

# What factors determine cyclic amplitude in the snowshoe hare (*Lepus americanus*) cycle?

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**Abstract:** Snowshoe hares (*Lepus americanus* Erxleben, 1777) fluctuate in 9–10 year cycles throughout much of their North American range. These cycles show large variations in cyclic amplitude and we ask what factors could cause amplitude variation. We gathered data from 1976 to 2012 on hare numbers in the boreal forest of Alaska, Yukon, Northwest Territories, and northern British Columbia to describe the amplitude of hare fluctuations and to evaluate four possible causes. First, weather could cause variation in amplitude via hare reproduction or survival, but this mechanism does not fit our data. Second, bottom-up processes involving forest succession could explain amplitude variation through changes in winter forage availability, but succession is too slow a variable in our study areas. Third, plant defenses entrained by hare over-browsing in one cycle can produce variation in plant quality and quantity in subsequent cycles. A mathematical model suggests this is a possible explanation. Fourth, predator recovery following the cyclic low is inversely related to hare cyclic amplitude, and the existing data are consistent with this mechanism. A standardized regional monitoring program is needed to improve our understanding of cyclic amplitude variation in hares and the possible role of predators and winter foods in affecting amplitude.

**Key words:** snowshoe hare, *Lepus americanus*, 10 year cycle, boreal forest, predation, Canada lynx, *Lynx canadensis*, succession, secondary chemicals, weather.

**Résumé :** L'abondance des lièvres d'Amérique (*Lepus americanus* Erxleben, 1777) fluctue selon des cycles de 9–10 ans dans une bonne partie de l'aire de répartition nord-américaine de l'espèce. Ces cycles présentent de grandes variations d'amplitude, et nous nous penchons sur les facteurs qui pourraient causer ces variations. Nous avons recueilli des données de 1976 à 2012 sur le nombre de lièvres dans la forêt boréale de l'Alaska, du Yukon, des Territoires-du-Nord-Ouest et du nord de la Colombie-Britannique afin de décrire l'amplitude des fluctuations des lièvres et d'évaluer quatre causes possibles. Premièrement, si la météo peut causer des variations d'amplitude en agissant sur la reproduction ou la survie des lièvres, ce mécanisme ne concorde pas avec les données. Deuxièmement, des processus ascendants associés à la succession forestière pourraient expliquer les variations d'amplitude par des variations de la disponibilité de nourriture durant l'hiver, mais la succession est une variable qui évolue trop lentement dans les zones étudiées. Troisièmement, les mécanismes de défense des plantes induits par le surbroutement des lièvres durant un cycle peuvent produire des variations de la qualité et de la quantité des plantes durant les cycles subséquents. Un modèle mathématique suggère qu'il s'agit d'une explication possible. Quatrièmement, le rétablissement de prédateurs suivant le creux d'un cycle est inversement relié à l'amplitude du cycle des lièvres, et les données concordent avec ce mécanisme. Un programme de surveillance régionale normalisé est nécessaire pour améliorer la compréhension des variations de l'amplitude des cycles des lièvres et de l'effet éventuel des prédateurs et de la nourriture hivernale sur cette amplitude. [Traduit par la Rédaction]

**Mots-clés :** lièvre d'Amérique, *Lepus americanus*, cycle décennal, forêt boréale, prédation, lynx du Canada, *Lynx canadensis*, succession, substances chimiques secondaires, météo.

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## Introduction

Snowshoe hares are a classic textbook example of animals with relatively regular population cycles (Elton and Nicholson 1942; Krebs 2009, p. 203). Three key questions arise from these cycles: first, what causes the changes in population growth rates; second, what causes regional synchrony; third, what produces variations in amplitude of cyclic peaks? In the past much interest has focused on the causes of hare population fluctuations, and both predation and food supplies have been manipulated to delimit the causal nexus (Keith 1990; Krebs et al. 1995; Boonstra et al. 1998; Sheriff et al. 2010). Regional synchrony and asynchrony have been addressed less, and both regional weather and predator movements have been suggested as the cause of synchronized dynamics (Ranta et al. 2006; Krebs et al. 2013). The question of what factors cause variation in cyclic amplitude has not been addressed directly, and the implicit assumption has been that the answer lies either in plant–herbivore interactions, in predator recovery rates from the cyclic low, or both (Blasius et al. 1999).

Much of the discussions of amplitude variations in hare cycles have centered on the fur return data of Canada lynx (*Lynx canadensis* Kerr, 1792), a specialist snowshoe hare predator (Ranta et al. 1997; Haydon and Greenwood 2000). Moran (1953) pointed out very early that the period between lynx cyclic peaks was remarkably constant, but the amplitude varied greatly. Analyses of fur return data have led to the development of a series of lynx dynamics models including chaotic food-web models that describe how synchrony can be maintained in coupled populations along with large variations in cyclic amplitude (Schaffer 1984; Blasius et al. 1999). The ecological mechanisms driving the amplitude variations in these models are not clear.

Limited long-term monitoring of snowshoe hares has been conducted at various locations throughout the north, but these data have never been collectively analysed to explore the variability of cyclic amplitudes and how they differ locally and regionally. Using data on snowshoe hare abundance from Alaska, Yukon, Northwest Territories, and British Columbia covering the period 1976–2012, we test four hypotheses that attempt to explain the variation in the hare cycle's amplitude.

We begin with three assumptions about snowshoe hare population cycles. First, we assume that a major factor affecting population increase and decline is predation by a suite of predators, typically Canada lynx, coyotes (*Canis latrans* Say, 1823), red foxes (*Vulpes vulpes* (L., 1758)), Northern Goshawks (*Accipiter gentilis* (L., 1758)), and Great-horned Owls (*Bubo virginianus* (Gmelin, 1788)) (O'Donoghue et al. 1997, 1998). Second, we assume that weather has some modifying effect on hare cycles, possibly by affecting early summer survival of juveniles (Kielland et al. 2010). Third, we assume that hares, like all herbivores, are strongly affected by the availability and quality of their forage plants, and that browsing may have delayed effects on vegetation condition. All hypotheses assume that sufficient quantities of good-quality food are necessary for the hares to increase in abundance.

