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POPULATION ECOLOGY – ORIGINAL RESEARCH

Contribution of late-litter juveniles to the population dynamics of snowshoe hares

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Abstract

Determining the factors driving cyclic dynamics in species has been a primary focus of ecology. For snowshoe hares (*Lepus americanus*), explanations of their 10-year population cycles most commonly feature direct predation during the peak and decline, in combination with their curtailment in reproduction. Hares are thought to stop producing third and fourth litters during the cyclic decline and do not recover reproductive output for several years. The demographic effects of these reproductive changes depend on the consistency of this pattern across cycles, and the relative contribution to population change of late-litter versus early litter juveniles. We used monitoring data on snowshoe hares in Yukon, Canada, to examine the contribution of late-litter juveniles to the demography of their cycles, by assigning litter group for individuals caught in autumn based on body size and capture date. We found that fourth-litter juveniles occur consistently during the increase phase of each cycle, but are rare and have low over-winter survival (0.05) suggesting that population increase is unlikely to be caused by their occurrence. The proportion of third-litter juveniles captured in the autumn remains relatively constant across cycle phases, while over-winter survival rates varies particularly for earlier-litter juveniles (0.14–0.39). Juvenile survival from all litters is higher during the population increase and peak, relative to the low and decline. Overall, these results suggest that the transition from low phase to population growth may stem in large part from changes in juvenile survival as opposed to increased reproductive output through the presence of a 4th litter.

Keywords Population cycles · Demography · Limitation · Snowshoe hare · *Lepus americanus*

Introduction

Population cycles have interested ecologists for decades, and examining the drivers of species' cycles has been the subject of intense investigation, providing considerable knowledge on the factors regulating density (Myers 2018). Several external factors such as disease, food availability, and predation have been proposed as mechanisms regulating population cycles, and numerous theoretical and experimental studies have tested the importance of these factors across species and populations (Krebs et al. 1995; Korpimäki et al. 2004; Redpath et al. 2006). However, the external factors driving cyclic dynamics for most species are still debated (Myers 2018), especially in regards to the mechanisms initiating population growth from low densities, or causing growing populations to rapidly decline (Andreassen et al. 2020). One approach to resolve such debate is to explore which demographic variables and life-history traits change in accordance with cycle phase (i.e. increase vs decline;

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Oli et al. 2020), so that previous and future experimental results can then be placed in the context of the parameters that appear to regulate species abundance (Oli 2019). That being said, several life-history traits vary across phases, and deciphering which changes represent a necessary requirement for population cycles, or an associated epiphenomena, requires more detailed consideration (Oli 2019).

The 10-year cycle of the snowshoe hare (*Lepus americanus*) across the boreal forests of North America is a prominent example of population cycles, with investigations into changes in their abundance dating back to the early twentieth century (Green et al. 1939). A typical cycle can be divided into four phases: increase, peak, decline, and low based on annual rates of population change (Keith 1990). The increase phase is characterized by high survival and recruitment rates, whereas the decline phase is associated with reduced survival and recruitment rates (Keith and Windberg 1978; Hodges et al. 2000; Krebs et al. 2001; Oli et al. 2020). The cessation of population growth at peak densities corresponds with decreased adult and juvenile survival, and a reduction in reproductive output. The reduction in reproductive output, caused by changes in the number of leverets produced and pregnancy rates, precedes peak hare densities by approximately two years (Cary and Keith 1979; Stefan and Krebs 2001). As a result, explanations of the cycle feature lethal effects of predators affecting both adult and juvenile survival rates, in combination with a factor driving the observed reproductive cut-back (Krebs et al. 2018). Changes in reproduction could be driven by variation in density-dependent winter food availability or quality (Cary and Keith 1979; DeAngelis et al. 2015), or indirect effects of predators mediated through predator-induced stress (Boonstra et al. 1998a; Sheriff et al. 2009, 2011), the latter of which is most widely accepted (Krebs et al. 2018).

