Finally, the index of generalist predation pressure was correlated with lower hare densities (Chapter 3), supporting the generalist predation hypothesis that cycles are dampened by an increase in generalist predators (Andersson and Erlinge 1977, Bjørnstad et al. 1995, Klemola et al. 2002).

Other biotic factors such as vegetation structure also influence southern hare dynamics. Consistent with previous studies, higher hare densities were associated with increased horizontal cover (Chapter 3, Pietz and Tester 1983, Lewis et al. 2011, Holbrook et al. 2017b) and stem densities (Chapter 3, Fuller et al. 2007, Lewis et al. 2011, Ivan and Shenk 2016). However, these structural features were significant after including the effects of direct predation risk in the model, implying that the benefit of these features extends beyond structural complexity enhancing predator evasion (Mowat et al. 2000, Fuller et al. 2007, Ivan and Shenk 2016). One possible mechanism is higher horizontal cover and stem densities reduce predator encounters and increase hare density partially through indirect predation effects (Sheriff et al. 2009, Krebs et al. 2018, MacLeod et al. 2018). Finally, landscapes with more open areas surrounding the trapping grids were associated with lower hare densities on the grids (Chapter 3), consistent with the landscape structure hypothesis, (Dolbeer and Clark 1975, Buehler and Keith 1982, Keith et al. 1993) which posits increased predation in open areas reduces cyclic dynamics (Dolbeer and Clark 1975, Sievert and Keith 1985, Griffin and Mills 2009).

In addition to biotic factors, abiotic effects, including temperature extremes also influenced hare density. Extremely cold winter temperatures and hot summer temperatures were associated with lower hare densities the subsequent summer (Chapter 2). Because predation accounts for >90% of hare mortality (Hodges 2000, Wirsing et al. 2002), cold winters may encourage riskier foraging (Hodges and Sinclair 2005) increasing predation (Chapter 2). The effects of hot summer temperature manifest only after one year implying either a delayed effect on adult survival or effect on juvenile survival (Chapter 2). Mechanistically, extremely hot summer temperatures may reduce milk production (Rhoads et al. 2009) lowering juvenile survival (sensu Krol et al. 2007). Finally, shorter snow durations can led to camouflage mismatched hares (Mills et al. 2018) that experience reduced survival (Zimova et al. 2016, Wilson et al. 2018). Indeed, increased durations of white hares on snowless backgrounds were associated with lower hare density the subsequent summer (Chapter 2). However, we were unable to consider mismatch in this analysis because we did not have snow data for one-third of the hare time series. We did, however, identify summer and winter temperatures as novel factors influencing southern hare densities, showing that the effects of climate change on collapsing hare cycles can manifest throughout the year.

What role do these biotic and abiotic factors have in influencing the cycles of northern hares? Interactive range-limit theory predicts that biotic and abiotic factors should influence both northern and southern range limits (Sirén and Morelli 2019). Although the hare cycle was initially thought to be driven by both food availability and predation (Keith et al. 1984, Krebs et al. 1995), it is now believed that predation plays the dominant role in driving hare cycles (Krebs et al. 2018, Oli et al. 2020). In addition to direct mortality, predation on hares may decrease reproduction via stress effects of chronic predator chases (Sheriff et al. 2009, Krebs et al. 2018, MacLeod et al. 2018). The other biotic and abiotic factors that we found to influence southern hare population dynamics appear to play less of a role in the northern boreal forest, although landscape structure may influence the variable amplitude of northern cycles (Krebs et al. 2018).

Finally, as severe winter conditions influence the entire boreal food web, the effects of climate change on cycles are uncertain (Barraquand et al. 2017, Krebs et al. 2018).

Increased direct density dependence and/or decreased delayed density dependence could contribute to cycle collapse (Williams et al. 2004). Biologically, increased predation from generalist predators whose populations can respond immediately to changes in their prey population size would be expected to increase direct density dependence (Hanski et al. 1991, Williams et al. 2004). Similarly, decreased predation from specialist predators whose populations track those of their prey with a lag would be expected to decrease delayed density dependence. Our findings of both increased direct density dependence and decreased delayed density dependence for acyclic Montana hares when compared to cyclic Yukon hares are consistent with a decreasing ratio of specialist to generalist predators in Montana compared to Yukon. This decreasing ratio is also consistent with the two other main factors influencing southern hare density: landscape structure and climate severity. Predation is expected to increase in landscapes with more open areas and in colder winters that encourage riskier foraging (sensu Hodges and Sinclair 2005) and predation in Montana is largely driven by generalists as opposed to specialists (Chapter 3).

Twelve of the fourteen Montana hare time series supported a cycle collapse through period lengthening, however, the time series of the average Montana hare densities supported period shortening. Cycles of European rodents and grouse appear to collapse primarily due to period shortening (Bjørnstad et al. 1995, Cattadori and Hudson 1999), contrasting with the North American grouse cycle collapse due to period lengthening (Williams et al. 2004). Biologically, we might expect a dominant role of period shortening in species that have multiple generations per year (e.g. rodents; Bjørnstad et al. 1995, Klemola et al. 2002) and a more prominent role of period lengthening in longer lived species (e.g. grouse and moose; Post et al. 2002, Williams et al. 2004) with hares falling in the latter category. Although there is support for both period lengthening and period shortening in the data, by additionally considering hare biology, we tentatively posit period lengthening as the mode of collapse, while emphasizing the need for more data to establish a more definitive conclusion.

Collectively we used a unified modeling framework to determine that Montana hare populations are acyclic, driven by generalist predation, landscape structure and climate severity. Individually many of these factors have been linked to cyclic collapse in other systems such as grouse, insects and rodents (Hanski et al. 1991, Klemola et al. 2002, Ims et al. 2008). However, as we demonstrated in hares, multiple factors may act simultaneously. Thus, applying a unified modeling framework which considers multiple drivers to other cyclic systems is crucial in order to better elucidate all of the factors that may contribute to the phenonium of cycle dampening or collapse.

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Tables

Table 1 - Evidence for cycles in snowshoe hares from 14 sites in western Montana and one study area in Yukon. Hare densities were first calculated using a spatially-explicit capture-mark-recapture framework and then true density was calculated with a state space model implemented in a Bayesian framework. The Yukon hare time series (Krebs et al. 2018) was also included for comparison. To directly compare the 21 year Montana time series to the 40 year Yukon time series, we also analyzed a 21 year portion of the Yukon data. C indicates cycles; W indicates weak cycles; A indicates acyclicity.

Grid	OUSS[1]	ACF[2]	ARMA[3]	S-index[4]
Booboo	A	W	C	C
Bullwinkle	A	W	A	W
Burn	A	W	C	C
INCO	A	A	A	W
INCY	A	A	C	W
INOO	A	A	A	W
INOY	A	A	C	C
Moosebutt	C	W	C	C
Pigskin	A	W	A	C
Rooster	A	A	C	W
SCCO	A	A	C	W
SCCY	A	A	C	C
SCOY	A	A	A	C
Vortex	A	A	A	C
Montana (Average All Sites)	A	A	A	W
Yukon (40 years)	C	C	C	C
Yukon (21 years)	C	W	C	C

[1] Significant periodogram maximum based on the null hypothesis of an Ornstein-Uhlenbeck state space (OUSS) process (Louca and Doebeli 2015).

[2] Significant peaks in the ACF (autocorrelation function) (Turchin 2003)

[3] The β_1 and β_2 coefficients from an ARMA (2,1) model (Williams et al. 2004)

[4] The S-index (SD of log transformed density estimates) (Hansson and Henttonen 1985).

Table 2 - Support for covariates on density estimates for snowshoe hares in western Montana from 1998-2018. Density estimates were obtained using a spatially-explicit capture-mark-recapture framework. Covariates were placed on true density using a state space model implemented in a Bayesian framework. Direct predation risk is one minus grid level survival. The cumulative predation index was calculated by multiplying each independent species detection by the importance of hares in their diet and summing for all species detected on each grid. Cold days is the number of days below -5^{o} C. Max temp is the yearly maximum temperature from the previous summer.

