Forest-Fire Regime: The Missing Link to Understand Snowshoe Hare Population Fluctuations?

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Introduction

The snowshoe hare (*Lepus americanus*) is actually recognized as a keystone species in North American boreal forests, having significant effects on vegetation and being one of the most relevant preys for several predators (Keith 1963; Keith and Cary 1991; O'Donoghue et al. 1998; Krebs 1996; Krebs et al. 2001a). According to the bottom-up theory, prey species at the base of the food chain are critical to maintain wildlife biodiversity at the landscape level (Noss 1987; Hunter 1999; Thompson 1988; Thompson and Angelstam 1999).

Population fluctuations in the snowshoe hare have thus fascinated biologists over the last 50 years (see Keith 1963 and 1990; Lidiker et al. 2000; Murray 2000; Krebs et al. 2001b). The snowshoe hare exhibits an 8- to 11-year cycle in the northern part of its geographical range, but this cycle is dampened or eliminated in the southern part of its range (Keith 1990; Murray 2000). Another characteristic of these fluctuations is that population trends are largely synchronous over large geographical regions (Murray 2000; Krebs et al. 2001b).

Numerous studies have explored this cycle and its causes, linking the hare cycle to exogenous or endogenous causes (see review in Murray 2003). Hypotheses in the first group (Murray 2003) are solar activity affecting plant productivity (Sinclair et al. 1993; Ranta et al. 1997; Sinclair and Gosline 1997), weather changing habitat quality (Grange 1949; Butler 1953), ultraviolet rays and forest fires modifying plant succession and composition (Rowan 1950; Grange 1965; Fox 1978), and plant nutrients varying naturally and cyclically (Lauckhart 1957). All these hypotheses emphasize that external causes affect food availability or quality for the snowshoe hare and consequently its population densities; the effect is bottom-up. Possible endogenous causes are numerous (Murray 2003): epidemics due to infectious diseases or shock (MacLulich 1937; Green and Larson 1938), physiological stress at high density

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reducing fitness (Christian 1950), polymorphic behavior according to population density (Chitty 1967; Krebs et al. 1992), overbrowsing at high density (Lack 1954), plant defenses induced by browsing (Fox and Bryant 1984; Bryant et al. 1985), predation according to density (Trostel et al. 1987; Royama 1992), and finally interaction between food shortage and predation (Keith 1974, Krebs et al. 1995; Sinclair et al. 2000). All hypotheses from this second group are based on intrinsic causes; some refer to predation whereas some other are based on food or an interaction between the two. Bottom-up as well as top-down hypotheses could thus explain the processes underlying this phenomenon (Keith 1963, 1974, 1990; Keith et al. 1984; Krebs et al. 1995, 2001a). The relative importance of these causes may vary in time, and the hare cycle is probably the resultant of the interaction among several of them.

Among all these causes, the most accepted point of view is the one taking into account food and predation. Keith (1974) have proposed that successive hare–food and hare–predator interactions cause declines of cycling hare populations, an hypothesis also tested and verified by Wolff (1980) in Alaska. In this experiment, Wolff (1980) have suggested that a steep increase in hare abundance can lead to overbrowsing and subsequently to individual shifts from optimal to suboptimal habitats where predation risk is higher. Reviewing causes of the snowshoe hare cycle, Keith et al. (1984) have concluded that starvation (bottom-up effect) can be considered as the cause of the first phase of population decline, followed by an increasing effect of predation, leading to a relative equilibrium between food and predator influence, and finally by a last period during which predation is solely responsible of the decline in abundance. Krebs et al. (2001a) have later considered that the three trophic levels are clearly involved in the control of those fluctuations: vegetation (hare food supply), snowshoe hare (as herbivore and prey) and predators. They have suggested that the 10-year cycle of the snowshoe hare is the result of the interaction between predation and food supply, but of these two factors, predation is clearly the dominant process. By comparing two hare populations found on an island and on close mainland sites, Krebs et al. (2002) have demonstrated the importance of predation as a major cause of hare population trends. Indeed, island-confined population exhibited lower amplitude of abundance fluctuations, and higher juvenile and adult survival rates during most years, except during years of population declines. Moreover, they observed that the predator guild exhibited lower densities and species richness on the island than on the mainland sites.

