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ARTICLE

Synchrony in the snowshoe hare (*Lepus americanus*) cycle in northwestern North America, 1970–2012

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Abstract: Snowshoe hares (*Lepus americanus* Erxleben, 1777) fluctuate in 9–10 year cycles throughout much of their North American range. Regional synchrony has been assumed to be the rule for these cycles, so that hare populations in virtually all of northwestern North America have been assumed to be in phase. We gathered qualitative and quantitative data on hare numbers and fur returns of Canada lynx (*Lynx canadensis* Kerr, 1792) in the boreal forest regions of Alaska, Yukon, Northwest Territories, and northern British Columbia to describe synchrony in the time window of 1970–2012. Broad-scale synchrony in lynx fur returns was strong from 1970 to about 1995 but then seemed to break down in different parts of this region. Hare populations at 20 sites in Alaska, the Yukon, and Northwest Territories showed peak populations that lagged by 1–4 years during the 1990s and 2000s cycles. The simplest hypothesis to explain these patterns of asynchrony in hare cycles is the movement of predators from British Columbia north into the Yukon and then east into the Northwest Territories and west into Alaska. A traveling wave of these cycles is clearly seen in the lynx fur returns from western Canada and Alaska from 1970 to 2009. One consequence of a failure of synchrony is that hare predators like Canada lynx and Great-horned Owls (*Bubo virginianus* (Gmelin, 1788)) can move from one adjacent area to the next within this region and survive long enough to prolong low densities in hare populations that have declined earlier.

Key words: Lepus americanus, 10 year cycle, boreal forest, Alaska, Yukon, British Columbia, Northwest Territories, predation, climate, traveling waves.

Résumé : Les populations de lièvres d'Amérique (*Lepus americanus* Erxleben, 1777) fluctuent selon un cycle de 9 à 10 ans dans une bonne partie de l'aire de répartition nord-américaine de l'espèce. Il était présumé que ces cycles étaient régis par une synchronie régionale faisant en sorte que les populations de lièvres de la presque totalité du nord-ouest de l'Amérique du Nord étaient en phase. Nous avons recueilli des données qualitatives et quantitatives sur le nombre de lièvres et le nombre de peaux de lynx du Canada (*Lynx canadensis* Kerr, 1792) rapportées dans les régions de forêt boréale de l'Alaska, du Yukon, des Territoires-du-Nord-Ouest et du nord de la Colombie-Britannique afin de décrire cette synchronie durant la période de 1970 à 2012. Une forte synchronie régionale du nombre de peaux de lynx était observable de 1970 à 1995 environ, mais semble s'être estompée par la suite dans différentes parties de cette région. Les populations de lièvres dans 20 localités en Alaska, au Yukon et dans les Territoires-du-Nord-Ouest montrent des maximums décalés de 1 à 4 ans durant les cycles des décennies 1990 et 2000. L'hypothèse la plus simple pour expliquer ces patrons d'asynchronie des cycles des lièvres est le mouvement de prédateurs vers le nord, de la Colombie-Britannique au Yukon, puis vers l'est, jusqu'aux Territoires-du-Nord-Ouest, et vers l'ouest, jusqu'en Alaska. Le nombre de peaux de lynx rapportées dans l'Ouest canadien et en Alaska de 1970 à 2009 témoigne clairement de l'évolution d'une onde progressive de ces cycles. Une des conséquences de l'interruption de la synchronie est que les prédateurs des lièvres comme le lynx du Canada et le grand-duc d'Amérique (*Bubo virginianus* (Gmelin, 1788)) peuvent se déplacer entre différentes zones attenantes à l'intérieur de cette région et survivre assez longtemps pour que perdurent les faibles densités des populations de lièvres déjà en baisse.

Mots-clés : Lepus americanus, cycle décennal, forêt boréale, Alaska, Yukon, Colombie-Britannique, Territoires-du-Nord-Ouest, prédation, climat, ondes progressives.

Introduction

Snowshoe hares (*Lepus americanus* Erxleben, 1777) are a classic textbook example of animals with relatively regular population cycles (Elton and Nicholson 1942; Krebs 2009, p. 203). While much interest has focused on the causes of these hare population fluctuations, less concern has been shown toward synchrony, the tendency of regional populations of hares to be in phase with one another (Ranta et al. 2006). Much of the analysis of synchrony has focused on small-rodent and game-bird populations (e.g., Ims and Andreassen 2005; Henden et al. 2009), partly because of rapid population turnover and partly because of extensive data from

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hunting statistics. Small-mammal ecologists have carried out extensive studies on synchrony on a local spatial scale of a few to tens of kilometres (Steen et al. 1996), but similar studies have not been carried out for snowshoe hare populations.

Much of the discussions of synchrony have centered on the fur return data of Canada lynx (*Lynx canadensis*), a specialist snowshoe hare predator (Ranta et al. 1997*a*; Haydon and Greenwood 2000). These analyses have led to a series of models describing how synchrony can be maintained in coupled populations. They are all based on the belief of a continent-wide synchrony of these populations, tempered partly by traveling waves (Smith 1983; Ranta et al. 1997*a*).

Unlike the fur data on lynx, there are few long time-series data on snowshoe hare abundance in Canada and Alaska, and this has hampered the development of sophisticated models for hare spatial dynamics. In this paper, we attempt to pull together the available data on hare population changes in northwestern North America from 1970 to 2012. We will explore the local synchrony and speculate on the reasons for a reduction of synchrony since the 1990s. We wish to evaluate three hypotheses from the theoretical and empirical synchrony literature:

1. Population synchrony is set by regional weather events (Ranta et al. 1997*b*).
2. The scale of local synchrony is driven by individual hare dispersal.
3. Traveling waves in hare synchrony occur and are driven by predator movements rather than weather events.

Both hypotheses 1 and 3 are consistent with the empirical finding that synchrony will decline with geographic distance (Ranta et al. 2006). Hypothesis 1 is tenable if weather events cause large changes in hare reproduction and mortality. Hypothesis 2 can be rejected if the spatial scale of hare dispersal is much less than the spatial scale of synchrony. Hypothesis 3 can be rejected if the scale of predator movements is much less than that of synchrony.

The most recent large-scale analysis of synchrony in the hare cycle (Smith 1983) suggested that hare cycle peaks in Canada began in central Saskatchewan (time 0) and the peak of the cycle spread in a spatial wave out to the east and west, with a time delay of the hare peak of 2–3 years by the time the Yukon was reached. We attempt here to test that part of Smith's hypothesis that maps on northwestern Canada and Alaska.

