Demography of snowshoe hare population cycles

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Abstract. Cyclic fluctuations in abundance exhibited by some mammalian populations in northern habitats ("population cycles") are key processes in the functioning of many boreal and tundra ecosystems. Understanding population cycles, essentially demographic processes, necessitates discerning the demographic mechanisms that underlie numerical changes. Using mark–recapture data spanning five population cycles (1977–2017), we examined demographic mechanisms underlying the 9–10-yr cycles exhibited by snowshoe hares (*Lepus americanus* Erxleben) in southwestern Yukon, Canada. Snowshoe hare populations always decreased during winter and increased during summer; the balance between winter declines and summer increases characterized the four, multiyear cyclic phases: increase, peak, decline, and low. Little or no recruitment occurred during winter, but summer recruitment varied markedly across the four phases with the highest and lowest recruitment observed during the increase and decline phase, respectively. Population crashes during the decline were triggered by a substantial decline in winter survival and by a lack of subsequent summer recruitment. In contrast, initiation of the increase phase was triggered by a twofold increase in summer recruitment abetted secondarily by improvements in subsequent winter survival. We show that differences in peak density across cycles are explained by differences in overall population growth rate, amount of time available for population growth to occur, and starting population density. Demographic mechanisms underlying snowshoe hare population cycles were consistent across cycles in our study site but we do not yet know if similar demographic processes underlie population cycles in other northern snowshoe hare populations.

Key words: boreal ecosystem; capture–mark–recapture analysis; Lepus americanus; *population growth rate; Pradel model; recruitment; snowshoe hare cycles; survival; wildlife's 10-yr cycle.*

Introduction

Cyclic fluctuations in abundance exhibited by some terrestrial mammals in northern latitudes, commonly called "population cycles," are considered to be one of nature's greatest mysteries (Keith 1962, Stenseth 1999, Myers 2018, Oli 2019). Cyclic mammals often are the most important herbivores in terms of biomass and impact across trophic levels, and their cyclic population dynamics are thought to be key processes in the structure and function of ecosystems where they occur (Krebs et al. 2001*a*, Ims and Fuglei 2005, Schmidt et al. 2012). In many North American boreal forests, snowshoe hares are the most important component of the food chain (Krebs et al. 2001*a*). Their population cycles are considered to be one of the most distinctive features of the ecology of the North American boreal forests, with

cyclic fluctuations in hare abundance influencing many ecological processes across trophic levels (Krebs et al. 2001*a*, Krebs et al. 2018).

The spectacular 10-yr cycles exhibited by snowshoe hares and their predators across the boreal forests of North America have fascinated generations of ecologists. Elton (1924) noted that "...every ten years the numbers of the rabbits increase to a maximum" and then "...the entire population is killed off by an epidemic disease" (Elton 1924:135–136). Green et al. (1939) subsequently proposed that "shock disease" was the cause of this mortality, and consequently, the population crash. Elton himself considered that the cyclic variation in reproductive capacity of snowshoe hare was the result of changes in climatic conditions affecting the food supply. However, he admitted a poor understanding of the physiology of hare reproduction. Elton's insightful analyses of snowshoe hare population cycles inspired many theoretical and experimental studies aimed at understanding causes and consequences of the cyclic fluctuations in hare abundance, notably by the research groups headed by Lloyd B. Keith (Keith 1962, Meslow and Keith 1968,

Cary and Keith 1978, Vaughan and Keith 1981, Keith 1990, Murray et al. 1997, Murray et al. 1998) and by Charles J. Krebs (Krebs et al. 1986, Sinclair et al. 1988, Smith et al. 1988, O'Donoghue and Krebs 1992a, Krebs et al. 1995, O'Donoghue et al. 1998, Boonstra et al. 1998a, Hodges et al. 1999, Krebs et al. 2001a, Sheriff et al. 2011, Krebs et al. 2018). Snowshoe hare population cycles have been a major contributor to our understanding of population regulatory mechanisms in vertebrates and feature prominently in most ecology textbooks (Ricklefs and Miller 2000, Krebs 2001).

The most notable feature of these cycles is the changes in abundance, with highly variable cyclic amplitudes (Hodges 2000, Hodges et al. 2001, Kielland et al. 2010). Cyclic changes in abundance are accompanied (or preceded) by phase-specific demographic changes, with the increase phase generally characterized by high survival and reproductive output, and the decline phase being associated with low survival and reproductive output (Cary and Keith 1978, Keith and Windberg 1978, Krebs et al. 1986, Krebs et al. 1995, Krebs et al. 2014). Although these broad demographic patterns are assumed to be consistent across hare populations and cycles (Keith and Windberg 1978, Hodges 2000, Hodges et al. 2001, Krebs et al. 2001a), rigorous empirical characterizations of demographic structure in cycling hare populations grounded in observational or experimental data are currently lacking (Barraquand et al. 2017).

Experimental and observational studies suggest that snowshoe hare population cycles are driven by one or more of the following factors: (1) direct mortality caused by their predators (Krebs et al. 1995, Krebs et al. 2018); (2) indirect, sublethal effects of predators mediated via predator-induced stress response (Boonstra et al. 1998a, Sheriff et al. 2009, 2011, Sheriff et al. 2017); and (3) winter food shortages (Cary and Keith 1978, Keith and Windberg 1978). Each of these potential causal mechanisms is predicted to impact demographic rates. The direct predation hypothesis predicts that a drastic reduction in survival due to direct predation leads to population crashes, and that reversal of these patterns would allow the hare population to increase. Thus, we predicted that the survival rate would exhibit strong phase-specific patterns, with the increase and decline phase of the cycles being characterized by the highest and the lowest survival, respectively. The winter food shortage hypothesis, on the other hand, predicts that population crashes are caused by reproductive failures following the peak phase; recovery of quantity and quality of winter food leading to improved reproductive functions would allow the hare population to stabilize. Under this hypothesis, we expected recruitment rate to exhibit a strongly phase-specific pattern, with the increase and decline phases being characterized by the highest and lowest recruitment, respectively. The indirect predation hypothesis predictions would be similar to those of the winter food shortage hypothesis, but acting more heavily during the decline and low phase because this hypothesis

postulates that population crashes are caused both by increased vulnerability to predation and to reproductive collapse due to predator-induced stress (Boonstra et al. 1998a, Sheriff et al. 2009, 2011, Sheriff et al. 2017). The indirect predation hypothesis also explains the low phase, arguing that predator-induced maternal stress would have intergenerational effects, delaying an immediate recovery after the decline phase (Boonstra et al. 1998b, Sheriff et al. 2010). Finally, the predation impact may be exacerbated by food shortages, with a greater impact of predation on survival when winter food supply is reduced (Krebs et al. 1995, Krebs et al. 2018), which would lead to the prediction that survival would be particularly low during the winter of the decline phase.

Using long-term field data spanning 40 yr (1977–2017) and temporal symmetry capture–mark–recapture (CMR) modeling framework (Pradel 1996, Nichols 2016), our goal was to discern demographic drivers of snowshoe hare population cycles in a boreal forest in southwestern Yukon, Canada. Specifically, we asked the following questions. First, what demographic changes cause an increasing population to stop growing and then to decline, and a declining population to stop declining and then to grow? Second, what demographic changes trigger the rapid population growth rate during the increase phase and the low population growth rate during the decline phase? Third, are the demographic mechanisms underlying changes in abundance consistent across cycles? Finally, what causes the variation in peak densities from one cycle to the next?