Covariate	Mean	95% CI	Probability $\beta \neq 0$
Horizontal Cover	0.155	(0.036, 0.275)	0.995
Sapling Density	0.191	(0.060, 0.325)	0.998
Landscape Structure	-0.145	(-0.299, -0.001)	0.976
Direct Predation Risk	-0.336	(-0.443, -0.230)	1.000
Generalist Predation Pressure	-0.111	(-0.258, 0.035)	0.932
Cumulative Predation Index	0.202	(0.058, 0.349)	0.997
Avian Detections	0.110	(-0.015, 0.236)	0.957
Lynx Probability of Use	0.301	(0.168, 0.437)	1.000
Cold Days	-0.103	(-0.202, -0.005)	0.980
Max Temp	-0.100	(-0.212, 0.011)	0.961

Figures

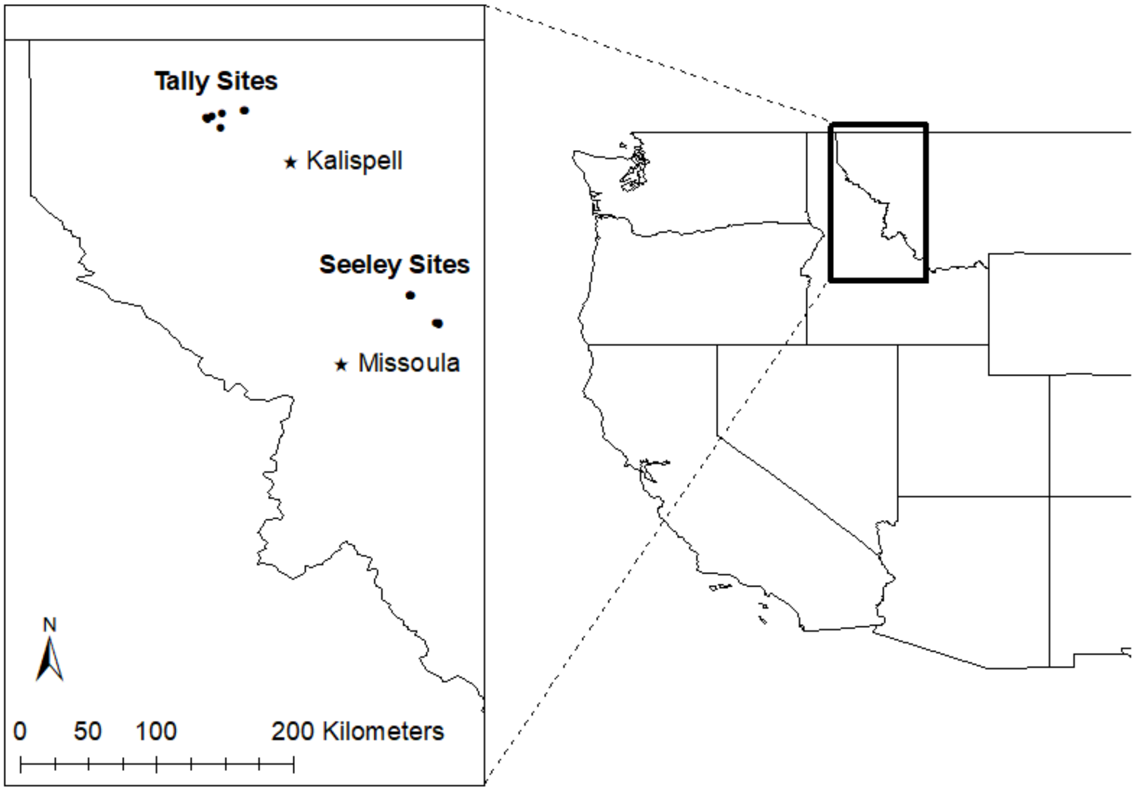

Figure 1 - Snowshoe hare study areas in western Montana from 1998-2018, with locations of the 7 Tally trapping grids and 7 Seeley trapping grids. In some cases, multiple sites are close enough to each other to appear as one dot.

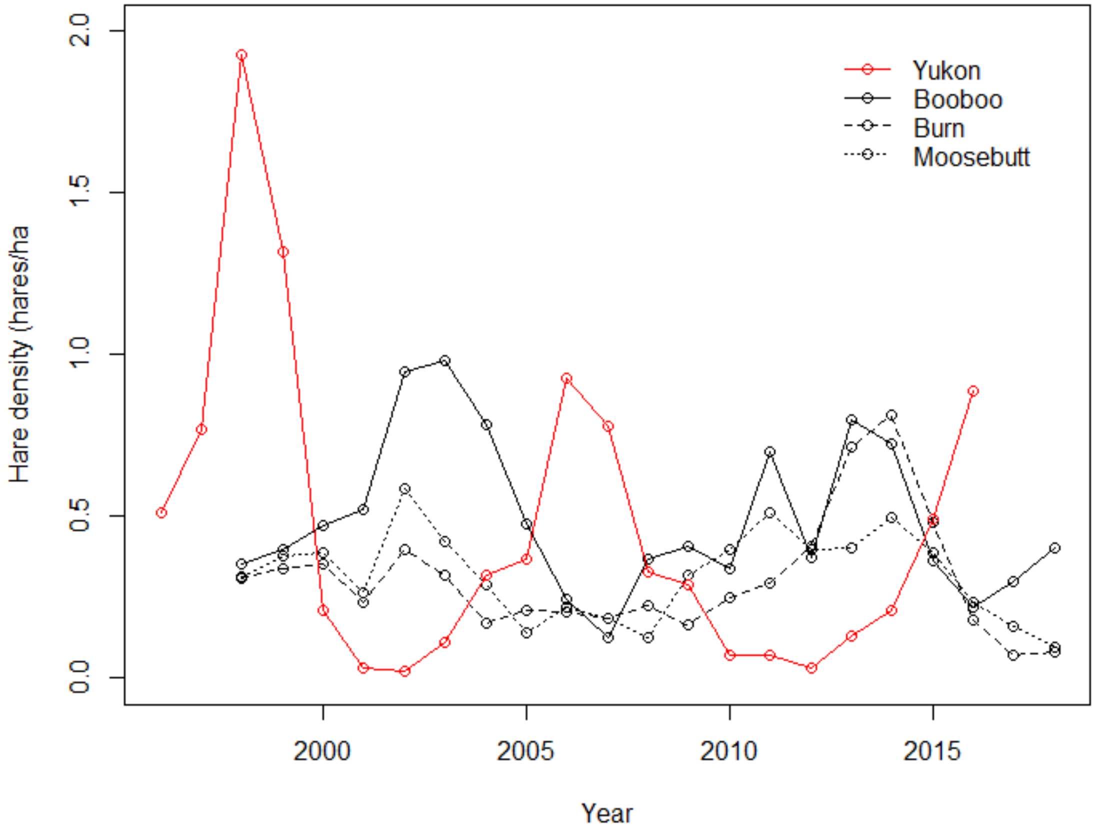

Figure 2 - Hare density from 3 sites in western Montana from 1998-2018 that display evidence of cycles (Table 1). Hare densities were first calculated using a spatially-explicit capture-mark-recapture framework and then measurement error was removed with a state space model implemented in a Bayesian framework. The Yukon hare time series (1996-2016) was also included for comparison (Krebs et al. 2018). Hare densities in Yukon were calculated using a spatially-explicit capture-mark-recapture framework and averaged across trapping sites (Krebs et al. 2018).