In a 16-year breeding experiment where they produce purebred lineages of high-phase and low-phase females, Sinclair et al. (2003) have recently observed that high-phase females exhibited lower reproductive rate, lower reproductive output, and earlier senescence than low-phase females. They thus concluded that an intrinsic mechanism operates in synergy with extrinsic causes of the 10-year hare cycle (predation and food shortage) in cycling populations.

The lower numerical variance in southern hare populations, which dampens the hare cycle, is considered to be the consequence of higher and steadier predation rates by a group of generalist predators typically common at lower latitudes (Howell 1923; Wolff 1980, 1981; Buehler and Keith 1982; Keith and Bloomer 1993; Stenseth et al. 1997). Several studies also suggest that the interaction between predation and food can explain the absence of snowshoe hare cycle in the south-eastern part of its distribution range, where richer forest ecosystems support constant predation pressure from generalist and specialist predators, along with constant and high food productivity (Keith 1990; Wirsing et al. 2002).

Krebs et al. (2001b) have suggested two general models to explain synchrony of hare population fluctuations across large geographic regions: one driven by weather and one by dispersal movements. Sinclair et al. (1993) have proposed a weather model, related to the sunspot cycle, to explain synchronicity of the hare cycle across North America. Sunspots and hare numbers are indeed highly correlated for three time periods during the past 250 years: 1751–1787, 1838–1870, and 1948–1986, which were all periods of high-amplitude sunspot fluctuations (Sinclair and Gosline 1997). Krebs et al. (2001b) have suggested that because sunspots affect broad weather patterns, they might, through weather, entrain snowshoe hare cycles across the continent when solar activity is unusually high. However, Sinclair et al. (1993) and Krebs et al. (2001b) were unable to put forward a mechanism for sunspot-affected weather patterns to translate into demographic impacts on hares.

Another interesting facet of hare cycle studies concern the temporal association between hare habitat and hare population level. The relationship between understory cover (as a protecting visual barrier against predators) and snowshoe hare abundance has been studied extensively and has clearly shown that the intensity of habitat use is positively correlated to lateral cover density (Grange 1932; Adams 1959; Bider 1961; Conroy et al. 1979; Wolff 1980; Orr and Dodds 1982; Wolfe et al. 1982; Pietz and Tester 1983; Parker 1984; Carreker 1985; Monthey 1986; MacCraken et al. 1988; Koehler 1991; Ferron and Ouellet 1992; Ferron et al. 1998; Litvaitis 2001; Beaudoin et al. 2004). Such studies have concluded that hares prefer feeding and hiding cover presenting a dense (>80% obstruction at 15 m) lateral cover, and use travel cover under dense canopy. Predation rates on hares are lower in dense cover than in sparser understory (Wolff 1980).

Surprisingly, the link between habitat selection and demography in the snowshoe hare has not yet been investigated. It is actually known that local and regional fluctuations in population abundance can be related to movements of hares searching for a habitat of better quality. Indeed, at high hare density, subordinate animals are likely driven into more open habitat were they are more vulnerable to predation, according to a small scale adaptation of multi-nodal diffusion model (Smith 1983) and individual-oriented model (Bascompte et al. 1997). At the landscape level, the availability of good cover is greatly dependent on the presence of regenerating forest stands. In the boreal forest, forest fires (and more recently logging) create those successional stages ideal for snowshoe hares (Radvanyi 1987). As fire has been a dominant disturbance regime in the Canadian boreal forest since the last ice age (Stocks et al. 2003), it can be presumed that the snowshoe hare has become adapted to it by being demographically opportunistic. Our objective is thus to establish correlative evidence of a relationship between geographical location, sunspot incidence, forest fire regime, and variations in hare abundance across Canada.

