FEATURE ARTICLE

Factors affecting hare–lynx dynamics in the classic time series of the Hudson Bay Company, Canada

Zhibin Zhang[1,*], Yi Tao[2], Zhenqing Li[3]

[1]State Key Laboratory of Integrated Management on Pest Insects and Rodents in Agriculture, Institute of Zoology, and
[2]Key Laboratory of Animal Ecology and Conservation Biology, Chinese Academy of Sciences, Beijing 100080, PR China
[3]Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, PR China

ABSTRACT: The 10 yr hare–lynx (*Lepus americanus–Lynx canadensis*) cycles in boreal forest of North America have been well known for >100 yr, but the underlying mechanism is still not fully understood. Prey–predator interactions are generally thought to be the major causative factor for the cycle. The effect of climate on the hare–lynx cycle has been largely ignored. By using partial cross correlation and stepwise multiple regression methods, we re-analyzed the Hudson Bay Company's well known hare–lynx time series (1847–1903), to evaluate effects of intrinsic self-regulation, prey–predator interactions and El Niño/Southern Oscillation (ENSO) on hare–lynx dynamics. Our results clearly indicate that the widely cited classic hare–lynx dynamic is mostly explained by intrinsic self-regulation factors, instead of by prey–predator interaction; ENSO has small effects on rates of increase in hare and lynx populations.

Hare–lynx dynamics is determined by intrinsic self-regulation, and by the El Niño Southern Oscillation (ENSO).

Photo: Tom and Pat Leeson

KEY WORDS: Snow hare · *Lepus americanus* · Canadian lynx · *Lynx canadensis* · Prey–predator interaction · ENSO · SOI · Population outbreaks · Self-regulation

1. INTRODUCTION

The 10 yr abundance cycles (varying often from 8 to 11 yr) of the snowshoe hare *Lepus americanus* Erxleben, 1777 and the Canadian lynx *Lynx canadensis* Kerr, 1792 in the boreal forest of North America have been well known for more than 100 yr (Stenseth et al. 1997), but the underlying mechanism for driving the cycles of snowshoe hares and lynx is still not fully understood. Nevertheless, 3 main hypotheses have been proposed for the hare–lynx cycles: (1) hare–lynx interaction, (2) plant–hare interaction, and (3) plant–hare–lynx interaction.

(1) The hare–lynx interaction hypothesis states that the cycle is caused by prey–predator interaction (e.g. as shown by the Lotka-Volterra model). The prey–predator model can produce coupled oscillations in abundance of prey and predator. The hare-lynx cycles are often cited as a textbook example of prey–predator oscillations in ecology (May 1973, Murray

1989, Stenseth et al. 1997, Krebs et al. 2001). How-
ever, both Leigh (1968) and Gilpin (1973) concluded
that the hare–lynx dynamic is not a prey–predator
oscillation because they found, when using the
classic Canadian data, that the regression fit to the
Lotka-Volterra model was poor.

(2) The plant–hare interaction hypothesis states that
the cycle results from the interaction between hares
and their winter food supply (Lack 1954, Fox & Bryant
1984): population crashes are triggered by a shortage
of palatable winter forage, and the duration of popula-
tion cycles is determined by the recovery time of the
browse. Accordingly, oscillations of lynx populations
are consequences rather than causes.

(3) The plant–hare–lynx interaction hypothesis views
the cycle as the consequence of interactions among the
3 trophic levels (Keith 1974). It is hypothesized that
starvation at high densities initiates the population de-
cline of hares, and the decline is further accelerated by
lynx predation. Stenseth et al. (1997) found the domi-
nant dimensional structure of the hare series appeared
to be 3, whereas that of the lynx was 2. Stenseth et al.'s
(1997) analysis suggests that the classic view of a sym-
metric hare–lynx interaction is too simplistic.

The role of climate in the hare–lynx cycle remains un-
certain. Since the oscillations of hare and lynx pop-
ulations are so strongly synchronized over all of Canada,
several ecologists have suggested that large–scale me-
teorological factors (e.g. sunspots) might be responsible
for this synchronicity (Moran 1949, 1953a,b, Sinclair
1993). But Lindstrom et al. (1996) and Ranta et al. (1997)
rejected the possibility of a solar cycle–climate–hare–
lynx causal relationship. Stenseth et al. (2004) suggested
the North Atlantic Oscillation (NAO) might synchronize
the lynx dynamics within the Atlantic, Continental, and
Pacific zones with different snow conditions, which may
influence the lynx–hare interaction.