Given these assumptions, we consider four hypotheses that could cause variations in hare cyclic amplitude:

1. Weather hypothesis: variations in weather, particularly May temperature and precipitation, affect juvenile hare mortality or reproduction directly and thus cause amplitude variations to be positively correlated spatially and temporally. This hypothesis predicts that nearby sites with the same weather will show the same amplitude sequence over time.
2. Forest succession hypothesis: the abundance of good winter food that occurs in the early to mid-stages of forest succession releases hares from food limitation allowing their numbers to increase. During forest succession, good winter food is replaced by poor winter food resulting in increasing food limitation that causes the cycle's amplitude to decline as forest succession proceeds.

3. Plant defense hypothesis: severe browsing by hares in the winter of a high amplitude peak increases the toxicity of hares' preferred winter food resulting in the next hare cycle of reduced amplitude because of higher plant chemical defense compounds.
4. Predator hypothesis: the abundance of predators during the cyclic low determines the time lag before predation mortality exceeds hare reproductive rates, and thus the cyclic peak density. This hypothesis predicts that a low amplitude cycle will be preceded by relatively high predator abundance in the previous low phase so that cyclic amplitude is negatively correlated with the minimum of predator abundance.

Figures 1a–1c gives a schematic illustration of the patterns expected from hypotheses 2, 3, and 4. Hypothesis 1 is not illustrated but would be expected to create a series of cycles of varying amplitudes that correlate with local weather conditions. More complex models involving two or all of these mechanisms could be postulated, but it seems difficult enough at present to evaluate the four simple models. Our analysis is based upon estimated hare abundance, amplitudes of hare cycles, and lynx population trends, as well as a mathematical model of plant defense, to demonstrate the possibility of hypothesis 3.

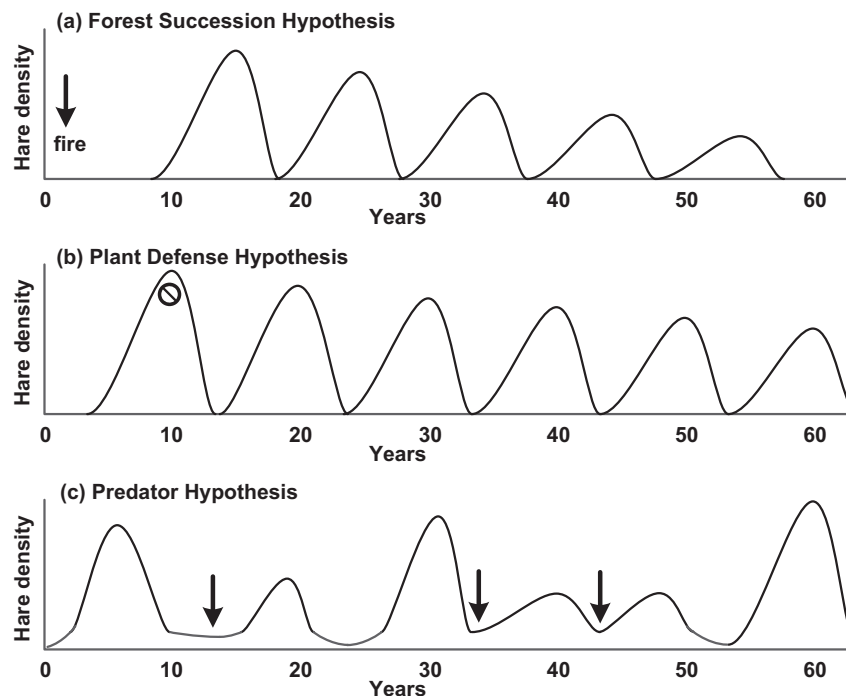
The limitations of the questions we are asking and the data we have available should be kept very clear in the evaluation that follows. We are asking about the amplitude of the hare cycle at the local scale within a study area (our measurement units) and the variation in amplitude over short periods of time of the order of two to four hare cycles within that study area. We cannot address here global issues of landscape ecology because we do not have data on a landscape scale, nor can we address the very long-term changes that might be associated with climate change over hundreds of years.

## Materials and methods

We have relied on three methods to estimate the abundance of hare populations. The most accurate method is mark–recapture estimation with at least two samples per year (Kluane Lake, Yukon, and Bonanza Creek, Alaska). The details of these mark–recapture methods are provided by Krebs et al. (2001b) and Kielland et al. (2010). This method is at a small spatial scale and very labor intensive. The majority of our hare data come from annual counts of hare pellets on fixed plots, following the standardized protocol described in Krebs et al. (2001a). This method is relatively quick and can be done over a large spatial scale. Pellets are cleared off these plots each year so the annual deposition of pellets is measured. These pellet counts have been transformed to absolute hare density by the use of the regression given for Kluane Lake in Krebs et al. (2001a). There is a large assumption built into this conversion, i.e., that the regression obtained for Kluane Lake will apply elsewhere in the boreal forests of northwestern North America. Present evidence suggests that this assumption is correct for other areas (Mills et al. 2005). Some limited data are based on road counts, which are the numbers of hares sighted along a standardized length of highway (Arthur and Prugh 2010) or the number of hares observed per field day (McIntyre and Schmidt 2012). These data are reliable for estimating population peaks and troughs if the density changes are sufficiently large and they have the advantage of large spatial scale. They produce data highly correlated with those obtained by pellet counts (Arthur and Prugh 2010).

We estimate the amplitude of the hare cycle in two ways. First, we estimate amplitude in the traditional manner as the ratio of peak density to low density. Cyclic peak density is the largest abundance estimate obtained and typically occurs in the autumn sampling. The cyclic low density is typically obtained in the spring sampling period. One difficulty with this ratio measure is that abundance in the low phase is difficult to estimate accurately. We use the ratio of the hare peak abundance to the abundance of

**Fig. 1.** Schematic representation of the predictions of three single-factor hypotheses to explain variations in snowshoe hare (*Lepus americanus*) cyclic amplitude. Hare cycles are highly simplified. (a) The arrow in the forest succession diagram indicates a fire or other disturbance after which there is a time lag before shrub regrowth provides adequate cover for hares. (b) The symbol in the plant defense diagram represents a very high peak year (a “super peak”) in which hares severely browsed the winter vegetation. We do not know how quickly vegetation recovers from severe browsing in the boreal forest, so this sequence is hypothetical. (c) Arrows in the predator diagram indicate low and increase phases in which either predators survived the low phase in moderate abundance or immigrant predators arrived in a local area from distant populations so that predator populations start increasing from relatively high levels. The time scale is indicative rather than absolute.



hares in the previous low as the first measure of amplitude. A second method is simply to use measures of peak abundance as an index of amplitude. This index is reliable only if the density in the low phase is nearly equal in all areas studied or in all cycles studied on the same study area.