Snowshoe hares breed during the summer, with a maximum of four litters produced in a single year that are locally synchronous, creating distinguishable juvenile cohorts (Cary and Keith 1979; O'Donoghue 1994). The majority of the reproductive collapse, in terms of number of offspring produced per female in a season, occurs via the cut-back of the third and fourth litters (Stefan and Krebs 2001). Specifically, fourth litters are thought to only occur in the late low and early increase phase, whereas third litters are curtailed during the decline (Stefan and Krebs 2001). First and second litters are produced in every cycle phase, with second litters exhibiting changes in the average litter size, whereas first litter sizes remain relatively constant (i.e., 0.5 leveret variation; Hodges et al. 2000). Monitoring reproduction in hares requires considerable effort as juveniles are not trappable until 35 days of age and locating litters at birth is nearly impossible (Hodges et al. 2001). This becomes particularly challenging during the low and early increase phase when there are few hares to capture (Gillis 1998; Hodges et al. 1999). Therefore, the consistency of the change in reproductive output over the cycle, particularly in regard to the production of a fourth-litter, has not been examined across multiple cycles.

Assessing the impact of changing reproductive output and juvenile recruitment on cycle dynamics warrants further consideration of survival differences between juveniles from different litter groups. The contribution of late-litter juveniles (i.e., third and fourth litters) to snowshoe hare population growth will depend on their survival rate relative to juveniles born earlier in the summer. Indeed, offspring of other lagomorph species born earlier in the breeding season have higher survival rates than individuals from later litters that may further extend into increased reproductive performance the following year (Iason 1989). Late-litter snowshoe hares enter the autumn with smaller body mass (O'Donoghue and Krebs 1992), presumably having higher foraging requirements to accommodate growth which may reduce over-winter survival, particularly during autumn and early winter (Gillis 1998). However, due to high pre-weaning mortality rates of leverets (Stefan 1998), monitoring an adequate sample of juveniles from birth to autumn is difficult. As a result, we lack knowledge on relative survival rates of different juvenile cohorts, and particularly in how this might vary across cycle phase.

In this study, we used long-term live-trapping data (42 years) on a snowshoe hare population from southwestern Yukon, Canada, to examine the potential contribution of late-litter juveniles to cycle dynamics. Specifically, we determine: (1) if the reduction of late litters is consistent across cycles, (2) how over-winter survival of late litters compare to that of early litters, and (3) how juvenile survival from each litter varies among cycle phases. In particular, we assess whether changes in production and/or over-winter survival of late-litter juveniles is (1) an important contributor to stopping population growth at the hare peak and (2) required to explain a return to population increase following the low phase. Broadly, this research addresses the degree to which population increase and decline in cyclic species is affected by changes in reproductive output versus juvenile survival.

Materials and methods

Study area and trapping methods

This study was conducted in the Kluane Lake region of Yukon, Canada (61°N, − 138°W). The boreal forest in this area is comprised primarily of white spruce (*Picea glauca*) with smaller amounts of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The shrub layer is dominated by gray willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*). The main predators of hares in the region are Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*), with other predators including great-horned owls (*Bubo virginianus*) and northern goshawks (*Accipiter gentilis*). Snowshoe hares have been monitored in the region over the last four decades (Krebs et al. 2018; Oli et al. 2020).

We captured snowshoe hares using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) on several study grids that were either 10 × 10 or 20 × 20 with 30 m spacing between traps (Krebs et al. 2001, 2018). Sex, age, reproductive status, body mass, and right hind foot length of each individual were recorded. Each hare received a Monel #3 eartag (National Band and Tag Co., Newport, KY, USA) on the first capture and the identity of a previously marked hare was recorded in each subsequent capture. Trapping occurred between autumn 1977 and autumn 2017, and all data used in this study came from unmanipulated control grids.