Recently, the El Niño Southern Oscillation (ENSO)
phenomenon has attracted enormous attention owing to
the significant ecological impacts it has been shown to
have at a global scale. A number of climate anomalies
(e.g. severe droughts, flooding, and hurricanes) are
linked to ENSO occurrences in many regions (Bjerknes
1969, Loon & Rogers 1981, Rasmusson & Wallace 1983,
Ropelewski & Halpert 1987). Several studies have
shown that some rodent outbreaks were associated with
ENSO events (Jaksic et al. 1997, Zhang & Wang 1998,
Zhang 2001, Zhang et al. 2003), although a small number
of studies (e.g. Krebs et al. 2004) found no such link. Be-
cause North America (including Canada and Alaska)
is significantly affected by ENSO episodes (Garnett
& Khandekar 1992, Shabbar & Khandekar 1996, Hoer-
ling et al. 1997, Shabbar et al. 1997, Hsieh et al. 1999,
Hsieh & Tang 2001; see also the website of Environ-
ment Canada: www.msc.ec.gc.ca/education/lanina/

index_e.cfm), it is possible that ENSO may have some
influence on the hare–lynx cycle; however, this has
not been investigated.

The classic hare–lynx time series based on the Hudson
Bay Company's historical records is widely used in most
ecological textbooks. In the present study, by using par-
tial cross correlation and multiple regression analysis,
we analyzed the hare–lynx time series to investigate the
role of self-regulation, prey–predator interactions, and
ENSO in hare–lynx cyclic dynamics. Our aim was to
test 3 hypotheses: (1) hare or lynx population cyclic
dynamics in the time series are mostly affected by self-
regulation; (2) hare–lynx cycles are mainly caused by
prey–predator interactions; and (3) ENSO affects hare or
lynx population dynamics.

2. DATA AND METHODS

2.1. Hare–lynx cycle data

This particular set of data was obtained from
MacLulich (1937). The data was mainly compiled from
historic pelt-trading records (Canadian lynx and snow-
shoe hare) of the Hudson Bay Company. The hare data
presented by MacLulich (1937) as one time series are
really 2 different sets of data. Data before 1903 repre-
sent fur records, whereas data after 1903 are derived
from questionnaires. The lynx fur data is also in-
complete after 1903 (see Elton & Nicholson 1942). The
hare–lynx data from the Hudson Bay Company is pre-
sented differently from author to author (e.g. Elton &
Nicholson 1942, Odum 1953). The hare–lynx data was
re-edited by Odum (1953) based on MacLulich's (1937)
data, and is cited in many books. In Odum (1953) the
lynx data before 1903 is about 1 yr earlier than
MacLulich's (1937) data; the lynx data after 1903 is
very different from MacLulich's data; the hare data
is also slightly different. Leigh (1968) tabulated the
1847–1903 hare and lynx fur data presented by Mac-
Lulich (1937) (Fig. 1). In this study, we used Leigh's
(1968) data for statistical analysis.

The annual increase rate of hare or lynx population
at Year t is defined as: $r = \log (N_{t+1}/N_t)$, where N_t is the
abundance of hare or lynx population at Year t (Zhang
et al. 2003).

2.2. Southern Oscillation Index (SOI) data

El Niño was originally used to describe the appear-
ance of a warming ocean current off the South
American coast adjacent to Ecuador and extending
into Peruvian waters around Christmas time. Today,
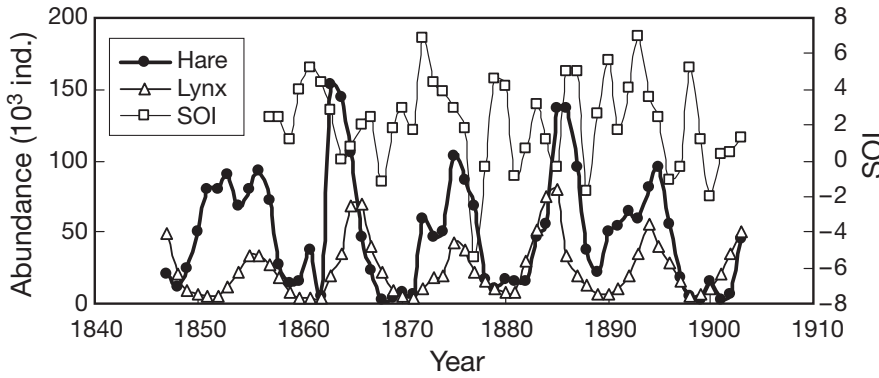the term El Niño refers to a sequence of changes (on