Methodology

We gathered data on hare abundance time series using different indices (i.e., bag count, hunting success, pellet count, number of furs sold); we used published data or graphs to estimate the amplitude of fluctuations in abundance or used databases from colleagues or from our research team. We considered only time series covering at least one period of abundance fluctuation (i.e., 10 years or more), the longest one covering 12 periods. For each time series, we first log-transformed hare abundances to minimize bias related to harvest statistics. Mean amplitude of fluctuations in abundance was calculated for a given time series by averaging cycle amplitude between successive minima and maxima.

Forest fire regime was calculated using the large fire database (LFDB) used by the Canadian Forest Service, which includes information such as annual fire abundance, fire location, and burned area for all fires larger than 200 ha in area censused in Canada for the 1959–1997 period, whatever they were caused by lightening or human activities. The LFDB divides Canada into territorial units according to three different spatial scales: ecozones (n = 15; mean area = 838,516 km^2), ecoregions (n = 219; mean area = 57,962 km^2) and ecodistricts (n = 1,031; mean area = 12,223 km^2). As the origin of hare time series were not always clearly identified, we used the ecoregion spatial scale as an interesting compromise between low geographical precision and high precision in fire regime calculation. We were thus able to define relative fire regime ranging from 1,000 to 1.6 million years, for each of these ecoregions (Fig. 1).

The geographical location of each time series of hare abundance was established with a GIS using the same ecoregions as for the LFDB, and a corresponding fire regime was thus paired to each time series. Pearson or Spearman ranked-correlations were used to test relationships between mean amplitude value in hare abundance fluctuation, latitude, longitude and fire regime, and between number of fires, total burned area and sunspot abundance (Legendre and Legendre 1998; Zar 1999). Number of fires, total burned area, and number of sunspots were previously standardized by the mean to be

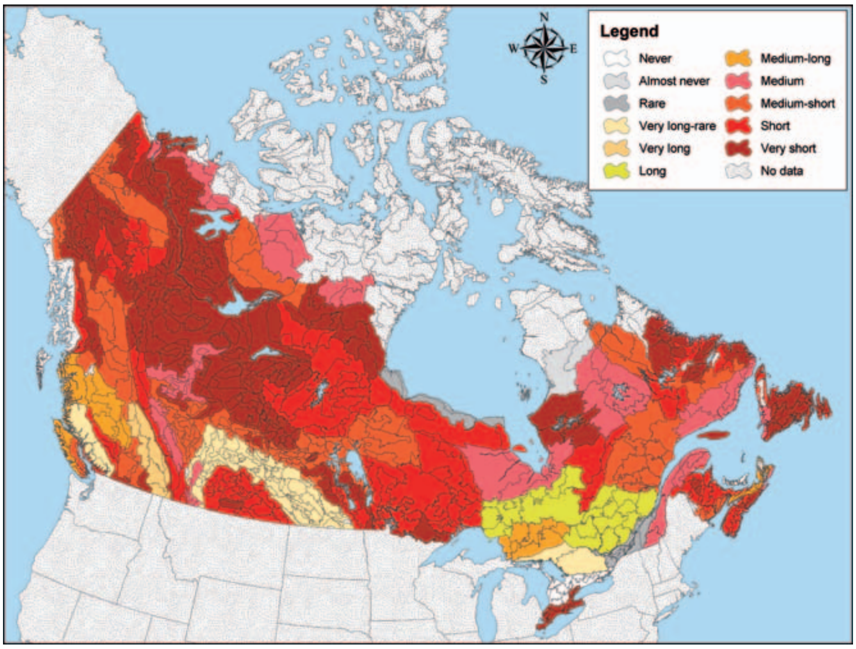

Fig. 1 Distribution of forest fire regime across Canada (large fire database (LFDB) from the Canadian Forest Service: all fires >200 ha during the 1959–1997 period)

compared on a similar scale. Data on annual sunspot abundance between 1959 and 1997 were freely downloaded from the Royal Observatory of Belgium website (http://sidc.oma.be/), which provides the Sunspot Index Data Center.