Lynx population numbers are available for the Kluane Lake site, and they were obtained from snow tracking data along a fixed 25 km trail counted as often as possible within 1–2 days of fresh snowfall during the winter months (O'Donoghue et al. 2001). For all other sites, we use an index of lynx abundance based on the number of lynx trapped per lynx trapper per winter. Because fur trapping is often prohibited or trappers choose not to trap in Yukon and Alaska when lynx are in low abundance, we cannot measure the abundance of lynx at their lowest density via fur returns. Instead, we use an estimate of lynx population growth from a log-linear regression of fur returns over time for the 3–5 years of the hare cycle increase. Lynx fur trapping indices map directly to the hare cycle but are not an absolute measure of lynx densities (McKelvey et al. 2000).

Statistical analyses of correlations, ANOVA, and simple linear regressions were carried out in NCSS version 8 (NCSS, LLC, Kaysville, Utah, USA; <http://www.ncss.com/>). All snowshoe hare abundance estimates used here are given in the Supplementary material in Krebs et al. (2013).

## Results

### General observations of geographic variation in hare cycle amplitude

Peak densities of snowshoe hares vary from one cycle to the next, and Table 1 summarizes this information for all our sites. Figure 2 illustrates box plots for the two possible measures of cyclic amplitude (high/low) depending on whether the previous

low is used or the following low. There is no significant difference between these amplitude estimates with median values of 14 and 18 (Mann–Whitney  $U$  test,  $p = 0.5$ ,  $n = 19$ ) and mean values of 28 and 29. There are a low number of replicated estimates of amplitude. Seven areas have two to four estimates of amplitude (Kluane, Delta Junction, Denali, Kenai, North Slave – South Slave, Inuvik, and Wrangell–St. Elias). We could detect no differences in amplitudes (high/previous low) among these seven areas (ANOVA,  $F_{[6,10]} = 0.74$ ,  $p = 0.6$ ). We conclude that over this geographic area, cyclic amplitudes (high/low) are about 20- to 30-fold, on average, with a range from 2- to 3-fold up to about 100-fold but with most cycles showing an amplitude of 10- to 50-fold.

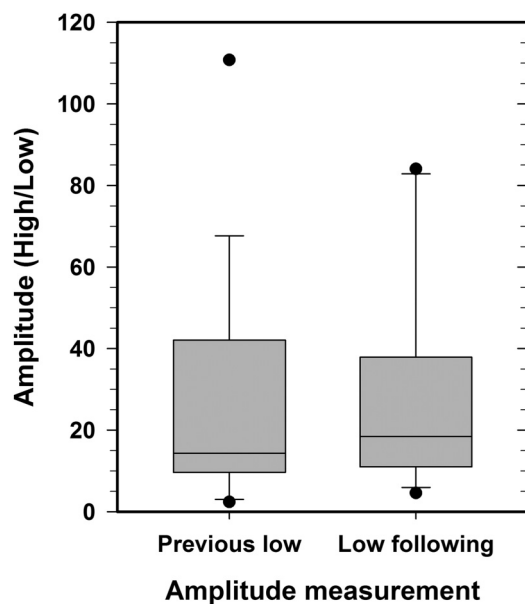
If cyclic amplitude is measured simply by the density of hares at the peak of the cycle, our data fall into two groups. Bonanza Creek in Alaska forms one group, with a mean peak density of 6.3 hares/ha ( $n = 2$  cycles), and all the seven other areas with more than two estimates of peak density form a second group with a mean peak density of 2.2 hares/ha. We note that this measure of amplitude is poorly correlated with the other two more conventional measures that utilize peak/low abundance ( $r = 0.32$ ,  $n = 15$  for both measures). We think, following McKelvey et al. (2000), that the intuitive idea that amplitude should be measured simply by the cyclic peak abundance is less informative than the measurements of amplitude that use the ratio of cyclic peak to cyclic low hare abundance. The main reason for this is that the cyclic low density is highly variable so that not all cycles start from the same baseline. The coefficient of variation of peak hare densities in our data are 63%, while the coefficient of variation of low densities is 83%. Whatever measure of cyclic amplitude is used, our results are based on relatively few hare peaks and further data on all sites would be desirable.

**Table 1.** Snowshoe hares (*Lepus americanus*) peak abundance estimates used in this analysis of cyclic amplitude, years of data since the previous low, and estimates of cyclic amplitude.

Area	Peak year	Season	Maximum density (no. of hares/ha) or maximum count	Minimum density (no. of hares/ha) or minimum count	Years since previous low	Amplitude (high to previous low)
Kluane Lake, Yukon	1981	Fall	4.43	0.04	4	110.75
	1990	Fall	1.68	0.12	4	14.32
	1998	Fall	2.73	0.07	4	42.06
	2006	Fall	1.15	0.02	4	67.65
Bonanza Creek, Alaska	1999	Fall	6.53			
	2009	Fall	6.00	0.26	7	23.08
Skeena River, British Columbia	2003	Fall	1.51			
	1999	BBS	851*	4*	4	21.25
Delta Junction, Alaska	2006	BBS	1291*	2*	2	64.50
	1989	Spring	6.971			
Denali National Park, Alaska	1999	Spring	8.031	0.63	5	12.66
	2009	Spring	40.351	0.63	7	63.65
Kenai Peninsula, Alaska	1983	Fall	3.55			
	1999	Fall	1.23	0.15	8	8.20
	2011	Fall	1.45	0.13	6	11.15
Mayo, Yukon	1999	Fall	2.741			
	2006	Fall	4.521	0.18	5	25.261
North Slave–South Slave, Northwest Territories	1990	Fall	2.98			
	1999	Fall	2.38	0.22	6	10.82
	2009	Fall	1.24	0.52	3	2.38
Inuvik, Northwest Territories	1997	Fall	2.20	0.64	8	3.44
	2009	Fall	1.11	0.37	4	3.00
Tetlin, Alaska	2008	Fall	0.95	0.04	7	23.75
Wrangell–St. Elias, Alaska	1991	Fall	2.85			
	2001	Fall	3.93	0.29	7	13.58
	2009	Fall	2.68	0.28	5	9.65

Note: Site locations are mapped in Fig. 3 (p. 566) and Table 1 (p. 566) of Krebs et al. (2013). BBS, Breeding Bird Survey routes.