Fig. 1. *Lepus americanus* and *Lynx canadensis*. Hare and lynx abundances (redrawn from Leigh 1968) and Southern Oscillation Index (SOI) (data from Shi & Wang 1989) during 1847–1903

average every 3 to 8 yr) in atmospheric circulation across the Pacific Ocean and the Indonesian Archipelago when warming is particularly strong. During El Niño episodes, lower than normal pressure is observed in the eastern tropical Pacific, and higher than normal pressure is found over Indonesia and northern Australia. These conditions characterize the warm phase of the Southern Oscillation (SO). La Niña is referred to as the cold phase of SO when the sea surface temperature (SST) becomes unusually lower. During La Niña periods, lower than normal pressure is found over Indonesia, and higher than normal pressure is observed over the eastern tropical Pacific.

The Southern Oscillation Index (SOI) is calculated from the monthly fluctuation in the sea-level air pressure between Tahiti and Darwin. Extreme negative values of SOI are usually associated with warm events, but not always. There are several SOI data sources (e.g. 1866–2004 SOI data is available on the website of University of East Anglia: www.cru.uea.ac.uk/cru/data/soi.htm, and 1876–2004 SOI data is available on the website of the Australian Government Bureau of Meteorology: www.bom.gov.au/climate/current/soi2.shtml). In the present study, we calculated the yearly SOI values using the SOI data provided by Shi & Wang (1989) (Fig. 1). Shi & Wang's (1989) data has the earliest SOI values, extending back to 1854. There are slight differences in SOI values among different sources, but the 3 different SOI time series share the same fluctuations. For the overlapping period, there are strong positive correlations between Shi & Wang's (1989) data and data from the University of East Anglia (r = 0.886, p = 0.000, n = 122); between Shi & Wang's (1989) data and data from the Australian Government Bureau of Meteorology (r = 0.871, p = 0.000, n = 112); and between the Australian Government Bureau of Meteorology and the University of East Anglia data (r = 0.982, p = 0.000, n = 112).

2.3. Population models

We assume the annual increase rate of hare population (r_t^H) at year t is determined by its own past abundance (H_{t-k}), the past abundance of lynx (L_{t-k}), and the past values of SOI (S_{t-k}); the annual increase rate of lynx population (r_t^L) at year t is determined by its own past abundance (L_{t-k}), the past abundance of hare (H_{t-k}), and the past values of SOI (S_{t-k}). The population models are given as below:

$$r_t^H = a_0 + a_{1,k}\sum_{k=0}^{m}H_{t-k} + a_{2,k}\sum_{k=0}^{p}L_{t-k} + a_{3,k}\sum_{k=0}^{q}S_{t-k} + \varepsilon(t) \quad (1)$$

$$r_t^L = b_0 + b_{1,k}\sum_{k=0}^{m}L_{t-k} + b_{2,k}\sum_{k=0}^{p}H_{t-k} + b_{3,k}\sum_{k=0}^{q}S_{t-k} + \varepsilon(t) \quad (2)$$

In Eqs. (1) & (2), H_t and L_t are log-transformed. $\varepsilon(t)$ denotes stochastic noise; m, p and q denote the time lag of H_t, L_t and S_t. a_0, $a_{1,k}$, $a_{2,k}$, $a_{3,k}$, b_0, $b_{1,k}$, $b_{2,k}$, and $b_{3,k}$ are model parameters, representing the positive or negative effect on increase rates. $a_{1,k}$ represents self-regulation or density dependency of hare; while $b_{1,k}$ represents self-regulation or density dependency of lynx. $a_{2,k}$ and $b_{2,k}$ represent predation effect. $a_{3,k}$ and $b_{3,k}$ represent climate effect of ENSO. k represents the time lag of effect; if $k = 0$, the effect on increase rate is direct; otherwise, the effect is k years delayed.