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). Average lifespan is about 1 yr, but they can live up to 7 yr (Keith and Windberg 1978, Boutin et al. 1986, Hodges et al. 2001, Krebs et al. 2018). At Kluane, ≥90% of hares die because they are killed by predators (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 1978, O'Donoghue and Krebs 1992a). Mean litter size varies between 3.2 and 6.9 leverets, depending on litter order and cyclic phase (Cary and Keith 1978, Hodges et al. 2001). Juveniles of both sexes disperse predominantly between 30 and 60 d of age; leverets typically disperse by September (Gillis and Krebs 1999, Hodges et al. 2001). Reproductive parameters typically show cyclic variation (Cary and Keith 1978, O'Donoghue and Krebs 1992a, Hodges et al. 2001), but there is no evidence that dispersal is phase-specific (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*) and willow (*Salix glauca*; 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*), with small areas of balsam poplar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*). 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*b*).

We captured snowshoe hares using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) located on 10 × 10 or 20 × 20 grids with 30-m spacing between traps (for details see Appendix S1: Table S1). Field methods are described in detail elsewhere (Krebs et al. 1986, Hodges et al. 2001, Hodges et al. 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 Fall 1977 and continued until Fall 2017. We considered two ~2.5-month capture occasions each year, Fall (hares captured during 1 September–15 November) and Spring (1 March–15 May). Multiple captures for a hare within one season, when they occurred, were considered to be a single encounter for that sampling occasion. All of our data came from unmanipulated (control) grids; no data from experimental grids were used (details in Krebs et al. 1995, 2001*b*, 2018). Finally, we excluded hares with unknown sex (*n* = 45 hares) from the present analyses. Grid size, trapping dates, and the number of hares captured in each grid are presented in Supporting Information (Appendix S1: Table S1).

Capture–mark–recapture analysis

Capture–mark–recapture analysis (CMR) has long been used to estimate various population parameters such as survival and recruitment rates from individually marked animals (Cormack 1964, Jolly 1965, Seber 1965). Recent developments in CMR models (Pollock et al. 1990, Lebreton et al. 1992, Nichols et al. 1992, Williams et al. 2002, Lebreton et al. 2009) have revolutionized the study of animal populations because they allow estimation and modeling of many important demographic quantities, including abundance, survival, recruitment, and population growth rates. Our primary goal in this study was to characterize phase-specific demography and to assess the relative contribution of survival and recruitment to population growth rate, so we focused on Pradel's temporal symmetry model (Pradel 1996, Nichols 2016). This approach permits estimation and modeling of the realized population growth rate and its constituents, survival and recruitment rates. The Pradel CMR modeling approach combines forward

time (i.e., starting with the first capture and ending with last capture) and reverse time (i.e., starting with the last capture and ending with the first capture) modeling of capture histories to estimate capture probabilities (p_t), apparent survival (ϕ_t), and seniority (γ_t). The latter two parameters are related to the realized population growth rate (λ_t) as follows (Pradel 1996, Nichols and Hines 2002, Nichols 2016):

$$E(\lambda_t) = \frac{\phi_t}{\gamma_{t+1}} \tag{1}$$

where E indicates expected value, and the subscript t indicates time. For clarity, p_t is the probability that a marked animal alive and in the sampled population is captured at time t; ϕ_t is the probability that an animal alive at time t survives to time $t + 1$ and remains in the population; γ_t is the probability that a marked animal that was in the population at time t also was alive and in the sampled population at $t − 1$ or earlier. Because an animal captured at time t must either be a previously marked animal that survived from time $t − 1$ to t, or a new recruit that was not in the population of marked animals at $t − 1$, λ_t can be written as the sum of survival and recruitment rates:

$$\lambda_t = \phi_t + f_t. \tag{2}$$

Rearranging, Eq. 2 yields

$$f_t = \lambda_t − \phi_t, \tag{3}$$

where f_t is the per capita recruitment rate, defined as the number of new recruits at time $t + 1$ per individual at time t. Equations 1–3 imply that the Pradel model can be reparameterized to permit direct estimation and modeling of the realized population growth rate λ_t, and its demographic determinants, ϕ_t and f_t.

Because we were interested in the relative contributions of survival and recruitment to population growth rate, we focused on the ϕ–f parameterization of the Pradel model. We used ϕ–λ parameterization of the Pradel model to obtain direct estimates of λ. Although hares were trapped every month in some years, the trapping schedule varied over time (Krebs et al. 1986, Hodges et al. 2001). Trapping data outside of Fall and Spring trapping sessions (see Study species, study area, and field methods) were not used. Henceforth, survival (or recruitment) from Fall to Spring sampling occasions is referred to as Winter survival (or recruitment); survival (or recruitment) from Spring to Fall sampling occasions is referred to as summer survival (or recruitment).

We used a sequential approach to CMR model fitting. First, we allowed *p* to be affected by phase of the cycle (increase, peak, decline, or low), season (Fall or Spring), and cycle number (cycle that peaked in 1980 = cycle 1 and the recent cycle that peaked in 2017 = cycle 5; Appendix S1: Fig. S1), and their singular, additive, and

two-way interactive effects. Second, we allowed all parameters (p, ϕ, and f) to be affected by singular, additive, and two-way interactive effects of phase of the cycle, season, and cycle number. The goal of the second analysis was to identify the model structure that best described our data. A secondary goal of our study was to answer the following question: which demographic change(s) stops population growth and then causes it to decline (and vice versa)? We addressed this question by examining if transition from one phase to another was accompanied by substantial change in one or both vital rates. We created a new temporal covariate such that the last phase of one cycle before the next phase begins to be a "transition" phase; this new variable (*trans_phase*) would have the same value as the cyclic phase except when the phase transition occurs (i.e., transitions from increase to peak, peak to decline, decline to low, and low to increase phase). We then allowed ϕ and f to be affected by the singular effect of *trans_phase*, and as well as additive or two-way interactive effects with season or cycle numbers as described previously. Our data were not sufficient to support fully time-dependent models or those involving three-way interactive effects of the aforementioned variables.

Following Keith (1990), we defined cyclic phases based on the finite rate of annual change (Spring to Spring) in snowshoe hare density (Δd). Specifically, decline and increase phases were characterized by $\Delta d < 0.44$, and $\Delta d > 1.89$, respectively. All years between the decline and increase phases were defined as the low phase, and years between increase and the next decline were defined as the peak phase (Keith 1990, Sheriff et al. 2015). Snowshoe hare densities were estimated using program DENSITY 5, which implements the spatial capture–mark–recapture model (Efford 2009). We trapped snowshoe hares on seven grids (Appendix S1: Table S1), 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 (Appendix S1: Table S1). To account for missing data, we fixed $p = 0$ 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. In all analyses, we specified the time intervals between successive samples in months (average interval between Fall to Spring sampling occasions was seven months, and between spring to fall sampling occasions was five months); thus, all estimated parameters are monthly rates or probabilities.

In CMR analyses, ϕ represents apparent (rather than true) survival in the sense that losses include both death and permanent emigration, and f represents gains from both birth and immigration. Thus, if the size of the study area changes during the course of a study, it could potentially affect estimates of ϕ, f, and, thus, λ (Hines and Nichols 2002, Williams et al. 2002). During the early part of our study (1977–1985), trapping occurred on 10×10 square grids with 30-m spacing (i.e., 300×300 m trapping grids) using 50 traps located in alternate positions. Some of these grids were discontinued after Spring 1985. Starting in Fall 1985, we trapped snowshoe hares using 86 traps spaced over 20×20 grids (600×600 m trapping grids). Details regarding the trapping protocol are provided in Appendix S1: Table S1; for trapping design details, see Fig. 4.3 in Krebs et al. 2001*b*:59). Thus, we also tested for the effect of grid size on ϕ and f. Increase in grid size would reduce the area-to-perimeter ratio, which would reduce the probability of permanent emigration but increase the probability of immigration. Thus, we expected grid size to affect apparent survival positively, and to affect recruitment negatively.