\*Abundance estimates based on road counts so these are not densities (numbers of hares/ha) but numbers of hares per unit distance.

**Fig. 2.** Box plots of the amplitude of snowshoe hare (*Lepus americanus*) cycles measured in all the areas listed in Table 1. The median amplitude if the previous low abundance is used was 14.3; if the following low is used, the median amplitude was 18.4.

The demographics of cyclic amplitudes are relatively simple: the starting low density of hares, their rate of population growth, and the number of years of the increase phase over which this growth rate is expressed all combine to determine the cyclic amplitude. We wish to determine which mechanistic drivers set this demographic stage.

### Tests of hypotheses

Given data on hare abundance over a limited number of cycles, we have attempted to evaluate the following predictions of each of the four hypotheses proposed in the Introduction:

1. Weather hypothesis: sites with similar climate or similar weather in May will have similar temporal patterns of amplitude variation.
2. Forest succession hypothesis: amplitude peaks occurring early in forest succession will be high because the quantity and quality of winter food will be high, and subsequent peaks will decline as succession proceeds and the quantity and quality of winter food declines.
3. Plant defense hypothesis: the increase in toxic antibrowsing defense of the hare's preferred winter browse species initiated by a very high peak hare density will result in a long period of amplitude decline followed by a toxin-determined food – hare density stable limit cycle.
4. Predator hypothesis: relatively high abundance of predators in the low and increase phase will generate a low amplitude hare peak and vice versa.

### Hypothesis 1: correlated regional weather determines amplitudes

The mechanism behind this explanation is that severe winters or summers affect hare mortality rates, which reduces the rate of population growth of hares, but not of their predators. This is a simplified landscape or regional hypothesis because it assumes that over a region of 500–1000 km, the weather is highly correlated. In our analysis, we consider both long-term weather trends (climate normals) and weather conditions during a specific time period when hares may be most vulnerable (May). We realize that there are a large number of weather hypotheses and it is not possible to test every one with the limited data. We have picked the biologically most realistic hypothesis to consider here.



**Table 2.** Relative peak density of snowshoe hares (*Lepus americanus*) in 12 areas of northwestern North America.

Location	1970s	1980s	1990s	2000s
Central British Columbia				High
Central Northwest Territories	Very high	High	Moderate	Low
Inuvik, Northwest Territories			High	Low
Kluane Lake, Yukon	Very high?	High	Moderate	Low
Mayo, Yukon			Low-moderate	Moderate
Tetlin National Wildlife Refuge, Alaska	Very high		Low?	High
Wrangell-St. Elias National Park, Alaska	Very high	High?	High	Moderate
Bonanza Creek, Alaska	Very high*	Moderate?	High	High
Denali National Park, Alaska	Very high	Low	Low	High
Delta Junction, Alaska	Very high		Moderate	High
Koyukuk National Wildlife Refuge, Alaska	Very high	Low	High	Moderate
Kenai Peninsula, Alaska	Very high	High	Low	Low

**Note:** Peaks are classified within the decade in which they occurred. The very high or “super peaks” of the 1970s were mostly qualitative natural-history observations.

\*Documented by Wolff (1980).

Our observations reveal that no clear trend in cyclic amplitude is common to all sites (Tables 1, 2). This observation suggests that regional weather does not affect the cycle's amplitude, thus throwing doubt on hypothesis 1. The regional weather hypothesis can be tested more rigorously by comparing pairs of sites located within a few hundred kilometres of each other (Kluane Lake, Yukon, versus Mayo, Yukon; Bonanza Creek, Alaska, versus Denali Park, Alaska). The Kluane site is located about 325 km south of the Mayo site, while the Bonanza Creek site is located about 130 km north of the Denali site.

The climate normals (30 year averages of temperature (°C), total precipitation (mm), and snowfall (cm); Supplementary Table S1<sup>1</sup>) of these four sites used to test hypothesis 1 do not differ greatly: all pairwise correlations exceed 0.82 (Supplementary Table S2).<sup>1</sup> The weather hypothesis would, therefore, predict no great differences in the temporal variation in cycle amplitude existing among these four locations. However, variation in amplitude among these four locations after the very high hare peak of the early 1970s (J. Bryant and C.J. Krebs, personal observations) has been significant (Fig. 3; Tables 1, 2). Kluane Lake hare peaks have declined in the 1990s and 2000s to much lower levels than they were in the 1970s and 1980s (Fig. 3), and while the Kluane hare peak in 2007 was the lowest observed, Mayo (325 km away) had a moderate hare peak at that time. Similarly, Bonanza Creek had very high hare peaks in both 1999 and 2009 at the same time that Denali Park (153 km away) had a low hare peak in 1999 and a much higher peak in 2009. Analyses of hare population data in interior Alaska from 1999 to 2008 indicate that the amplitudes of hare cycles in this area were only moderately affected by variation in common weather parameters such as precipitation and temperature (Kielland et al. 2010).

We conclude that at each site in Yukon and Alaska, the amplitudes of hare cycles vary greatly over time and space. On a local scale of 100–200 km, amplitudes match, but on spatial scales greater than about 400 km, amplitudes do not match even though weather does (McCabe et al. 2012). These observations are inconsistent with the hypothesis that correlated weather determines cyclic amplitudes in this region of the snowshoe hare's range.

However, the possibility remains that variations in weather of a critical month in the hare's life cycle may influence regional variation in the cycle's amplitude. May is the most likely month in which regional differences in weather could result in regional differences in the cycle's amplitude. For example, a cold and wet May could reduce survival of the hare's first litter of leverets, thus affecting the amplitude of the hare cycle. However, the data pre-

sented in Supplementary Fig. S1<sup>1</sup> strongly suggest that variation in May temperature and precipitation is unrelated to the amplitude variation occurring among these four sites. Since hares have two to four litters during the summer, there is ample opportunity for compensatory survival of later litters if the May litter is affected by weather. O'Donoghue (1994) found that predation was the most common cause of death of juvenile hares during their first 30 days of life and weather was rarely a factor causing juvenile losses. It seems unlikely that weather will affect juvenile survival after the snow has melted in May in these northern localities.

