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Estimating abundance, temporary emigration, and the pattern of density dependence in a cyclic snowshoe hare (*Lepus americanus*) population in Yukon, Canada

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Abstract: Estimates of demographic parameters based on capture–mark–recapture (CMR) methods may be biased when some individuals in the population are temporarily unavailable for capture (temporary emigration). We estimated snowshoe hare abundance, apparent survival, and probability of temporary emigration in a population of snowshoe hares (*Lepus americanus* Erxleben, 1777) in the Yukon (Canada) using Pollock's robust design CMR model, and population density using spatially explicit CMR models. Survival rates strongly varied among cyclic phases, seasons, and across five population cycles. We found strong evidence that temporary emigration was Markovian (i.e., nonrandom), suggesting that it varied among individuals that were temporary emigrant in the previous sampling period and those that were present in the sampled area. The probability of temporary emigration for individuals that were in the study area during the previous sampling occasion (γ'') varied among cycles. Probability that individuals that were temporarily absent from the sampled area would remain temporary emigrants (γ') showed strongly seasonal pattern, low in winter and high during summers. Snowshoe hare population density ranged from 0.017 (0.015–0.05) hares/ha to 4.43 (3.90–5.00) hares/ha and showed large-scale cyclical fluctuations. Autocorrelation functions and autoregressive analyses revealed that our study population exhibited statistically significant cyclic fluctuations, with a periodicity of 9–10 years.

Key words: autoregressive analysis, boreal ecosystem, capture–mark–recapture analysis, capture probability, *Lepus americanus*, density dependence, Pollock's robust design, snowshoe hare cycles, survival, spatial capture–recapture model, temporary emigration, wildlife's 10-year cycle.

Résumé : Les estimations de paramètres démographiques reposant sur des méthodes de capture–marquage–recapture (CMR) pourraient être biaisées dans les situations où certains individus de la population sont provisoirement non disponibles pour la capture (émigration temporaire). Nous avons estimé l'abondance, le taux de survie apparent et la probabilité d'émigration temporaire au sein d'une population de lièvres d'Amérique (*Lepus americanus* Erxleben, 1777) au Yukon (Canada) en utilisant le modèle CMR à schéma robuste de Pollock, et la densité de la population en utilisant des modèles CMR spatialement explicites. Les taux de survie variaient considérablement au fil des phases du cycle et des saisons et entre cinq cycles démographiques. Nous avons relevé des indices solides du caractère markovien (c.-à-d., non aléatoire) de l'émigration temporaire, donnant à penser que cette dernière diffère entre les individus qui étaient des émigrants temporaires durant la période d'échantillonnage précédente et ceux qui étaient présents dans le secteur échantillonné. La probabilité d'émigration temporaire pour les individus qui étaient dans le secteur d'étude durant l'occasion d'échantillonnage précédent (γ'') variait entre les cycles. La probabilité que des individus qui étaient temporairement absents du secteur échantillonné demeurent des émigrants temporaires (γ') présentait une forte saisonnalité, étant faible en hiver et élevée durant les étés. La densité de la population de lièvres d'Amérique allait de 0,017 (0,015–0,05) lièvres/ha à 4,43 (3,90–5,00) lièvres/ha et présentait de vastes fluctuations cycliques. Des fonctions d'autocorrélation et des analyses autorégressives ont révélé que la population étudiée présentait des fluctuations cycliques statistiquement significatives, d'une périodicité de 9–10 ans. [Traduit par la Rédaction]

Mots-clés : analyse autorégressive, écosystème boréal, analyse de capture–marquage–recapture, probabilité de capture, *Lepus americanus*, dépendance sur la densité, schéma robuste de Pollock, cycles des lièvres d'Amérique, survie, modèle spatial de capture–recapture, émigration temporaire, cycle démographique décennal.

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Introduction

Studies of population dynamics often rely on individual-based data collected by following fates of individuals that are uniquely marked. When such data are available, capture–mark–recapture (CMR) methodologies offer a variety of tools to rigorously estimate many population parameters such as survival, recruitment, population growth rate, and abundance (Pollock et al. 1990; Lebreton et al. 1992; Williams et al. 2002; Lebreton et al. 2009). Because CMR methods are powerful, flexible, applicable in a variety of contexts, and can adequately account for imperfect detection, they have become the method of choice for studying wildlife populations (Williams et al. 2002; Lebreton et al. 2009). An assumption inherent in most open population CMR studies is that all emigration from the study site is permanent and that temporary emigration does not occur. In reality, however, temporary emigration can occur in a variety of contexts (Kendall et al. 1997). For example, if the sampling area encompasses only a portion of the home ranges of animals, some individuals may be temporarily unavailable for sampling if they are outside the study area at the time of sampling. Other situations when temporary emigration is possible include (but are not limited to) temporary absence of nonbreeders on breeding grounds and temporary unavailability of individuals that are underground or inactive due to torpor (Kendall et al. 1997; Kendall and Bjorkland 2001; Bailey et al. 2004; Penaloza et al. 2014). We note that temporary emigration in the CMR context refers to temporary unavailability of organisms to be sampled, and not permanent emigration (i.e., migration away from their home ranges) as is commonly used in dispersal or metapopulation literature.

Because temporary emigration can potentially introduce bias in the estimates of demographic parameters, it is desirable to account for temporary emigration when possible (Kendall et al. 1997; Kendall 1999; Bird et al. 2014). Pollock's robust design CMR modelling approach offers a flexible way to obtain unbiased estimates of demographic parameters in the presence of temporary emigration (Kendall et al. 1997; Williams et al. 2002). Here, we apply a robust design CMR modelling framework to field data spanning 43 years (1977–2020) to estimate temporary emigration, apparent survival, and abundance of a cyclic snowshoe hare (*Lepus americanus* Erxleben, 1777) population in a boreal forest in southwestern Yukon, Canada. Snowshoe hares are the most important component of the food chain in many North American boreal forests, where snowshoe hare populations exhibit cyclic fluctuation in abundance with peak densities occurring every 9–11 years (Elton 1924; Krebs et al. 1995, 2001, 2018). Although several aspects of snowshoe hare population dynamics have been studied (e.g., Krebs et al. 1986, 2018; Hodges et al. 2001; Oli et al. 2020; Peers et al. 2021), estimates of population size that take temporary emigration into consideration are currently not available for our study population. Thus, our goal was to provide unbiased estimates of temporary emigration and abundance, and to determine how they vary across season, cyclic phases, and five population cycles.