We implemented the Pradel model using program MARK (White and Burnham 1999) Version 6.2 implemented in the RMark package (Laake 2013) for program R, Version 2.2.0 (R Core Team 2014). 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 (Williams et al. 2002, Burnham and Anderson 2002). The effect of aforementioned covariates was determined by comparing AIC_c among models with and without covariates. Models with difference in AIC_c (ΔAIC_c) ≤ 2 were considered to be equally plausible.

Life table response experiment analysis

The contribution of a demographic variable θ to population growth rate λ depends on the sensitivity of λ to changes in θ, and the amount of observed change in θ. This contribution can be decomposed using the life table response experiment (LTRE) analysis (Caswell 1989, 2001, Dobson and Oli 2001, Oli and Armitage 2004). Specifically, the observed change in population growth rate ($\Delta \lambda$) can be decomposed as

$$\Delta \lambda \approx \sum_i \Delta \theta_i \frac{\partial \lambda}{\partial \theta_i} \qquad (4)$$

where $\Delta \theta_i$ is the observed difference (or change) in ith parameter θ_i (f or ϕ) and $\partial \lambda / \partial \theta_i$ is the sensitivity or partial derivative of λ with respect to θ_i; the sum is calculated over all vital demographic parameters that contribute to λ. In our case, λ is simply the sum of ϕ and f (Eq. 2). Differentiating λ with respect of ϕ and f, we find that $\partial \lambda / \partial f = \partial \lambda / \partial \phi = 1$. Consequently, Eq. 4 reduces to

$$\Delta \lambda = \Delta \phi + \Delta f. \qquad (5)$$

Using this approach, we decomposed phase-specific differences in λ within each season, and seasonal differences in λ within each phase.

<div style="text-align:center">R<small>ESULTS</small></div>

Excluding hares captured outside of the Fall and Spring capture seasons, we captured 5,296 unique hares 10,459 times (5,085 captures of 2,664 females and 5,374 captures of 2,632 males). Mean body mass at first capture ($\pm$SE) was 1,274.99 $\pm$ 3.51 g (range: 310–2,180 g). The number of hares captured per sampling occasion ranged from 2 in Spring 2002 to 555 in Fall 1980. More snowshoe hares were captured during Fall than Spring, and during the increase or peak phase of population cycles than during the decline or low phase. More hares were captured on Sulphur (2,886 captures) than on other trapping grids (Appendix S1: Table S1).

Phase-specific, cycle-specific, and seasonal demographic patterns

Virtually all well-supported single covariate CMR models included the effect of cyclic phase on ϕ and season on f, suggesting that survival varies most strongly across cyclic phases, whereas recruitment shows strong seasonal variation (Table 1A). Based on this model, ϕ was highest during the increase phase and lowest during the decline phase (overall estimate $\pm$1 SE per month: increase: 0.911 $\pm$ 0.003; peak: 0.870 $\pm$ 0.003; decline: 0.803 $\pm$ 0.003; low: 0.884 $\pm$ 0.004), and f per month was substantially higher during summer (0.280 $\pm$ 0.007) than winter (0.042 $\pm$ 0.003).

Next, we fitted a series of two-variable models to test simultaneously for the effects of the cyclic phase, cycle number, and season on ϕ and f. The most parsimonious model suggested that the phase-specific ϕ varied across cycles (Table 1B), with cycle 1 generally characterized by high survival rates and cycle 3 characterized by low ones; ϕ for the low phase of cycle 3 (0.730 $\pm$ 0.033) was the lowest across all phases and cycles (Fig. 1A). On the other hand, seasonal f also varied across cyclic phases. Summer recruitment was the lowest during the decline phase (0.204 $\pm$ 0.009) and the highest during the increase (0.350 $\pm$ 0.010) and low phases (0.358 $\pm$ 0.023). Winter recruitment was low ($f < 0.1$) across all phases; there was virtually no overwinter recruitment during the low phase (Fig. 1B). Based on a model that allowed demographic parameters to vary simultaneously across phases and seasons, ϕ was higher during summer than winter; it was the lowest during the decline phase and highest for increase and low phases. Winter recruitment was low across all phases, but summer recruitment was the highest during the increase and lowest during the decline and low phases (Fig. 2).

Last, we tested simultaneously for the effects of all covariates to discern phase-, season- and cycle-specific patterns in ϕ and f. The most parsimonious three-variable model included additive effects of all covariates and interactive effect of phase and cycle number on ϕ, and an additive effect of all covariates and an interactive effect of phase and season on f (Table 1C).

This model revealed that (1) winter survival was lower and more variable across cycles and phases than summer survival; (2) summer recruitment was more variable across cycles and phases than winter recruitment; the latter was close to zero across all phases and cycles; and (3) the decline phase was characterized by low winter survival and summer recruitment, and this pattern was consistent across all phases and cycles (Fig. 3A–D). A competing model (model 2, Table 1C) differed only in model structure for p and yielded similar results.

As expected, the realized population growth rate also exhibited strongly phase-specific patterns, with the highest and lowest growth rate observed during the increase and decline phase, respectively (monthly $\lambda \pm$ SE for increase phase: 1.041 $\pm$ 0.002; peak phase: 1.009 $\pm$ 0.002; decline phase: 0.928 $\pm$ 0.002; and low phase: 1.038 $\pm$ 0.003). Considered seasonally, the hare population always increased during summer and always declined during winter (monthly summer λ: 1.182 $\pm$ 0.006; winter λ: 0.887 $\pm$ 0.003). The rate of population decline was the highest (19% per month) during the winter of the decline phase; the rate of increase was the highest during the summer of the increase phase (39% per month). The season- and phase-specific pattern in λ was generally consistent across cycles (Fig. 4).

The parsimony of the top single covariate model did not substantially improve when grid size was allowed to affect ϕ and f additively (ΔAIC_c = 0.459). This model revealed that grid size positively influenced ϕ (regression coefficient for 20 $\times$ 20 grids: β = 0.016 $\pm$ 0.039; 95% CI = −0.061 to 0.092) but negatively influenced f (regression coefficient for 20 $\times$ 20 grids: β = −0.046 $\pm$ 0.035; 95% CI = −0.114 to 0.023). Although these results are consistent with our predictions that increase in grid size would increase ϕ and reduce f, the fact that confidence intervals for both βs straddled zero suggests that the grid size effect on these parameters were insubstantial. Grid size-specific estimates of ϕ and f are presented in Supporting Information (Appendix S1: Table S2).

The overall monthly capture probability, estimated using the constant parameter model, was 0.592 $\pm$ 0.013, but it varied substantially depending on phase, season, and cycle number. Capture probability was generally high during Spring when the population was in increase or peak phase; it was the lowest during Fall when the population was in low phase (Appendix S1: Table S3).

Life table response experiment analysis

We applied LTRE analysis to decompose phase-specific differences in λ within each season, and seasonal differences in λ within each phase. During winter, λ declined as the hare population transitioned from increase to peak phases, and from peak to decline phases. Nearly all the phase-specific changes in λ were due to changes in apparent survival, with a negligible

TABLE 1. Model comparison statistics testing for the effect on capture probability (*p*), apparent survival (ϕ), and recruitment rate (*f*) of: (A) singular effect of each covariate; (B) additive and interactive effects of two covariates; (C) additive and interactive effects of three covariates; (D–E) same as A–B except that the covariate phase was replaced by covariate trans_phase; and (F) comprehensive model selection table that includes all one-, two- and three-variable models.