Results

We found no correlation between annual sunspot abundance and number of fires ($r_p = 0.24$; Bartlett $\chi^2 = 2.33$; $p = 0.13$; $P = 0.33$), nor between sunspot abundance and total burned area between 1959 and 1997 ($r_p = 0.22$; Bartlett $\chi^2 = 1.92$; $p = 0.17$; $P = 0.28$) (Fig. 2). However, total burned area and sunspot abundance were related before 1990 ($r_p = 0.55$; Bartlett $\chi^2 = 10.08$; $p < 0.01$; $P = 0.90$).

The amplitude of fluctuations in hare abundance in the boreal forest was correlated to latitude ($r_p = 0.61$; Bartlett $\chi^2 = 6.66$; $p = 0.01$; $P = 0.78$), but not to longitude ($r_p = -0.39$; Bartlett $\chi^2 = 2.42$; $p = 0.120$; $P = 0.36$) (Fig. 3). Forest fire regime was influenced by latitude (Zk $r_p = -0.68$; Bartlett $\chi^2 = 8.91$; $p < 0.01$; $P = 0.89$) but not by longitude ($r_p = 0.34$; Bartlett $\chi^2 = 1.73$; $p = 0.189$;

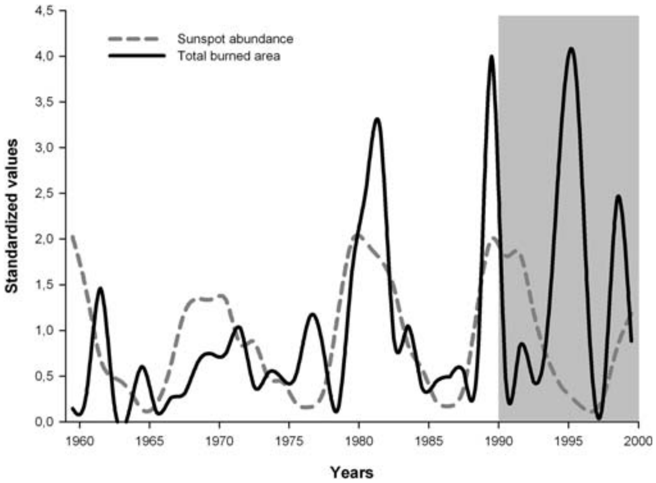

Fig. 2 Relationship between annual sunspot abundance and total burned area, between 1959 and 1999. *Shaded area* refers to years following 1990, for which correlation between the two variables decreased

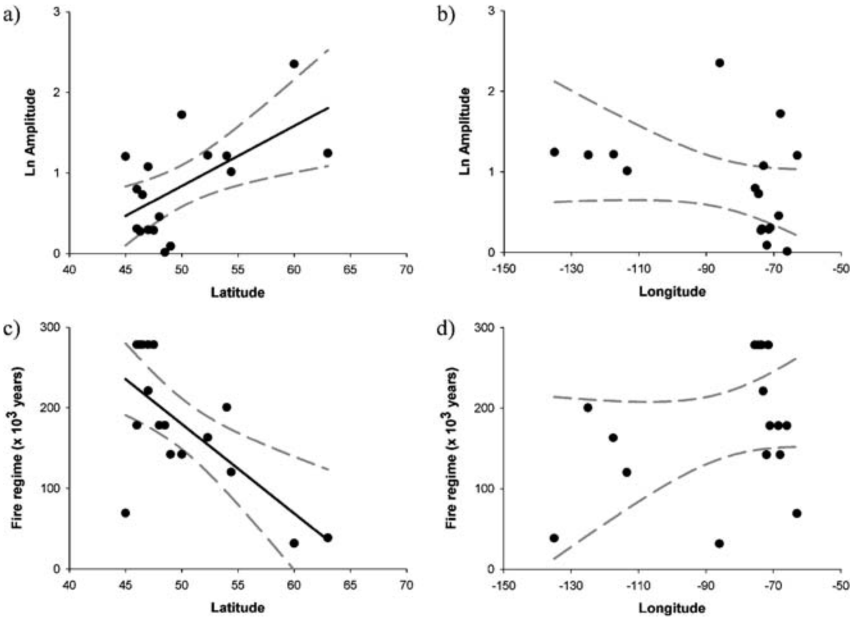

Fig. 3 Relationships between mean amplitude of hare fluctuations and latitude (a) or longitude (b), and between ecoregion fire regime and latitude (c) or longitude (d). Solid black lines represent significant relationships while dashed grey lines refer to 95% confidence intervals