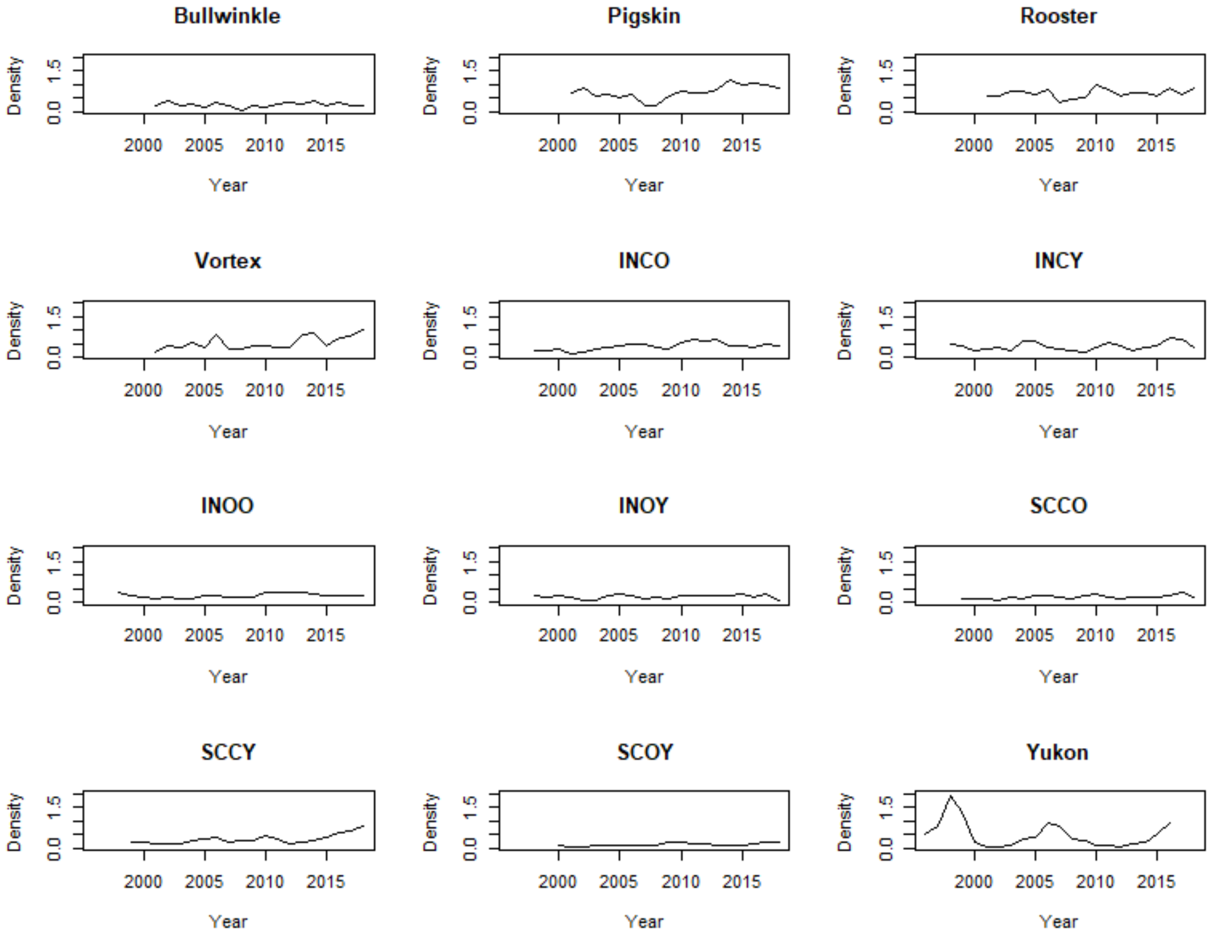

Figure 3 - Hare density from 11 sites in western Montana from 1998-2018 that do not display evidence of cyclic behavior (Table 1). Hare densities were first calculated using a spatially-explicit capture-mark-recapture framework and then true density was calculated with a state space model implemented in a Bayesian framework. The Yukon hare time series (1996-2016) was also included for comparison (Krebs et al. 2018). Hare densities in Yukon were also calculated using a spatially-explicit capture-mark-recapture framework and averaged across trapping sites (Krebs et al. 2018).

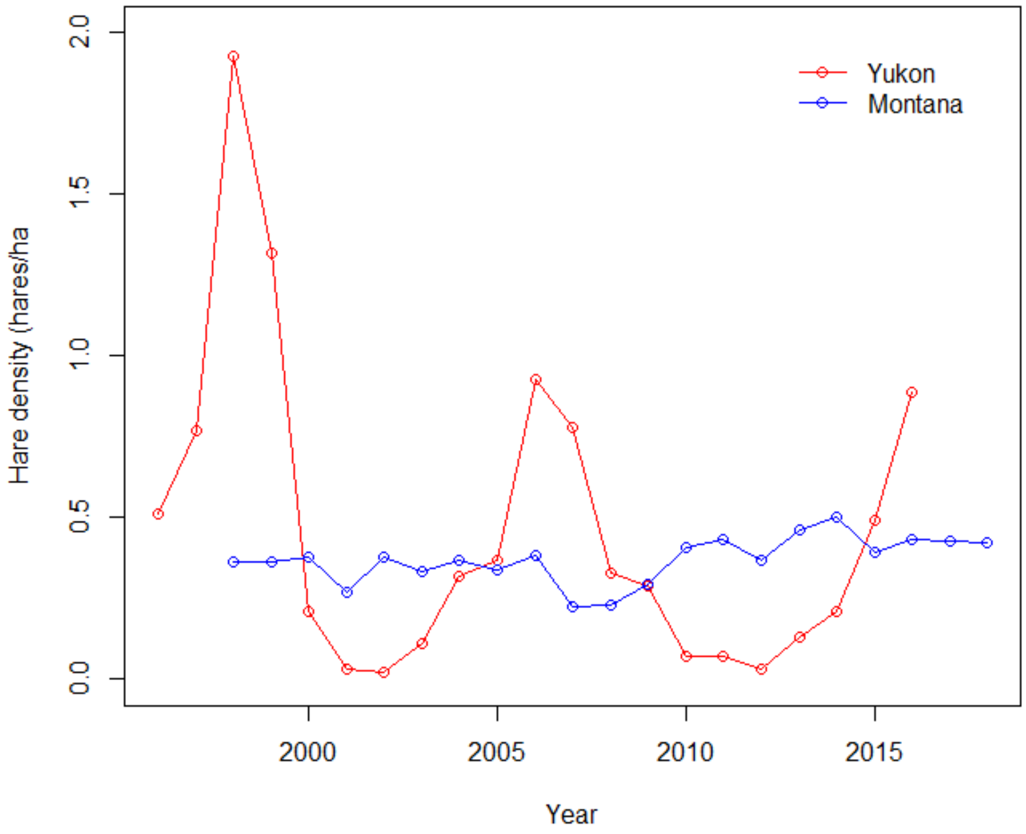

Figure 4 - Average hare density from 14 sites in western Montana from 1998-2018. Hare densities were first calculated using a spatially-explicit capture-mark-recapture framework and then measurement error was removed with a state space model implemented in a Bayesian framework. The Yukon hare time series (1996-2016) was also included for comparison (Krebs et al. 2018). Hare densities in Yukon were also calculated using a spatially-explicit capture-mark-recapture framework and averaged across trapping sites (Krebs et al. 2018).

