Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior Alaska [1]

K. Kielland, K. Olson, and E. Euskirchen

Abstract: We monitored populations of snowshoe hares *(Lepus american us,* Erxleben) in interior Alaska for 10 years from 1999 to 2008. During this period, fall densities of hares tluctuated approximately 14-fold. High population growth rates over summer (∧ = 1.83-8.00) were followed by large population declines over winter (X = 0.16-0.82). Young-of-the-year hares tended to gain mass over winter, while adult hares tended to loose body mass. The average mass of adult hares was significantly lower during the low phase of the cycle compared with when hares were abundant. Overwinter survival of juveniles relative to adults decreased strongly as a function of the frequency of snowfall events. However, effects of temperature and precipitation on hare demography were season dependent and appear to act as modifiers of the primary controls over population dynamics (predation and food) rather than as direct sources of mortality. The rapid changes in green-up and snow-up in interior Alaska may affect forage conditions as well as the timing of molt in snowshoe hares. The strength of these interactions may increase in importance if the asynchrony of environmental seasonality and life history traits of snowshoe hares becomes more pronounced as the climate continues to change.

Résumé : Nous avons effectué un suivi annuel des populations de lièvre d'Amérique (*Lepus americanus*, Erxleben) de l'intérieur de l'Alaska de 1999 à 2008. Au cours de cette période, la densité automnale du lièvre a fluctué d'un facteur 14. Les taux élevés de croissance des populations en été (λ = 1,83–8,00) ont été suivis d'importants déclins des populations en hiver (λ = 0,16–0,82). Les levreaux tendaient à augmenter leur masse corporelle en hiver tandis que les adultes tendaient à la voir diminuer. La masse moyenne des lièvres adultes était significativement plus faible durant le creux du cycle que durant la période d'abondance. La fréquence des chutes de neige influençait davantage la survie hivernale des juvéniles que celle des adultes. Toutefois, les effets de la température et des précipitations sur la démographie du lièvre dépendaient de la saison et semblaient agir comme agents modificateurs des principaux facteurs de la dynamique des populations (prédation et nourriture) plutôt que comme causes directes de mortalité. Les transitions rapides entre les saisons avec et sans neige à l'intérieur de l'Alaska peuvent influencer les conditions d'alimentation ainsi que la période de mue du lièvre d'Amérique. L'intensité de ces interactions pourrait s'amplifier si l'asynchronie entre la phénologie et les caractéristiques du cycle biologique du lièvre d'Amérique s'accentue en lien avec la progression des changements climatiques.

[Traduit par la Rédaction]

Introduction

The distribution of mammalian herbivores in the boreal forest of interior Alaska is controlled by physical disturbances such as flooding and fire (Wolff and Zasada 1979; Wolff 1980) insofar as these factors modify habitat structure and food availability for herbivores. Snowshoe hares *(Lepus americanus,* Erxleben) are widely distributed herbivores throughout the boreal forest whose biomass during population peaks is nearly twice as high as that of moose or microtines (Rexstad and Kielland 2006). Snowshoe hares occupy a variety of upland and floodplain habitats but tend to favor relatively dense forest stands that provide both food and cover. Thus, hares are typically not found at great densities in midsuccessional forests dominated by balsam poplar *(Populus balsamifera* L.) stands (floodplain forests) or birch - white spruce *(Picea glauca* (Moench) Voss) stands (upland forests). Rather, hares are most abundant in early-successional willow/alder stands that provide both high food availability and cover from avian and mammalian predators. Areas of dense cover also tend to afford thermal protection during winter. Recent studies in the Yukon Territory have demonstrated the complexity of biotic interactions (mainly predation and food) that appear to control population fluctuations in snowshoe hares (Krebs et ai. 1995,2001). Climatic factors controlling the dynamics of snowshoe hare populations have invoked sunspot cycles (Sinclair et a1. 1993), although no clear functional relationship between the broad-scale weather patterns, sunspot activity, and hare demography has been demonstrated. Climatic factors have also been

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implicated as direct controls in some species of small mammals (Rexstad and Debevec 2002) and hares, especially in winter (Meslow and Keith 1971),