2.4. Statistical analysis

In a preliminary analysis, we found strong autocorrelations of variables H_t, L_t, and S_t and strong cross correlations among the variables. Thus, simple correlation is not suitable for evaluating effects of variables H_t, L_t, and S_t on population dynamics. Partial cross correlation has been widely used for causal analysis by controlling co-varying variables (Stark et al. 2006). Partial cross correlation is very useful for inferring direct or spurious causes of control variables. In this study, partial cross correlation is used to identify effects of hare and lynx abundance and SOI on the increase rates in Eqs. (1) & (2). Because the period of population cycle of hares and lynx is about 10 yr, we assume that the maximum time lag of hare abundance, lynx abundance or SOI on increase rate of hare or lynx populations is 5 yr.

Stepwise multiple regression analysis (Philippi 1993) is used to identify factors affecting increase rate of hare or lynx population in Eqs. (1) & (2). There is no obvious multicollinearity effect in the multiple regression mod-

els since all variance inflation factors (VIF) are <10. Statistical software SPSS v. 13.0 was used for the statistical analysis. Significance level was set at p < 0.05.

3. RESULTS

3.1. Partial cross correlation

When variables of lynx abundance and SOI are controlled, increase rate of hare population at Year t is negatively and significantly correlated to the hare abundance at Year t (H_t) (r = −0.496, p = 0.006, n = 27). When variables of hare abundance and SOI are controlled, increase rate of lynx population at Year t is negatively and significantly correlated to the lynx abundance at Year $t-1$ (L_{t-1}) (r = −0.548, p = 0.002, n = 27), at Year $t-2$ (L_{t-2}) (r = −0.700, p = 0.000, n = 27), and at Year $t-3$ (L_{t-3}) (r = −0.600, p = 0.001, n = 27). When variables of hare abundance and lynx abundance are controlled, increase rate of hare population at Year t is positively correlated to SOI at Year t (S_t) with an approximate significance ($r = 0.337$, p = 0.073, n = 27); the rate of increase of lynx population is negatively correlated to SOI at Year t (S_t), and close to being statistically significant (r = −0.322, p = 0.089, n = 27).

In general, the partial cross correlation analysis indicates that the increase rates of hare or lynx populations are mostly explained by their own previous abundances. The effect of SOI on the rates of increase of hare or lynx populations is nearly significant. No predation term enters into the partial correlation models for either hare or lynx populations.

3.2. Stepwise multiple regression analysis

Stepwise multiple regression analysis indicates that the rate of increase of hare population at Year t is negatively and significantly affected by hare abundance at Year t (H_t) (Fig. 2) and hare abundance at Year $t-3$ (H_{t-3}), with an R^2 value of 0.381. The regression model is as follows:

$$r_t^H = 4.452 - 0.507H_t - 0.514H_{t-3} \qquad (3)$$
$$(0.961) \quad (0.116) \quad\;\; (0.160)$$

Here, the numbers in the brackets in Eqs. (3) & (4) are standard deviations of the relevant estimated parameters in the model. The rate of increase of lynx population at Time t is negatively and significantly affected by lynx abundances at Time t (L_t) (Fig. 2) and Time $t-3$ (L_{t-3}) and by SOI at Time $t-4$ (S_{t-4}), the latter with an R^2 value of 0.790. The regression model is as follows:

$$r_t^L = 4.308 - 0.441L_t - 0.558L_{t-3} - 0.017S_{t-4} \qquad (4)$$
$$(0.372) \quad (0.057) \quad\;\; (0.052) \quad\;\; (0.008)$$

In general, the result achieved by using stepwise multiple regression analysis is very similar to that obtained by using partial cross correlation analysis. A significant effect of SOI on the rate of increase of lynx population is found. No significant predation term enters into the regression models for both hare and lynx populations.