To summarize, because we found no relationship between regional variation in the cycle's amplitude and regional variation in weather either at the level of climate normals or May temperature and precipitation, we have tentatively rejected the weather hypothesis as an explanation of amplitude variation in the hare cycle.

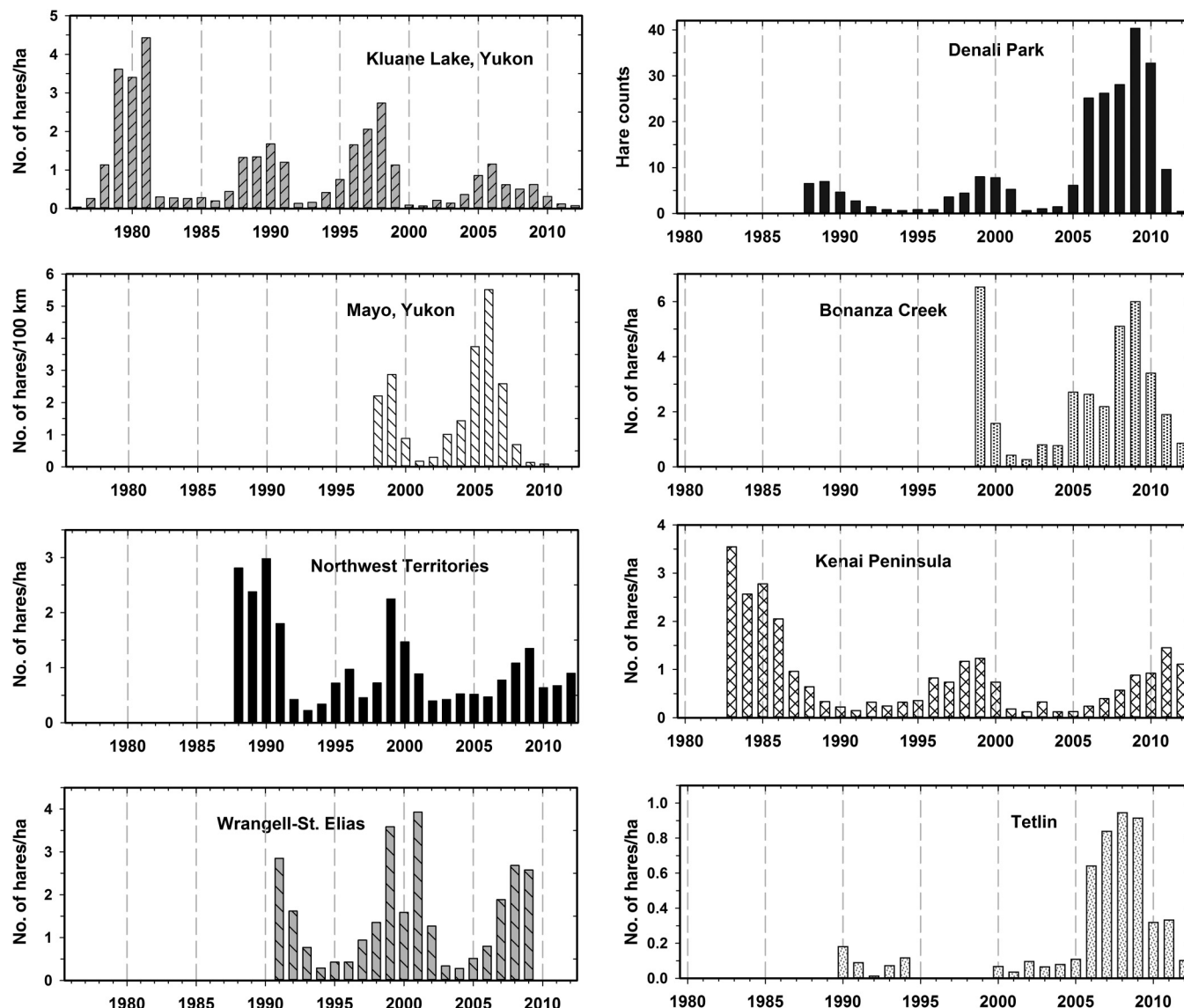
### Hypothesis 2: forest succession hypothesis

This hypothesis is based upon the widespread observation that both the quantity and the quality of the snowshoe hare's preferred winter browse, which is primarily the twigs of rapidly growing deciduous woody species such as willows (genus *Salix* L.) and birches (genus *Betula* L.), peaks relatively early in forest succession and then declines as these preferred browse species are replaced by slowly growing species such as evergreen spruces (genus *Picea* A. Dietr.) that are poor winter food for hares (Fox 1978; Bryant and Kuropat 1980; Bryant et al. 1983; Sinclair et al. 1988). Extensive work in eastern North America has shown that the initial stages of succession after logging are not preferred by hares and it is only after 10–35 years that optimal hare habitat is achieved in the southern part of the hare's range (de Bellefeuille et al. 2001; Homyack et al. 2007). High amplitude hare peaks that often occur relatively early in forest succession after disturbances such as wildfire or logging are generally followed by a period of amplitude decline during subsequent forest succession (e.g., Grange 1949, 1965; Bookhout 1965; Fox 1978; Bryant et al. 1983). The three most likely causes of declining amplitude are (1) increasing toxicity to snowshoe hares of slowly growing late-successional species such as spruce (Bryant and Kuropat 1980; Bryant et al. 1983); (2) declining quantity of suitable and accessible browse as the forest matures; and (3) decreasing horizontal cover in the form of dense thickets of tall deciduous shrubs and spruce saplings that snowshoe hares use to evade predators (Wolff 1980).

The following quote was taken from a “Refuge Notebook” written for the *Peninsula Clarion* newspaper by Ted Bailey, retired

<sup>1</sup>Supplementary text, Tables S1 and S2, and Fig. S1 are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2014-0159>.