Because snowshoe hares have a limited capacity to store fat (Whittaker and Thomas 1983; Hodges et al. 2001), they rely on a constant and frequent food supply. As a medium-sized herbivore. the daily food intake of snowshoe hares equates to approximately 10% of their body mass (Pease et al. 1979; Bryant 1987; Keith 1990). This high food requirement could render them increasingly vulnerable to directional changes in climate that reduce forage availability (e.g., higher snow fall) and (or) compromise their foraging time (e.g., very low temperatures). For example. the length of the season of snow cover in interior Alaska extends from late October through April with approximately 30 cm of snow by the end of October (Alaska Climate Research Center 2009, http://climate.gi.alaska.edu). Further, periods of cold air temperatures (-40 °C) are fairly common during winter in this region, a circumstance that could pose additional energetic challenges to snowshoe hares. Whereas snowshoe hares have very low foot loadings (Buskirk et al 2000) and thus are seemingly well adapted to snow, snow depth and cold temperatures have been reported to be inversely correlated with overwinter survival of adult hares (Meslow and Keith 1971).

Here, we examine a 10-year data series (from August 1999 through November 2008) on snowshoe hare abundance and associated demographic parameters in interior Alaska and further juxtapose these temporal patterns of population dynamics with patterns of regional climate variability. Because of the short time period for which we have reliable population estimates, we did not seek to analyze climatic controls over the snowshoe hare population *cycle* as such. Rather, we sought to examine how local weather conditions could ameliorate or exacerbate intra- and interannual variability in demographic processes of snowshoe hares. Our focal question was how sensitive are snowshoe hares to intra- and interannual variation in climate as manifested in changes in population growth. survival, and body mass over the same time scales? Given the apparent regularity in population fluctuation of snowshoe hares in the historical record (Elton and Nicholson 1942), we hypothesized that snowshoe hares are behaviorally, if not physiologically, buffered from climate fluctuations. Here, we examine this null hypothesis in a boreal forest ecosystem that has undergone marked changes in climate, disturbance regime, and hare populations over the last few decades.

Study area

The study area is part of the Bonanza Creek Long Term Ecological Research (BNZ LTER) project in interior Alaska. The Riparian trap grid, from which these data were obtained, is located along the Tanana River near the Bonanza Creek Experimental Forest 20 km south of Fairbanks (64°41'36.6"N. 148°l7'30.3"W). The site is characterized as successional stage IV, closed alder and willow shrubs (Viereck et al. *1993b),* and is dominated by willow *(Salix* spp.), thinleaf alder *(Alnus incana* ssp. *tenuifolia* (Nutt.) Breitung), and some balsam poplar with an herbaceous understory of forbs (e.g., *Epilobium angustifolium* L. and *Equisetum hyemale* L.) and several grasses. The climate is strongly continental and semiarid with cold winters and warm, dry summers (Viereck et al. *1993a).* Mean annual temperature is -3.3 °C with temperature extremes ranging from -50 °C in winter to 30 °C in summer. Mean annual precipitation is 269 mm-year^{-1} with approximately 37% falling as snow. The growing season is approximately 100 days.

Methods

Live-trapping snowshoe hares

The Riparian trap grid is approximately 9 ha and consists of 50 traps arranged in a 5 x 10 grid with a 50 m intertrap distance. This design was chosen because home ranges of snowshoe hare are typically 5-10 ha and overlap is common (O'Farrell 1965; Wolff 1980; Hodges et al. *1999a, 2000).* The live-traps are Havahart size 3 and model 1079. The size of the snowshoe hare population is estimated by mark-recapture methods during four primary encounter occasions (sensu Nichols and Pollock 1990) per year (June, August, November, and March) that correspond to life history stages of hares. Primary encounter occasions at the site occur over the course of 1 week and consist of four secondary encounter occasions (individual examinations of trap grids) at the site. Similar to other studies of snowshoe hares, the traps are baited with carrots for hydration and alfalfa for nourishment (Wolff 1980; O'Donoghue and Krebs 1992; O'Donoghue et al. 1997; Hodges et al. 2001). Traps are set during the late afternoon and checked the next morning over 4 subsequent days.