Our study population exhibits the classic 10-year population cycles (Krebs et al. 1995, 2001, 2018). Theory suggests that density-dependent feedback mechanisms that permit populations to grow at faster rates when density is low (and at a slower rates when density is high) are necessary and often sufficient for regulation of biological populations (Royama 1992). The structure and strength of density dependence determine the pattern of population fluctuations. Whereas direct (first-order) density dependence leads to a stable equilibrium, delayed (second or higher order) density dependence is thought to be a necessary condition for cyclic fluctuations in abundance (Royama 1992; Turchin 1999; Oli 2019). Although density dependence in snowshoe hare populations has been examined by several authors (Royama 1992; Stenseth et al. 1997; Turchin 2003), previous studies were based primarily on the analysis of fur return data. To our knowledge, no study has examined density dependence in snowshoe hare populations using actual estimates of hare population size or density as opposed to indices of hare abundance. Thus, our second goal was to investigate the pattern and strength of density dependence in our study population using actual estimates of hare abundance.

Materials and methods

Study species, study area, and field methods

Snowshoe hares are distributed across North American boreal forests (Hoffman and Smith 2005) where they are one of the most important herbivores in terms of biomass and impact across trophic levels (Boonstra et al. 2016). Their coat colour is white in winter but rusty brown during summer. Mean lifespan is about 1 year, but they can live up to 4 years in the wild and up to 7 years in captivity (Keith and Windberg 1978; Boutin et al. 1986; Hodges et al. 2001; Krebs et al. 2018). At Kluane, predation is the most important cause of hare mortality, with ≥90% of hare deaths occurring due to predation (Boutin et al. 1985; Hodges et al. 2001; Krebs et al. 2018). Hares breed from May to September; females typically produce up to three (and occasionally four) litters per breeding season, with the first litters being born in May (Cary and Keith 1979; O'Donoghue and Krebs 1992; Boutin et al. 2002; Peers et al. 2021). Mean litter size varies between 3.2–6.9 leverets, depending on litter order and cyclic phase (Cary and Keith 1979; Hodges et al. 2001). Juveniles of both sexes disperse predominantly between 30 and 60 days of age; leverets typically disperse by September (Gillis and Krebs 1999; Hodges et al. 2001; Boutin et al. 2002). Dispersal rate is generally low (≤0.14) and it plays a relatively minor role in snowshoe hare population dynamics (Boutin et al. 1985). Reproductive parameters typically show cyclic variation (Cary and Keith 1979; O'Donoghue and Krebs 1992; Hodges et al. 2001; Stefan and Krebs 2001), but there is no evidence that dispersal varies depending on the phase of the population cycle (Boutin et al. 1985). During summer, hares consume forbs, grasses, leaves, and some woody browse, but their winter diet in Kluane consists primarily of the twigs of dwarf birch (*Betula glandulosa* Michx.) and willow (*Salix glauca* L.) (Krebs et al. 2018).

Our field study was conducted near Kluane Lake in the southwestern Yukon, Canada. Vegetation in this region is boreal forest dominated by white spruce (*Picea glauca* (Moench) Voss), with small areas of balsam poplar (*Populus balsamifera* L.) and trembling aspen (*Populus tremuloides* Michx.). Climate is cold, with mean monthly temperature falling below −20 °C during the winter months. The study area is typically under snow cover for about 8 months from October to May. A detailed description of the study area is given by Krebs et al. (2001).

We captured snowshoe hares using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) located on 10 grid × 10 grid or 20 grid × 20 grid with 30 m spacing between traps. For details of grid layout see Krebs et al. (2001: p. 59) and Oli et al. (2020: Appendix S1, Table S1). Field methods are described in detail elsewhere (Krebs et al. 1986; Hodges et al. 2001, 2006). Each hare received a Monel #3 ear tag (National Band and Tag Co., Newport, Kentucky, USA) at first capture; identity of previously marked hares was recorded in subsequent captures. Live trapping began in autumn 1977 and continued until autumn 2020. We considered two 2.5-month primary sampling occasions each year: autumn (hares captured during 1st September – 15th November) and spring (1st March – 15th May). Our secondary samples consisted of each month within primary sampling occasions; thus, we had three secondary samples within each primary sample (autumn: September, October, and November; spring: March, April, and May). Additional details regarding the field study are presented elsewhere (Krebs et al. 2001, 2018).

Ethics approval

All live-trapping procedures were approved by the Yukon Territorial Government Scientists and Explorers Act Licenses and Wildlife Permits, The University of British Columbia Animal Care Committee, the University of Alberta Animal Use and Care Committee, and the University of Toronto Animal Care Committee, and followed the guidelines of the American Society of Mammalogists (Sikes 2016).

Pollock's robust design CMR analysis

Traditionally, CMR methods are divided into two broad categories: closed population models and open population models (Otis et al. 1978; Williams et al. 2002). Typically, closed population models provide estimates of capture probabilities and abundance and assume that population size remains unchanged during the sampling period. Open population models, on the other hand, permit gains and losses during the sampling periods and provide estimates of survival, recruitment, abundance, and other demographic parameters, but they assume that any movement away from the sampled area is permanent. Pollock's robust design combines features of both closed and open population models (Pollock 1982; Lebreton et al. 1992; Pollock et al. 1993; Williams et al. 2002). Under this design, a distinction is made between primary and secondary sampling occasions. Within the secondary sampling occasions, the population is assumed to be closed (as in closed population CMR models), but primary sampling sessions are separated by longer time intervals (primary sampling sessions) during which populations can experience gains and losses (as in open population CMR models). Because the robust design modelling approach allows a flexible framework for estimating and modelling temporary emigration (Kendall et al. 1997; Kendall 1999; Williams et al. 2002), we used this modelling approach for our study.