Fig. 3. Snowshoe hare (*Lepus americanus*) abundance at two Yukon sites, Northwest Territories, and five Alaskan sites showing the discrepancies in peak amplitudes from sites near each other. Kluane Lake and Mayo are 325 km apart and Denali Park and Bonanza Creek are 153 km apart.



Supervisory Biologist of the Kenai National Wildlife Refuge (KNWR), Alaska. This quote suggests that the forest succession hypothesis could explain the amplitude decline that has been observed on KNWR since 1983 (Fig. 3):

On the Kenai Peninsula peak snowshoe hare densities in the 1947 burn declined about 50% between the 1984–85 and 1997–98 peaks. Measurements of vegetation in these habitats suggests less food is available to hares in the winter because of heavy browsing by hares during the past cycle, competition with and concurrent heavy browsing by moose, and a less dense protective understory. In contrast, hare densities in the younger 1969 burn were higher than in the 1947 burn area during the 1997–98 peak because of a more abundant food supply and increasing protective cover from spruce trees in the understory.

Although this hypothesis is generally supported by research done throughout the lowland boreal forests of North America (Fox 1978) such as the forest on the KNWR, there are notable examples of amplitude variation that this hypothesis cannot explain. In Alaska, Yukon, and Northwest Territories, the open forest that

occurs near treeline contains an abundance of comparatively poorly defended shrubs such as willow and shrub birch (*Betula glandulosa* Michx.) irrespective of the stage of forest succession after disturbances such as wildfire. Yet in these forest habitats, amplitude varies in the absence of recent disturbances. An example of this amplitude variation is the amplitude decline that has occurred at Kluane, Yukon, since hare cycle research began in the late 1970s (Fig. 3). The Kluane region has a low percent annual area burned, which ranges from 0.001% to 0.01% (Stocks et al. 2002). This indicates that fire return intervals in this region range from 100 to 1000 years. The estimated fire return interval on the specific 350 km<sup>2</sup> Kluane study site is in the order of 300–400 years (Dale et al. 2001).

To summarize, the forest succession hypothesis can explain some, but not all, of the observed variation in the hare cycle's amplitude. Thus, factors other than disturbance followed by forest succession must be involved in determining amplitude variation over the 20–40 year time scale that we deal with in this paper. This is especially true in subalpine forest ecosystems such as the Kluane, Yukon, site. The remaining two hypotheses, the plant

defense hypothesis and the predator hypothesis suggest two such factors.

### Hypothesis 3: plant defense hypothesis

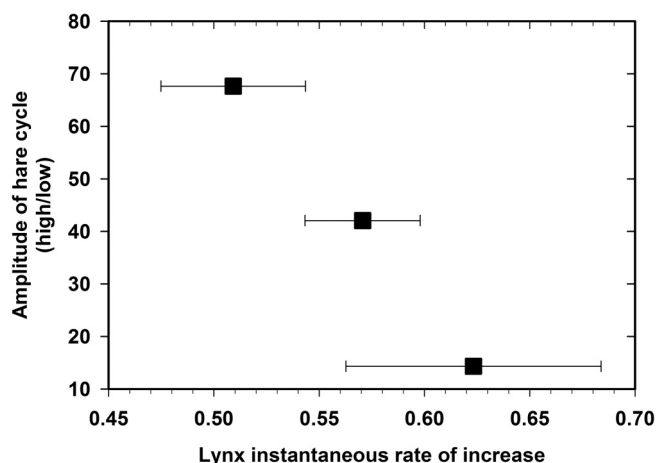
The biological basis of this hypothesis is that if, at the start of a cycle, the hare's favored food plants have minimal plant defenses, a super peak will be produced because the hares' nutritional condition will be optimal, improving both reproduction and survival. The physiological foundation of this hypothesis is the process of woody plant aging and the reversal of aging by pruning (Kozłowski 1971, chapter 4). Aging and its reversal by pruning (e.g., hare browsing) affect the toxic antibrowsing defenses of the snowshoe hare's preferred winter foods, the twigs of rapidly growing deciduous species such as willow and birch. The biological basis for this effect is given in Liu et al. (2012). The problem with evaluating this hypothesis is that we do not yet have replicated field studies of hare population dynamics and food-plant chemical defenses throughout several hare cycles in different parts of the geographic range of hares. Here we consider only the physiological basis of such a mechanism for variable cyclic amplitude.

Rongsong Liu (University of Wyoming, Mathematics Department) has used the simpler version of her model (Liu et al. 2012) to predict qualitatively how severe browsing by snowshoe hares in the winter of a very high hare peak should affect the amplitude of the hare cycle during subsequent cycles. *Betula glandulosa* was selected for the simulation because its twigs are a highly preferred winter food of snowshoe hares (Grange 1965; Pease et al. 1979; Smith et al. 1988; Krebs et al. 2001b) and the dammarane triterpenes that defend birch *B. glandulosa* twigs against hare browsing in winter have been chemically identified (Reichardt 1981; Reichardt et al. 1987; Williams et al. 1992). In the simulation, the duration of toxicity was set to 3 years, which is the period of time that the twigs of *B. glandulosa* growing near Fairbanks remain unpalatable to snowshoe hares after a severe browsing event (Fox and Bryant 1984) and is also the period of time that the concentration of dammarane triterpenes in the smaller diameter segments found at the tip of a *B. glandulosa* twig remains high (P.B. Reichardt, unpublished data). The twig's maximum diameter was set to 3 mm because at Kluane, Yukon, during the winters of the cyclic low and the early increase phase, the diameter at which snowshoe hares bite off *B. glandulosa* twigs ranges from about 2 to 4 mm (Smith et al. 1988). This also is the diameter at the point of clipping observed during the cyclic low in interior Alaska (Wolff 1980) and in northern Alberta (Pease et al. 1979). Neither predation nor any disturbance such as wildfire has yet been included in this model.