Materials and methods

Fur production data on Canada lynx were obtained from the Alaska Department of Fish and Game (courtesy of S. Arthur) and from Statistics Canada for British Columbia, Yukon, and Northwest Territories (Census of Wildlife Pelt Production, Table 003-0013; accessed 23 February 2012). These data are tallied by government statistics agencies and are typically grouped over large political areas like the entire Yukon. Consequently, these data are less useful to determine local dynamics. The assumption is made that lynx reach a peak 1–2 years after hares (O'Donoghue et al. 2010).

We have relied on four methods to estimate the abundance of hare populations. The first and most accurate is mark–recapture estimation with at least two samples per year (Kluane Lake, Yukon, and Bonanza Creek, Alaska). This method suffers from being small scale and very labor intensive. The details of these mark–recapture methods are provided by Krebs et al. (2001*b*) and Kielland et al. (2010). Second, 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. (2001*a*). This method is relatively quick and can be done over a large spatial scale. Pellets are cleared off these plots each year, so the deposition measured is annual. These pellet counts have been transformed to absolute hare density by the use of the regression given in Krebs et al. (2001*a*). There is a large assumption built into this conversion—that the regression obtained for Kluane Lake will apply elsewhere in the boreal forests of northwestern North America. There is strong support for this assumption where it has been tested (Mills et al. 2005; Murray et al. 2005). We do not know if this assumption is correct everywhere; however, since we are less concerned with absolute abundance but rather with identifying cyclic peaks and troughs, this assumption is not critical for the analysis that follows. Third, 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 sufficient to recognize population peaks and troughs if the density changes are sufficiently large and they have the advantage of large spatial scale. They produce data similar to that obtained by pellet counts (Arthur and Prugh 2010) and are more quantitatively reliable than observations given in newspaper articles. Finally, trapper questionnaires have been used in the Yukon to identify trends in hare numbers in the same way that early statistics were gathered (Chitty and Elton 1939; B.G. Slough, personal communication). Typically, trappers are asked each year if hares are scarce, common, or abundant on their trap lines, and the replies summarized. We have put all these methods together to characterize the pattern of hare cycles in northwestern North America.

The definition of the years of the cyclic peak are clear when mark–recapture estimates are available; however, with many indices, peak years are less clear. In particular during some hare cycles a single year is clearly the peak, while in other cycles hares may remain at high density for 2–4 years in a row. We have defined the peak year in our analyses as that year with the highest recorded abundance of hares. There is the possibility with index data that small peaks are completely missed, but we will continue our analysis with the assumption that hare peaks are clearly visible to a naturalist or trapper. We have indicated extended peaks in our discussion of particular data sets.

To obtain a quantitative measure of synchrony among populations, the traditional analysis proceeds by calculating cross-correlation coefficients (Ranta et al. 2006). But we cannot use this approach for hare data because of low sample size of overlapping data and time shifts in synchrony. Unless the data are a continuous time series of at least 15 points, cross-correlation analysis is unreliable because of large standard errors and adds little to visual examination of synchrony from plots like those presented here. For periods of overlap in our data sets, we can calculate Pearson correlation coefficients (zero time lag) to determine if synchrony declines with geographic distance.

Statistical analyses were carried out in NCSS version 8 (NCSS, LLC, Kaysville, Utah, USA; http://www.ncss.com/). All time-series data were detrended before calculating cross-correlations, as recommended by Ranta et al. (2006). All snowshoe hare population estimates used here are given in the supplementary material data file[1] following this paper.

In this paper, we use "local" to indicate areas within a 75–100 km circle and "regional" to indicate areas within a 200–400 km circle.

Results

Lynx fur data

Large-scale regional synchrony can be detected readily from lynx fur returns. Figure 1*a* shows these returns for the Yukon, Northwest Territories (N.W.T.), and British Columbia (B.C.). There was a peak in the early 1970s, another in 1980–1981, and a third in

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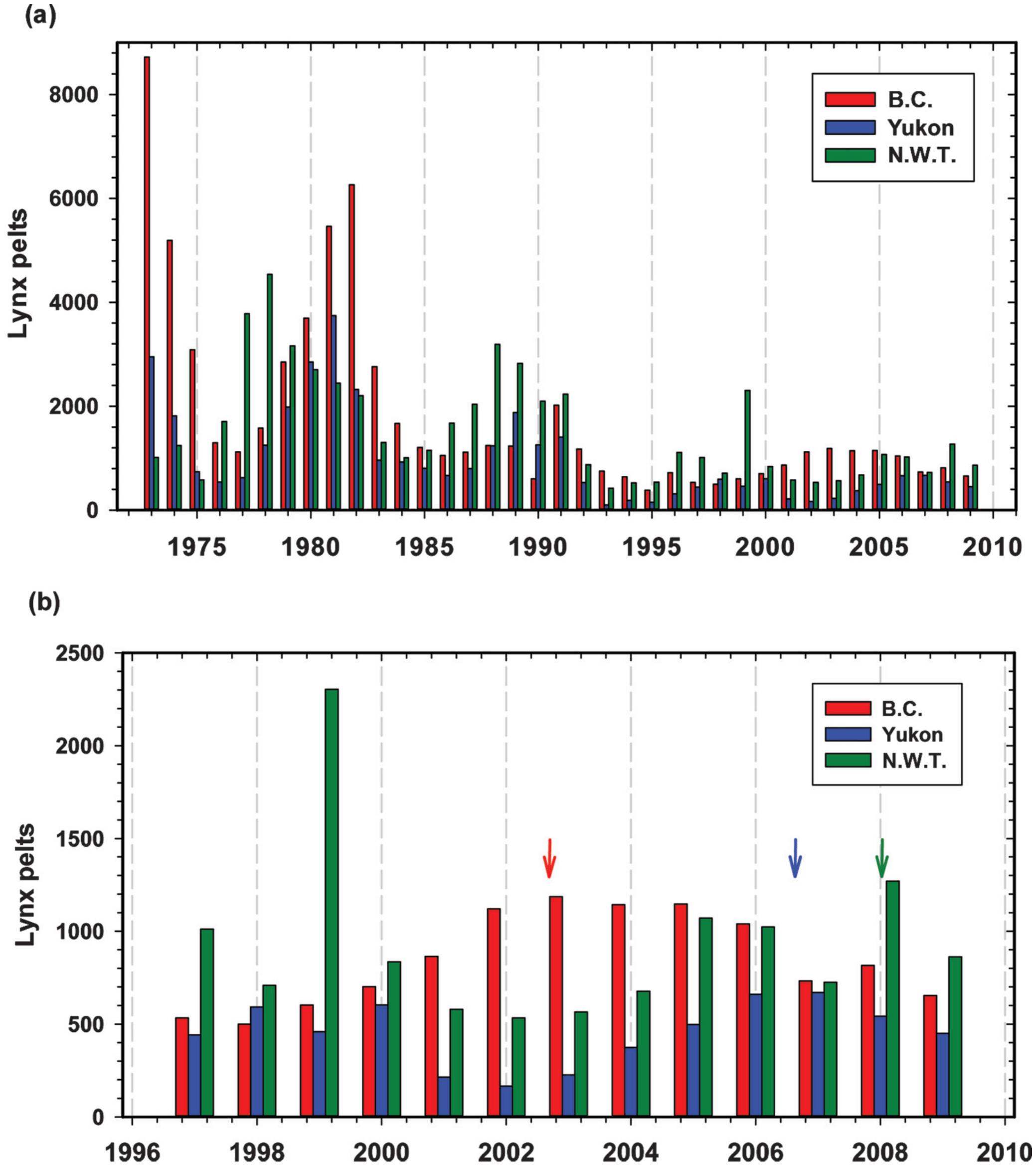
[1] Supplementary material Figs. S1, S2, and S3, as well as the data file, are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2013-0012.