The robust design approach to estimating temporary emigration envisions a superpopulation consisting of N_i^0 individuals that are associated with the sampling area (Kendall et al. 1997). Of these, N_i individuals are available for capture with capture probability $p_i{}^*$ during the primary sampling occasion i. However, in the presence of temporary emigration, some of these individuals would not be exposed to sampling because they would be temporarily absent from the study area. If the temporary emigration is completely random, then the expected number of individuals that are exposed to sampling during the primary sampling at primary sampling occasion i is $E(N_i) = (1 - \gamma)N_i^0$, where γ is the probability that an individual temporarily emigrates prior to primary sampling occasion i. However, if temporary emigration is Markovian, then the probability that an individual is a temporary emigrant during primary sampling occasion i depends on whether or not it was a temporary emigrant during $i - 1$. Specifically, the probability of temporary emigration is γ' for $\left(N_i^0 - N_{i-1}\right)$ individuals that were temporary emigrants during $i - 1$; it is γ'' for the N_{i-1} individuals that were exposed to sampling during $i - 1$ (Kendall et al. 1997; Kendall 1999). In other words, this approach allows temporary emigration to be different for individuals that were in the study area during the previous sampling and those that were away; γ'' represents the probability of temporary emigration for individuals that were in the study area during the previous sampling occasion, whereas γ' represents the probability that individuals that were temporary emigrants during the previous sampling occasion will remain temporary emigrants in the current sampling occasion. We note that, under this study design, a hare would be considered a temporary emigrant if it were present in that portion of home range outside of the trapping area.

We used a robust design CMR approach to estimate and model temporary emigration and other demographic parameters. For each year of study, we had two sampling occasions (autumn and spring), and within each primary sampling occasion, we had three secondary sampling occasions. We considered three sets of models. In the first set, we assumed Markovian temporary emigration; in the second set, we assumed random temporary emigration; and in the third set, we assumed no temporary emigration. To facilitate parameter estimation, we constrained probability of first capture p in a secondary period and subsequent secondary-period recaptures c within the same primary period to be the same, and allowed them to be affected by singular, additive, and interactive (two-way only) effects of phase of the cycles (increase, peak, decline, and low), season (autumn or spring), and cycle number (cycle that peaked in 1980 = cycle 1 and the recent cycle that peaked in 2017 = cycle 5; cycle number was treated as a discrete variable). Cyclic phases were defined following Keith (1990), based on previous estimates of finite rate of annual change (spring to spring) in snowshoe hare densities (Krebs et al. 2018).

We trapped snowshoe hares on seven control (unmanipulated) grids, but not all grids were trapped simultaneously. Gribble's, Grid 1050, and Kloo Lake grids were not trapped after spring 1985, and Chitty grid was trapped intermittently (Oli et al. 2020). To account for missing data, we fixed $p = c = 0$ for grids when they were not trapped. Preliminary analyses provided no evidence of sex-specific differences in model parameters (also see Krebs et al. 1986; Hodges et al. 1999), so sex effect was not included in the final analyses. Previous analyses have shown that apparent survival (φ) and capture probabilities (p) are strongly influenced by phase, season, and that they also vary across cycles. Thus, we allowed additive and interactive effects (only two-way interactions) of these covariates on φ and p. Thus, in addition to constant parameter models, we allowed singular effect of phase, season, and cycle number on γ' and γ''; our data were insufficient to support more complex models. In all analyses, we specified the time intervals between successive samples in months (mean interval between autumn and spring sampling occasions was 7 months, and between spring and autumn sampling occasions was 5 months); thus, all estimated parameters are monthly rates or probabilities. There was no evidence that capture probability differed among secondary samples. Thus, the probability of at least one encounter during a primary sampling occasion is given by $1 - (1 - p_j)^3$, where p_j is the capture probability during a secondary sample, j.

We implemented the robust design CMR model using program MARK (White and Burnham 1999) version 6.2 implemented in the RMark package (Laake 2013) for program R version 3.6.1 (R Core Team 2019). We used an information-theoretic approach for model selection with Akaike's information criterion corrected for small sample size (AIC$_c$) as a measure of model parsimony (Burnham and Anderson 2002; Williams et al. 2002). The effect of aforementioned covariates was determined by comparing AIC$_c$ among models with and without covariates. Because the random and no temporary emigration models are special cases of the Markovian temporary emigration model, we could compare these models both within and among sets based on AIC$_c$ values. Models with difference in AIC$_c$ (ΔAIC$_c$) ≤ 2 were not considered to be substantially different in terms of the model likelihood. We expected that temporary emigration would be (*i*) higher during summer than winter because snow cover would reduce the ability of snowshoe hares to move; (*ii*) higher during the peak and early decline phases, compared with the late decline or low phases (high population sizes during late increase and peak density phases would mean a greater competition for resources and a higher probability of temporary emigration); and (*iii*) higher during cycle 1 because of smaller effective sampling area during this cycle compared with later cycles. We also expected that apparent survival would be (*i*) higher during the increase and lower during the decline phase compared with other phases; (*ii*) higher during summer than winter because of harsh winter conditions and reduced food availability or accessibility during winter; and (*iii*) lower during cycle 1 compared with subsequent cycles because of higher temporary emigration during first cycle as described above. Finally, we expected capture probability to vary over time depending on environmental context, season, cyclic phases, or across

Table 1. Model comparison statistics testing for the effect of various covariates on capture probability (p), apparent survival (φ), and temporary emigration parameters for snowshoe hares (*Lepus americanus*) (γ'' is the probability of temporary emigration for hares that were exposed to sampling during $i - 1$; γ' is the probability that hares that were temporary emigrants during $i - 1$ will remain as temporary emigrants during sampling occasion i).