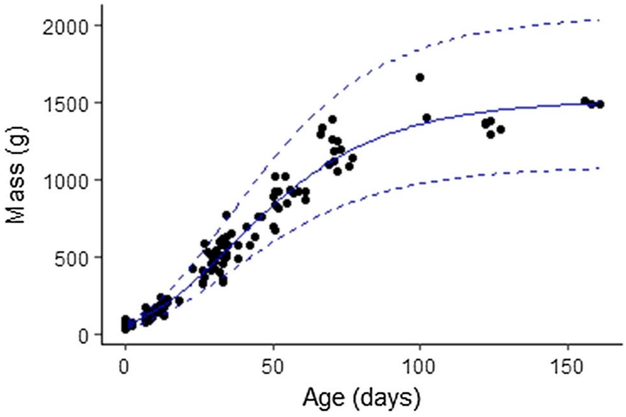

Fig. 1 Gompertz growth curves (solid) and 95% CIs for juvenile snowshoe hare fit using maximum likelihood with lognormal errors. The points represent 209 mass measurements recorded for 69 known-age individuals

Calculating growth rates and designating litter groups

Using 209 body mass measurements on 69 known-age juveniles from earlier monitoring in this population (O’Donoghue and Krebs 1992), we fit Gompertz growth curves using maximum likelihood, assuming lognormal errors. The Gompertz growth equation is:

$$\text{mass} = a\mathrm{e}^{-e^{\mu(\lambda-\text{age})e/a+1}},$$

consistent with the formulation used in the grofit package in R (Kahm et al. 2010). These 69 known-age individuals were monitored during the cyclic increase and peak (i.e. 1989 and 1990), and were from the first (25), second (36), and third (8) litter cohorts. Due to the limited sample size for individuals older than 50 days, we combined juveniles from multiple litter groups in the same growth curve, and fixed the asymptotic mass as the average adult mass in December and January (1518 g; Fig. 1). We choose these dates for our average asymptotic mass as it represents when individuals will be adult size, but prior to over-winter mass loss (Hodges et al. 2006).

We used mass data for individuals captured between September–November to determine the presence of fourth-litter juveniles each year. We classified suspected fourth-litter hares as any individual who was less than the projected mass obtained from the lower 95% confidence interval of a juvenile born on August 13th. This date represents the latest recorded birth date of a third-litter, when hare reproduction was intensively monitored from 1988 to 1996 (Hodges et al. 2001). Therefore, we are assuming individuals captured in autumn weighing significantly less than the growth rate of a juvenile born on the latest known date of a third-litter to likely come from a fourth-litter born later in the breeding season.

We distinguished early (i.e., first and second) and third-litter juveniles for comparisons of over-winter survival based on body mass similar to above. Third-litter hares were classified as any individual who was less than the mass obtained by the upper 95% confidence interval of an individual born on the earliest recorded date of a third-litter, July 20th (Hodges et al. 2001). However, we restricted this analysis to trapping that occurred between the week of August 01 and September 18, the latter date being when third-litter juveniles would reach 1000 g according to our Gompertz growth curve, as we considered hares larger than 1000 g impossible to assign to a litter group. Here, we are assuming individuals are most likely from a third-litter if they weighed less than the maximum growth rate of an individual born after the earliest known third-litter. We classified early litter juveniles during this same time period (i.e., August 01–September 18) as any juvenile hare that was not considered as being from a late-litter. Individuals who were caught for the first time in summer or autumn were classified as juveniles (as in Hodges et al. 1999; Peers et al. 2020), and therefore we restricted data in this analysis to study grids where monitoring occurred in the previous year. There is a potential that our classification of juveniles includes dispersing adults; however, this likely had minimal impact on our analysis as instances of adults dispersing into the population over the summer are rare (Boutin et al. 1985).

To calculate the proportion of the autumn population that was from either early or third-litter juveniles, we further restricted the data to include trapping records that occurred only between August 14 and September 18, which represents the time period after the last known date of the third-litter births, and prior to them reaching 1000 g. In this calculation, we use August 14th as our cut-off to ensure third litters have occurred and were therefore trappable.