Fig. 1. (*a*) Number of Canada lynx (*Lynx canadensis*) trapped in three of the western provinces of Canada from 1973 to 2009. (*b*) Expanded data set from 1997 to 2009 showing the apparent peak years in B.C. (2003), Yukon (2007), and N.W.T. (2008?) (data from Statistics Canada 2011, available from http://www.statcan.gc.ca/).



1989–1991 in all three jurisdictions. But after 1995, there was no general agreement among areas and no clear sign of a strong cyclic peak in these fur data. Figure 1*b* shows these latter years, which suggest peaks in separate years for each of these three jurisdictions. Hare peaks would be expected to be 1–2 years before the lynx capture peaks.

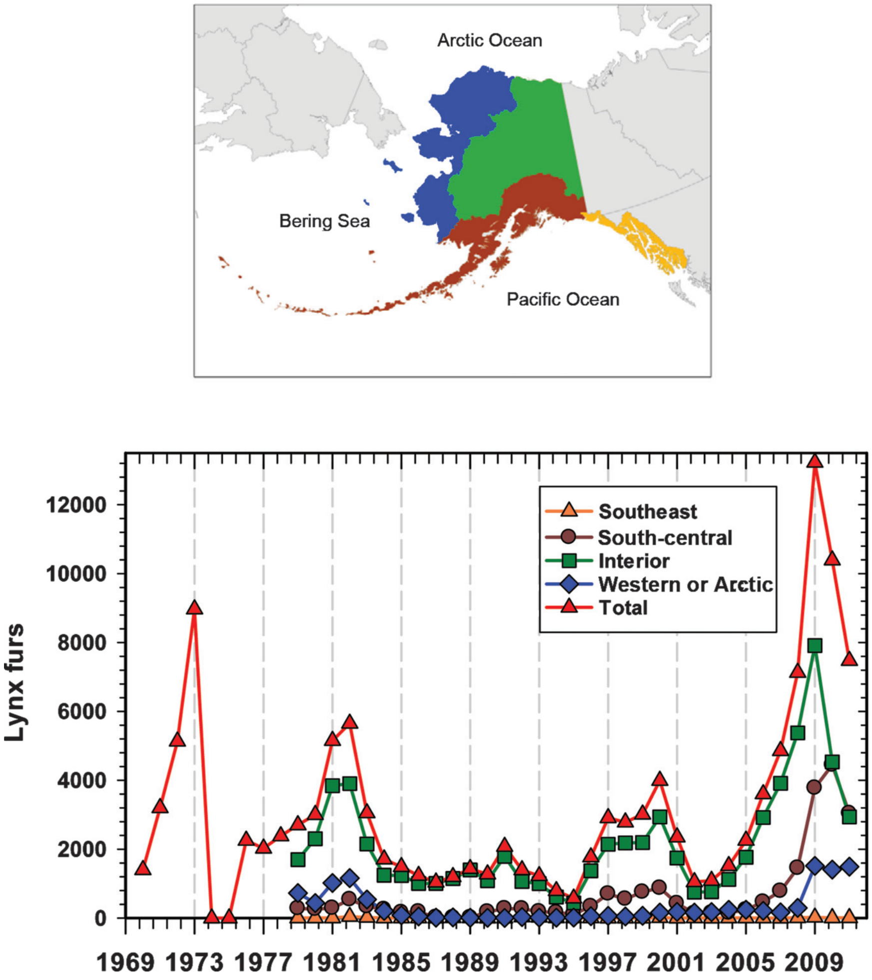
Figure 2 shows similar lynx fur trapping data from four broad regions of Alaska. Most lynx furs in Alaska come from the interior region around Fairbanks. Peaks in general seemed to occur in all fur trapping areas of Alaska in the years 1973, 1981–1982, 1991, and 1997–2000, but after 2000, there was some evidence of out-of-phase fluctuations measured by lynx fur trapping. In 2009, the Alaska Interior reached a peak, while the south-central (Glennallen region) peaked in 2009–2010. The Kenai Peninsula lynx trap catch reached a peak in 2010–2011 (T. Burke, personal communication). The Western or Arctic region of Alaska was anomalous in reaching a low peak in 1981–1982 and again only in 2009–2011. There is a slight suggestion that until the early 1990s, the Alaskan lynx peaks may have occurred 1–2 years after the Yukon peaks and possibly 2–3 years after the N.W.T. lynx peaks (see supplementary material Fig. S1),[1] but since 2000 lynx peaks seem to be out of phase in different parts of Alaska.

Snowshoe hare indices

Figure 3 shows the geographic location of the 20 areas from which we have some snowshoe hare data, and Table 1 lists these locations and the number of years of data available from each. For some sites, there are gaps in the years sampled, which limits some of the statistical analyses that follow.

Coarse-grained data such as that obtained from lynx fur statistics (and shown in Figs. 1 and 2) are valuable for suggesting large-scale patterns, but need to be broken down on a finer scale to look at local synchrony. We have 12 sets of local data of snowshoe hare indices of varying length to present, and we will begin by looking at data within Canada. Figure 4 shows hare population trends for the six Canadian sites. The Kluane time series is the longest. Hares peaked in the Kluane region in 1971, 1979–1981, 1988–1990, 1997–1998, and 2006. The central N.W.T. hares reached peaks in 1988–

Fig. 2. Number of sealed Canada lynx (*Lynx canadensis*) pelts taken in four areas of Alaska since 1970. All lynx taken in Alaska are required to be recorded and tagged with a seal if they are to be sold. Almost no lynx are caught in southeast Alaska (data from the Alaska Department of Fish and Game 2012).