The prediction of the Liu et al. (2012) model that is relevant to amplitude variation is the following: severe browsing in winter by hares on *B. glandulosa* such as that observed at Kluane, Yukon, by Smith et al. (1988) in the winters of 1980–1981 and 1981–1982 will result in a hare cycle with declining amplitude. This prediction is qualitatively supported by the dampening of the hare cycle that has been observed at Kluane, Yukon, since the hare peak that occurred in the winters of 1980–1981 and 1981–1982 (Fig. 3). However, since *B. glandulosa* does not occur at all of the sampling plots at Kluane, this simulation, which used *B. glandulosa* as the browse species of interest, is insufficient to totally account for the amplitude decline observed at Kluane. But, as noted by Smith et al. (1988), browsing by the snowshoe hare on its second most preferred browse species, the grayleaf willow (*Salix glauca* L.), resulted in a growth response similar to that of *B. glandulosa*. This observation indicates that if *S. glauca* uses toxins for antibrowsing defense, then the explanatory value of the Liu et al. (2012, 2013) model at Kluane will increase. The chemical identification of the specific secondary metabolites that defend *S. glauca* against hare browsing and their mode of action need to be determined before a robust test of the Liu et al. (2012, 2013) hypothesis can be done at Kluane.

The Alaska paper birch (*Betula neoalaskana* Sarg.) (previously *Betula papyrifera* Marshall) is the most important winter food of

**Fig. 4.** Amplitude of the snowshoe hare (*Lepus americanus*) cycle at Kluane Lake, Yukon, over three cycles in relation to the instantaneous rate of increase of Canada lynx (*Lynx canadensis*) during the hare population increase phase. Lynx abundance was estimated by snow tracking counts. The amplitude of the hare cycle is measured as the peak hare density/previous low hare density. Error bars are 1 SE.



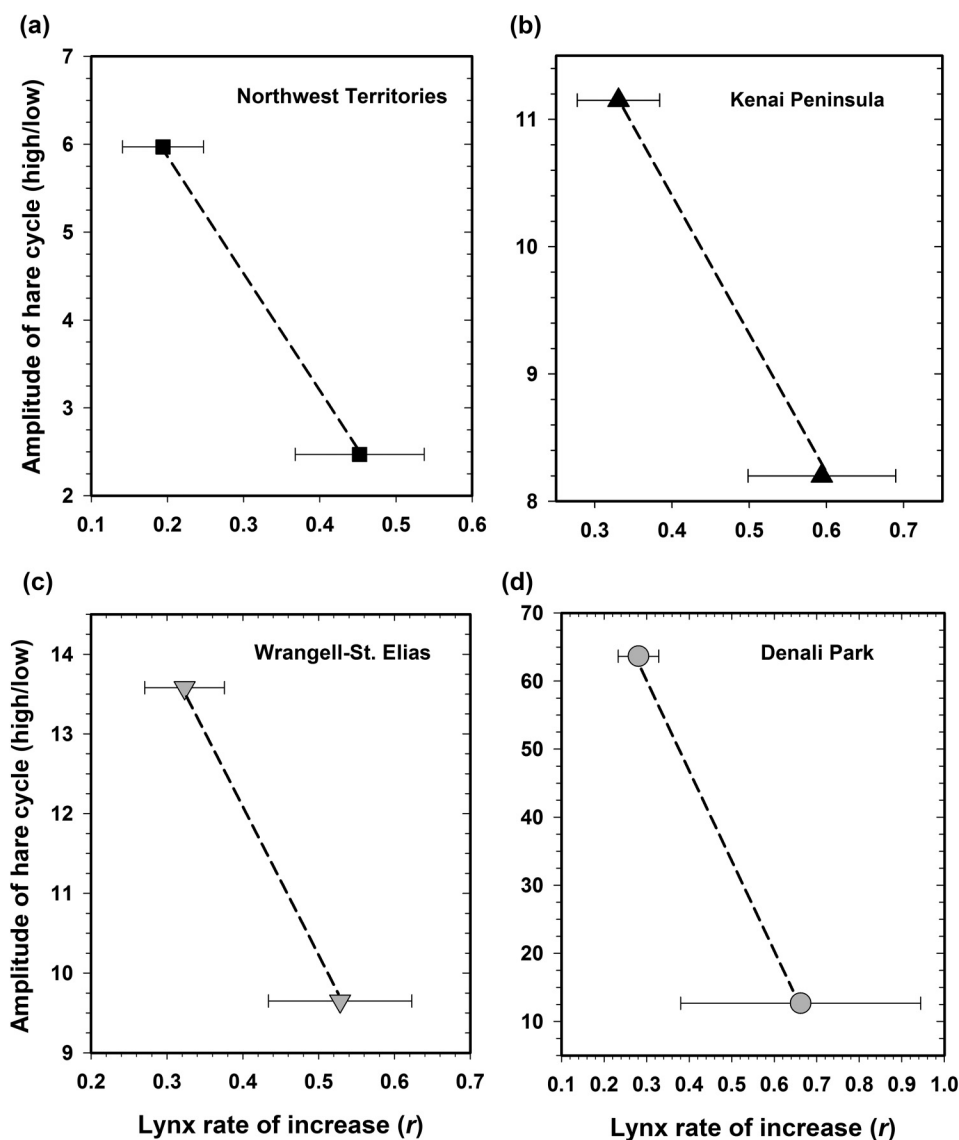
snowshoe hares and moose (*Alces alces* (L., 1758)) living on the Kenai National Wildlife Refuge (KNWR) (Oldemeyer 1983). The twigs of the *B. neoalaskana* saplings are defended against snowshoe hare browsing in winter by papyriferic acid (PA), which as mentioned above, both deters feeding by the snowshoe hare (Reichardt et al. 1984) and is also toxic to the snowshoe hare (Forbey et al. 2011). The duration of time that the segments of the twigs of *B. neoalaskana* saplings growing on the KNWR produce enough PA to deter hare browsing is about the amount of time required by the Liu et al. (2012) model to generate the hare cycle that occurs on the KNWR (Fig. 3). Thus, this model may also partially explain the amplitude decline that has been documented at the KNWR (Fig. 3).

The hare cycle that has occurred at Denali National Park, Alaska, clearly does not support the first prediction of Liu et al.'s (2012) simulation. After the spectacular high hare peak that occurred at Denali in the winters of 1970–1971 and 1971–1972 (J. Bryant, personal observation), the amplitude of the cyclic peak did decline (C. McIntyre, unpublished data) as predicted by the Liu et al. (2012) model. However, the occurrence of another very high amplitude hare peak at Denali in the winter of 2009 (Fig. 3) is clearly inconsistent with Liu et al.'s (2012) prediction of a long period of amplitude decline followed by the emergence of a stable limit cycle driven by toxic defense against hares. Thus, other factors must be affecting amplitude variation at Denali.