Examining survival rates and the presence of fourth litters

First, we examined the cycle phase of each year where fourth-litter juveniles occurred, to determine their consistency across cycles. Cycle phase was based on criteria from Keith (1990), where finite rate of annual change (spring to spring) less than 0.44 equals a decline, more than 1.89 equals an increase phase, and the years between these phases correspond to either peak or low. Next, we examined the over-winter survival probability for juveniles from each litter group (i.e. early, third, or fourth). For this analysis, we considered over-winter survival as any juvenile captured in the previous autumn that was captured after March 01 of the following spring, which encompasses the period when we conducted live-trapping for a spring population estimate. We acknowledge this represents apparent survival, as loss will include both death and emigration (Sandercock 2020). However, we expect emigration to have limited impact on our results, as there is no suspected difference in dispersal rates between litter groups and cycle phase (Boutin et al. 1985; Gillis and Krebs 1999), and our goal was to compare relative changes in winter survival between cohorts and cycle phase (see further discussion below). For simplicity, we therefore refer to the probability of being captured the following spring as apparent survival for the rest of our analyses. We calculated the proportion of juveniles from each litter group that survived over winter by comparing the apparent survival rates of 500 bootstrapped datasets of individuals within each litter group. Sample size of our bootstrapped datasets corresponds to the total number of individuals captured during the autumn for each litter group.

We then compared differences in apparent survival between early and third-litter juveniles, as well as adults, across cycle phases. We assigned cycle phase as the phase of the hare population determined at the spring census (i.e. when juveniles were recaptured), as our goal was to describe over-winter survival rates that cause the proceeding phase (see supplement for results from phase classifications as the autumn, or previous spring phase). Given the low sample size within some years, calculating average survival for litter and cycle phase as the mean across years was not feasible. Instead, we assessed relative differences in apparent survival by comparing the survival rates of 500 bootstrapped datasets of individuals from each age group and phase. Each bootstrapped dataset included resampled individuals, with replacement, until the number of individuals in the resample equaled the original dataset for each age group and cycle phase. We repeated this same analysis, including only years that represented transitions between ycle phases to determine the demographic change that may signal such transitions.

We then examined the drivers of juvenile over-winter apparent survival across our entire dataset using generalized linear models (GLM) with a binomial distribution and a logit link in the program R (3.3.1). We used an information theoretic approach to determine which variables best-characterized whether a juvenile hare was captured the following spring. Models consisted of all combinations of litter group, cycle phase, mass, and sex. We selected the top model using Akaike's Information Criterion, corrected for small sample sizes (AICc; Burnham and Anderson 2002). Covariates used for our analyses had a variance inflation factor less than 2 (Graham 2003), signifying covariates were not correlated in our models.

Results

Litter production

We captured a total of 40 individual hares suspected to be from a fourth-litter between September and November over the 42 years of monitoring in the region (3680 total individuals were captured on control grids between September–November). Fourth litter individuals were present in 12 years across the five cycles and occurred primarily during the low and increase phases of the cycle (11 cases) with a single case during the decline (Fig. 2). The percent of the autumn population (September–November) that was made up of 4th litter juveniles was never more than 10%. Proportion of the autumn population (i.e., August 14–September 18) that was early or third-litter juveniles differed across cycle phases (Fig. 3). However, given the restricted trapping period included in the analysis, only 25 years had trapping data that could be included. The proportion of the total hares caught during the autumn (i.e., August 14–September 18) that were third-litter juveniles was highest during the low phase (0.36) and was lower but consistent during the increase (0.15), peak (0.21), and decline (0.15) phases of the cycle (Fig. 3). For early litter juveniles, proportions were relatively constant during the increase (0.50), peak (0.47), and decline (0.47), with values somewhat lower during the low phase (0.36; Fig. 3 and Table S2). These patterns were similar regardless of the classification of cycle phase, except when cycle phase was classified as the phase during the previous spring, where the proportion of late-litter juveniles was consistent across phases (see Fig S1).