Model no.	Model	K	AIC$_c$	ΔAIC$_c$	Weight	Deviance
A. Markovian temporary emigration.						
1	φ(cycle_no * season + phase) γ''(cycle_no) γ'(season)p(cycle_no * season + phase)	33	38 960.172	0.000	0.586	47 948.071
2	φ(phase * cycle_no + season) γ''(cycle_no) γ'(season)p(phase * cycle_no + season)	48	38 961.358	1.186	0.324	47 919.006
3	φ(cycle_no * season + phase) γ''(cycle_no) γ'(season)p(phase * cycle_no + season)	41	38 965.106	4.934	0.050	47 936.882
4	φ(phase * cycle_no + season) γ''(cycle_no) γ'(season)p(cycle_no * season + phase)	40	38 965.485	5.313	0.041	47 939.278
5	φ(phase * cycle_no + season) γ''(cycle_no) γ'(phase)p(phase * cycle_no + season)	50	38 978.226	18.055	0.000	47 931.834
6	φ(cycle_no * season + phase) γ''(season) γ'(cycle_no)p(phase * cycle_no + season)	41	38 980.826	20.654	0.000	47 952.602
7	φ(cycle_no * season + phase) γ''(season) γ'(cycle_no)p(cycle_no * season + phase)	33	38 982.729	22.557	0.000	47 970.628
8	φ(phase * season + cycle_no) γ''(cycle_no) γ'(season)p(phase * cycle_no + season)	40	38 982.780	22.608	0.000	47 956.573
9	φ(phase * cycle_no + season) γ''(cycle_no) γ'(phase)p(cycle_no * season + phase)	42	38 984.456	24.284	0.000	47 954.215
10	φ(phase + cycle_no + season) γ''(cycle_no) γ'(season)p(phase * cycle_no + season)	37	38 985.319	25.148	0.000	47 965.161
B. Random temporary emigration.						
1	φ(cycle_no * season + phase) γ''(.)p(phase * cycle_no + season)	35	39 045.560	0	0.685	47 863.965
2	φ(cycle_no * season + phase) γ''(season)p(phase * cycle_no + season)	36	39 047.571	2.015	0.254	48 029.428
3	φ(cycle_no * season + phase) γ''(phase)p(phase * cycle_no + season)	38	39 051.602	6.045	0.034	48 029.428
4	φ(cycle_no * season + phase) γ''(cycle_no)p(phase * cycle_no + season)	39	39 053.618	8.061	0.012	48 029.428
5	φ(cycle_no * season + phase) γ''(.)p(cycle_no * season + phase)	27	39 057.297	11.741	0.002	48 057.271
6	φ(cycle_no * season + phase) γ''(season)p(cycle_no * season + phase)	28	39 059.309	13.752	0.001	48 057.271
7	φ(phase * cycle_no + season) γ''(.)p(phase * cycle_no + season)	42	39 061.155	15.598	0.000	48 030.914
8	φ(phase * cycle_no + season) γ''(season)p(phase * cycle_no + season)	43	39 063.172	17.616	0.000	48 030.914
9	φ(cycle_no * season + phase) γ''(phase)p(cycle_no * season + phase)	30	39 063.333	17.776	0.000	48 057.271
10	φ(cycle_no * season + phase) γ''(cycle_no)p(cycle_no * season + phase)	31	39 065.345	19.789	0.000	48 057.271
C. No temporary emigration.						
1	φ(cycle_no * season + phase)p(phase * cycle_no + season)	34	39 043.542	0.000	0.997	48 029.428
2	φ(cycle_no * season + phase)p(cycle_no * season + phase)	26	39 055.286	11.744	0.003	48 057.271
3	φ(phase * cycle_no + season)p(phase * cycle_no + season)	41	39 059.138	15.595	0.000	48 030.914
4	φ(phase * season + cycle_no)p(phase * cycle_no + season)	33	39 068.814	25.271	0.000	48 056.712
5	φ(phase + cycle_no + season)p(phase * cycle_no + season)	30	39 075.126	31.583	0.000	48 069.063
6	φ(cycle_no * season + phase)p(phase * season + cycle_no)	25	39 077.159	33.616	0.000	48 081.154
7	φ(phase * cycle_no + season)p(cycle_no * season + phase)	33	39 087.464	43.921	0.000	48 075.363
8	φ(phase * cycle_no)p(phase * cycle_no + season)	40	39 088.565	45.022	0.000	48 062.358
9	φ(phase * cycle_no)p(phase * cycle_no + season)	40	39 088.565	45.022	0.000	48 062.358
10	φ(phase * cycle_no + season)p(phase * season + cycle_no)	32	39 093.677	50.135	0.000	48 083.590

Note: We considered three sets of models, assuming (A) Markovian temporary emigration, (B) random temporary emigration (i.e., $\gamma'' = \gamma'$), and (C) no temporary emigration (i.e., $\gamma'' = \gamma' = 0$). Covariates are cyclic phase (phase; increase, peak, decline, low); season (autumn or spring sampling occasions), and cycle number (cycle_no; cycle peaking in 1980–1981 is cycle number 1; current cycle peaking in 2016–2017 is cycle number 5). For each model, we report the number of parameters (K), Akaike's information criterion corrected for small sample size (AIC$_c$), difference in AIC$_c$ (ΔAIC$_c$), model weight, and model deviance.

cycles, but we did not have specific expectations. For clarity, we refer to survival (or temporary emigration) from spring to autumn as summer survival (or temporary emigration), and survival (or temporary emigration) from autumn to spring as winter survival (or temporary emigration).

The size and number of trapping grids changed during the course of this study (Oli et al. 2020). Thus, we calculated the population density (along with 95% confidence intervals (95% CI)) by dividing the estimated population size by the area of the sampled grids. Our intention was not necessarily to report unbiased estimates of population density but to provide a standardized estimate of abundance to permit comparison across the entire study period. Whereas the robust design CMR models provide unbiased estimates of abundance, density estimated as above may be biased because difficulties inherent in estimating effective trapping area (Otis et al. 1978; Efford 2004; Borchers and Efford 2008). Further complications may arise if the number and location of trapping grids change over time. Thus, we also estimated snowshoe hare population density using the spatially explicit capture–recapture model (Efford 2004; Borchers and Efford 2008; Royle et al. 2014) using data from Silver and Sulphur (both control or unmanipulated) grids that were continuously trapped during each season and year of our study (autumn 1977 to spring 2020). We implemented the spatially explicit capture–recapture model in program DENSITY (Efford 2014).

Analysis of density dependence

Density dependence in population dynamics is typically studied within the framework of time-series analyses using autoregressive models. We considered an autoregressive process of order k, generally referred to as AR(k), of the following form (Royama 1992; Stenseth et al. 1997; Oli 2019):

$$X_{t+1} = a_0 + (a_1 + 1)X_t + a_2 X_{t-1} + a_3 X_{t-2} + \cdots + a_k X_{t-k} + \varepsilon_t \tag{1}$$

where X_t is log-transformed population size or density at time t, a_0 is the intercept term, a_i is the autoregressive coefficient of degree i, and ε_t is the independently and identically distributed process variance, assumed to be normally distributed with $\varepsilon_t \sim \text{Normal}(0,\sigma^2)$. Ecologically, the parameters a_1 and a_2 (and higher order coefficients) quantify the strength of direct and delayed density dependence, respectively. Populations experiencing direct density dependence converge to stable equilibria, whereas those experiencing delayed density dependence exhibit

Fig. 1. Model-averaged monthly estimates of apparent survival (φ, with 95% confidence intervals (95% CI)) for a snowshoe hare (*Lepus americanus*) population in Kluane, Yukon, Canada, during Autumn 1977 – Spring 2020. Color version online.