Model no.	Model	K	AIC_c	ΔAIC_c	Weight
A					
1	ϕ (phase)*p*(phase*cycle_num + season)*f*(season)	26	45,744.274	0.000	1.000
2	ϕ (phase)*p*(phase*cycle_num)*f*(season)	25	45,853.438	109.163	0.000
3	ϕ (phase)*p*(phase*season + cycle_num)*f*(season)	18	45,858.117	113.842	0.000
4	ϕ (phase)*p*(phase + season + cycle_num)*f*(season)	15	45,943.666	199.392	0.000
5	ϕ (phase)*p*(phase*season)*f*(season)	14	45,990.589	246.315	0.000
B					
1	ϕ (phase*cycle_num)*p*(phase + season + cycle_num)*f*(phase*season)	36	45,005.299	0.000	0.867
2	ϕ (phase*cycle_num)*p*(phase*season + cycle_num)*f*(phase + season)	36	45,009.348	4.049	0.115
3	ϕ (phase*cycle_num)*p*(phase*season)*f*(phase + season)	32	45,013.027	7.728	0.018
4	ϕ (phase*cycle_num)*p*(phase*cycle_num + season)*f*(phase + season)	44	45,067.639	62.340	0.000
5	ϕ (phase*cycle_num)*p*(phase + season + cycle_num)*f*(phase + season)	33	45,088.589	83.290	0.000
C					
1	ϕ (phase*cycle_num + season)*p*(phase*season + cycle_num)*f (phase*cycle_num + season)	52	44,823.909	0.000	0.706
2	ϕ (phase*cycle_num + season)*p*(phase*season)*f*(phase*cycle_num + season)	48	44,825.664	1.755	0.294
3	ϕ (phase*cycle_num + season)*p*(phase*season + cycle_num)*f (cycle_num*season + phase)	45	44,851.798	27.889	0.000
4	ϕ (phase*cycle_num + season)*p*(phase*cycle_num + season)*f (phase*cycle_num + season)	60	44,861.929	38.020	0.000
5	ϕ (phase*cycle_num + season)*p*(phase*season)*f*(cycle_num*season + phase)	41	44,867.914	44.005	0.000
D					
1	ϕ (trans_phase)*p*(phase*cycle_num + season)*f*(season)	32	45,398.921	0.000	1.000
2	ϕ (trans_phase)*p*(phase*season + cycle_num)*f*(season)	24	45,426.276	27.355	0.000
3	ϕ (trans_phase)*p*(phase*season)*f*(season)	20	45,435.589	36.668	0.000
4	ϕ (trans_phase)*p*(phase*cycle_num)*f*(season)	31	45,477.544	78.622	0.000
5	ϕ (trans_phase)*p*(phase + season + cycle_num)*f*(season)	21	45,527.299	128.378	0.000
E					
1	ϕ (trans_phase + cycle_num)*p*(phase*season + cycle_num)*f (trans_phase + season)	37	44,982.494	0.000	0.999
2	ϕ (trans_phase + cycle_num)*p*(phase*season)*f*(trans_phase + season)	33	44,996.946	14.452	0.001
3	ϕ (trans_phase + cycle_num)*p*(phase*cycle_num + season)*f (trans_phase + season)	45	44,999.207	16.713	0.000
4	ϕ (trans_phase + cycle_num)*p*(phase + season + cycle_num)*f (trans_phase + season)	34	45,012.565	30.071	0.000
5	ϕ (trans_phase + cycle_num)*p*(phase + season)*f*(trans_phase + season)	30	45,029.233	46.740	0.000
F					
1	ϕ (phase*cycle_num + season)*p*(phase*season + cycle_num)*f (trans_phase*cycle_num + season)	75	44,662.976	0.000	1.000
2	ϕ (trans_phase*cycle_num + season)*p*(phase*season + cycle_num)*f (cycle_num*season + trans_phase)	51	44,714.273	51.297	0.000
3	ϕ (trans_phase*cycle_num + season)*p*(phase*season)*f (trans_phase + cycle_num+season)	69	44,731.841	68.865	0.000
4	ϕ (trans_phase*cycle_num + season)*p*(phase*cycle_num + season)*f (phase*cycle_num + season)	80	44,742.982	80.006	0.000
5	ϕ (phase + cycle_num+season)*p*(phase*season)*f (trans_phase*cycle_num + season)	81	44,744.416	81.440	0.000

Notes: The covariates phase and trans_phase were not used in the same model because they are identical except when the phase transitions occur. Covariates are: phase = phase of the cycle (increase, peak, decline, low); cycle_num = cycle number (cycle peaking in 1980–1981: cycle number 1; current cycle peaking in 2016–2017: cycle number 5), season: season corresponding to capture occasion (Fall or Spring), and trans_phase = same as the cyclic phase, but this covariate also includes a transitional phase when the population transitions from one phase of the cycle to the next.

influence of recruitment (Fig. 5); this occurred in part because winter recruitment was low and showed little variation across phases (Fig. 1B). During summer, λ always declined when the population transitioned from increase to peak phase and peak to decline phase. In contrast, it was always associated with substantial
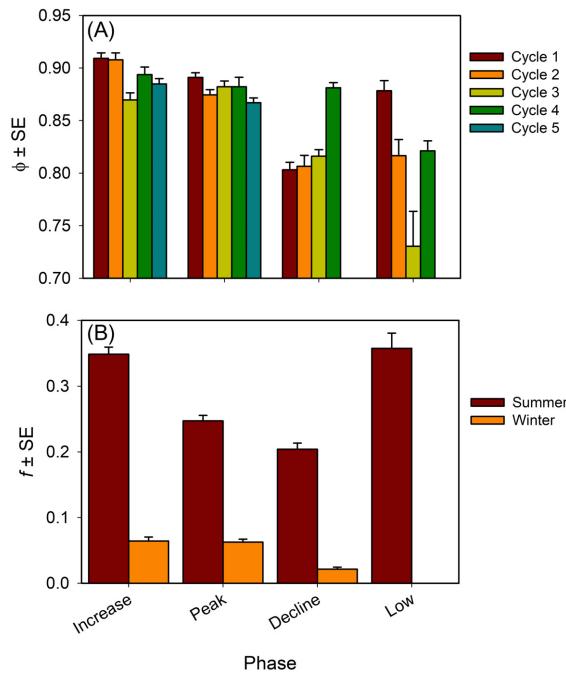
FIG. 1. Phase- and cycle-specific estimates (±standard error [SE]) of monthly apparent survival, ϕ (A), and phase- and season-specific estimates of monthly recruitment rate, f (B) for snowshoe hares in Kluane, Yukon, Canada from Fall 1977 to Fall 2017. These estimates were obtained using the most parsimonious two-variable Pradel's capture–mark–recapture model (model 1, Table 1B).

increases in λ when the population transitioned from decline to low and from low to increase phase. Phase-specific changes in λ during summer were generally larger than those in winter. Changes in recruitment made larger contributions to phase-specific differences in λ during summer. In contrast, changes in survival were the primary demographic determinants of phase-specific differences in λ during winter (Fig. 5). Seasonal patterns of the relative contribution of recruitment and survival to $\Delta\lambda$ were broadly consistent across cycles.

Because the hare population always declined during winter and always increased during summer regardless of cyclic phase, within-phase, seasonal differences in λ were substantial, ranging from 0.23 to 0.54. Changes in f made larger contributions to the seasonal differences in λ across all phases and cycles, with seasonal variation in ϕ playing only a secondary role.