Apparent over-winter survival

Apparent over-winter survival rates varied among litter groups, with early litter juveniles having 4.7 times higher

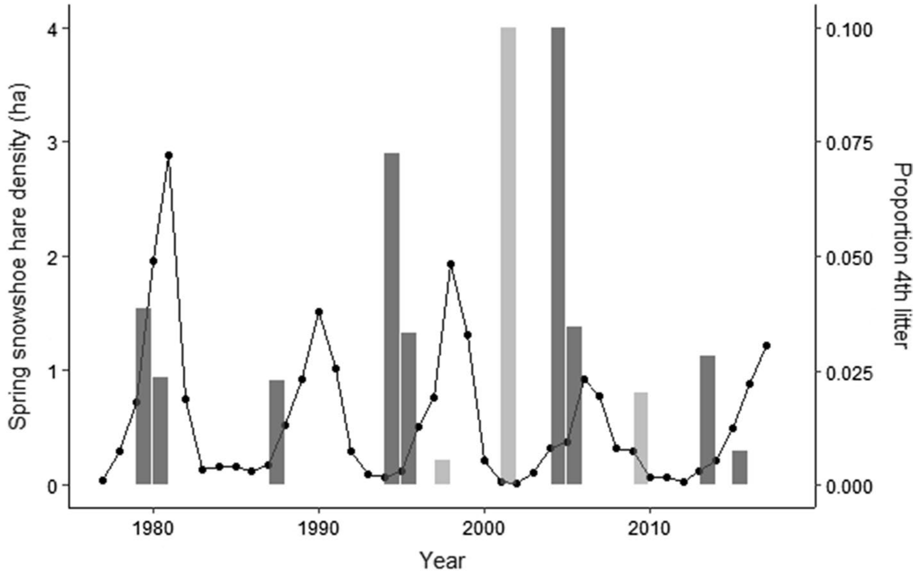

Fig. 2 Spring snowshoe hare density (dotted line) in southwestern Yukon since 1977 with the proportion of the total individuals captured in September–November that were suspected to be from a fourth-litter (gray bars). Light gray bars represent years where only one individual fourth-litter juvenile was captured

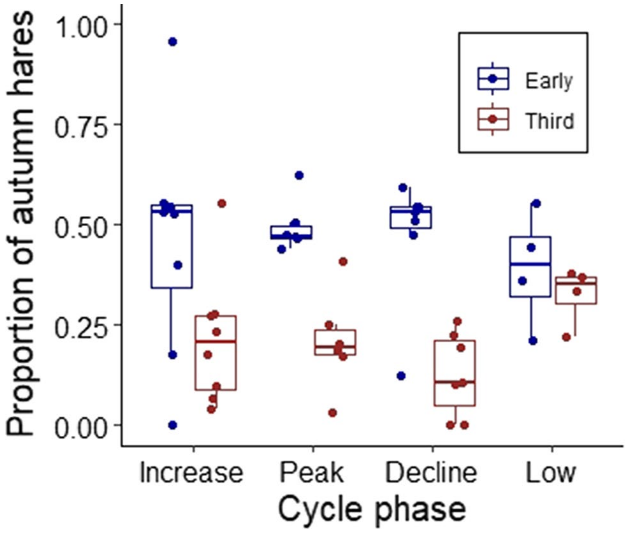

Fig. 3 Boxplots of the proportions of the autumn population (Aug 14–Sep 18) that were either early litter (blue; left), or third-litter (red; right) juveniles for each phase of the cycle. Individual dots represent the values for each year that correspond to the cycle phase and litter group