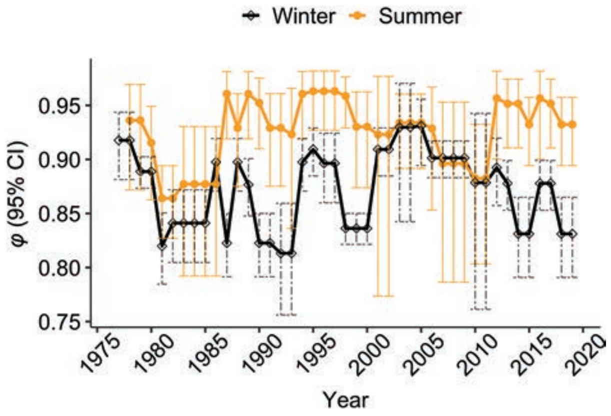
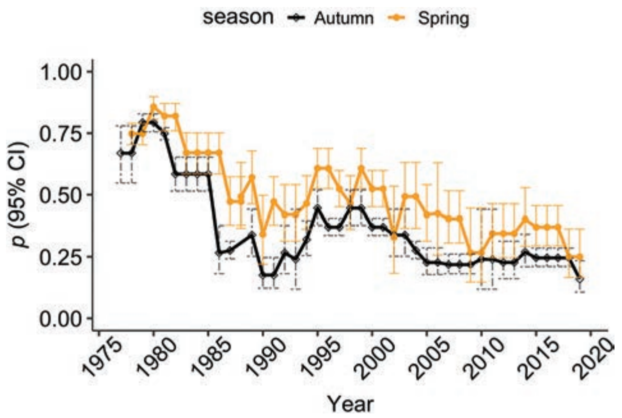


Fig. 2. Model-averaged estimates of capture probability (p, with 95% confidence intervals (95% CI)) for a snowshoe hare (*Lepus americanus*) population in Kluane, Yukon, Canada, during autumn 1977 – spring 2020. For these analyses, the probability of first-time capture and subsequent recaptures were assumed to be the same. These estimates were obtained using the most parsimonious robust design capture–mark–recapture model that assumed Markovian temporary emigration (model 1 in Table 1A). We note that these estimates of capture probability are expected to differ from those reported in previous analyses (Oli et al. 2020) because of nonzero temporary emigration (Kendall et al. 1997). Color version online.



a variety of dynamical behaviors, ranging from damped oscillations to cycles and chaos (Royama 1992). The periodicity of the second-order autoregressive process is determined by values of parameters a_1 and a_2 (Royama 1992; Bjørnstad et al. 1995; Turchin 2003).

Estimates of autoregressive parameters can be affected by both sampling and process variances, but conventional time-series models (e.g., Royama 1992; Turchin 2003) do not adequately consider sampling and process variances of the response and predictor variables. Thus, we used a Bayesian state-space modelling approach to fit the AR(k) model to the snowshoe hare density data (Viljugrein et al. 2005; Rotella et al. 2009; Ims et al. 2011; Ahrestani et al. 2013). We modelled the state process as specified in eq. 1 with $\varepsilon_t \sim$ Uniform(0,1) The state process was then linked to the observation process as $Y_t = \text{Normal}(X_t, \eta_t^2)$, where Y_t is the log-transformed population density at time t and η_t^2 is its variance estimated as $\eta_t^2 = \text{var}(D_t)$, where D_t is the log-transformed variance of the density at time t estimated from the spatially explicit capture–recapture model. We fitted the state-space models to spring to spring, and autumn to autumn density estimates (time interval = 1 year). For each analysis, we ran four chains each with 6 000 000 iterations with 500 000 burn-ins and retained results for every 50 iterations to minimize autocorrelation in parameter estimates. Convergence of Markov chains was assessed using Gelman–Rubin statistics ($\hat{R}$); $\hat{R} \leq 1.1$ generally indicates convergence proper mixing of Markov chains. We report mean, median (50th percentile), and 95% credible intervals (95% CrI) for each parameter monitored. We fitted state-space model in JAGS version 4.3 (Plummer 2003) in R computing environment (R Core Team 2019) with vague priors: $a_i \sim$ Normal(0,10^{-7}); $x_i \sim$ Normal(Y_1,10^{-7}) for i = {1, 2} for spring to spring and autumn to autumn density data; and $\varepsilon_t \sim$ Uniform(0,1). We fit AR(k) models to the estimated population density obtained from the spatially explicit capture–recapture models (SECR-based estimates). We did not fit AR(k) models to naïve density estimates (i.e., population density estimated using the robust design abundance estimates) because these estimates have correlation structure that is not appropriately accounted for in AR(k) analyses.

We used autocorrelation function (ACF) to reveal the trend and periodic patterns of the time series of abundance (Box et al. 2008). The ACF is estimated by calculating the correlation between the pairs of log-transformed densities $X_{t-\tau}$ and X_t separated by time lag τ, τ = 1, 2, ... The correlation coefficients were then plotted against τ to reveal the trend and periodicity in the time series of log-transformed snowshoe hare densities (Turchin 2003). The ACF analyses were conducted using the point estimates of snowshoe hare population densities obtained from the spatially explicit capture–recapture analysis.