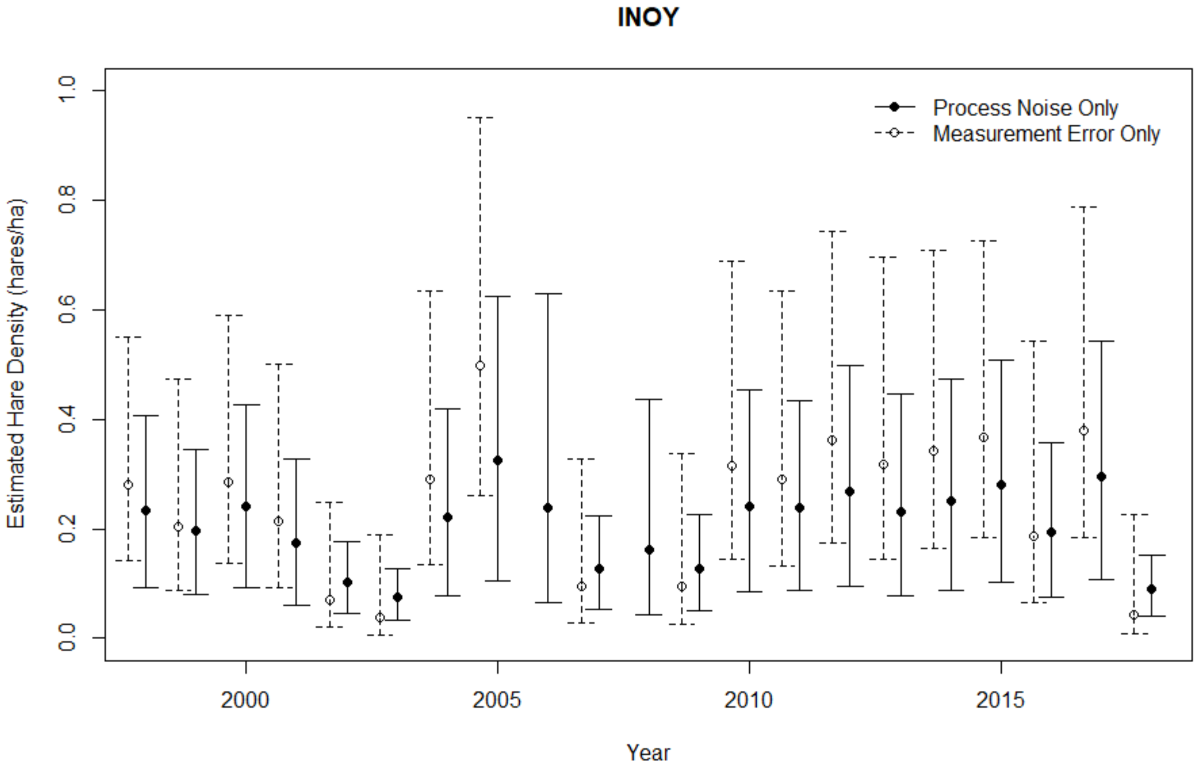

Figure 5 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

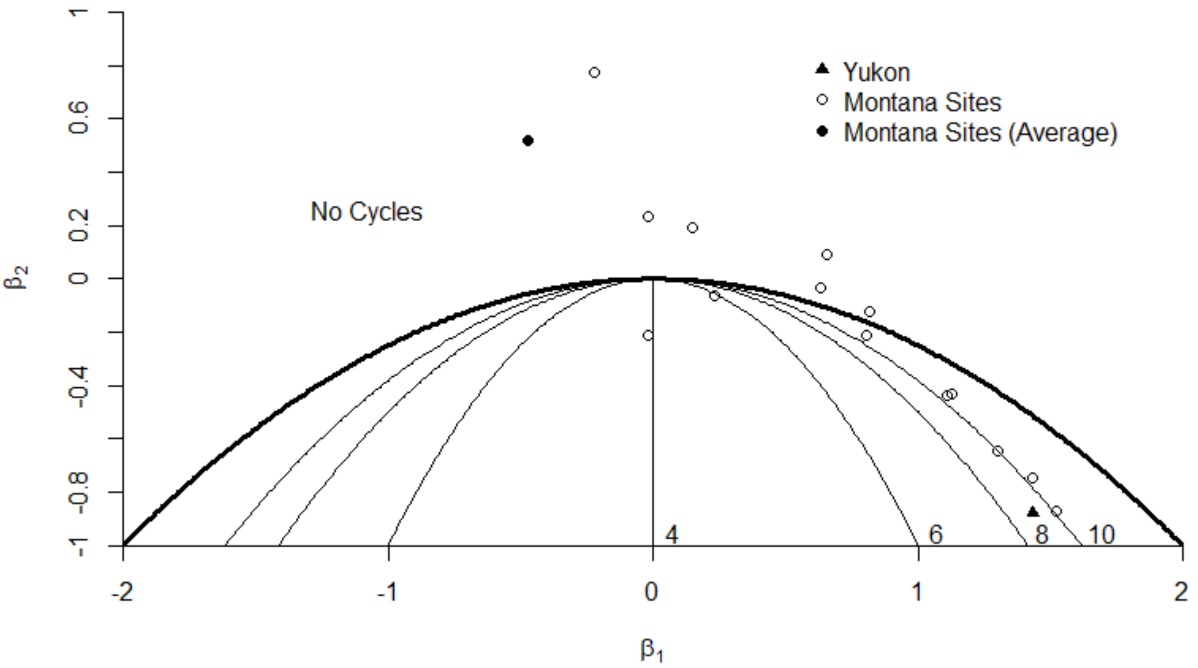

Figure 6 - Estimated values of β_1 and β_2 from an ARMA(2,1) model. Combinations that occur under the bold parabola exhibit cyclic behavior, while combinations above do not provide evidence for cycles. The period of the cycle is represented as various parabolas and is labeled above the x-axis. β_1 represents direct density dependence while β_2 represents delayed density dependence. The effects of density dependence grow stronger as the beta coefficients become more negative. Cycles can collapse through increasing strength of direct density dependence (more negative β_1) leading to period shortening or through decreasing strength of delayed density dependence (more positive β_2) leading to period lengthening.