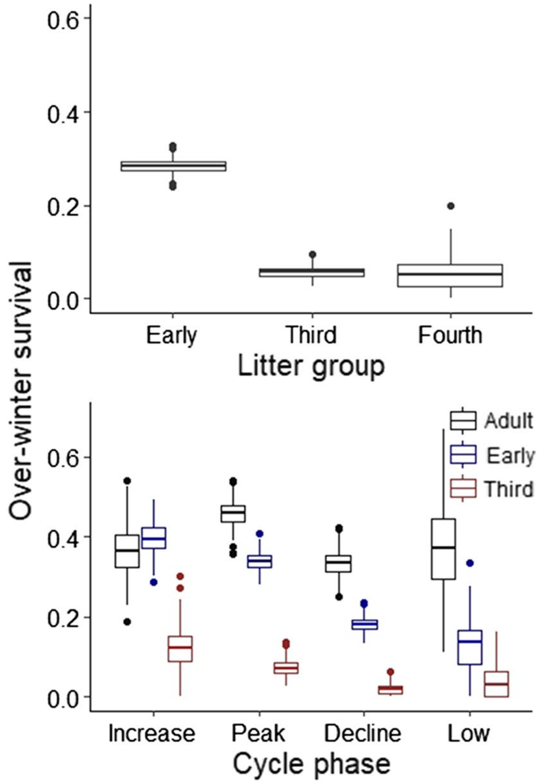

Fig. 4 The probability of being captured the following spring among **a** litter groups, and **b** cycle phase for adults (black; left), early litter (blue; middle), and third-litter (red; right) juveniles, based on recapture rates from 500 bootstrapped datasets

survival (0.28, 95% CI based on bootstrap recruitment: 0.26, 0.31) than third-litter (0.06, 95% CI 0.04, 0.08). Only, two of the 40 fourth-litter individuals we tagged were recaptured the following spring (Fig. 4a). Apparent survival also varied between cycle phases, and each litter had qualitatively similar patterns. Lowest survival occurred during the decline and low phase for both early (decline = 0.18, CI 0.15, 0.21; low = 0.14, CI 0.06, 0.22) and third litters (decline = 0.02, CI 0.00, 0.05; low = 0.03, CI 0.00, 0.10). Apparent survival rates increased during the increase and peak phase for both early (increase = 0.39, CI 0.34, 0.46; peak = 0.34, CI 0.31, 0.37) and third litters (increase = 0.12, CI 0.03, 0.21; peak = 0.07, CI 0.04, 0.10; see Fig. 4b). These patterns were similar in years that were transitions between cycle phases

(Fig S3). Over-winter survival appears less variable across phases for adults, with highest rates during the increase and peak (Fig. 4b). Survival patterns across phase and age groups appear similar if examining yearly percentages as opposed to the pooled bootstrap models (Fig S4), however, there is large variation among years within the same phase and age group. Yearly patterns should be taken with caution, as some years were severely limited by sample size (i.e. < 5 individuals captured in the autumn).

Our top model explaining whether a juvenile was recaptured the following spring included cycle phase, litter group, and body mass ($w = 0.79$; Table S3) and was the only model within 2 ΔAICc. Likelihood of being recaptured in the spring was higher for early litter juveniles (1.35 ± 0.26, $z = 5.2$, $P < 0.01$; Fig. 5) and increased with larger body mass (0.002 ± 0.0002, $z = 4.6$, $P < 0.01$). In reference to the decline phase, apparent survival was higher during the increase (1.18 ± 0.20, $z = 6.0$, $P < 0.01$) and peak (0.77 ± 0.154, $z = 5.0$, $P < 0.01$) whereas apparent survival in the low phase did not significantly differ from rates during the decline phase (-0.26 ± 0.46, $z = -0.6$, $P = 0.58$; Fig. 5).