1990, 1999, and 2008–2009. The southeastern N.W.T. hares were almost always at very low numbers, and if any peak is visible in these data, it is coincident with the central N.W.T. in 1988–1990 and 1999 with no clear peak after that time. The Inuvik area by contrast showed peak hare numbers in 1992–1993 and again in 1996–1998, and a low density peak in 2008–2009. Mayo populations peaked in 1999–2000 and again in 2006–2007.

Figure 5 shows hare data from six sites in Alaska. The Kenai Peninsula hares reached a peak in 1983–1984 and again in 1998–1999. Denali hares peaked in 1988–1989, 1999–2000, and again in an extended peak from 2006 to 2009. Bonanza Creek hares were at a peak in 1999 and again in 2008–2009. Tetlin hares reached an extended peak in 2007–2009. Delta Junction hares were at peak numbers in 1998–1999 and again in an extended peak in 2006–2009. Wrangell–St. Elias hares were at a peak in 1991, 1999–2001, and again in 2008. In western Alaska at Galena hares reached peak numbers in 1999–2001 and again in 2008–2009 (K. Bodony, personal communication). At Wiseman, Alaska, in the Brooks Range the hare peaks occurred in 2000–2001 and again from 2009 to 2012.

Figure 6 illustrates how synchrony in hare abundance declines with distance. Two points emerge from Fig. 6. First, there is a high degree of synchrony among many pairs of populations up to 1700 km apart, illustrating the large-scale regional synchrony over this time period. But second, there are many low correlations, leading to a wide scatter of points. In part these low correlations can be explained by the landscape of the Yukon and Alaska, which can render airline distance a poor measure of biotic connectedness. For example, the Kluane hare data are poorly correlated with the Wrangell–St. Elias data ($r = -0.07$) even though these sites are only 214 km apart. But the airline distance is measured across the St. Elias Mountains and their associated glaciers.

An independent set of data on snowshoe hare abundance in the Yukon has been gathered from 1977 to 2011 by the Yukon Territorial Government in questionnaires to registered trappers who hold trap lines (M. O'Donoghue, personal communication). Figure 7 shows the groupings of trap lines that we have used to gather data on hare abundance trends. All the Yukon groups showed cyclic dynamics. Table 2 shows that in the broad sense most Yukon sites were in phase with one another over this time period with the exception of Watson Lake, which seemed to peak 1 year ahead of the other sites, and Old Crow, which tended to peak 1 year later. Figure 8 shows that within the Yukon, synchrony declined slowly with distance with a drop in the correlation coefficient of 0.3 for every 1000 km distance. This is the same as the slope in Fig. 6 (also 0.3 for every 1000 km) and these estimates completely overlap in their confidence limits.

Table 3 presents the peak years for hares in all these regions from all the data presented here. It provides a visual assessment of what appears to be a traveling wave of hare peaks particularly since 1990.

Fig. 3. Locations of 20 sites from which snowshoe hare (*Lepus americanus*) data were available. Each site is listed by a number, which is also given in Table 1, that lists the number of years of data available from each site.

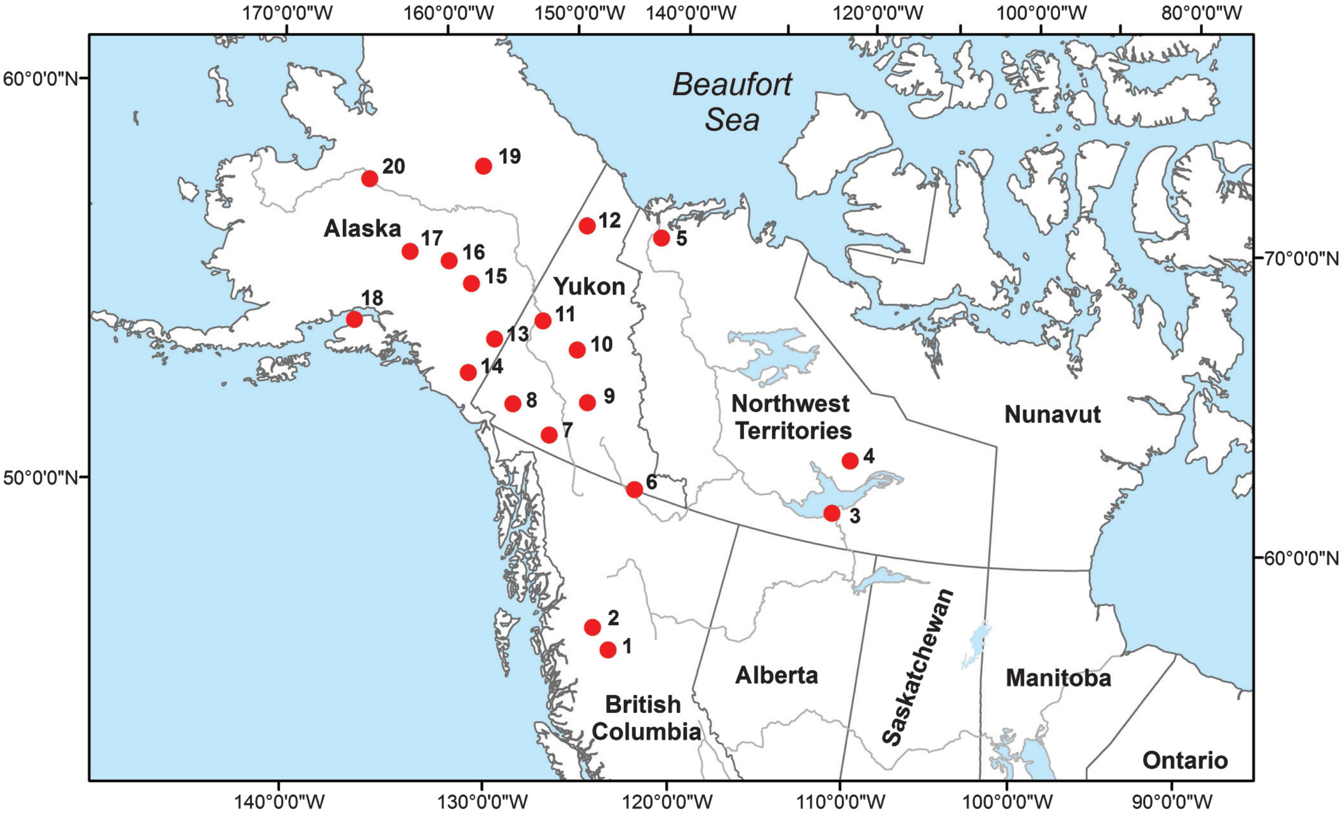


Table 1. Sites (mapped in Fig. 3) used in this analysis, years of data available for each, and type of data utilized.