Each trapped snowshoe hare is sexed, weighed (± 109), and the right hind foot measured (millimetres). Newly captured hares are tagged in each ear with No. 3 Monel tags from the National Band Company (Boonstra et al. 1998; Hodges et al. *1999a,* 2001). Adult males are defined as those with a pointed penis, while juveniles are those with a smaller, blunt, and barely eversible penis (Keith et al. 1968; Keith 1990). Females are described as adult when lactating or carrying a fetus according to the criteria of Keith et al. (1968) and O'Farrell (1965). When other methods were not applicable, those hares weighing less than 1100 g or with foot sizes less than 130 mm in June, August, or November were categorized as juveniles and became adults the March following their summer of birth. In this paper, population growth rate (A) was calculated from population abundance estimates during each primary occasion (Krebs 1999). Recruitment was estimated from the proportion of juveniles in the population in August each year. Differential survival of juveniles versus adults was estimated from the change in this proportion over winter. Body condition was estimated by dividing mass (grams) by right rear foot length (millimetres) (Bailey 1968). We used this estimate to describe the possible impact of climate variables that in turn might influence intra- and interannual population dynamics (O'Donoghue and Krebs 1992; Hodges et al. *1999b).*

Population density estimation

Snowshoe hare abundance was obtained from maximum likelihood estimators (Otis et at. 1978) assuming population closure. Moreover, these methods require that each marked animal can be uniquely identified and that at least three sampling periods are used. The abundance estimates were

used to inform a recent model of population density (Elford 2004) that relies on neither the size of the trapping grid nor estimation of the effective trapping area. The method relies on the estimated population size (M and capture probability *(p)* as wen as the mean distance between successive captures *(d),* which provide an estimate of the scale of individual movements. These closed-population capture-recapture data were used as inputs to the simulation model of the trapping process based on *(i)* spatially defined trap locations, *(ii)* the magnitude of individual hare movements, *(iii)* the overall capture probability, and *(iv)* the spatial scale of the detection function describing capture probabilities (Efford 2004). Density estimates were derived from this method based on model M_o (Otis et al. 1978). This model assumes equal capture probabilities and is generally biased low if these assumptions are not met (Otis et al. 1978). Although other available models accounting for changes in individual capture probabilities (M_h), behavior (M_b), and time effects (M_t) provided a better fit to the data at some capture occasions, we decided upon consistent use of this model (M_0) with a known bias as is recommended for such longer-term data sets (Menkins and Anderson 1988; Boulanger and Krebs 1994; Krebs 1999).

Data analyses

Climate data pertainmg to daily air temperature (mean, minimum, and maximum) and precipitation (as both rain and snow) were obtained from the National Climatic Data Center for a climate station in Fairbanks, Alaska, for the period of our time series, 1998-2008. We performed simple and multiple regression models with climate variables and interactions among the climate variables (temperature, growing degree-days, freezing degree-days, precipitation, and frequency of snow fall events) against several demographic parameters, including population density, recruitment, apparent survival, and age structure. All analyses were performed using PROC GLM in the statistical software package SAS v. 9.1.3 (SAS Institute Inc., Cary, North Carolina).

Results

Population dynamics, 1999-2008

The abundance of snowshoe hares varied over 14-fold from the peak in 1999 through 2008. The highest densities were found during the fall (August) trapping sessions in 1999 (6.6 ± 1.9 hares·ha^{-1}) and 2008 (3.2 ± 0.6 hares-ha^{-1}) compared with 0.4-0.8 hares·ha^{-1} during the low of the population cycle (2001-2004) (Fig. 1). Apparent rates of population growth (∧)during summer varied over fourfold from a low (∧∼ 1.83) in 2002 to a high (^~8.00) in 2008. Finite population growth rates during summer decreased over threefold during the population decline from 1999 to 2003 (Fig. 2), which was followed by a significant downturn in overwinter abundance (^~ 0.16-0.27) during these years. A lower rate of overwinter population decline in 2004 started the population on recovery after which recruitment during summer exceeded mortality over winter, especially during 2007-2008 (Fig. 2).

During the study period reported here, annual air temperatures broken down by season (fall, spring, summer, and winter) were fairly stable (Fig. *3a).* Summer temperatures typically averaged 15 °C and winter temperatures averaged about -20 °C. Winter and autumn temperatures tended to be a bit warmer during the decline and low phase of the snowshoe hare cycle. Overall, annual mean temperature increased slightly over the study period yielding an 8-day longer growing season (Alaska Climate Research Center 2009, http://climate.gi.alaska.edu/Fairbanks). Total snowfall decreased steadily from a high of about 175 cm following the 1999 population peak to approximately 110 cm at the end of the low in the cycle (Fig. *3b).* By contrast with winter, the duration of the decline and low phase was associated with increased (eightfold) spring precipitation but no change in summer rainfall. Further, the increase phase of the cycle was associated with greater summer precipitation but no change in fall and winter precipitation (expressed as snow-water equivalents) (Fig. *3b).*

Fig. 1. Densities of snowshoe hares on the BNZ LTER riparian trap grid, 1999–2008.