Discussion

Our goal was to examine the presence and survival rates of juveniles from different litter groups to provide insight into the contribution of different litters to the demographic variables most strongly influencing population cycles in this species. Our results demonstrate that 4th litters are present consistently across cycles, and primarily occur during the increase phase (Fig. 2; Stefan and Krebs 2001). However, the capture of 4th litter juveniles was extremely rare and their apparent over-winter survival was low making it unlikely that the transition from a cyclic low to population increase is driven by increased reproduction through the addition of this litter group. This suggests that a change in fecundity is not necessarily the important driver of the increase phase of the cycle, as the increase in leverets produced per female during this period is driven by the occurrence of the 4th litter (Stefan and Krebs 2001). Furthermore, the proportion of third-litter juveniles captured in the autumn remains relatively constant across cycle phases and may be highest in the low phase (see Fig. 3 and Fig S1). In contrast, apparent survival rates vary between phases particularly for early litter juveniles (Fig. 4). Juveniles from all litters were more likely to be recaptured in the following spring during the increase and peak, and less likely during the decline and low (Fig. 4). This suggests that any recovery of survival during the low phase may stem primarily from adult survival (Hodges et al. 1999), and the lack of summer recruitment considered critical for the decline and low phase (Oli et al. 2020) may be caused by lowered juvenile survival. Therefore, snowshoe hare populations do not increase, following decline, until mortality rates have decreased.

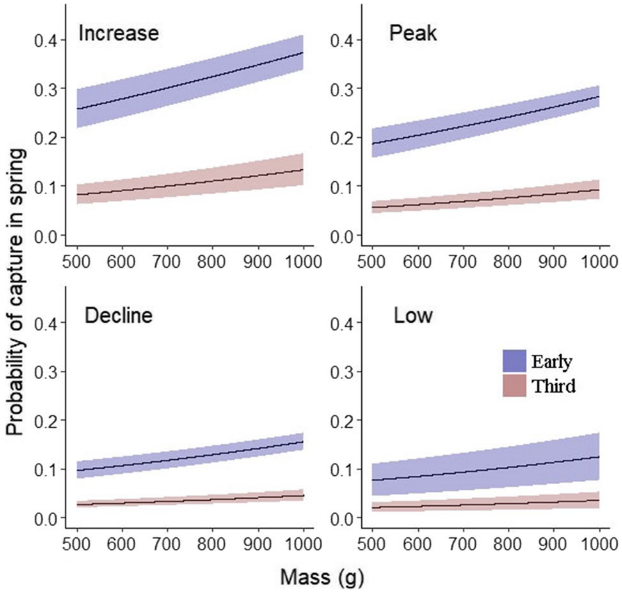

Fig. 5 Modeled effect of body mass at first capture on the probability of being captured the following spring for early (blue; top) and third (red; bottom) litter juveniles across each phase of the cycle, using coefficients from the strongest supported model. Confidence bars represent predicted response standard errors

We can think of two potential hypotheses that may drive the pattern of juvenile survival we observed. First, high-predation risk during population declines causes higher stress levels in females (Boonstra et al. 1998a, b; Sheriff et al. 2011), which leads to lower reproductive rates and offspring quality (Sheriff et al. 2009). These offspring may have reduced survival, and continue to produce lower quality offspring through maternal effects (Sheriff et al. 2010). Under this hypothesis, recruitment of juveniles into the spring increases when stress levels are reduced and offspring quality improves, which subsequently improves juvenile survival. Second, predators exist at high enough densities following population decline to maintain similar consumption rates on juveniles in proportion to prey density during the low phase. Predators such as great-horned owls that have a slower numerical response relative to other predators (O'Donoghue et al. 1997), and show preference for juvenile over adult hares (Rohner and Krebs 1996), may have a particularly important role during this phase of the cycle (Rohner et al. 2001; Tyson et al. 2010). Juvenile survival increases when relative consumption rates finally decrease, which causes population growth. However, there was substantial variation in apparent survival and the proportion of late-litter hares across years, even within cycle phases (see Fig S1, S2, and S4). Therefore, the relative contribution of specific demographic parameters driving the reduced summer recruitment during the low phase (Oli et al. 2020) may vary across cycles (King and Schaffer 2001). Regardless, future research should focus on early litter production and survival given the relatively low over-winter survival rate of juveniles born later in the summer, which may be broadly applicable across other lagomorph species (Iason 1989).