Appendix A

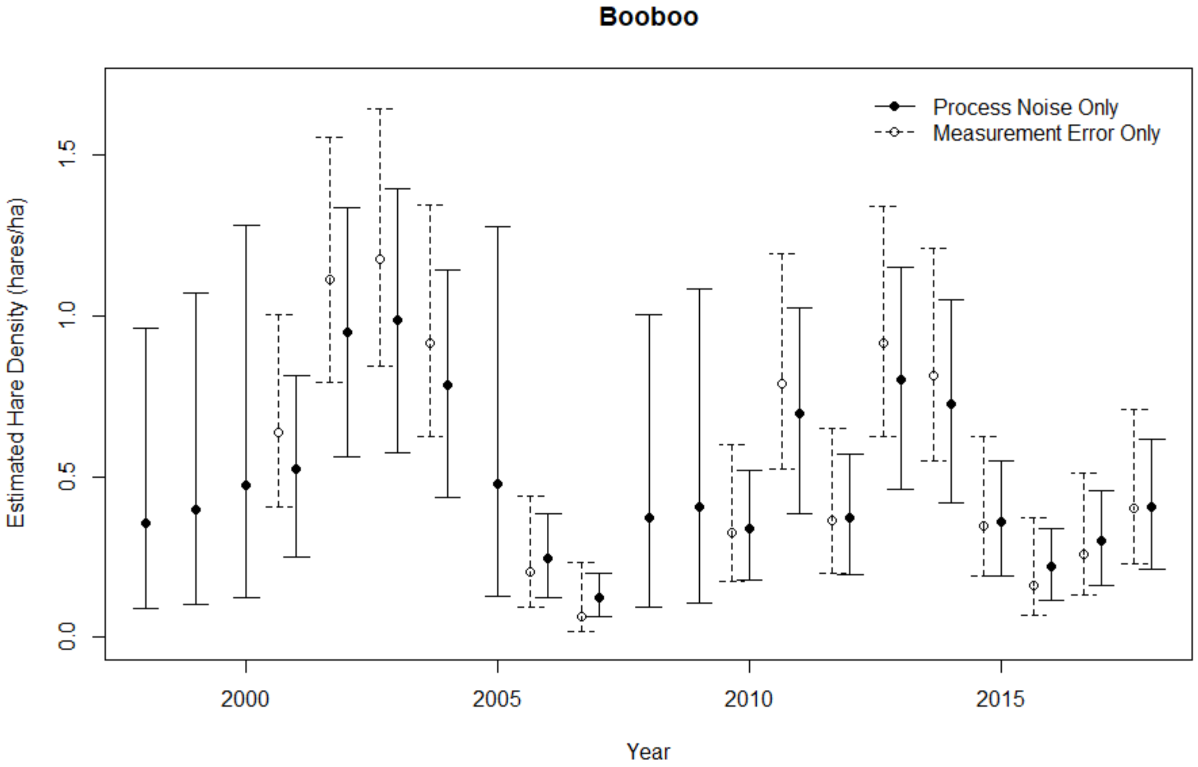

Figure S1 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

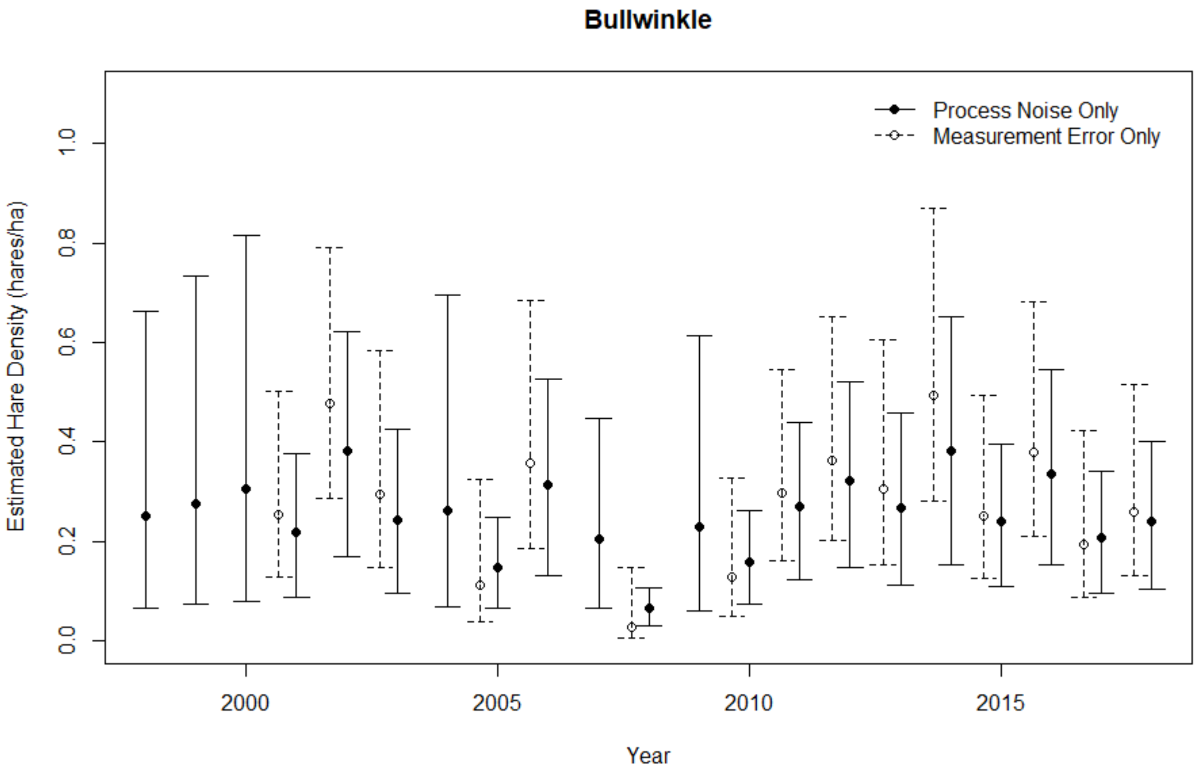

Figure S2 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

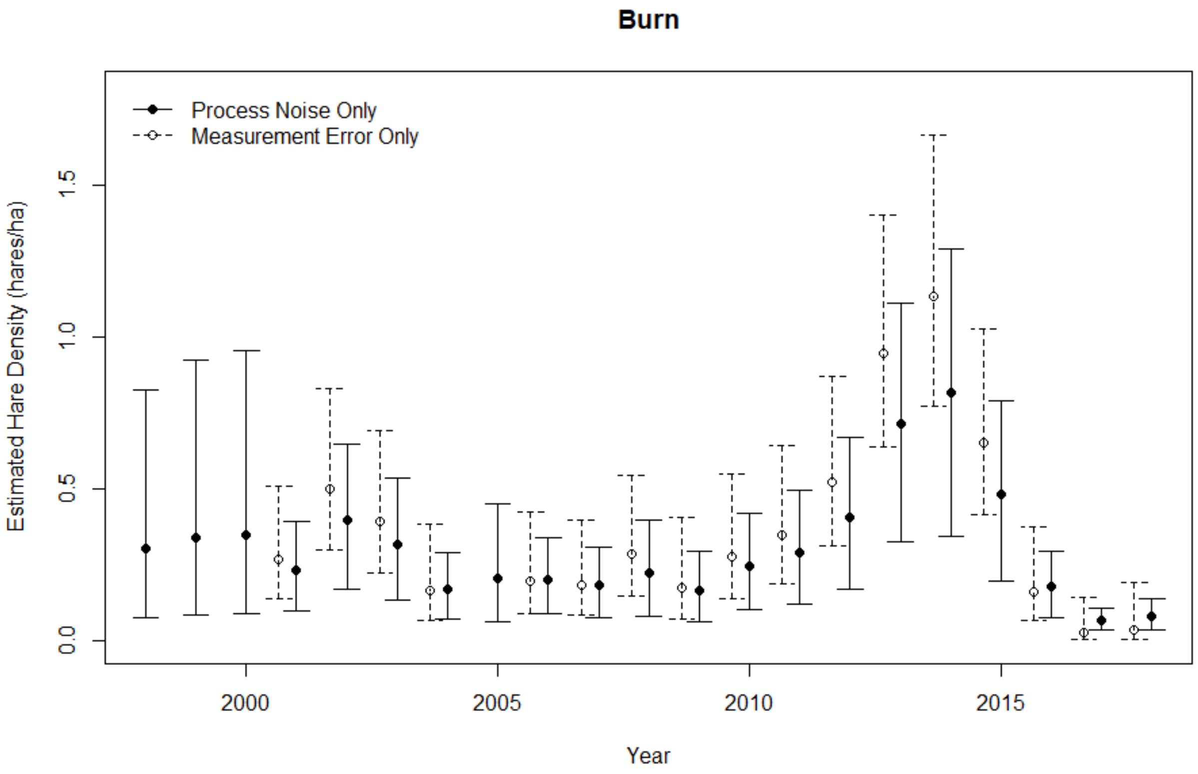

Figure S3 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

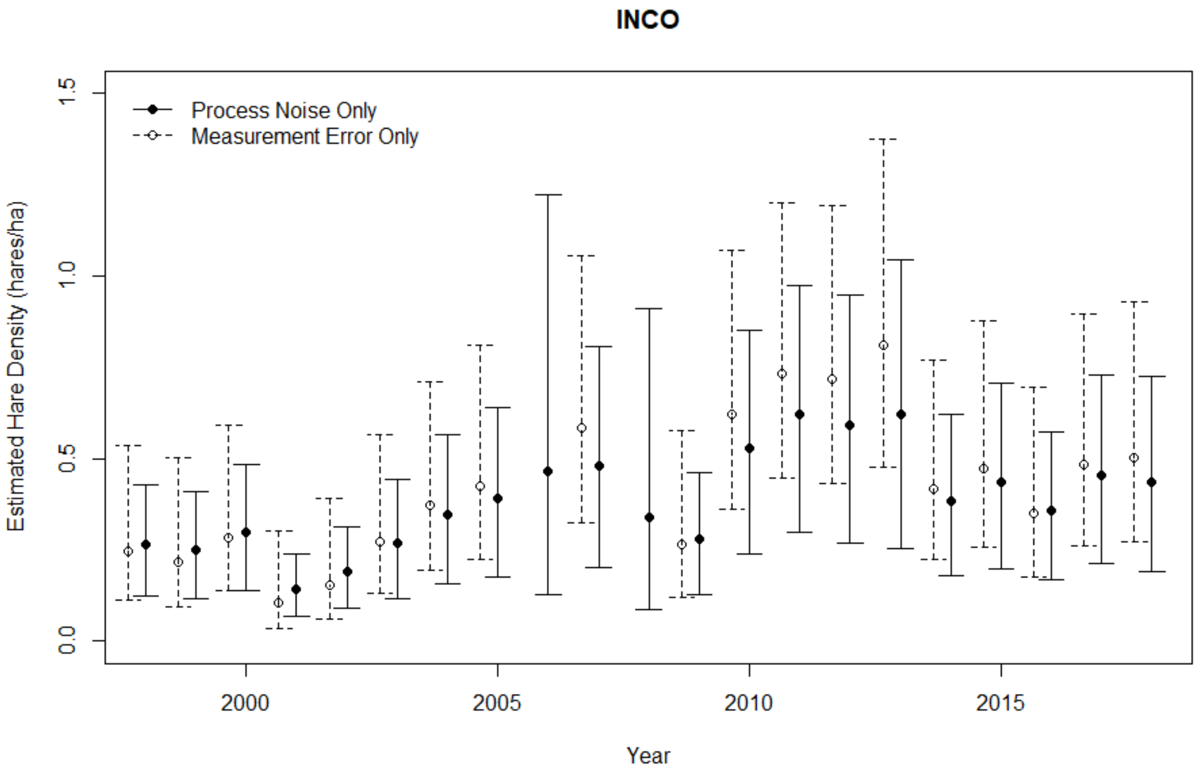

Figure S4 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

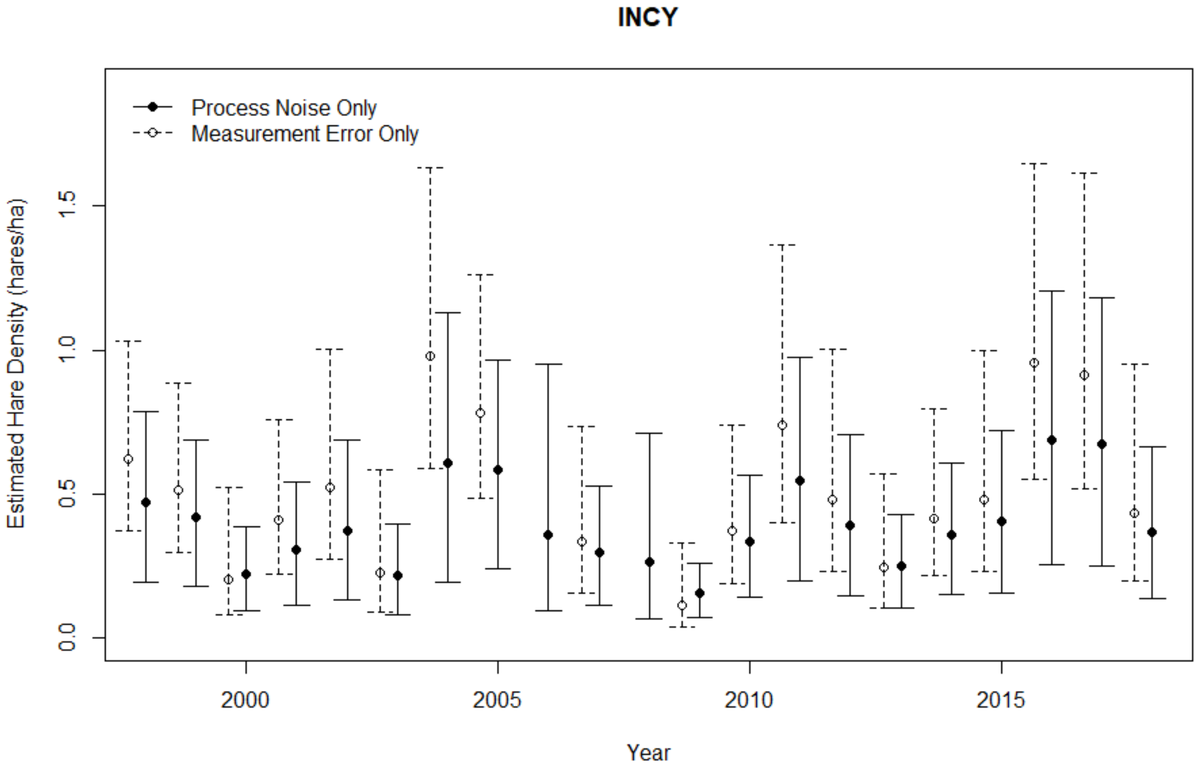