Phase transitions

To discern demographic changes that triggered transitions from one cyclic phase to the next, we repeated the analyses testing for the singular, additive, and interactive effects of phase, season, and cycle number described in Phase-specific, cycle-specific, and seasonal demographic patterns, except that we used the covariate *trans_phase* (instead of phase), which allowed demographic
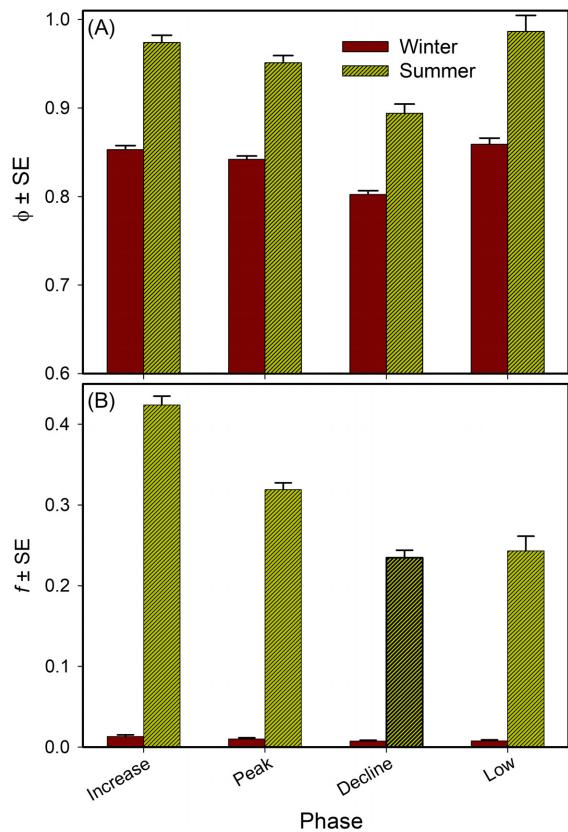

FIG. 2. Phase- and season-specific estimates (±standard error [SE]) of monthly apparent survival (ϕ; A) recruitment rate (f; B) for snowshoe hares in Kluane, Yukon, Canada during Fall 1977–Fall 2017. These estimates were obtained using the most parsimonious Pradel's capture–mark–recapture model that allowed ϕ and f to be affected by phase and season. The model structure was ϕ(phase * season)p(phase * cycle_num + season)f(phase + season).

parameters to be different when a population transitioned from one phase to the next during a cycle. The most parsimonious model testing for the singular covariate effects (Table 1D) yielded season-specific estimates of f and phase-specific estimates of ϕ described previously, but also provided additional information regarding the phase transitions (Appendix S1: Table S4): (1) the end of the increase phase was characterized by substantial reduction in survival; this parameter declined further as the population transitioned from decline to low phase; and (2) the transition from low to increase phase was characterized by the highest survival (0.980 ± 0.007).

The most parsimonious two-variable phase transition model included an additive effect of *trans_phase* and cycle number on ϕ and *trans_phase* and season on f (Table 1E, model 1). This model suggested three things. First, that the aforementioned *trans_phase*–specific pattern in ϕ was generally consistent across cycles, but also revealed that there was substantial variation across cycles. The transition from decline to low phase
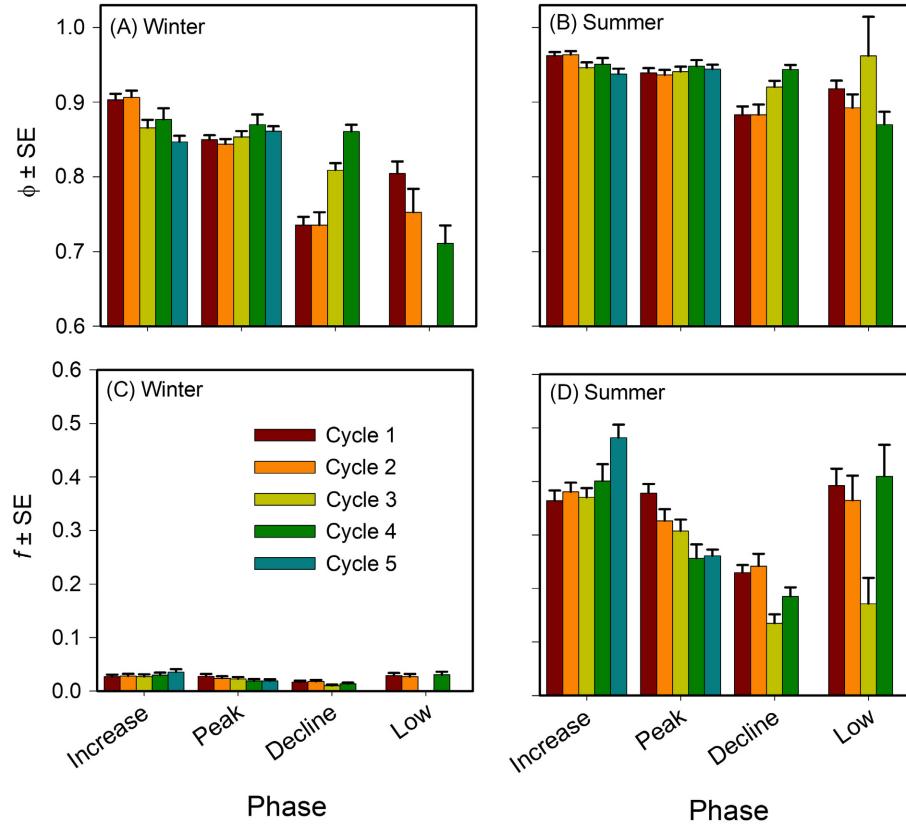
FIG. 3. Phase- and cycle-specific estimates (±standard error [SE]) of monthly apparent survival (φ) during winter (A) and summer (B); and phase- and cycle-specific estimates of monthly recruitment rate (*f*) during winter (C) and summer (D) for snowshoe hares in Kluane, Yukon, Canada from Fall 1977 to Fall 2017. These estimates were obtained using the most parsimonious three-variable Pradel's capture–mark–recapture model (model 1, Table 1C).
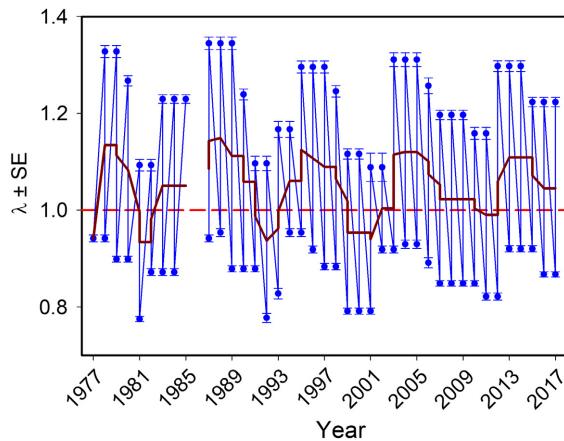

FIG. 4. Estimates of monthly realized population growth rate (λ ± standard error [SE]) for snowshoe hares in Kluane, Yukon, Canada for each sampling interval from Fall 1977 to Fall 2017. Dark red lines represent moving average of monthly λ across two seasons. The realized population growth rate was estimated using the most parsimonious three-variable Pradel's capture–mark–recapture model (φ–λ parameterization). Trapping did not occur during Fall 1985 and Spring 1986.

(Fig. 6A) was characterized by low survival across all cycles, with the lowest survival observed in cycle 3. Second, the transition from decline to low phase (Fig. 6B) also was characterized by the lowest summer recruitment (*f* = 0.246 ± 0.016), whereas that from low to increase phase (*trans_phase* = *l*; Fig. 6B) was characterized by the highest summer recruitment (*f* = 0.495 ± 0.033). Third, winter recruitment was low across all phases, and phase transitions (Fig. 6B).