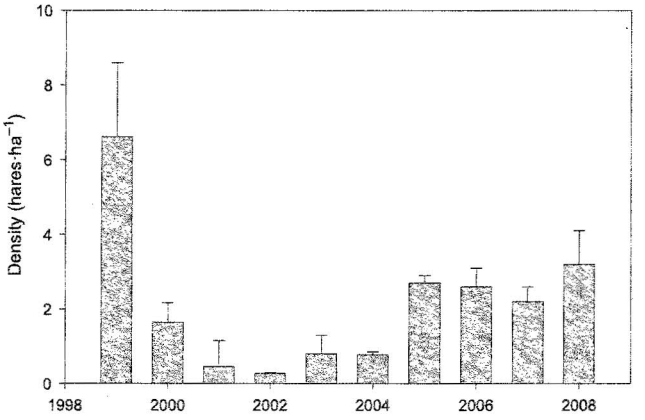
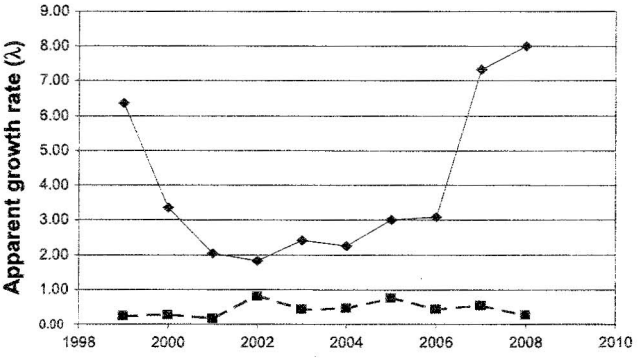


Fig. 2. Rates of finite population growth during summer (solid line) and winter (broken line) on the BNZ LTER riaparian trap grid, 1999–2008.



Age structure

The proportion of juveniles in the population varied from a high of 83% in August 1999 to a low of 17% in March 2005 (Fig. 4). The large overwinter reduction in the proportion of juveniles in all years except 2007-2008 suggests that overwinter mortality disproportionately affects the young-of-the-year and is a major factor contributing to the population decline. During 2007-2008 (corresponding to the near-peak

Fig. 3. Interannual patterns of (*a*) average seasonal air temperatures and (*b*) precipitation distribution, Fairbanks Alaska, 1999–2008. Data are from the National Climatic Data Center for a climate station in Fairbanks, Alaska.