Site	Location	No. of years of hare data	Type of data available
	British Columbia (B.C.)		
1	Nadina Forest District	5	Pellet counts
2	Skeena–Stikine Forest District	10	Pellet counts
	Northwest Territories (N.W.T.)		
3	South Slave	24	Pellet counts
4	North Slave–Sahtu	24	Pellet counts
5	Inuvik	18	Pellet counts
	Yukon		
6	Watson Lake	34	Questionnaires
7	Whitehorse	34	Questionnaires
8	Kluane Lake	37	Livetrapping
9	Faro	34	Questionnaires
10	Mayo	13 (34)	Road counts (questionnaires)
11	Dawson	34	Questionnaires
12	Old Crow	34	Questionnaires
	Alaska		
13	Tetlin National Wildlife Refuge	17	Pellet counts
14	Wrangell–St. Elias National Park	21	Pellet counts
15	Delta Junction	17	Road counts
16	Bonanza Creek LTER	14	Livetrapping
17	Denali National Park	23	Road counts
18	Kenai Peninsula	17	Livetrapping
19	Brooks Range (Wiseman)	5	Pellet counts
20	Galena	16	Natural history

Note: Two areas with few years of data (sites 1 and 19) were used to pinpoint recent peak populations of snowshoe hares (*Lepus americanus*). LTER, long-term ecological research site.

Discussion

We have reached two conclusions from our analysis of these spatial synchrony data. First, there was widespread synchrony among snowshoe hare populations in northwestern North America from the 1970s to the early 1990s as indexed by lynx fur returns. Second, since 1995 many local hare populations (and thus lynx) were out of synchrony with one another by up to 5 years. We discuss each of these in turn.

Widespread synchrony among hare populations in northwestern North America appeared to be the rule in the 1970s to the early 1990s. Synchrony among hare populations declines with distance (Figs. 6 and 8) with nearly the same slope, supporting both hypotheses 1 and 3. This synchrony is reflected in analyses of lynx fur returns indicating substantial but not perfect synchrony (Haydon and Greenwood 2000). But analyses of continental-wide synchrony may be biased by the use of fur return data over long time periods as a surrogate for accurate population data. At best they could suggest hypotheses for more empirical investigation. In this paper, we use lynx fur data only to pinpoint the timing of cyclic peaks.

There is a very large literature on synchrony in fluctuating populations, particularly in small rodents and game birds (Bjørnstad et al. 1999; Ims and Andreassen 2005; Korpimäki et al. 2005; Ranta et al. 1997*c*). Three general mechanisms for intraspecific population synchrony have been suggested—correlated regional weather, dispersal among populations, and trophic interactions with mobile predators (Liebhold et al. 2004). These are the three general mechanisms that we attempt to evaluate here.

Regional weather over scales of 200–400 km could synchronize local populations and this is an attractive hypothesis if there is some direct or indirect path from weather to hare reproductive

Fig. 4. Population changes in snowshoe hares (*Lepus americanus*) at six sites in western Canada. Note that the *y*-axis scales differ. All the sites except Mayo provide estimates of the number of hares per hectare. Mayo counts are a road-count index of number seen per 100 km of driving. British Columbia is the mean of sites 1 and 2 in Fig. 1, Central N.W.T. is site 4, southeast N.W.T. is site 3, and Inuvik is site 5.