4. DISCUSSION

The hare–lynx cycle has been interpreted as a textbook example of a prey–predator oscillation, but this has been disputed (Krebs 2001), although Trostel et al. (1987) argue that predation may at least be responsible for the snowshoe hare cycle. May (1973) regards the Hudson Bay lynx and hare population oscillation as an example of a Lotka-Volterra oscillation. However, Leigh (1968) and Gilpin (1973) found the hare–lynx dynamic is not a prey–predator oscillation. We also found no significant predation effect for both hare and lynx populations; furthermore, we demonstrate that the rates of increase of hare or lynx populations are basically self-regulated or density dependent. Thus we
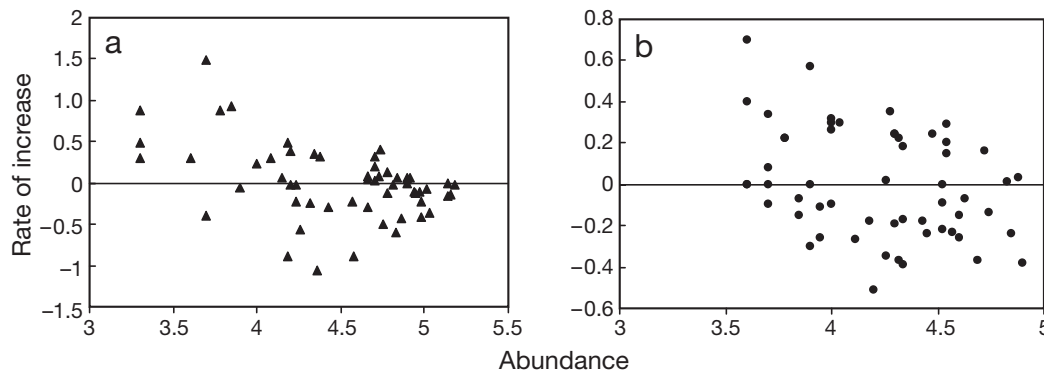

Fig. 2. *Lepus americanus* and *Lynx canadensis.* Relationships between rate of increase and abundance of (a) hare, and (b) lynx at Year t. Note the different scales on axes

conclude that self-regulation or density dependence may be the major forces driving population cycles of hare and lynx for this time series.

The mechanism of self-regulation in both hare and lynx populations is hard to infer from the modeling studies. Because some studies indicated that interventions providing additions of artificial or natural food could not prevent hare crash (Krebs et al. 2001), hare crash might be caused by social stress or maternal stress linked to food shortage or crowding. Lifetime reproductive output of hares taken from small populations was more than double that of hares taken from peak populations; the different lifetime reproductive outputs suggest that maternal effect might be important for hare cycle dynamics (Krebs et al. 2001). Our modeling results indicated that both direct and delayed density dependency are important in population cycles of hare and lynx.

The fact that the present study was based on the classic Hudson Bay Company hare–lynx time series introduces the potential for error on a number of fronts. We do not assert that predation is not important in hare–lynx dynamics. In fact, several previous studies have demonstrated the predation effect in hare–lynx cycling (e.g. Stenseth et al. 1997, 2004). Because the classic time series might have been edited by several different sources and is derived mostly from historical fur records of the Hudson Bay Company, it is possible that a number of disturbances (e.g. scale, time delay in space, fur price fluctuation in the market) could have affected data quality. Predation effects may be more obvious at local scales, but this effect may be reduced at large scales when data of different places or times are not appropriately pooled together. It is common that population outbreaks may have time delay among neighboring sites; this is also true for hare and lynx outbreaks (Krebs et al. 2001). Furthermore, the fur price of hares or lynx may be unstable due to fluctuations in market demand, and there may also be fur imports from other regions, which will then affect data quality. Finerty (1979) pointed out that hare and lynx data presented by MacLulich are in fact from different regions of Canada. Thus, care should be taken when basing explanations of population cycle dynamics on this time series. However, the observation of strong self-regulation or density dependency of both hare and lynx population (see Fig. 2) should not be neglected when looking for causative factors in hare–lynx cycle dynamics. The furs could have been recorded under different calendar years by the Hudson Bay Company, such as year of production, year of record, or year of sale (for more detail, see Elton & Nicholson 1942), which could have caused a time shift between hare and lynx. To confirm the effect of time shift on predation interaction, we repeated the analysis by moving

the calendar of lynx abundance 1 or 2 yr later than that of hare abundance. Still, we did not find any predation effect for both hare and lynx populations.