There are several key uncertainties and limitations in our data that should be considered for future research. The timing of reproduction in the spring may depend on yearly variation in weather (Angerbjörn 1986; Visser et al. 2009), and leverets can vary in body size and growth rates (O'Donoghue and Krebs 1992), both causing some juveniles to be inaccurately classified as either early or late-litter individuals. However, our results demonstrate that larger individuals in late summer/early autumn are more likely to be recaptured in the spring (Fig. 5), and that the relative probability of their occurrence and survival changes across the cycle. Larger individuals at this time period will more likely represent early as opposed to late-litter juveniles. These patterns are also consistent with earlier work examining juvenile survival rates between litter groups (Gillis 1998). Furthermore, as expected, we documented 4th litters primarily during the late low and early increase phase of the cycle (Stefan and Krebs 2001), suggesting our methods of classification were accurate. Regardless, our main goal was to compare survival rates and autumn proportions across cycle phases, which is more robust to the limitations outlined above.

A more important uncertainty is the potential differences in dispersal rates that may bias our estimates of apparent survival. Although earlier work suggests juvenile dispersal does not differ between litter groups and cycle phase, these results are based on low sample sizes (Boutin and Krebs 1986; Gillis and Krebs 1999). Late-litter juveniles may also disperse at an older age (O'Donoghue and Bergman 1992; Gillis and Krebs 1999), causing a higher percentage of late-litter juveniles captured in the autumn to be pre-dispersal, reducing their probability of capture the following spring. Future studies should examine dispersal patterns across litter groups, and whether this pattern is dependent on population density, as changes in survival rates between phases may represent differences in dispersal. That being said, the proportion of individuals caught in spring that are new hares does not vary widely across cycle phases (Hodges et al. 2001), suggesting higher survival in the increase versus low phases is not driven by differences in dispersal. Variation in capture probability across cycle phase or litter cohort may further cause uncertainty in our results, and warrants further investigation.

This research indicates that snowshoe hare populations may transition from the low to increase phase due to improvement in over-winter survival of early born juveniles (see Fig. 4, 5). Indeed, reproductive output does change throughout the cycle (Cary and Keith 1979; Stefan and Krebs 2001); however, we did not find evidence that the low phase is characterized by a reduced proportion of third-litter juveniles, nor that the population increase out of the low coincides with a higher proportion of third-litter juveniles. Modeling exercises are therefore required to estimate the degree that the autumn populations could be changed had females produced at their maximum capacity. That being said, the main change in reproductive output between the low and increase phase, or increase and peak, in our population is caused by the occurrence of the 4th litter (Stefan and Krebs 2001), and given the low survival rate relative to early litter juveniles, it seems unlikely population growth at this phase is driven largely by their occurrence. Instead, changes in reproductive output may be indicative of overall patterns in individual condition (i.e. stress; Boonstra et al. 1998a). This may influence offspring quality (Sheriff et al. 2009) and their likelihood of survival, as the low to increase phase corresponds with changes in relative survival (Fig. 4b).

These patterns further resemble environmental canalization; fitness or demographic components whose variation has greater effects on overall fitness or population growth should be less variable across time (Gaillard and Yoccoz 2003). The third and fourth litters have greater temporal variation relative to early litters (Stefan and Krebs 2001), due to their lower contribution to fitness and demography (Pfister 1998). Although changes in late-litter occurrence constitutes the majority of the collapse in reproductive output, differences in pregnancy rates and litter size within earlier litters (Stefan and Krebs 2001), may have a larger effect on population growth. However, given the uncertainty in our estimates of survival and classification of litter groups, as well as the limited sample size within phases, we strongly recommend future studies investigate late-litter survival and reproduction during the low and early increase phase of the snowshoe hare cycle. The challenge will be to capture enough hares to overcome sample size limitations, but success will provide critical information at this important phase of the cycle.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-021-04895-x.

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Author contribution statement MJLP, JRR, and SB conceived and designed the study. All authors contributed to data collection and logistical support. MJLP and JRR led data analyses and drafted the manuscript with significant input from all authors.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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