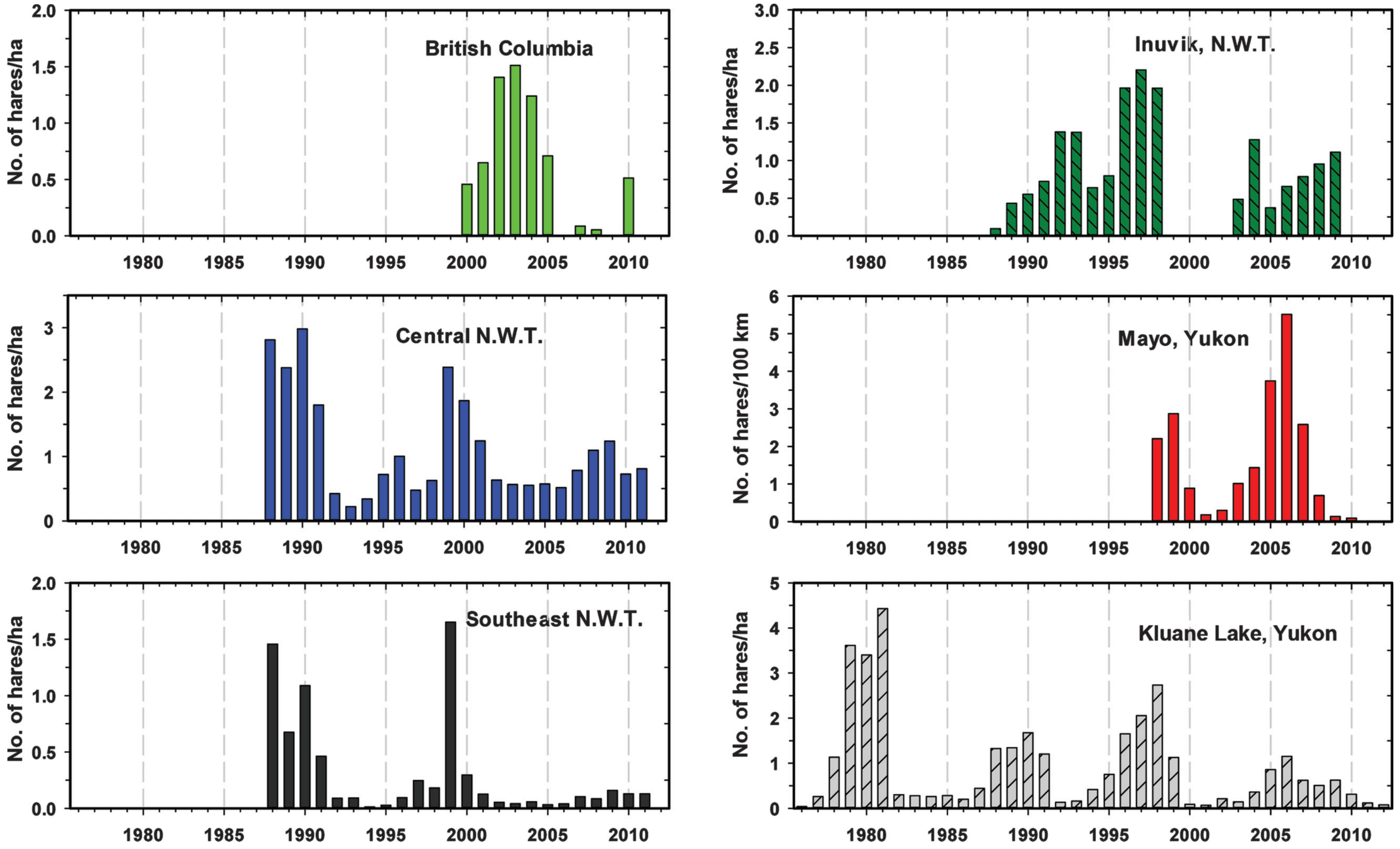


Fig. 5. Population changes in snowshoe hares (*Lepus americanus*) at six sites in Alaska. Hare densities were estimated by pellet counts at Tetlin, Wrangell–St. Elias, and Kenai, and by livetrapping at Bonanza Creek. Delta Junction counts were taken along Breeding Bird Surveys on the Richardson Highway and Denali counts were taken along bird survey routes in Denali National Park; both are mean counts per day. Note that the *y*-axis scales differ.

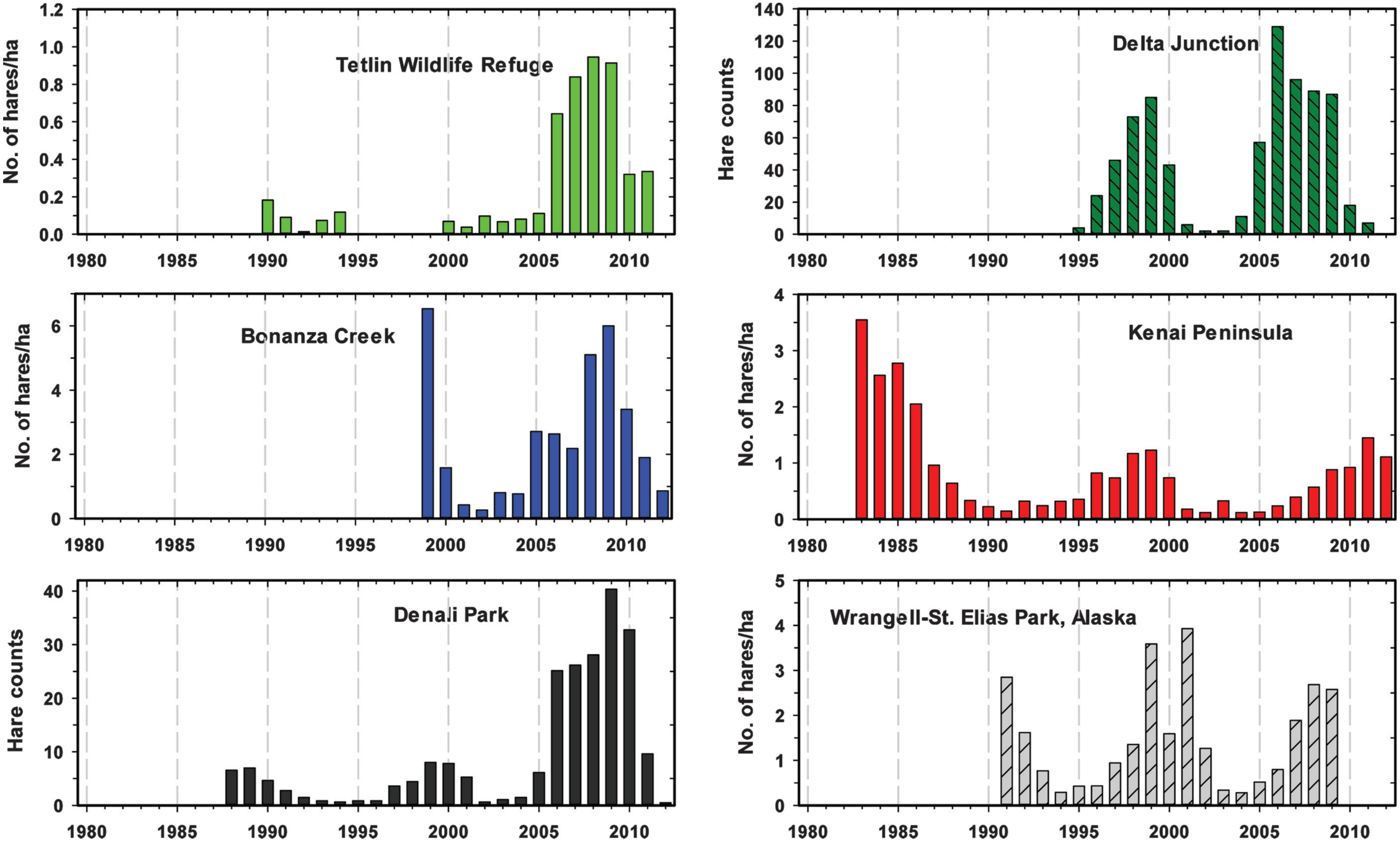


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Fig. 6. Correlations of snowshoe hare (*Lepus americanus*) abundance estimates between pairs of samples and straight-line geographic distance, $n = 40$. Data from 1988 to 2012. Only samples with 12 or more annual points are plotted. The regression is highly significant ($r = 0.51$, correlation = 0.0003·distance + 0.62, $p < 0.001$).