Previous studies suggest that sub-continental Canada — where snowshoe hare and lynx are widely distributed — is affected by El Niño and La Niña episodes (Garnett & Khandekar 1992, Shabbar & Khandekar 1996, Hoerling et al. 1997, Shabbar et al. 1997, Hsieh et al. 1999, Hsieh & Tang 2001; see also the website of Environment Canada: www.msc.ec.gc.ca./education/lanina/index_e.cfm). In El Niño years, the sub-continent will become warm and dry; while in La Niña years, it will become cold and wet, especially from late autumn to next spring (Fig. 3). It is likely that abundant precipitation during La Niña or high SOI years increases food resources, which probably facilitates hare population recovery, and/or it may affect
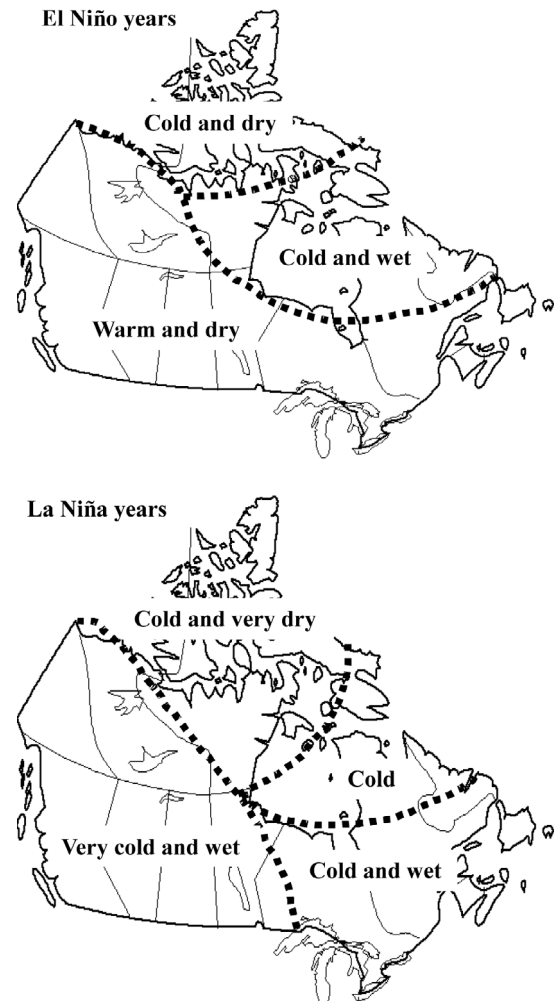

Fig. 3. Influences of El Niño and La Niña on climate of Canada during late fall to the following spring. Based on information from Environment Canada (see www.msc.ec.gc.ca/education/lanina/index_e.cfm)

hunting efficiency of lynx (Stenseth 2004) through changing snow coverage in winter. The mechanism linking ENSO and rate of increase of hare or lynx therefore needs further investigation.

Several studies have suggested that rodent outbreaks may be associated with ENSO events (e.g. Zhang & Wang 1998, Zhang 2001). Jaksic et al. (1997) reported that rodent irruptions during 1991-1992 (after an El Niño event) in certain semi-arid regions of South America were due to increases in seed bank following abundant rainfall. Using historical records of Brandt's vole *Microtus brandtii* population outbreaks in Inner Mongolia from 1948 to 1998, Zhang et al. (2003) found significant, positive correlations between monthly averages of SOI and vole population outbreaks; on the other hand, Krebs et al. (2004) found no correlation between outbreaks of house mice in Australia and ENSO. In the present study, we found that SOI has a significant but small effect on the rate of increase in the lynx population and a near-significant effect on increase rate of hare population. It can be seen from Fig. 1 that both hare and lynx peaks have a tendency to follow SOI peaks.

In summary, our results clearly indicate that the widely cited classic hare–lynx cycle, based on the Hudson Bay Company's data on fur collection, is not explained by predation between hare and lynx; strong negative self-regulation or density dependency effect is found for both hare and lynx populations; ENSO has small effects on the rates of increase of hare and lynx populations. The quality of the historical data is probably a reason for the lack of predation effects in the classic hare–lynx time series. Nevertheless, intrinsic self-regulation likely plays a significant role in hare–lynx cycles.

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