Generally, models that included the covariate *trans_phase* were better supported than comparable models that included phase as a covariate (Table 1). Analyses that considered all covariates simultaneously revealed that a model with φ (phase*cycle_num + season) and *f* (trans_phase*cycle_num + season) was substantially better supported than any other model in the set, suggesting that phase transitions are more strongly predicted by changes in *f*. However, *trans_phase* appeared as a covariate for φ, *f*, or both in all well-supported models in the set (Table 1F). Parameter estimates based on the best overall model (Appendix S1: Table S5) were generally consistent with aforementioned pattern in φ
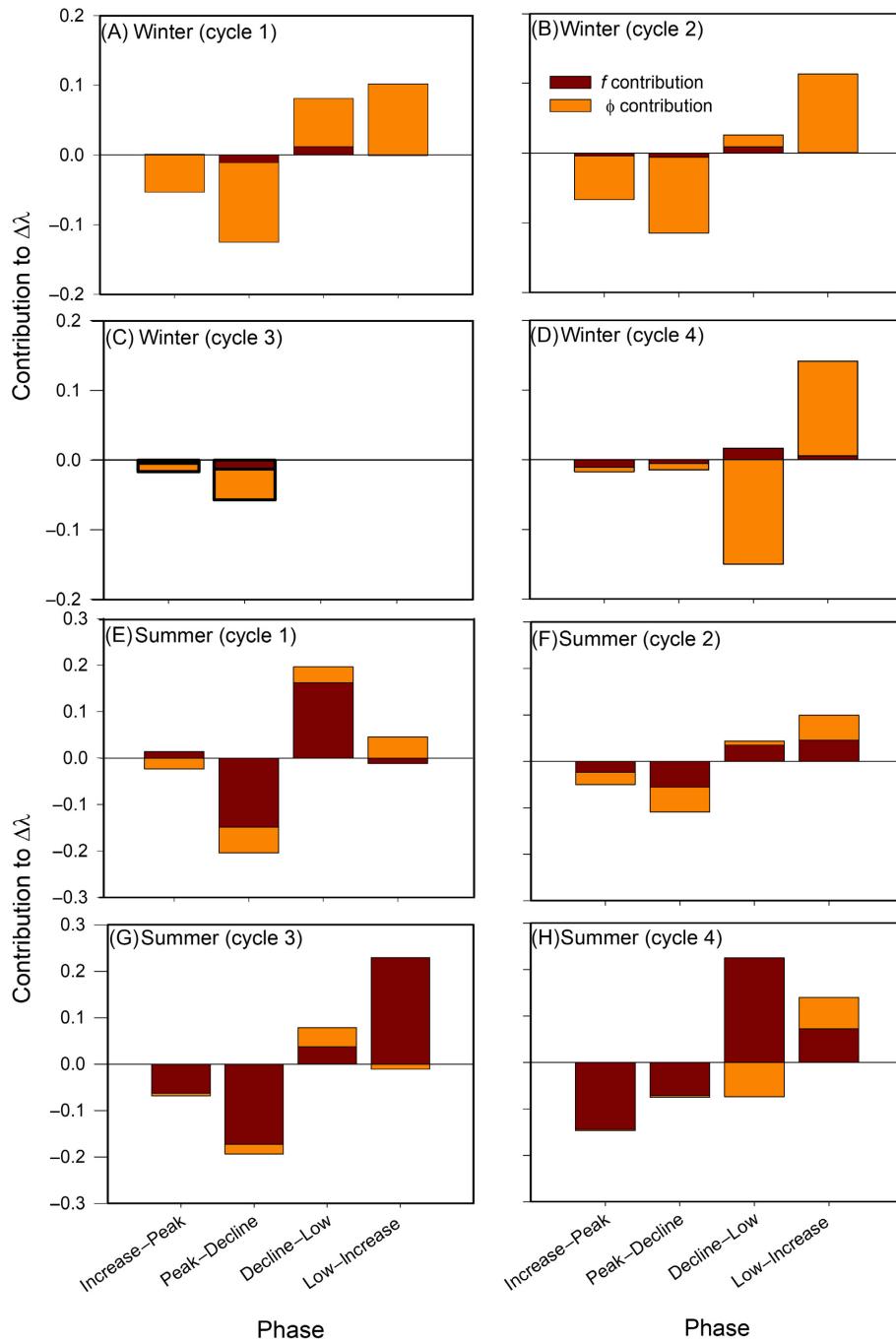
Fig. 5. Life table response experiment (LTRE) contribution of recruitment (f contribution) and survival (ϕ contribution) to phase-specific differences in realized population growth rate ($\Delta\lambda$) during winter (panels A–D); and during summer (panels E–H). These analyses are based on the parameter estimates obtained from the most parsimonious three-variable Pradel's model (model 1, Table 1C).

and f, but also highlighted the fact that changes in f during phase transitions are important determinants of population cycles. Phase- and season-specific estimates of λ for each cycle are presented in Appendix S1: Table S6.

DISCUSSION

Consistent with earlier observations (Keith and Windberg 1978, Krebs et al. 1986, Hodges 2000, Hodges et al. 2001), apparent survival of snowshoe hare in our study
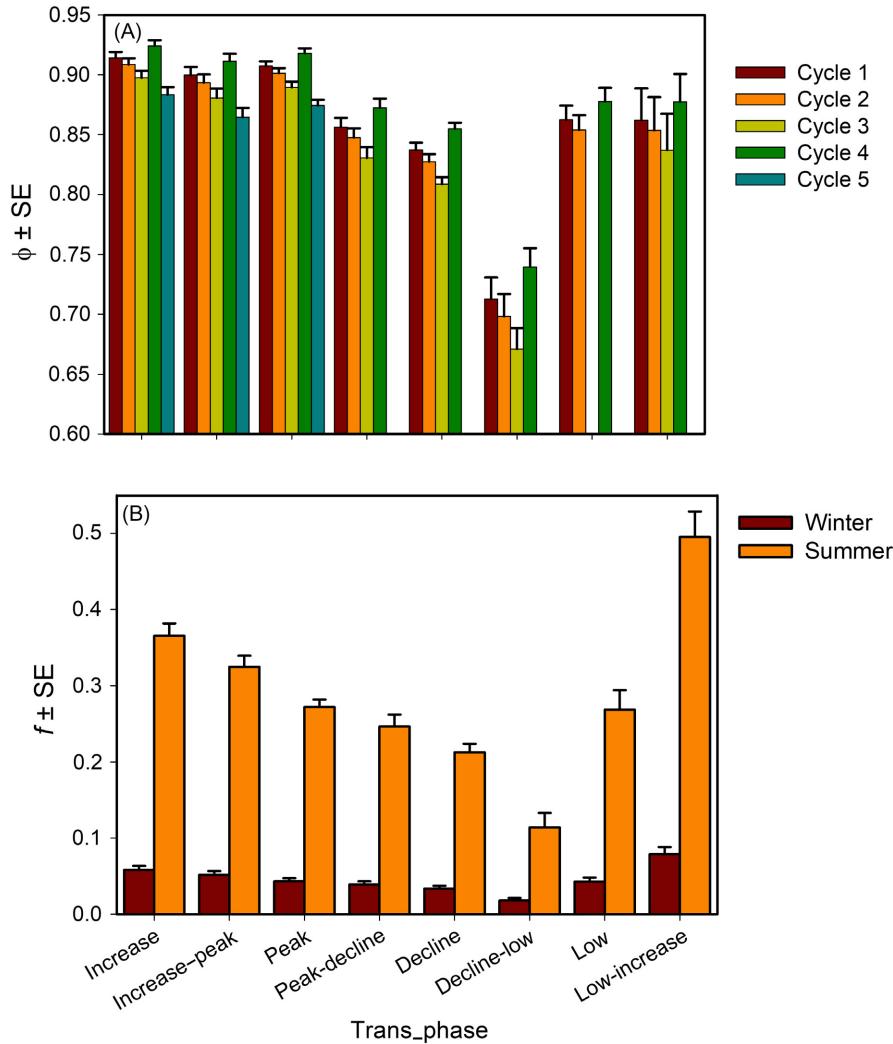
FIG. 6.   *Trans_phase* and cycle-specific estimates (±standard error [SE]) of monthly apparent survival, φ (A) and *Trans_phase* and season-specific estimates (±standard error [SE]) of monthly recruitment rate, *f* (B) for snowshoe hares in Kluane, Yukon, Canada during Fall 1977–Fall 2017. The *Trans_phase* covariate was the same as the cyclic phase except that the last instance of each phase was treated as a transition phase as the population moved from one phase of a cycle to the next. These estimates were obtained using the most parsimonious two-variable Pradel's model that included *Trans_phase* covariate (model 1, Table 1D).