Results

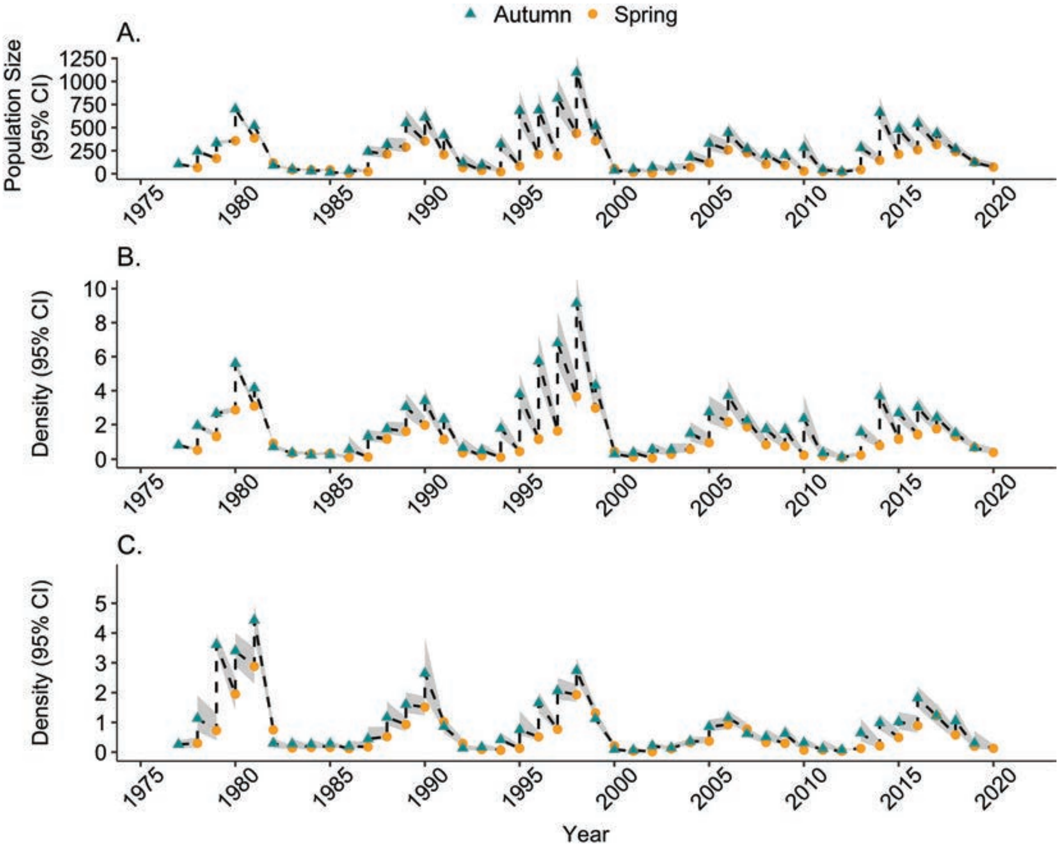
We live-trapped 5502 unique hares (2781 males and 2721 females) on control (unmanipulated) grids a total of 11 246 times during 1977–2020. More hares were encountered during autumn (3140 females and 3178 males) than spring (2314 females and 2614 males).

Robust design CMR models that assumed Markovian temporary emigration (Table 1A) were substantially better supported than those that assumed random temporary emigration (Table 1B) or no temporary emigration (Table 1C). The most parsimonious Markovian temporary emigration model (model 1 in Table 1A) indicated that both φ and p were influenced by an interactive effect of cycle number (treated as a categorical variable) and season, as well as an additive effect of phase; however, an equally well-supported model included an interactive effect of phase and cycle number and an additive effect of season on both of these parameters.

Model-averaged estimates of φ were higher during summer than winter, and generally higher during the increase or peak phase than during the decline phase. Generally, φ varied across cycles, but there was no apparent temporal trend (Fig. 1). Model-averaged estimates of p also varied across seasons (it was generally higher during spring than autumn), cycles (it was higher during cycle 1 compared with subsequent cycles), and phases (it was generally higher during the peak or late increase phase) (Fig. 2).

Virtually all well-supported Markovian temporary emigration models (Table 1A) included an effect of cycle number on γ'', indicating that this parameter strongly varied across cycles. Parameter estimates revealed that γ'' was nonzero only during cycle 1 (γ'' = 0.336; 95% CI = 0.252–0.432); it was practically zero for all other cycles. In contrast, most well-supported models for γ' included an effect of season. Estimates of γ' revealed that the snowshoe hares that are temporarily outside of the sampled area are highly unlikely to return to the sampled area during summer (γ' = 0.999; 95% CI = 0–1; $1 - \gamma' \approx 0$); they were much more likely to return to the sampled area during winter (γ' = 0.46; 95% CI = 0.15–0.79; $1 - \gamma' \approx 0.54$). Model-averaging did not substantially alter these patterns.

Fig. 3. Model-averaged time-specific estimates of snowshoe hare (*Lepus americanus*) population size (A) and naïve estimates of population density (hares/ha) obtained by dividing the population size estimates obtained from the robust design model of the trapping grid (B), population density (hares/ha) estimated using the spatially explicit capture–recapture model (C) in Kluane, Yukon, Canada, during autumn 1977 – spring 2020. Estimates in A and B were obtained using the most parsimonious robust design capture–mark–recapture model that assumed Markovian temporary emigration (model 1 in Table 1A). Color version online.



Estimates of population size (i.e., abundance in all sampled grids) exhibited distinctly cyclic patterns, with higher population size during autumn than during spring; increase and peak phases were generally characterized by high population sizes and low phases were characterized by very low population sizes (Fig. 3A). Population density estimated from the spatially explicit capture–recapture (SECR) model ranged from 0.017 (0.015–0.05) hares/ha in spring 2002 to 4.43 (3.90–5.00) hares/ha in autumn 1981. Although there were sometimes substantial differences in hare density estimated from the two methods (SECR-based estimates were generally lower than those obtained from the robust design CMR approach; Otis et al. 1978), the pattern of cyclic population fluctuations was almost identical (Figs. 3B and 3C). Based on SECR-based estimates of population densities, the amplitude of cycles (amplitude = highest population density/lowest density of the same cycle) was 38, 40, 164, 16, and 55 for cycle 1, cycle 2, cycle 4, and cycle 5, respectively. The amplitude of cycles based on naïve density estimates was 56, 29, 143, 18, and 38 for cycle 1, cycle 2, cycle 4, and cycle 5, respectively. We note, however, that cycle 5 was still in the decline when this study concluded.

The autocorrelation function (which reveals how correlation between population size at different points in time changes as their separation in time changes) using spring and autumn population density data revealed distinctly cyclic population dynamics with periodicity of ∼10 years (Figs. 4A and 4B). Bayesian autoregressive models fitted to log-transformed population density converged with $\hat{R} \leq 1.001$ for all parameters.

The first-order autoregressive coefficient (β_1) was negative for both autumn and spring density data, suggesting evidence for direct density dependence (Tables 2A and 2B). Using Royama's (1992; fig. 2.9) parameter plane scheme, we find that the term $(1 + \beta_1)$ was 0.16 for autumn density data and –0.060 for spring density data; β_2 (second-order autoregressive coefficient) was –0.329 for autumn density data and –0.308 for spring density data. These autoregressive coefficients (Tables 2A and 2B) were broadly consistent with those expected for a cyclic population with a periodicity of ∼10 years (Royama 1992).

Discussion

Temporary emigration is commonplace in studies of animal populations and can arise when a portion of the population is unavailable for sampling for a variety of reasons (Kendall et al. 1997; Kendall 1999; Penaloza et al. 2014; Gowan et al. 2019). Failure to account for temporary emigration when it occurs can result in biased estimates of demographic parameters that can also lead to incorrect inferences or management decisions, especially when temporary emigration is nonrandom (Kendall et al. 1997; Kendall 1999; Williams et al. 2002). When temporary emigration is suspected (a likely scenario in most open populations), it is advisable to use models that allow estimation and modelling of parameters related to temporary emigration (Schaub et al. 2004).