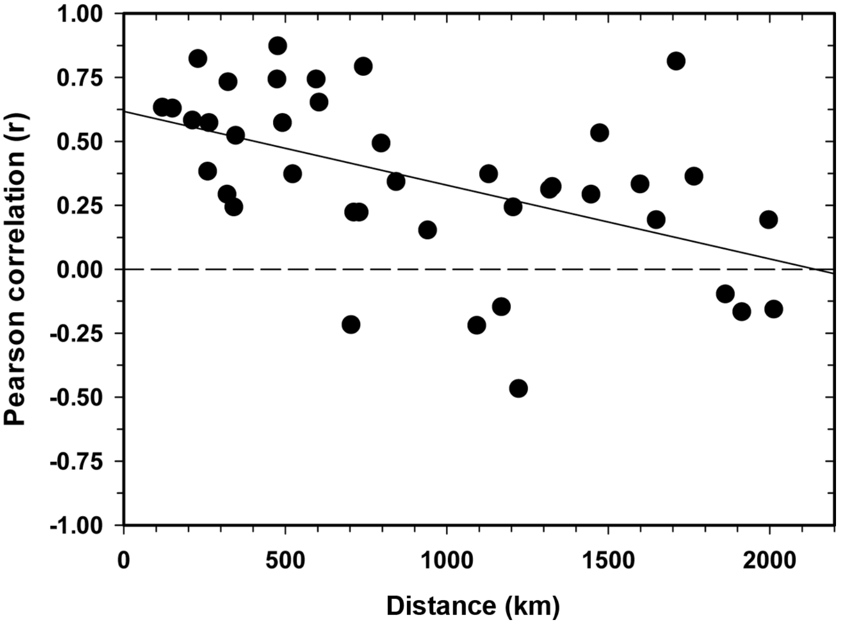
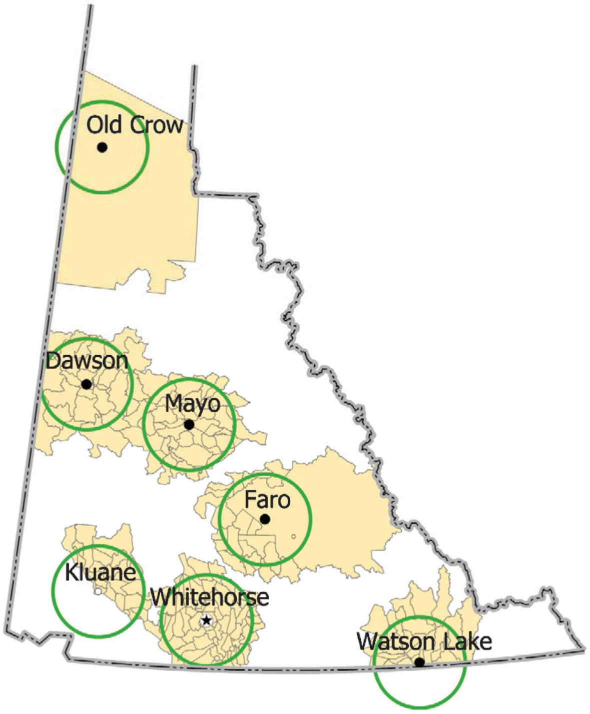


Fig. 7. Locations of questionnaire data from the Yukon that were aggregated into regional areas and tested in Fig. 8 for synchrony. Questionnaires were utilized from trappers whose trap lines were partly covered in the circles 75 km in radius around existing towns. The central Yukon sites appear to reach peak densities in the same years, whereas those in the southeast reach a peak 1 year earlier, and those in the north peak 1 or 2 years later.



rates and survival. The problem so far has been to specify a mechanism by which weather can drive changes in hare numbers. Weather hypotheses are difficult to test (Berteaux et al. 2006) and we require a specific model before we can make progress evaluating this idea. Detailed studies of the causes of death of snowshoe hares have always shown that predation is the immediate cause of death of more than 90% of hares (O'Donoghue et al. 2010), suggesting that if weather is responsible for the observed synchrony, then it must act indirectly via predation. We realize that the regional weather hypothesis is difficult to test directly, but we think it is logically inconsistent with the spatial pattern of asynchrony shown since 1995.

For snowshoe hares dispersal is not a viable explanation. The scale of movements of dispersing hares is local, and a maximum of about 20 km would be the limit of possible movements (Gillis and Krebs 1999, 2000; Hodges et al. 2001). Regional synchrony occurs on a much larger scale than that of individual hare dispersal and we reject this mechanism as sufficient to explain the scale of synchrony shown in Figs. 6 and 8.

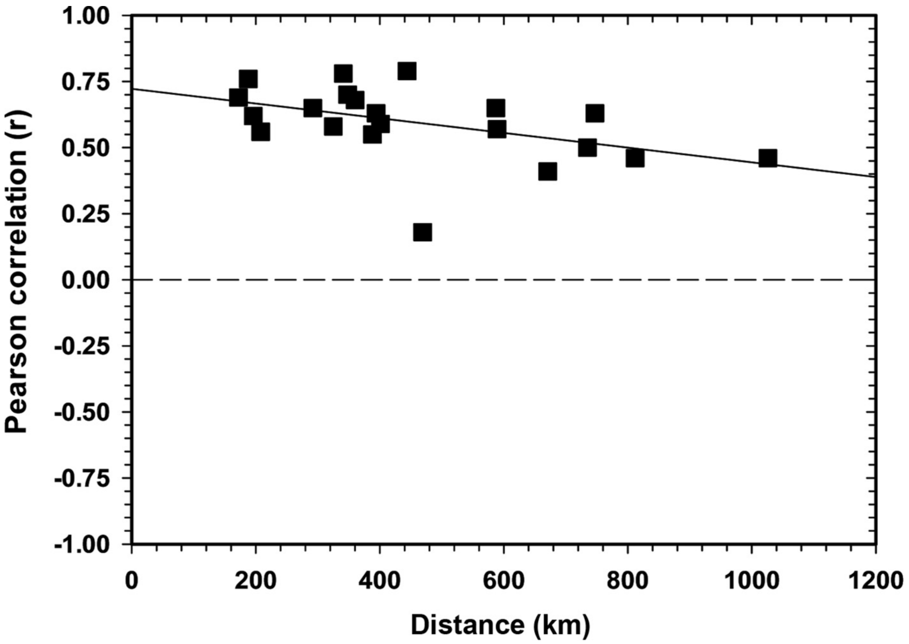
We suggest that the data summarized here are most compatible with the mobile predator hypothesis for generating synchrony in snowshoe hare populations in northwestern North America, as suggested by Ydenberg (1987). In particular, we note that predator movements can produce both broad synchrony and traveling waves among local populations that are not quite in phase or completely out of phase (Table 3). This is most clear in the 1990s and 2000s cycles in hares and also in the fur return data from Alaska and northwestern Canada shown in Figs. 1 and 2; both of which are consistent with a traveling wave of peaks moving to the northwest from central Canada (see also supplementary material Figs. S1 and S3).[1] In B.C., hares were completely out of phase with all the northern populations by 4–5 years in the early to mid-2000s. Central Alaskan populations were generally in phase with Yukon populations, but towards the periphery of Alaska (Brooks Range, Galena, Kenai Peninsula), cyclic peaks were delayed 1–2 years. Similarly the hare peaks in the north Yukon and the northern N.W.T. appeared to be delayed 1–2 years from those in the central and southern Yukon. These differences are not large and they are broadly consistent with the pattern of traveling waves for western North America suggested by Smith (1983). Our results with snowshoe hares cast possible doubt on the conclusion of Haydon and Greenwood (2000) that lynx cycles are synchronous across all of Canada. Clearly, additional data on hare numbers from central

Table 2. Synchrony of Yukon peak snowshoe hare (*Lepus americanus*) populations determined from trapper questionnaires, 1977– 2011.