area was strongly phase-dependent, with the highest and lowest monthly survival during the increase and decline phases, respectively. Recruitment rate, on the other hand, exhibited a strongly seasonal pattern, with little recruitment during winter. Snowshoe hares cannot replace themselves overwinter (0.04*7 = 0.028 recruits/ hare overwinter); however, each hare on average replaces itself by 1.4 recruits during summer (0.28*5 = 1.40 recruits per hare during summer). The strongly seasonal pattern of recruitment is consistent with snowshoe breeding biology; hares reproduce during spring and summer, with the first litters being born in May (Cary and Keith 1978, O'Donoghue and Krebs 1992a). Apparent winter recruitment, albeit small, can arise from some late litter three juveniles not being available for capture

in September/October trapping sessions, or from immigration.

Considering phase and season simultaneously (Fig. 2), annual apparent survival (calculated as $\phi_{summer}^{5} * \phi_{winter}^{7}$) was 0.288, 0.233, 0.122, and 0.322 for the increase, peak, decline, and low phases, respectively. Summer recruitment, on the other hand, continued to decline from increase to decline phases, and remained low during the low phase. These numbers suggest that survival has recovered during the low phase, but this does not result in population increase. This, in turn, would suggest that the low phase is not maintained by direct predation on adult hares or juveniles >3–4 weeks old.

As expected from seasonal and phase-specific variation in survival and recruitment rates, monthly λ

exhibited a strong seasonal and phase-specific pattern. During winter, λ was always <1.0 because hares are lost to death or dispersal during winter but there is little or no winter recruitment because hares do not reproduce during winter. However, the rate of population decline during winter varied among cyclic phases, ranging from a 13% monthly decline during the increase phase to a 19% monthly decline during the decline phase. In contrast, the hare population, on average, grew during summer months due to summer reproduction, but the rate of monthly population growth ranged from 40% during the increase phase to 13% during the decline phase. After accounting for winter declines, the snowshoe hare population would almost double every year during the increase phase, decline by 60% annually during the decline phase, and would remain fairly stable during the peak and low phases. Based on a 15-yr study of a cyclic snowshoe hare population near Rochester, Alberta, Canada Keith and Windberg (1978) reached a similar conclusion.

The season- and phase-specific demographic patterns were generally consistent across cycles, so an interesting question is: what caused the substantial variation in the peak density across cycles? Our results suggest that variation in peak density is primarily determined by the overall (cycle-specific) population growth rate and the number of available summers over which the population can grow. Cycle 1 was characterized by the highest overall monthly λ of 1.02 (~27% annual growth), and had five summers of population growth. In contrast, Cycle 4 was characterized by monthly λ of 0.99 (~5% annual decline) and only experienced three summers of growth before the decline began. Correspondingly, Cycle 1 and Cycle 4 achieved the highest and the lowest peak density, respectively. Our results further suggest that cycles that begin with low density or following longer periods of low annual population growth rate tend to achieve lower peak densities. For example, Cycle 4 (2006), which attained the lowest peak density among the five cycles, was preceded by 4 yr with low annual population growth rate (Fall 1998–Spring 2002; Fig. 4), which would have inevitably led to small starting population size when the increase phase of Cycle 4 began. Sheriff et al. (2015) show that the duration of the low phase (which ranges from 1 to 5 yr) is possibly caused by the severity of the predation risk during the decline phase, which determines the generational impacts on population demography via maternal effects. When the decline phase is rapid, the ensuing low phase is longer; when the decline phase is slower, the ensuing low phase is shorter.

We now return to the questions that motivated our study: what are the demographic drivers of snowshoe hare population cycles? Our results clearly show that annual fluctuation in snowshoe hare population numbers is the net result of the interplay between population decline during winter and population growth during summer, both of which exhibit phase-specific patterns. The life table response experiment analyses revealed that phase-related changes in survival drive the phase-specific patterns of winter population declines (Fig. 5A–D). For example, monthly winter λ declined from 0.877 during the peak phase to 0.752 during the decline phase (Δλ = 0.877–0.752 = 0.125); differences in winter survival between the peak and decline phases were responsible for 91.2% of this decline. In contrast, phase-specific differences in summer population growth rate were primarily determined by phase-related changes in summer recruitment, with differences in survival playing a secondary role (Fig. 5E–H).

Our results of phase transition analyses revealed that decreases in winter survival and summer recruitment stops population growth and triggers the decline phase. However, precipitous declines in winter survival trigger the population crash, leading to the low phase. During the low phase, survival typically returns to levels comparable to the increase phase, but summer recruitment remains low. The transition from low to increase phase, on the other hand, is triggered primarily by a substantial (~twofold) increase in summer recruitment, which further increases as the population enters the increase phase; coincident with improvements in survival, these demographic changes allowed the population to achieve higher growth rates during the increase phase, thus triggering a rapid population growth. These demographic indicators of transitions in cyclic phases were broadly consistent across cycles. Finally, λ was more strongly correlated with recruitment ($r = 0.983$, $P < 0.0001$) than survival ($r = 0.772$, $P < 0.0001$). Our results lead us to conclude that snowshoe hare population cycles are driven primarily by phase-specific variation in summer recruitment, with variation in winter survival playing a secondary role. Using a subset of the same data set, Krebs et al. (1986) reached a similar conclusion.

This conclusion naturally leads to the following question: what causes variation in winter survival and summer recruitment? We believe that phase- and season-specific differences in predation are the primary factor driving the observed pattern in snowshoe hare survival. Snowshoe hares in our study site are killed by a variety of mammalian and avian predators, including Canada lynx, coyotes (*Canis latrans*), northern goshawks (*Accipiter gentilis*), and great horned owls (*Bubo virginianus*). Radio-tracking studies suggest that predation is by far the most important mortality factor, accounting for ≥90% of deaths of adult hares in our study area (Boutin et al. 1986, Hodges 2000, Hodges et al. 2001, Krebs et al. 2018), and 86% of hare deaths in Alaska (Feierabend and Kielland 2015). Snowshoe hares potentially experience higher predation during winter because there are fewer alternative prey available to their predators (Feierabend and Kielland 2015) and the necessity of foraging during harsh environmental conditions (i.e., winter) make hares more vulnerable to predators (Curio 1976, Keith et al. 1984, Murray et al. 1997, Murray 2002). Evidence of starvation in our study site is rare (Boutin et al. 1986, O'Donoghue and Krebs 1992*a*,

Hodges et al. 2006), but winters in the western boreal forest are extremely cold (Seager 2005, Boonstra et al. 2016), and winter food shortages could potentially affect hare survival (Keith and Windberg 1978). Feierabend and Kielland (2014) reported that about ~3% of snowshoe hare deaths were attributable to apparent starvation, suggesting that death due to starvation is rare, but it is possible that hungry hares will be less vigilant and more susceptible to predation (McNamara and Houston 1987, Sullivan 1989). In addition to the lower availability of food, which makes hares less vigilant during the decline and therefore more vulnerable, the chronic stress, which leads to loss of muscle mass and condition (Boonstra et al. 1998a, Hodges et al. 2006) and decline in cognition, also contributes to this increased vulnerability. Results of an earlier experiment showing that hares in our study area survived substantially better on a grid that received both the experimental predator exclusion and food supplementation, compared to a grid receiving only predator-exclusion treatment (Krebs et al. 1995) suggests that food resources can interact with predation to affect snowshoe survival. However, results of natural feeding and food supplementation experiments in open populations provide no evidence that food supply can substantially improve snowshoe hare survival (Sinclair et al. 1988, Smith et al. 1988, Krebs et al. 1995).