The difference in AIC$_c$ between the most parsimonious model that assumed Markovian emigration and the most parsimonious model that assumed random emigration was 87.4; the difference in AIC$_c$ between one that assumed Markovian emigration and one that assumed no temporary emigration was 83.4 (Tables 1A–1C). These results provide strong evidence that temporary emigration

Fig. 4. Autocorrelation functions (ACF) fitted to spring to spring (A) and autumn to autumn (B) density estimates for snowshoe hares (*Lepus americanus*) in Kluane, Yukon, Canada, during autumn 1977 – spring 2020. Analyses were performed using the hare population density estimated using the spatially explicit capture–recapture model. Note that time intervals between spring to spring and autumn to autumn samples were 1 year; thus, the time lag are in years in both panels. Color version online.

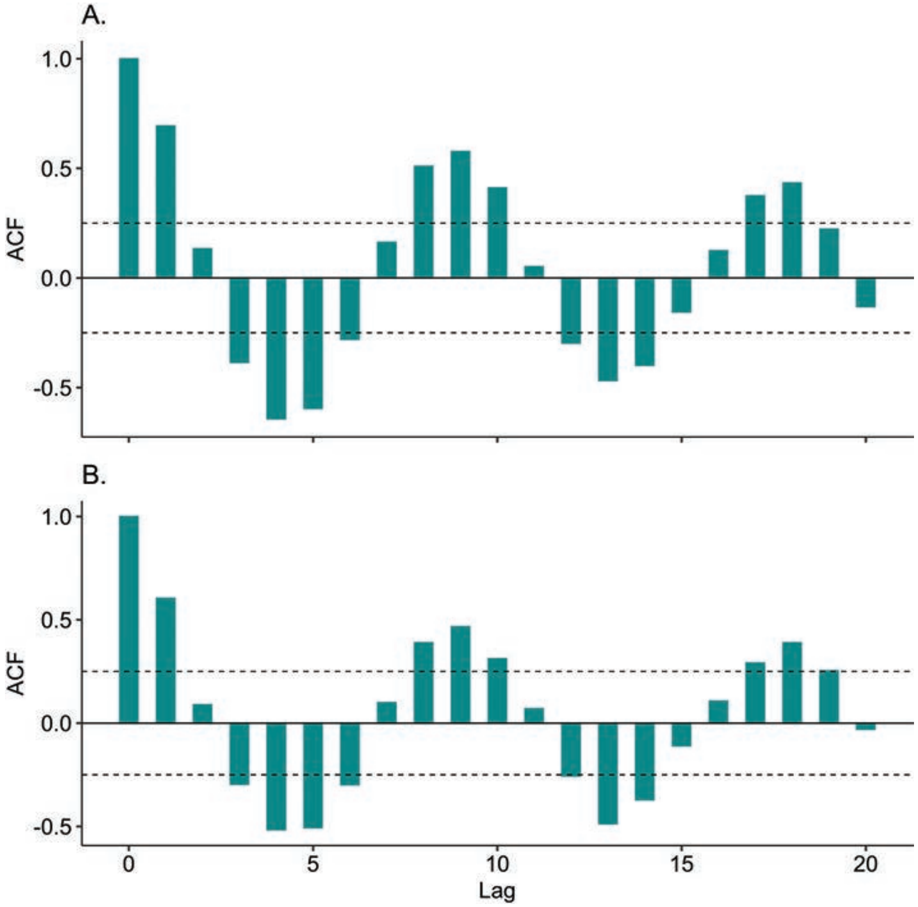


Table 2. Mean, median (50th percentile), standard error (SE), and 95% credible intervals (95% CrI) for the estimates of autoregressive parameters (a_0 is the intercept term; a_k is *k*th-order autoregressive parameter) for snowshoe hares (*Lepus americanus*) in Kluane, Yukon, Canada.

Parameter	Mean	SE	95% CrI
(A) Spring.			
a_0	−0.724	0.648	−2.301, 0.267
a_1	−1.060	0.601	−2.213, 0.153
a_2	−0.308	0.370	−0.908, 0.485
(B) Autumn.			
a_0	−0.259	0.409	−1.248, 0.482
a_1	−0.840	0.738	−2.179, 0.484
a_2	−0.329	0.399	−0.966, 0.517

Note: Results are presented for population density estimated using the spatially explicit capture–recapture model for spring (A) and autumn (B). Note that time interval for autumn to autumn and spring to spring is 1 year, whereas the time interval between seasons is about 6 months.

occurred in our study population and that it was not random. We note, however, that estimated γ'' was nonzero only for cycle 1. Comparing model-averaged estimates of apparent survival based on models that assumed Markovian temporary emigration (Table 1A; Fig. 1) with those that ignored temporary emigration (Table 1C), we find that models that ignored temporary emigration underestimated monthly apparent survival during cycle 1 by about 0.04 (or annual apparent survival by $1 - (1 - 0.4)^{12} = 0.39$); the influence of ignoring temporary emigration on apparent survival estimates for cycles 2–5 were less dramatic with a mean difference in monthly survival of 0.008 (or annual apparent survival of $1 - (1 - 0.008)^{12} = 0.09$). These results are consistent with the expectation that failure to account for temporary emigration would introduce negative bias in estimates of apparent survival (Kendall et al. 1997; J.D. Nichols, personal communication).

Nearly all well-supported Markovian temporary emigration models suggested that γ'' varied across cycles. Model-averaged estimates revealed that γ'' was generally high during cycle 1 ($\gamma'' \approx 0.34$) and close to zero during all other cycles. This pattern in γ'' was consistent with our expectations because the effective sampling area was the smallest during cycle 1 (~9 ha per trapping grid) compared with subsequent cycles (60 ha per trapping grid). The perimeter to area ratio increases as the size of the effective sampling area decreases, increasing the probability that snowshoe hares would have a portion of their home ranges outside the area that was sampled. As the size of the effective sampling area increases, the perimeter to area ratio decreases, reducing the likelihood that sampled hares would have a portion of their home range outside the sampled area, thereby reducing the probability of temporary emigration (Boutin 1984).

In contrast, γ' exhibited a strong seasonal pattern, evidenced by the fact that the most well-supported Markovian temporary emigration models included an effect of season on γ' (Table 1A).