Kluane	Whitehorse	Watson Lake	Faro	Dawson	Mayo	Old Crow
1979–1981	1979–1981	1978–1980	1979–1981	1979–1981	1978–1980	1980–1982
1988–1990	1988–1990	1987–1989	1988–1990	1988–1990	1988–1990	1988–1990
1997–1999	1997–1999	1995–1998	1997–1999	1998–2000	1997–1999	1997–2000
2006–2008	2007–2008	2006–2008	2005–2008	2006–2009	2006–2008	2006–2009

Note: The areas sampled are shown in Fig. 7.

Fig. 8. Correlation of Yukon snowshoe hare (*Lepus americanus*) abundance estimates from trapper questionnaires and geographic distance between pairs of samples, $n = 21$. Samples from 1977 to 2010. Hare abundance was estimated from the fraction of trappers reporting hares as abundant. The linear regression is correlation = 0.0003·distance + 0.72, $r = 0.46$, with $p < 0.04$ for slope and $p < 0.01$ for intercept.



and eastern Canada would complete the picture of traveling waves hypothesized by Smith (1983).

We do not see any clear variation in correlated regional weather that would be consistent with the patterns of synchrony we have just described. This can at best be a tentative rejection of the regional weather mechanism for synchrony and lack of synchrony among regional hare cycles. Regional weather might be a possible reason for variation in the amplitude of hare cycles, but at present, we do not have clear predictions for how this might be achieved. Understanding the factors causing variations in synchrony and the factors causing variations in cyclic amplitude are two distinct issues.

If predator movements are one key to local variation in the synchrony of hare populations, we need to do additional monitoring to test this hypothesis. Radio-collaring of both avian and mammalian predators of hares on a broad scale could add an important dimension to our understanding of how these northern cyclic systems operate. Any type of traveling wave must have a mechanistic explanation, and theoretical analyses of traveling waves (Blasius et al. 1999; McKelvey et al. 1999) suggest that predator dispersal could be the critical link worthy of study. We have some data on lynx movements (O'Donoghue et al. 2010) but not the detailed data we could now get from satellite radios. We also know that lynx are genetically panmictic across Canada (Row et al. 2012), suggesting widespread mixing, but we need more data on local movements to be able to explain the asynchrony that we have observed.

Specific testable predictions follow from the predator movement hypothesis. If traveling waves move from south to north, or east to west, we predict that mobile predators moving in those directions would survive longer than those moving in the opposite directions. Lynx clearly move in all directions once the hare population begins to collapse (supplementary material Fig. S2)[1] because they have no knowledge of the regional abundance of hares. The majority of these lynx die from starvation and only some survive to exploit the next hare peak. If by chance hare populations are declining or low on one area that is adjacent to a peak hare population, mobile predators moving from the peak area should both drive hare numbers down further on the area that is already low and hold them down longer on that area than if the entire region is in phase. More specific quantitative models would certainly be needed to ensure that these predation effects are necessary and sufficient to explain the changes in hare demography.

We do not know the conditions that favor regional synchrony (as we apparently had during the 1970s and 1980s) or those that cause regional asynchrony (as we have observed in the 1990s and 2000s). There are clear cases in the data that we have presented in which two areas were in phase in one hare cycle and several years out of phase in the following cycle. We can see a mechanism for testing the predator movement hypothesis if we had regional data on the abundance and movements of the major predators, as well as the local abundance of hares. Such a coordinated, large-spatial scale landscape study is the next step needed to understand these spatial dynamics.

The recommendations we make here for long-term monitoring of snowshoe hare populations has important economic value because it allows us to predict within any given region the current

Table 3. Summary of snowshoe hare (*Lepus americanus*) peak years of the population cycle from 20 areas of British Columbia (B.C.), Northwest Territories (N.W.T.), Yukon, and Alaska, 1980–2012.

		1980s										1990s										2000s										2010s		
Site	Location	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12
	B.C.																																	
1	Nadina Forest District																							x	x									
2	Skeena–Stikine Forest																							x	x									
	N.W.T.																																	
3	South Slave									x											x													
4	North Slave									x	x	x									x													
5	Inuvik			x	x									x	x				x						?									
	Yukon																																	
6	Watson Lake	#							#	#	#						#	#	#									#	#	#				
7	Whitehorse	#	#							#	#	#							#	#	#							#	#	#				
8	Kluane Lake	x	x								x	x								x								x						
9	Faro	#	#							#	#	#							#	#	#						#	#	#	#				
10	Mayo	#								#	#	#								x	x							x						
11	Dawson	#	#							#	#	#								#	#	#						#	#	#	#			
12	Old Crow	#	#	#						#	#	#							#	#	#	#						#	#	#	#			
	Alaska																																	
13	Tetlin National Refuge																													x	x			
14	Wrangell–St. Elias National Park											?	x								x	x	x							x	x			
15	Bonanza Creek		#									#									x									x	x			
16	Denali National Park									x	x										x	x								x	x	x		
17	Delta Junction																				x							x	x					
18	Kenai Peninsula				x	x	x													x	x												x	
19	Brooks Range (Wiseman)																					x	x								x	x	x	x
20	Galena	#																			x	x	x							x	x	x	x	

Note: Sites are mapped in Fig. 3. Not all areas had data for all these years. Peaks reported from questionnaire data are given by a pound (#) sign, since these are probably less precise than those obtained from quantitative data (x). A question mark indicates possibly a peak from natural history observations.

phase of the hare cycle. Monitoring data in central B.C. is currently being used in forestry management to determine when to plant tree seedlings, as trees planted close to the time of the hare peak are browsed by hares. This hare browsing results in wasted investment both from replanting costs and from a longer term impact on the forest industry because fewer trees are available for harvest in the future. As forest harvesting expands across the southern parts of the boreal forest, knowing when the hare peak occurs within any given area will become a necessary part of the foresters' silvicultural requirements. Large burned areas at the present time in B.C. cannot be replanted if hares are at peak numbers.

In conclusion, we appreciate that our attempts to analyze the spatial dynamics of snowshoe hare peaks are limited because of the length of the time series and the fact that not all areas have data from the same years. To further our understanding of these large-scale population events, we require a long-term, standardized monitoring program that extends over not only northwestern Canada and Alaska but also over the eastern part of the continent. This should ideally be combined with studies of the large-scale movements of predators to provide a formal test of the mobile predator hypothesis and the traveling wave hypothesis. In particular, we need detailed studies of predator movements over large spatial areas over the entire hare cycle. The data that we have represents a good start, and the monitoring programs now in place in Alaska, the Yukon, and the N.W.T. are well designed and need only be expanded to additional long-term sites. The continuation of such long-term time series is important if we wish to see how ecosystem changes associated with global warming will impact cyclic events in the boreal forest.

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