Figure S5 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

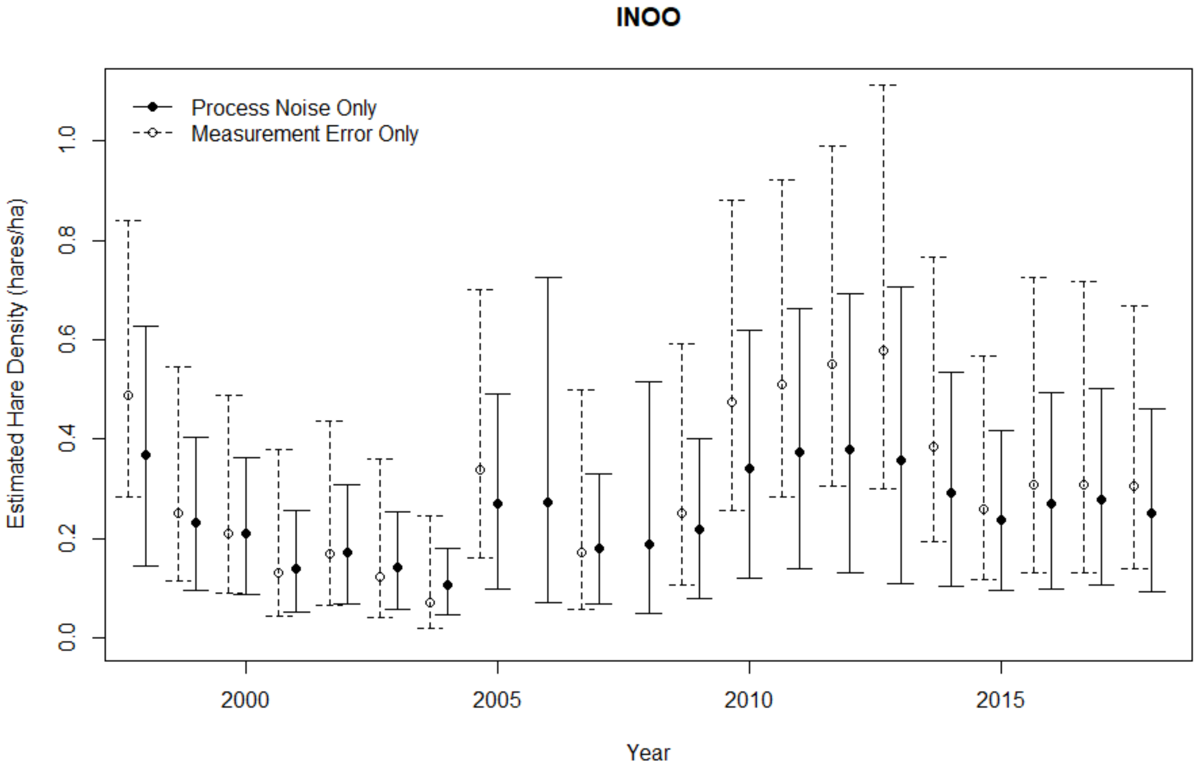

Figure S6 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

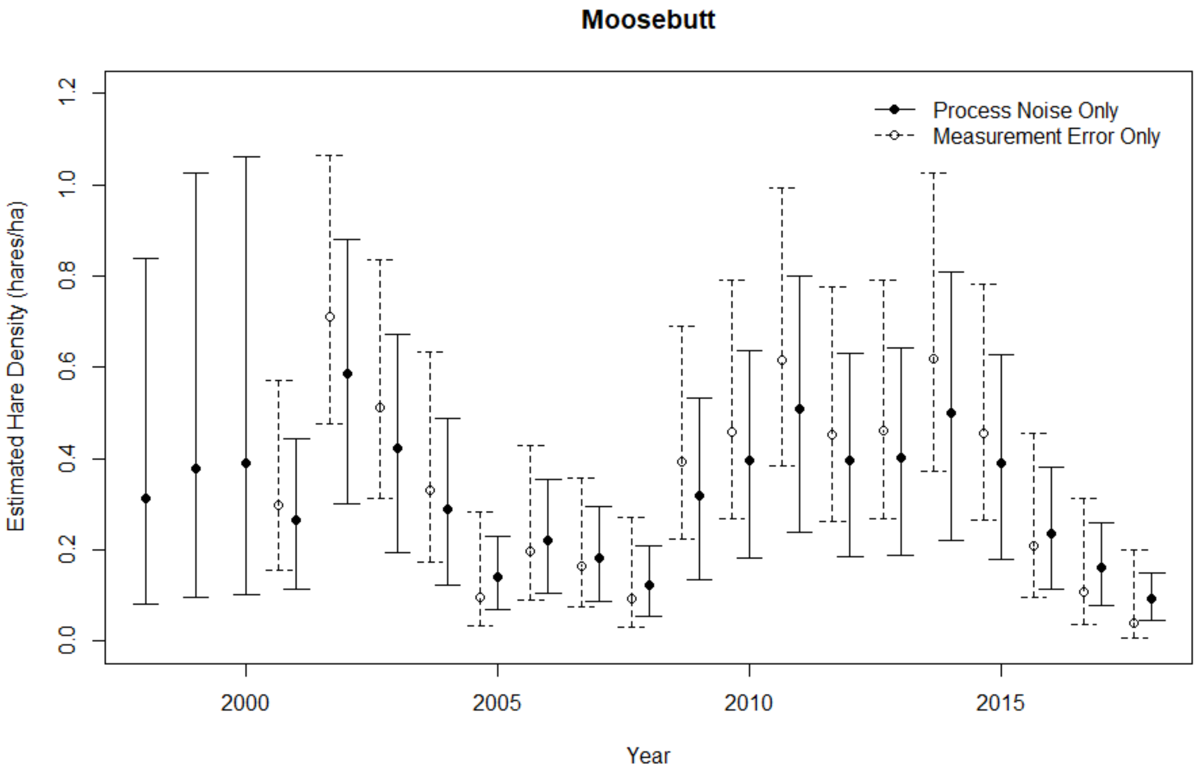

Figure S7 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

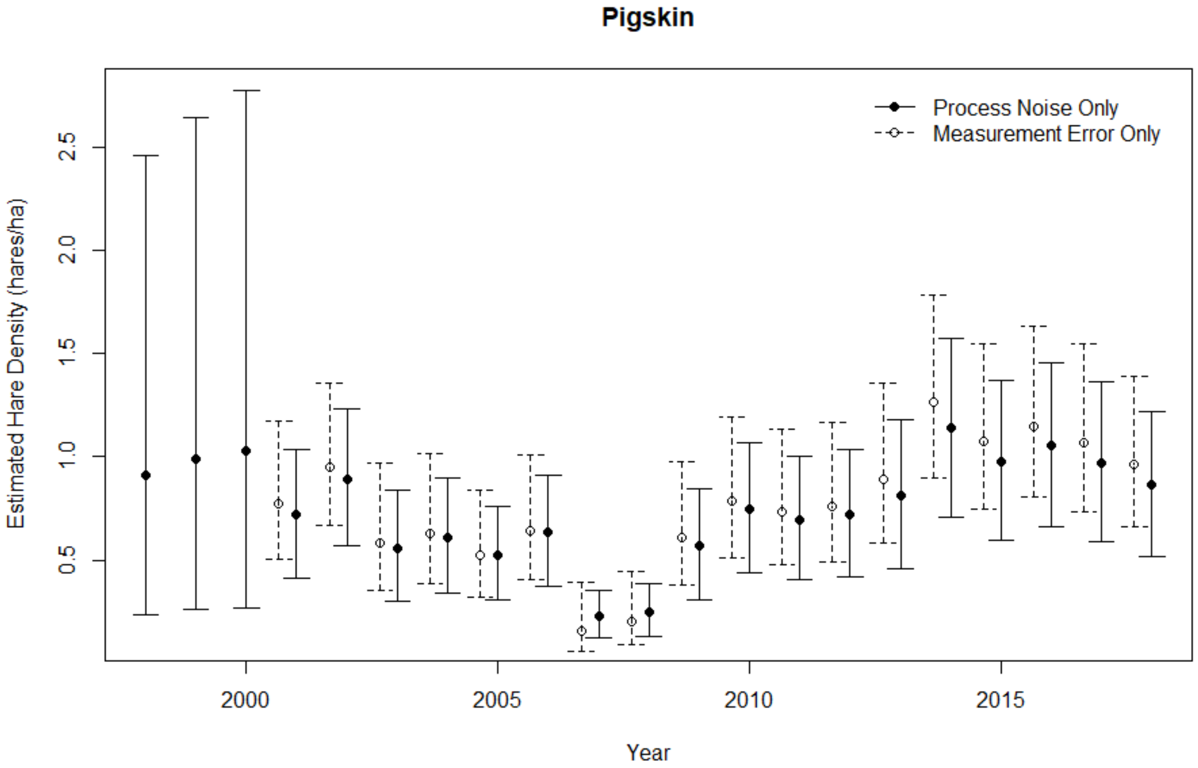

Figure S8 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

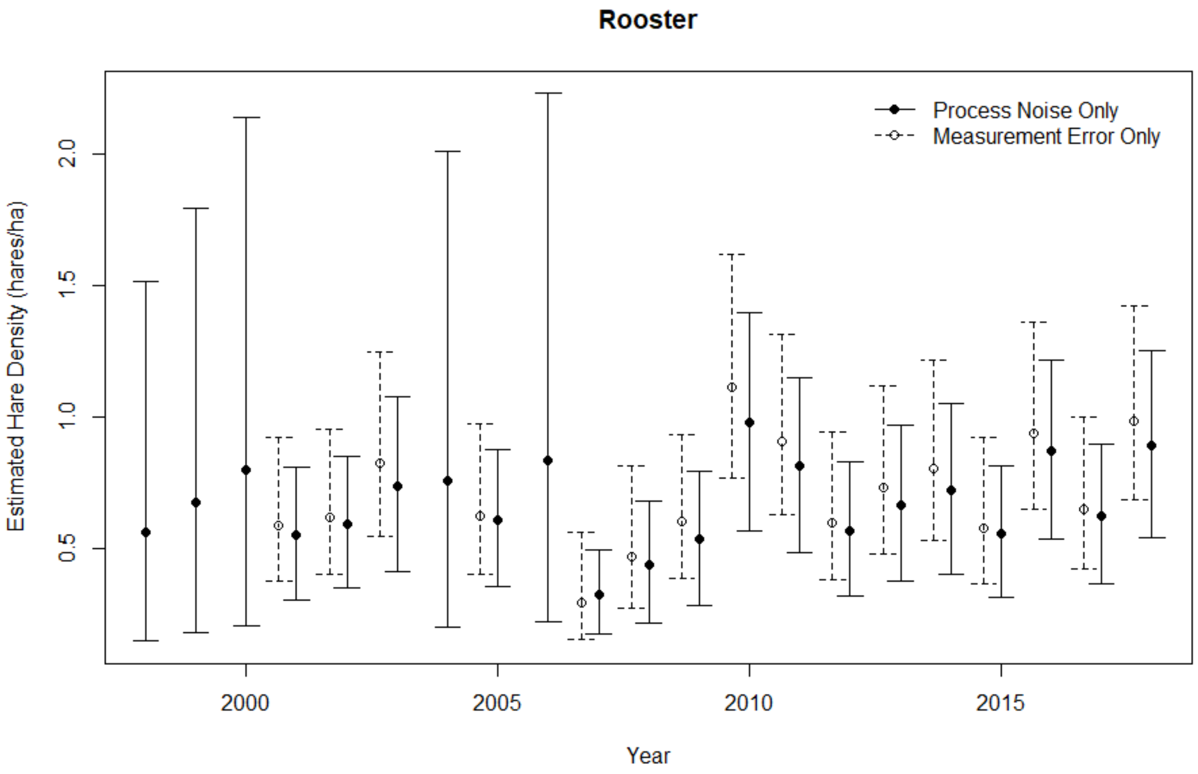