Recruitment is a composite function of births, early juvenile survival until trappable age (minimum mass at first capture was 310 g, or ~16–18 d of estimated age), and natal dispersal. Snowshoe hares reproduce during spring and summer, with the first litters being born in May and last litter by the end of August (Cary and Keith 1978, O'Donoghue and Krebs 1992a). Juveniles of both sexes disperse predominantly between 30 and 60 d of age; leverets typically disperse by September (Gillis and Krebs 1999, Hodges et al. 2001). Also, dispersal rate is generally low, with little or no phase-specific variation (Boutin et al. 1985), and cannot explain the substantial seasonal and phase-specific variation in recruitment. On the other hand, reproductive parameters of cyclic snowshoe hare populations show cyclic variation. Cary and Keith (1978) found that the number of young produced varied from 7.5 (decline phase) to 17.9 (low–early increase phase) young/female/yr, and that virtually all reproductive parameters showed cyclic variation, consistent with population cycles of snowshoe hares in Alberta, Canada. In Kluane, pregnancy rate and litter size exhibited phase-specific variation, with the increase and decline/low phase being characterized by the best (18.9 young female/yr) and worst (6.9 young female/yr) reproductive output, respectively (Hodges et al. 2001, Stefan and Krebs 2001). Thus, it is reasonable to conclude that phase-specific differences in recruitment rate are due primarily to phase-specific variation in *in situ* reproduction and possibly survival of juveniles until trappable age (Cary and Keith 1978, Krebs et al. 1986, Hodges et al. 2001, Stefan and Krebs 2001).

What causes phase-specific variation in summer recruitment? There are at least two possibilities. First, per capita food availability could potentially cause phase-related changes in recruitment. Keith (1974) proposed that food shortages in winter could affect hares' body condition and depress summer recruitment. However, food supplementation experiments revealed that supplemental food had little or no effect on snowshoe hare reproduction, survival, or population growth (O'Donoghue and Krebs 1992a, Krebs et al. 1995, Krebs et al. 2018). Furthermore, winter shrub biomass in Kluane has been increasing because of climate change over the last three decades (Boonstra et al. 2018); however, there has been no concomitant improvement in hare reproductive output during this period. Second, chronic stress due to predator chases could potentially depress reproduction during the decline and low phases. (Boonstra and Singleton 1993, Boonstra et al. 1998a). This is a working hypothesis at the present time. Rudy Boonstra and colleagues (Boonstra et al. 1998a, Sheriff et al. 2009, 2011, Boonstra 2013, Sheriff et al. 2015, Sheriff et al. 2017) have shown that snowshoe hares are sensitive to stress caused by predation risk. The hypothesis is that predator-caused stress is maternally programmed and epigenetically inherited (so stress is passed from one generation to the next), and that chronic stress depresses females' reproductive output. This epigenetic inheritance could explain the low recruitment during the low phase and improving recruitment as the population transitions from low to increase phase as the epigenetic signal is lost. Phase-related changes in predator-induced stress may be an important cause of phase-related changes in summer recruitment (Krebs et al. 2018) and, combined with increased predation on juvenile hares, can explain variations in recruitment. Our results are consistent with this hypothesis. Snowshoe hare juvenile survival is close to zero during the decline or early low phase (Keith and Windberg 1978, Hodges et al. 1999). However, seasonal and phase-specific patterns in juvenile survival rates and factors influencing them are not well understood for the low phase, and deserve additional research.

Cyclic populations of snowshoe hares are often characterized by prolonged low phases, and explaining this phenomenon has been a persistent challenge (Boonstra et al. 1998b, Krebs et al. 2001a). Our results show that, on average, snowshoe hare populations experience net annual growth even during the low phase. What, then, prevents snowshoe hare populations from starting to grow immediately? We propose two factors. First, we surmise that though the hare populations at low phase are characterized by positive *per capita* growth rates, starting population sizes are too small during the early low phase to create noticeable numerical increases. Furthermore, demographic stochasticity due to processes such as the Allee effect can potentially increase demographic variance, reduce population growth, and prevent small populations from growing (Caswell 2001, Brashares et al. 2010, Melbourne 2012). In effect, when the

numbers are too low it takes time for the population to experience visible numerical growth even through the *per capita* growth rate is positive. Second, we hypothesize that predator-induced maternally inherited stress during the decline results in offspring that have lower rates of reproduction and/or poorer survival than offspring at the start of the increase phase and that the legacy of these maternal effects take time to be removed from the population. Evidence from both human and laboratory studies indicates that such maternally inherited stress causes lifelong epigenetic effects in offspring (Meaney et al. 2007, McClelland et al. 2011, McGowan and Matthews 2018). Evidence from hares from different phases and brought to the laboratory maintain fitness traits of their counterparts in the field, indicating that these differences are intrinsic (Sinclair et al. 2003).

Recent findings on wild hares indicate that such phase-based differences are associated with organizational changes in brain function that then likely impact fitness. During the increase phase, the evidence indicates these organizational changes will result in adaptive behavior of adults and young (Lavergne 2018, Lavergne et al. 2019), resulting in enhanced survival. During the decline phase, the changes are expected to reduce reproductive rate (fewer pregnancies/summer) and offspring survival. Although transitions from increase to decline phase can be satisfactorily explained by low winter survival because of direct predation and stress-induced reproductive depression caused by predator chases, the duration of low phase, and factors and processes driving transitions from low to increase phase, require additional research in both field and laboratory.

Population cycles are essentially demographic processes, and cannot be fully understood or explained without first understanding demographic mechanisms that underlie cyclic changes in abundance (Oli and Dobson 1999, Krebs 2002). Despite seven decades of theoretical and empirical research, a thorough demographic characterization of snowshoe hare population cycles grounded in observational or experimental data had not been performed, and our understanding demographic mechanisms underlying cyclic changes in abundance remained incomplete until now (Barraquand et al. 2017). Given the cycle length, it had been difficult to test for the consistency of demographic patterns across cycles, because such research would necessitate decades of field data. Through a combination of parameters of statistically rigorous capture–recapture modeling framework and 40 yr of field data on the same population, our study fills the aforementioned knowledge gaps by (1) providing the first rigorous, empirically based demographic characterization of the rates of population change that must be explained; (2) providing evidence that the demography of snowshoe hare cycles showed a repeatable pattern over five population cycles; (3) discerning demographic mechanisms underlying the increase, peak, and decline phases; and (4) explaining the variation in peak densities achieved by the same population across different cycles. Cyclic mammals inhabit variety of habitats across northern hemisphere and exhibit diverse life histories, but they all show similar dynamical patterns (Krebs 2013, Myers 2018, Oli 2019). Similar analyses of other cyclic mammal populations would help us understand whether or to what extent cyclic mammalian populations are demographically similar.

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