P = 0.27) (Fig. 3). Finally, the mean amplitude of fluctuation in hare abundance was negatively correlated to the length of forest fire regime in the Canadian boreal forest ($r_p = -0.60$; Bartlett $\chi^2 = 6.99$; $p < 0.01$; P = 0.77)

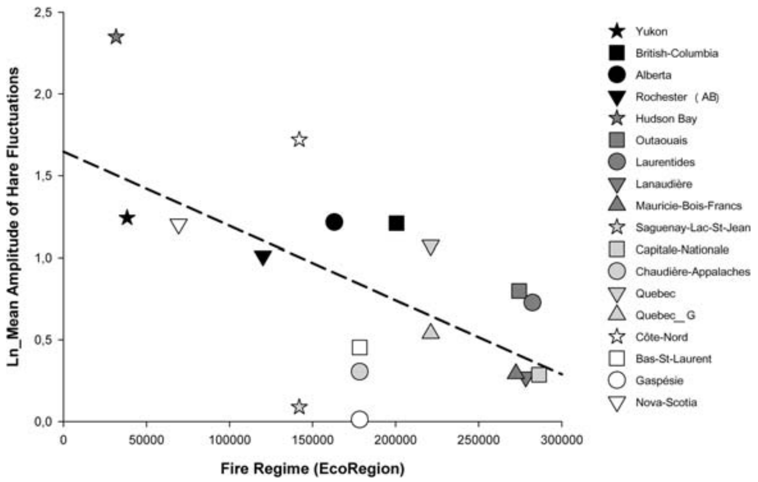

Fig. 4 Mean amplitude of hare abundance fluctuations in relation to forest fire regimes. Each *point* corresponds to a different hare time series, and *colors* refer to a longitudinal gradient from west (*black*) to east (*open white*). Sources of hare time series data: Yukon, British Columbia, Rochester and Alberta (Krebs et al. 2001b); Hudson Bay: (MacLulich 1957); Bas-St-Laurent, Saguenay-Lac-Saint-Jean, Capitale-Nationale, Mauricie-Bois-Francs, Outaouais, Côte-Nord, Gaspésie, Chaudière-Appalaches, Lanaudière, Laurentides and Quebec_G: Godbout (1999); Nova-Scotia and Quebec: Murray, D.L. Data gratefully provided

(Fig. 4). This suggests that forest fires, through their effects on hare habitat, directly influence hare abundance.

Discussion

Analyses of available data on hare populations, forest fires, and sunspots suggest that there are correlative evidences of relationship between these variables across the North American boreal forest.