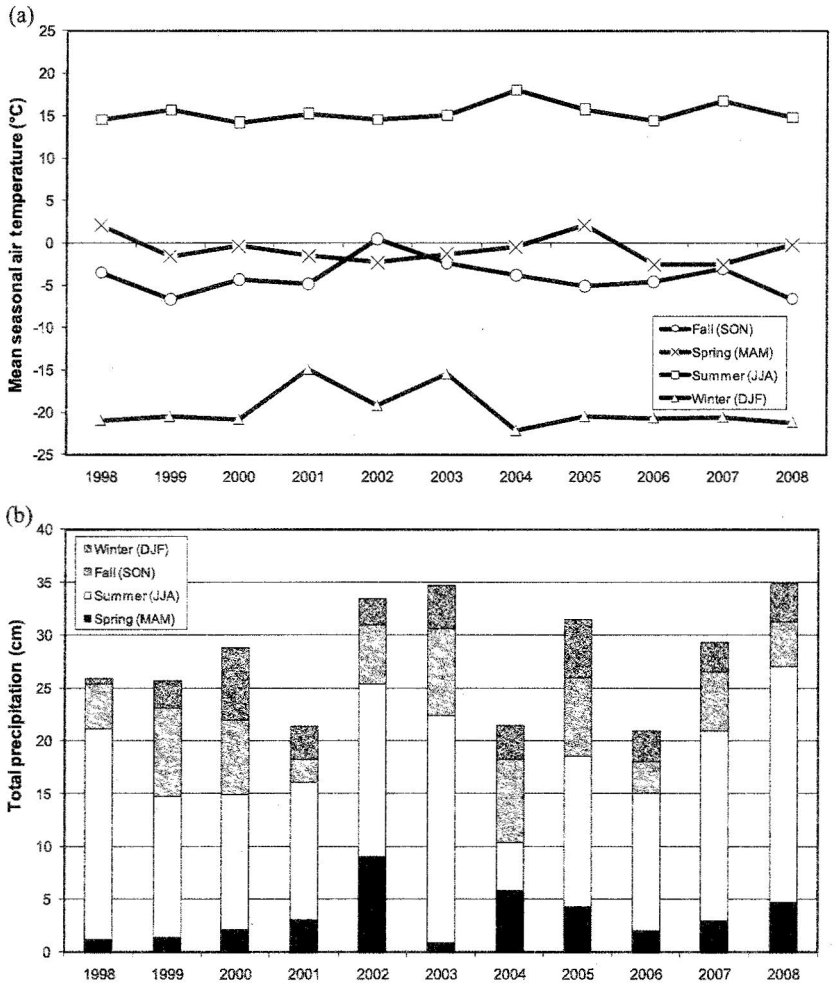
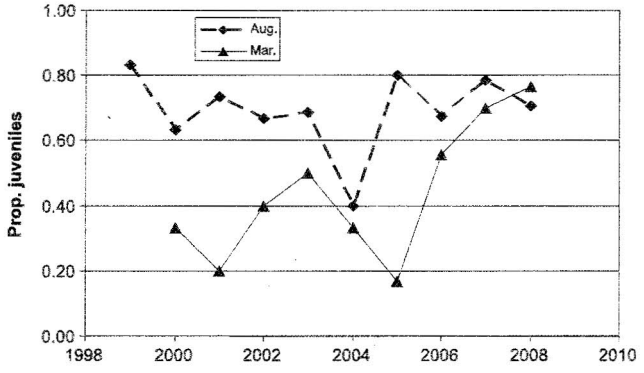


Fig. 4. Proportion of juveniles in the population of snowshoe hares during fall (August) and late winter (March) on the BNZ LTER riparian trap grid, 1999–2008.



of the cycle), the proportion of juveniles in the population remained fairly stable over winter, suggesting that juvenile mortality rates were indistinguishable from those of the adult segment of the population (Fig. 4).

Temporal trends in body mass

Body mass of adult hares averaged about 1600 g in the fall, while the average hind foot length was 138 mm, giving a body condition score of 11.6. Body condition scores ranged from 10.8 to 14.0. Both adult and juvenile hares exhibited changes in body mass over winter as a function of body mass in the fall, but in opposite trajectories. On an individual basis, most adult hares lost mass over winter, while most juveniles gained mass (Fig. 5). The rate of change was greatest for hares weighing less than 1200 g or more than 1800 g in August. The lightest hares gained over 60% mass over winter. while the heaviest hares lost nearly 20% of their autumn mass. Mass of adult hares over winter was inversely related to cumulative winter precipitation ($F_{[1,8]} = 8.38$, $p = 0.027$) but not winter temperature ($F_{[1,8]} = 1.61$, $p = 0.184$).

Body mass of adult hares also changed during the population cycle. Following the population peak in 1999, body mass decreased significantly along with population density until 2003 (Fig. 6), after which body mass gradually recovered, especially during the latter stages of the cycle (2006-2008). Body condition scores for adult hares varied from approximately 8 to 14 during the recent population cycle.

Fig. 5. Changes in overwinter body mass of individual snowshoe hares in relation to body mass in autumn, BNZ LTER riparian trap grid.

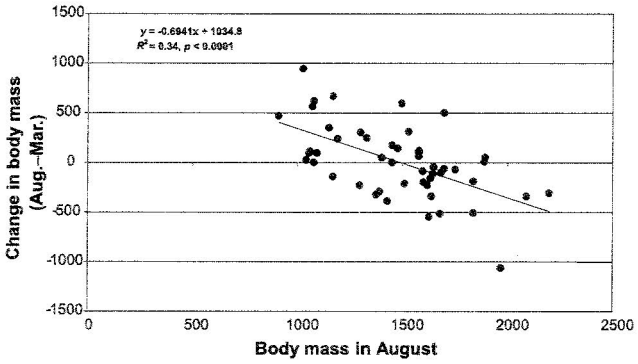
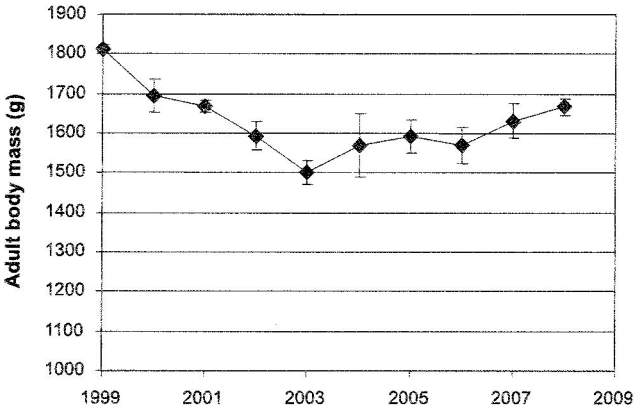