During summer, model-averaged estimates of γ' were very high (~0.999), suggesting that snowshoe hares that were temporarily away from the sampled area were highly unlikely to return during the next primary sampling occasion, because an estimate of the probability of return is given by $1 - \gamma' = 1 - 0.999 \approx 0$. In contrast, estimated γ' during winter was 0.455, suggesting that about 54% of snowshoe hares that were temporarily away from the sampled area would return. Although it was not one of our predictions (because we did not know if the pattern of temporary emigration would be nonrandom), this result would make biological sense if hares move less in winter (but we do not have home-range data for all these cycles), and if hares are less likely to wander off too far away from the sampled area in winter, which, if correct, would increase the probability of returning to the sampled area. As noted above, our inferences regarding γ'' and γ' apply primarily to cycle 1, because $\gamma'' \approx 0$ for cycles 2–5. Our expectation that temporary emigration would be higher during the late increase or peak phase due to increased competition for resources at high densities was not supported by our data.

Apparent survival probabilities were strongly phase- and season-specific, with generally higher survival during the increase and peak phase and the lowest survival during the decline phase. Hares survived substantially better during summer than winter; however, there was substantial variation across cycles in phase-specific and seasonal survival. The pattern of phase-, season-, and cycle-specific apparent survival and capture probabilities was consistent with those reported in earlier studies (Boutin and Krebs 1986; Hodges et al. 2001; Oli et al. 2020).

An important goal of this study was to estimate the size and density of our study population. Estimated population sizes of the sampled area and densities (which exhibited almost identical patterns) were generally precise and followed the expected phase- and season-specific patterns, but also revealed variation across cycles. Autumn sampling occurred after the conclusion of the summer breeding season, whereas spring sampling occurred at the end of winter when hares do not reproduce; hence, autumn densities were always higher than spring densities. As expected, peak phase within a cycle was characterized by higher densities compared with other phases. The amplitude of the snowshoe hare population cycles was remarkably variable, ranging from 18 for cycle 4 to 142 for cycle 3. Likewise, duration of low phase was highly variable (Figs. 3A–3C). We note, however, that estimates of population size, density, and cyclic amplitudes of cycle 1 may not be directly comparable with those of the subsequent cycles. This is because size of the trapping grids (9 ha) was substantially smaller than those for subsequent cycles (60 ha), which could have affected our estimates of population size. However, grid size and other aspects of the sampling protocol remained unchanged for cycles 2–5, so the estimates of abundance and densities should be directly comparable for all cycles except for cycle 1.

Although the robust design CMR model provides rigorous estimates of abundance and other demographic parameters, estimates of density obtained by dividing abundance estimates by the area of trapping grids should be viewed as naïve density estimates. This is because effective trapping area is difficult to objectively estimate (Williams et al. 2002; Efford 2004). In our study, the naïve estimates of hare population density were generally higher than those estimated by the SECR method. These differences arise primarily because the SECR models use information on the location of capture and explicitly estimate population densities, whereas the naïve estimates do not. Another factor that may have contributed to the observed differences include the fact that, for SECR analyses, we used data from two grids (Sulphur and Silver) that were trapped throughout our study. On the other hand, the robust design CMR analyses used data from all control (unmanipulated) grids because we were also interested in estimating and modelling other demographic parameters such as the probability of survival and temporary emigration; the size and the number of grids trapped varied over time. The result that SECR-based density estimates where generally lower than the naïve estimates suggests that the area of the trapping grids generally underestimates effective trapping area, leading to an overestimation of hare population density. Despite these differences, the estimates of hare density obtained from the two methods exhibit a near-identical pattern of population fluctuations (Figs. 3B and 3C) and autocorrelation functions (Figs. 4A and 4B).

Population regulation — the study of why populations fluctuate the way they do — is frequently guided by the "density paradigm" of population ecology (Krebs 2002*a*, 2002*b*), which posits that density-dependent feedback mechanisms that permit populations to grow at faster rates at low densities (and at slower rates when densities are high) are necessary and often sufficient for preventing unlimited population growth (Royama 1992; Turchin 1999, 2003). It has been suggested that population regulation necessarily implies density dependence and that unregulated populations cannot persist (Royama 1992). The structure of density dependence, possibly arising from direct or lagged effect of predation (Krebs et al. 1995), determines the pattern of population fluctuations; direct (or first-order) density dependence typically leads to stable equilibrium with the population size ultimately converging to some equilibrium values (but see May 1974), whereas delayed (or second-order) density dependence can generate a variety of dynamical patterns, including cyclic and chaotic fluctuations, depending on the strength of direct and delayed density dependence (Royama 1992; Turchin 2003). Ecologically, the first-order autoregressive parameter quantifies the strength of direct density dependence, whereas the second-order autoregressive parameter quantifies the strength of delayed density dependence (Royama 1992; Oli 2019). Population cycles, often considered to be the foundational problem in animal ecology (reviewed in Stenseth 1999; Lambin et al. 2002; Krebs et al. 2018; Myers 2018; Oli 2019), can be viewed as a special case of population regulation, where direct and delayed density dependence interact to cause a variety of dynamical behaviors including cyclic fluctuations (Royama 1992; Oli 2019). Thus, we applied this analytical framework to understand structure and pattern of density dependence in the fluctuations of our study population in our study area.

Autocorrelation functions (Figs. 4A and 4B) clearly revealed cyclic population dynamics with a periodicity of ~9- to 10-year density cycles, as indicated by the highest positive autocorrelation at lags of 9–10 years. These results held regardless of whether spring to spring or autumn to autumn data were used in the analyses. Likewise, autoregressive parameters (Tables 2A and 2B) also were broadly consistent with persistent or convergent population cycles with a periodicity of ~9–10 years, based on the parameter plane scheme proposed by Royama (1992; figs. 2.9–2.12). Our study is the first to report autocorrelation functions and autoregressive parameters for a snowshoe hare population using actual estimates of population density across five cycles and a Bayesian state-space model that appropriately accounts for both sampling and process variances (Viljugrein et al. 2005; Rotella et al. 2009; Ahrestani et al. 2013). Finally, we note that the mechanisms driving cyclic fluctuations in our study population remain to be completely ascertained. Field experiments suggest that predators, primarily through direct predation and possibly through maternally inherited stress, are likely to be important drivers of snowshoe hare population cycles (Krebs et al. 1995, 2018; Boonstra et al. 1998; Sheriff et al. 2010), although the possibility of three trophic (vegetation – snowshoe hares – predators) interactions cannot be conclusively ruled out at this time (Stenseth et al. 1997).

Competing interests statement

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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