Figure S9 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

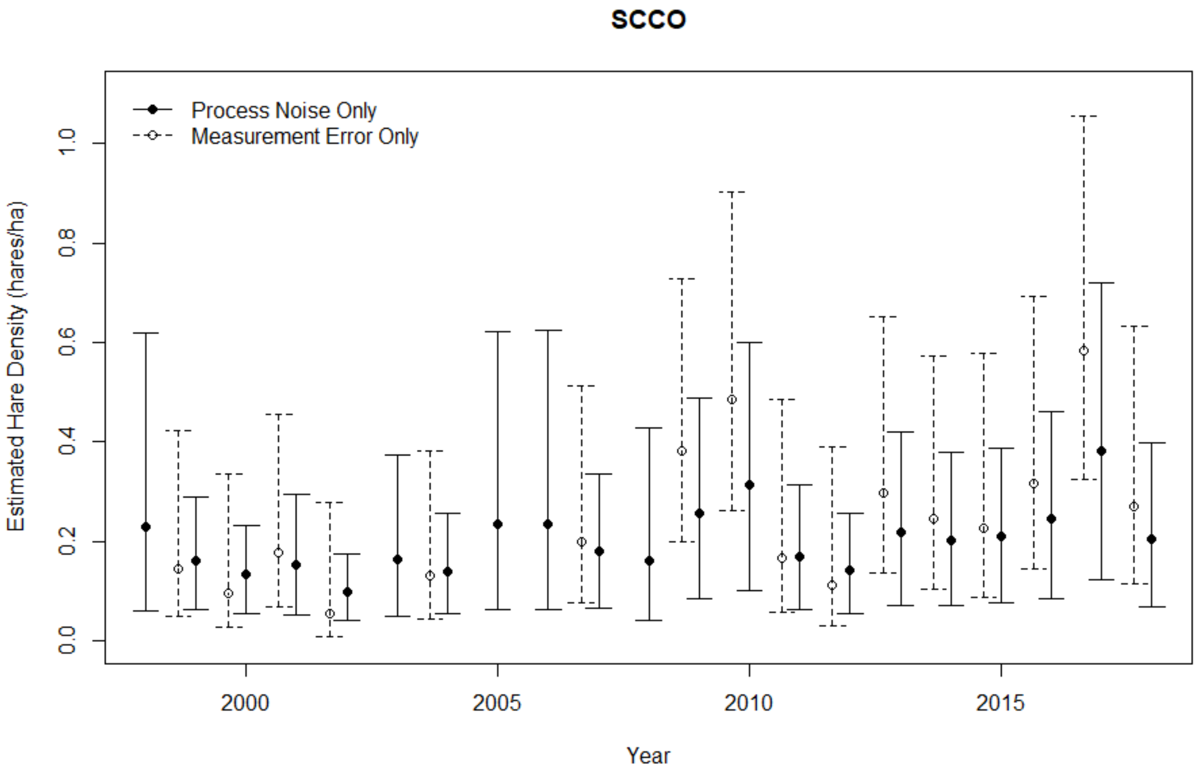

Figure S10 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

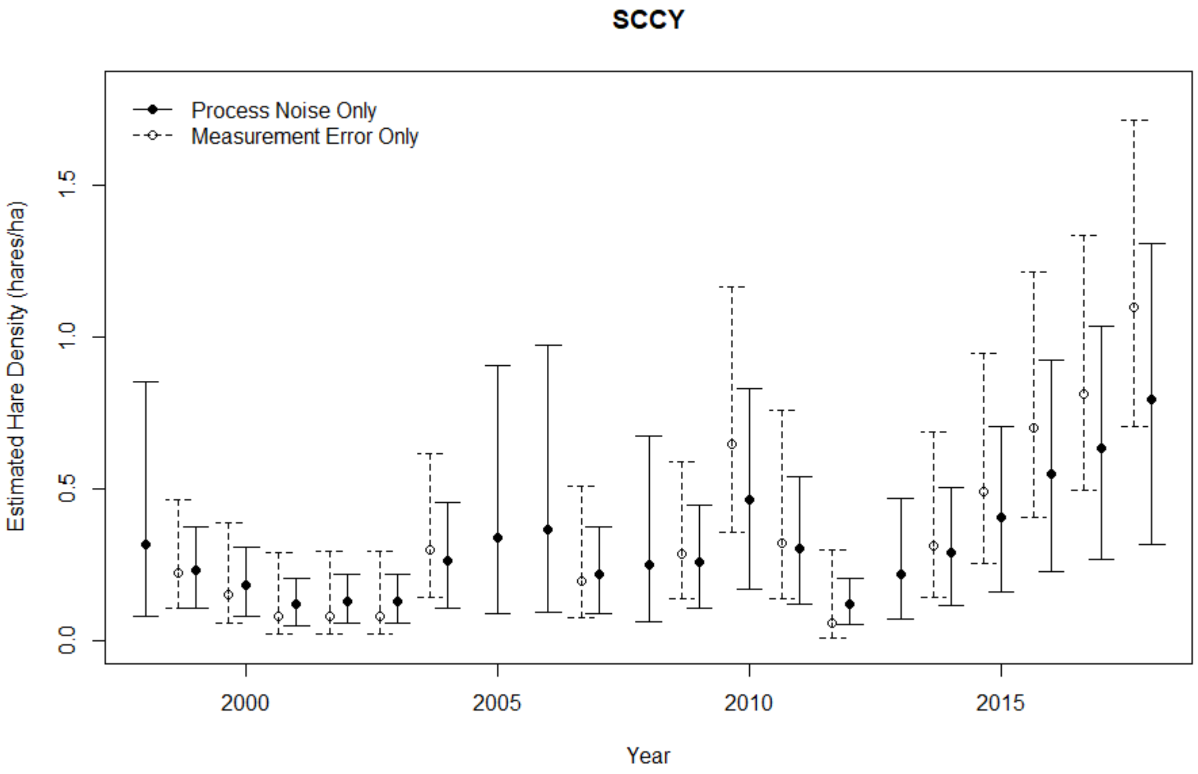

Figure S11 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

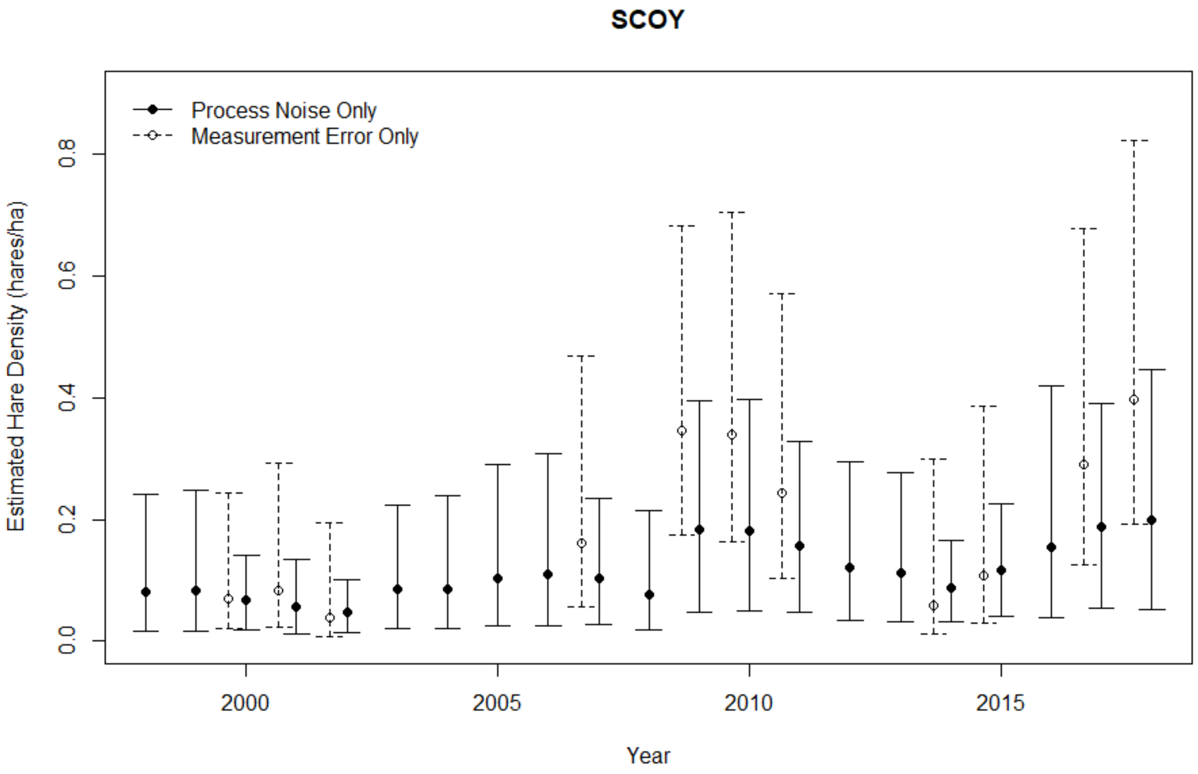

Figure S12 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.

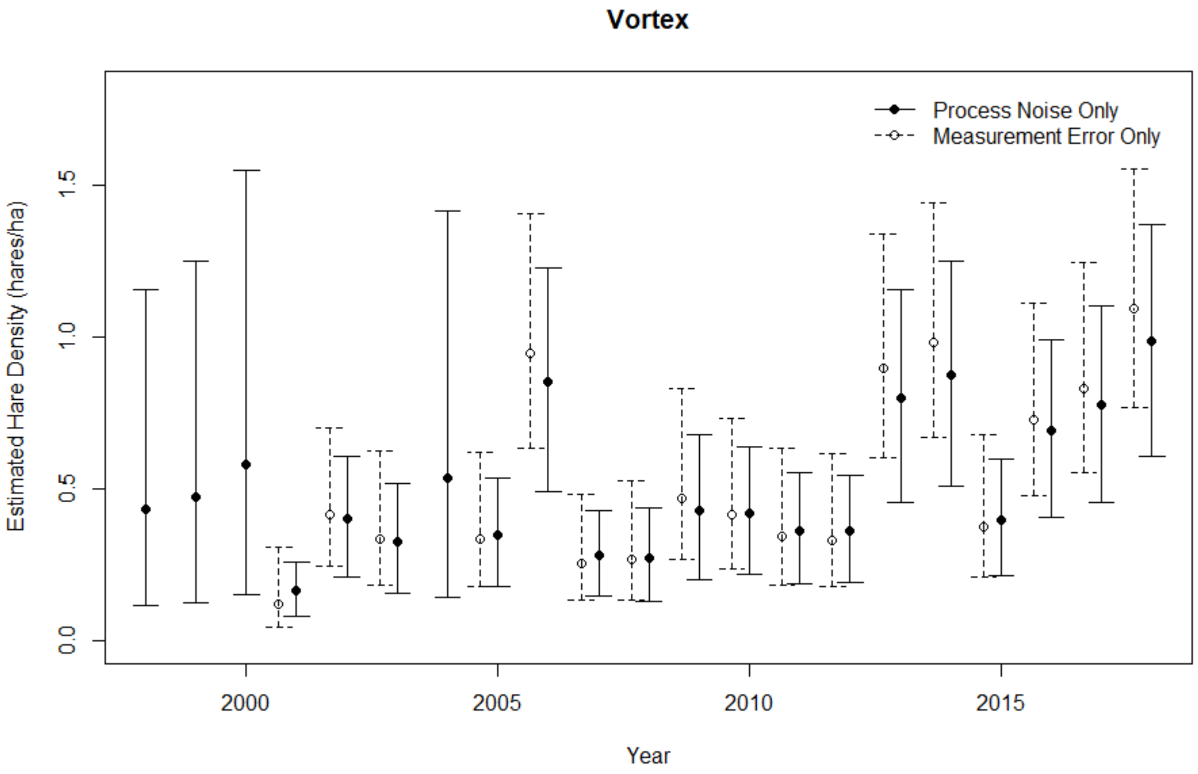

Figure S13 - Hare density from one site in western Montana from 1998-2018. Hare densities and 95% confidence intervals for the measurement error only estimate were calculated using a spatially-explicit capture-mark-recapture framework. Hare densities and 95% credible intervals with the measurement error component removed (process noise only) were then calculated with a state space model implemented in a Bayesian framework. Missing values for the measurement error only estimates occur when the site was not trapped that year.