Fig. 6. Changes in body mass of adult snowshoe hares on the BNZ LTER riparian trap grid, 1999–2008.



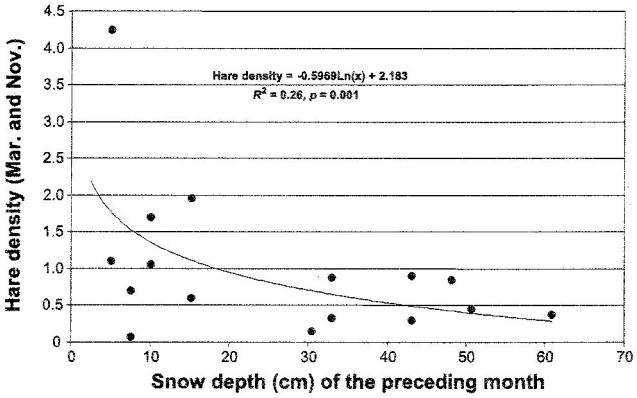
However, body condition was unrelated to population density, indicating that the reduction in body mass of hares during the low of the cycle represented smaller hares rather than hares in poor body condition.

Effects of climate parameters on snowshoe hare demography

We detected a moderate, inverse relationship between late-winter densities of snowshoe hares and snow depth (Fig. 7), suggesting that greater snow depth imparts a negative effect on hare populations during winter, as has been suggested in previous studies (Meslow and Keith 1971). However, this effect may be better explained by changes in the timing of snowfall, For example, early-winter population declines were greatest in years with shallow snow in early winter and in years of deep snow in early winter, resulting in a significant curvilinear relationship (Fig. 8), The same functional relationship described population decline over the entire winter: however, this relationship was not statistically significant.

Summer precipitation regimes exhibited a similarly weak, although positive relationship to snowshoe hare population growth (Fig. *9a).* Summer heat sum (growing degree-days) explained more of the variation in population growth rate (32%) than did total precipitation (Fig. *9b),* However, population growth appeared to be greatest during summers of intermediate growing degree-days, i.e., relatively cold or hot summers curtailed population growth rates.

Fig. 7. Densities of snowshoe hares in relation to snow depth on the BNZ LTER riparian trap grid, 1999–2008.



Overwinter population declines are associated with a reduction in the proportion of juveniles in the population (Fig. 4), which appears to be related to the frequency of snowfall events (Fig, 10). Despite large variation in body condition as noted above, we did not detect a consistent trajectory in this parameter over the population cycle. Likewise, cold winters had insignificant effects on body condition. Thus, overwinter body condition appeared to be insensitive to air temperature, suggesting that hares are able to compensate behaviorally for low winter temperatures.

Discussion

Snowshoe hare populations in the northern boreal forests, such as interior Alaska, typically exhibit greater population fluctuations than more southern populations of snowshoe hares (Murray 2000). Although we observed order-of-magnitude differences in population densities during this study, over the last 4 years of the data series (2005-2008), the fall population of snowshoe hares remained high and stable. This population trend follows 4 years, with a l-year time lag, of above-normal temperatures for October and below-normal snow fall. Moreover, the start of this significant rate of population recovery occurred following two very high wildfire years, which were also associated with greater over-winter survival of juveniles relative to adult snowshoe hares Over all years, the snowshoe hare population increased significantly (up to eightfold) during summer and strongly declined (down to 84% reductions) during winter. We found no relationship between the rate of population increase during summer and decline over winter, however, suggesting that these processes are largely independent. Population growth during summer was proportional to precipitation and growing degree-days, suggesting that increased food abundance, and possibly food quality, favor population growth. However, litter size is fairly constant in northern populations of snowshoe hares (Hodges et al, 2001), so other factors, such as survival of juveniles, which can vary by sixfold depending on the phase of the cycle (O'Donoghue 1994; Gillis 1998: Krebs et al. 2001), probably exerted a more significant control over population growth.