Sunspot abundance is cyclic and presents superimposed periodicities of 11 and 22 years (Sinclair et al. 1993; Klvana et al. 2004). The present study indicates that at the continental scale, the total burned area in the boreal forest between 1959 and 1990 was related to the annual abundance of sunspots, but this relationship did not hold after 1990 (Fig. 2). There is growing evidence that a link exists between sunspot abundance and weather but the exact mechanism underlying this relation is still unclear (Rind 2002). The incidence of forest fires, which is the main stand-replacing process in the boreal forest, is greatly influenced by weather (Stocks et al. 2003). Fires thus generate more or less abundant regenerating stands depending on weather. Regenerating stands presenting a dense lateral cover are known to be a prime habitat for the snowshoe hare as they provide food and protection from predators (Brocke 1975; Conroy et al. 1979; Wolff 1980; Parker 1984; Monthey 1986; Ferron and Ouellet 1992; Ferron et al. 1998; Litvaitis 2001). Consequently, there is possible link between sunspot abundance and snowshoe hare habitat through a sunspot–weather–forest fires–hare habitat relationship. This relationship is all the more interesting as periodicities of sunspots and hares are similar. Indeed, Sinclair et al. (1993) have previously pointed out that hare numbers are correlated with sunspot numbers and that there is a 10 to 11-year periodicity in the correlograms. They also suggested that the snowshoe hare cycle is modulated indirectly by solar activity through an amplified climate cycle that affects the whole boreal forest. However, they, as well as Krebs et al. (2001b), were unable to put forward a mechanism for sunspot-affected weather patterns to translate into demographic impacts on hares. The relationship suggested here might be the missing link in the understanding of this large-scale zeitgeber of snowshoe hare population fluctuations. Some other indications suggesting that this may be the case can be found in the literature. Fox (1978) has pointed out a coincidence between the Canada lynx cycle, an important predator of the snowshoe hare, and the occurrence of forest and brush fires. Grange (1965) has suggested that fires set in motion plant succession, potentially leading to an increase in snowshoe hares. Another interesting facet of our hypothesis is that it also takes into account the synchronicity of hare cycles across large areas of North America; the effect of sunspots on weather, and ultimately on forest fire, is indeed a continental phenomenon (Krebs et al. 2001b).

Our results indicate that there is however a lack of coincidence between sunspot abundance and total burned area in the boreal forest after 1990. Similarly, Murray (2003) have reported that synchrony in hare population cycle across North America have recently declined. He also indicated that the cause of this decoupling is under investigation as the exact cause of this phenomenon is still unknown. Weber and Flannigan (1997) have recently suggested that climate change is changing fire regime in the boreal forest. This recent perturbation of the boreal ecosystem along with increasing logging activities may have contributed to desynchronize hare population cycle across the continent.

Fire intensity rapidly responds to local weather and regional climate (Weber and Flanagan 1997). The fire regime thus naturally differs across different zones of the boreal forest. The LFDB supports this conclusion. The present study suggests that the amplitude of the snowshoe hare cycle apparently reacts, at least at the regional scale, to the length of the fire regime (Fig. 4). We suggest that at the landscape level, if the fire regime is very long, the availability of good habitat, that is regenerating stands, is limited but relatively constant over time. However, in other boreal ecoregions where the forest fire cycle is very short, good habitat will be more available, providing more opportunity for exponential growth of hare populations. Consequently, hare density will be more constant in the former situation whereas it will be more variable in the latter case. Despite the fact that forest fires occur in other often more fertile forest ecosystems of Canada, they are not an essential stand-replacing process as in the boreal forest. Using paired data on hare abundance time series and fire regime in those ecosystems, we were thus not surprised to find no correlation under such conditions.

Our study also reveals that forest fire regime was influenced by latitude and that amplitude of fluctuations in hare abundance in the boreal forest was also correlated to latitude (Fig. 3). The north-south gradient of reduction in amplitude of hare fluctuations is in accordance with Murray's (2000). In the boreal forest, forest fires may contribute to this dampening, as suggested by our analyses. In more southern forest ecosystems, the most prevalent hypothesis is that lower population densities and increased stability are probably related to the effects of strong and consistent predation by a suite of facultative and generalist predators, combined with the greater patchiness of suitable hare habitat (Wolff 1980, 1981). Recent investigations have however failed to exhibit clear north–south disparity in survival and reproductive rates of hares, and it is consequently unclear which factor causes this demographic trend at the continental level (Murray 2003).

Regenerating stands are an excellent feeding habitat for the snowshoe hare (Pease et al. 1979; Litvaitis et al. 1985; MacCraken et al. 1988; Smith et al. 1988; Scott and Yahner 1989; De Bellefeuille et al. 2001), and their availability not only reduces predation risk but also provides abundant food, another condition favoring population growth. The relation between forest fire regime and the amplitude of hare population cycle in the boreal forest thus supports the conclusion of Krebs et al. (2001b) that fluctuations of snowshoe hare population are the result of the interaction between predation and food supply.

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