### Hypothesis 4: predator hypothesis

If predators are the chief determinant of the amplitude of any particular cycle, it should be possible to predict the peak hare density from the density and rate of increase of all hare predators from the previous low phase. This prediction would assume that the initial density and rate of growth of predator populations is variable rather than constant, and that the growth rate of the hare population is controlled by mortality caused by predation. Our index of hare predators is the lynx. The lynx population of a local area could increase because of reproduction or immigration or both. Figure 4 illustrates the data available from Kluane Lake to test this prediction, and Figs. 5a–5d show similar data from Northwest Territories, Kenai Peninsula, Wrangell–St. Elias, and Denali National Park. In three hare cycles from Kluane Lake and two cycles in Northwest Territories (NWT), the Kenai, Wrangell–St. Elias, and Denali, there is a consistent negative correlation between hare cyclic amplitude (peak/low) and lynx population rate of increase from the previous

**Fig. 5.** Amplitude of the snowshoe hare (*Lepus americanus*) cycle (a) in Northwest Territories, Canada, (b) on the Kenai Peninsula, Alaska, (c) in the Wrangell–St. Elias National Park region (Game Management Unit 11) of Alaska, and (d) Denali National Park over two cycles in relation to the instantaneous rate of population increase per year of Canada lynx (*Lynx canadensis*) from the previous low. Lynx abundance was estimated from fur trapping records. For Denali Park, the hare data amplitude was calculated from road counts and the lynx data are from Game Management Units 20 A & C South. The amplitude of the hare cycle is measured as the peak hare density/previous low hare density. Error bars are 1 SE.



low phase. The same pattern is obtained from the Kluane Lake data if we use the abundance of lynx from the low rather than their rate of increase. The pattern is clear: the slower the rate of lynx population increase, the higher the amplitude of the hare cycle, and the faster the rate of increase of lynx, the lower the amplitude of the hare cycle. This prediction is in need of further testing but provides evidence in agreement with hypothesis 4. The initial abundance and rate of increase of lynx is a mix of survival during the low of hare abundance and influx of individuals from distant populations.

This association neglects the abundance of the other major hare predators such as the coyote and the Great-horned Owl. A much better analysis could be done if data were available of predator-caused mortality rates of hares over several 10 year cycles, but at present we have these detailed data for only one cycle (O'Donoghue et al. 1997, 1998). Coyote abundance at Kluane Lake is highly cor-

related with lynx abundance over the hare cycle ( $r = 0.97$ ,  $n = 14$  years; O'Donoghue et al. 2001).

## Discussion

We began our search for the causes behind variations in cyclic amplitude of snowshoe hare cycles by specifying four single-factor hypotheses. Although weather can affect snowshoe hare survival (Kielland et al. 2010), weather effects do not appear to produce the degree of variation in cyclic amplitude that we have observed. Nor do we see long-term trends in forest succession resulting from fires or logging that produce the dramatic differences that we have observed in cyclic amplitude over the short time periods for all the areas for which we have data. We think the most likely factors driving cyclic amplitude are predation mortality and (or) severe browsing causing changes in plant defence of the hare's winter food supplies.



Additional hypotheses can be generated by using two or more of these factors acting in concert. We prefer not to speculate about multifactor hypotheses until we have more understanding of the single-factor explanations that are most likely. We have tentatively rejected hypotheses 1 (correlated climatic variation) and hypothesis 2 (plant succession) for most areas for the variations in amplitude that we have described over the 20–40 year time scale. The Kenai Peninsula is an exception, which supports hypothesis 2, but its data are also consistent with hypothesis 4. Additional data will be most useful for this site and for Tetlin, since they are two of four sites currently being sampled (two also at Mayo) that have had recent fires in areas with records of hare numbers. We view the role of fire and plant succession as slow variables that affect hare cyclic amplitudes in the long term (50–200+ years) and over broad landscapes, and we have concentrated here on trying to explain the short-term variation shown over 20–40 years. It is possible that a two-factor explanation of predation pressure and browsing impacts will be needed to understand the details of why cycles vary so much in amplitude, or even a three-factor explanation of predation, browsing, and succession could be required. For the present we recommend two foci for study:

1. Movement of predators from regions with an increasing amplitude cycle to regions with a dampening one is a plausible explanation for amplitude dampening. Thus, we suggest the primary focus should be a major landscape study of predator density, survival, and movements through at least two hare cycles to determine where lynx, Great-horned Owls, coyotes, American marten (*Martes americana* (Turton, 1806)), and other major predators go when hares decline. Radio-collaring methods with satellite collars have now made these studies feasible.
2. The secondary focus should be testing the three assumptions made by the plant-quality model of Liu et al. (2012) at several locations across the geographical range of hare cycles, combined with data on hare demography.

In an ideal world, these two foci could be combined in a major collaborative, large-scale study across northwestern North America to bring together the information needed to understand the ecosystem dynamics of this important part of the boreal forest biome.

We recognize that our attempts to analyze the variations in amplitude of snowshoe hare peaks are limited because of the length of the time series and the fact that not all areas have data on hare and predator abundances, as well as forage availability and quality from the same years. To further our understanding of these population events, we need to expand our long-term, standardized monitoring program of hares, their predators, and food plants to extend over not only northwestern Canada and Alaska but also over the eastern part of the continent. The continuation of long-term time series is important if we wish to see how ecosystem changes associated with climate change will impact cyclic variation in the snowshoe hare cycle and community dynamics.

The concern about collapsing population cycles (Ims et al. 2008) is not visible in the data that we have assembled, but our results emphasize the continuing importance of maintaining long-term monitoring in the boreal forest. A better understanding of predator movements relating to the hare cycle could improve our understanding of the landscape dynamics of lynx and other predators.

We hypothesize that the models we have tried to evaluate here for snowshoe hare cycles should also apply to other species of mammals and birds that show cycles of variable amplitude. Snowshoe hare cycles might be a simple case in which predation is the main cause of amplitude variation, but since cycles occur in many diverse species in different ecosystems, one explanation for variable amplitudes may not fit all species or all populations. The question remains open and in need of additional experimental work.

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