Fig. 8. Effect of early-winter snowfall on the population growth of snowshoe hares on the BNZ LTER riparian trap grid.

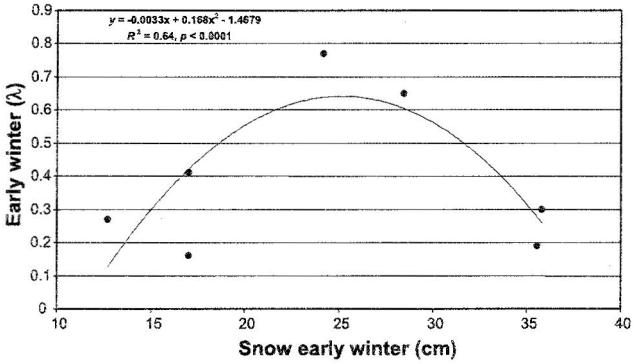
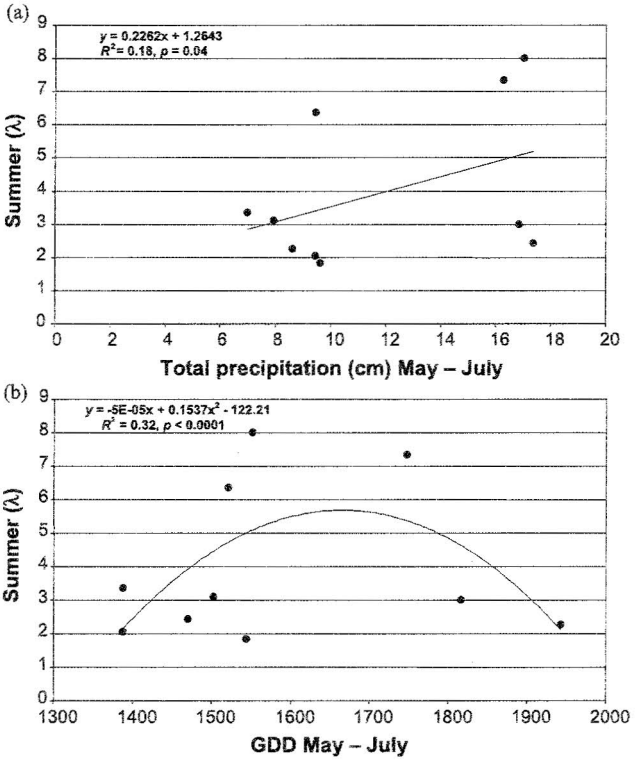
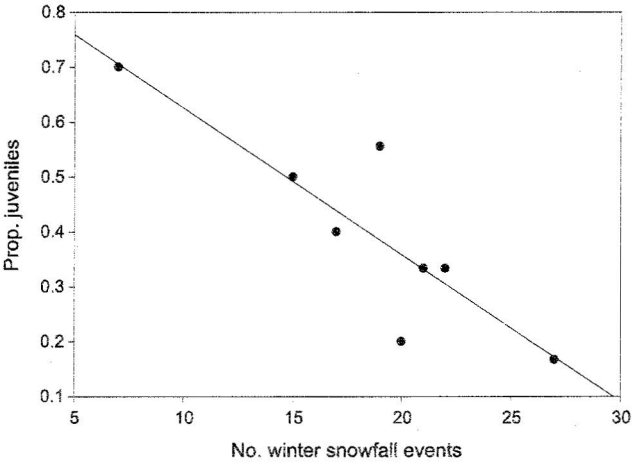


Fig. 9. Relationship between summer population growth of snowshoe hares and (*a*) total precipitation and (*b*) summer growing degree-days (GDD) on the BNZ LTER trap grid.



The abundance of snowshoe hares at our study site typically declined significantly during early winter, and this rate of population decline was much greater than later in the winter. Ongoing mortality studies using radiotelemetry support this observation (K. Kielland, unpublished information). One obvious factor in the population decline in early winter is the high proportion of juveniles in the population that generally exhibit much greater mortality rates than do adults (O'Donoghue 1994; Hodges et al. 2001). The onset of cold temperatures, snowfall and decreased cover as well as the physiological changes associated with molt and a radical change in diet represent a plethora of challenges to survival of young snowshoe hares, despite being in a positive growth

Fig. 10. Proportion of juveniles in the snowshoe hare population BNZ LTER riparian grid in relation to frequency of overwinter snowfall events (WSE), 1999–2008. Proportion of juveniles = 0.973 – 0.029(WSE) (R^2 = 0.61, p = 0.023).



phase. However, we did not detect a significant relationship between body condition and population density. Similar observations have been made of snowshoe hares in the Yukon (Hodges et al. 2006). Nor did winter weather appear to have a significant effect on body condition as such. Body condition decreased approximately 12% in early winter as a function of precipitation, but the latter explained less than 20% of this variation. Moreover, early winter also represents a time of increased predation rates from mammalian predators (Hodges et al. 2001), especially coyotes and lynx, which are common in the study area. These predators appear to have a negligible impact on leveret survival during summer but become major sources of mortality in winter (O'Donoghue et a1. 1997, 1998). Whereas the cumulative effects of temperature (expressed as freezing degree-days) had no detectable impact on the population decline, snow depth did have a significant, but variable, effect (Fig. 8). We hypothesize that the relationship between early-winter population decline and snow depth could stem from an interaction between cover and predation. During years of shallow snow, cover is relatively poor and mortality increases. In years of intermediate snow depth (15-30 cm), hares are afforded better cover and can also move with relative ease resulting in reduced mortality rates. However, when snow depths are greater than 30 cm, the mobility of snowshoe hares may be reduced disproportionately relative to their mammalian predators, such as coyotes and lynx, and mortality rates increase accordingly. It is relevant to note that this is largely an early-winter phenomenon during a time when the snow has a low density and provides poor mechanical support for the hares. As the snowpack settles over winter and snow density increases, snowshoe hares move with ease on top of the snowpack, and by late winter, it makes no locomotive difference to them if the snow depth is 50 or 100 cm. In a similar vein, the greater reduction in proportion of juveniles in the population during winter of more frequent snowfalls suggests that these weather events have a greater impact on young hares than does snow depth per se.

Climate-induced changes to the boreal forests

The mosaic of ecosystem types that characterize the landscape of interior Alaska is the result of both physiographic variation and disturbance history. In particular, the distribution pattern of coniferous and deciduous forests reflects the fire history of the region (Viereck 1973; Dyrness et al. 1986). Fire is the most common natural disturbance in the boreal forest, and the importance of this agent of ecosystem change has increased in the last two decades, during which the annual area burned in western North America has nearly doubled (Kasischke and Turetsky 2006; Kasischke and Chapin 2008). In Alaska, the frequency and intensity of fires have similarly increased, with 80% of the land area burned over the last 21 years occurring in only seven of those years. Whereas postfire vegetation development in boreal ecosystems may follow several pathways of succession, depending on fire severity (Van Cleve et al. 1996; Johnstone and Kasischke 2005), fire is undoubtedly an important factor shaping the habitats of many mammalian herbivores in Alaska, including snowshoe hares (Wolff 1978). Because the amplitude of the snowshoe hare cycle is related to fire history (Grange 1965; Fox 1978), the projected increases in fire frequency and severity (Flannigan et al, 2005) suggest increased cyclicity in snowshoe hare populations. Moreover, broad-scale climate factors controlling fire regimes in North America provide a convincing explanation for significant biogeographic variation in the toxicity of forage species sought by snowshoe hares (Bryant et al. 1994, 2009), which has a range of indirect effects on ecological functions of boreal forests (e.g., browsing intensity, herbivore abundance, and carbon cycling).

Lastly, the rapid warming of interior Alaska has resulted in longer growing seasons (50% increase over the last century). Whereas snowmelt and snow-up are governed by temperature (growing degree-days), molt in snowshoe hares is largely controlled by photoperiod. Thus, an extension of the snow-free period during these shoulder seasons represents an evolutionary bottleneck for hares, the magnitude of which is proportional to the asynchrony between the timing of molt and presence-absence of snow cover resulting in greater vulnerability to predation. The stochastic interaction between abiotic and biotic factors may have strong synergistic effects on snowshoe hare populations. The strength of these interactions may increase in importance if the asynchrony of environmental seasonality and life history traits of snowshoe hares becomes more pronounced as the climate continues to change.

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