Population regulation in snowshoe hare and Canadian lynx:
Asymmetric food web configurations between hare and lynx

(statistical modeling/generalized additive models/population dynamics/dimension)

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Communicated by Robert M. May, University of Oxford, Oxford, United Kingdom, March 3, 1997 (received for review May 30, 1996)

ABSTRACT  The snowshoe hare and the Canadian lynx in the boreal forests of North America show 9- to 11-year density cycles. These are generally assumed to be linked to each other because lynx are specialist predators on hares. Based on time series data for hare and lynx, we show that the dominant dimensional structure of the hare series appears to be three whereas that of the lynx is two. The three-dimensional structure of the hare time series is hypothesized to be due to a three-tripod level model in which the hare may be seen as simultaneously regulated from below and above. The plant species in the hare diet appear compensatory to one another, and the predator species may, likewise, be seen as an internally compensatory guild. The lynx time series are, in contrast, consistent with a model of donor control in which their populations are regulated from below by prey availability. Thus our analysis suggests that the classic view of a symmetric hare–lynx interaction is too simplistic. Specifically, we argue that the classic food chain structure is inappropriate; the hare is influenced by many predators other than the lynx, and the lynx is primarily influenced by the snowshoe hare.

The cyclic changes in abundance of the snowshoe hare (Lepus americanus Erxleben, 1777) and the Canadian lynx (Lynx canadensis Kerr, 1792) are well known (1–4). These 9- to 11-year fluctuations are commonly discussed in ecology texts (e.g., refs. 5 and 6) as examples of coupled predator–prey cycles (7–13).

Even though the biodiversity of the boreal forest is low (14), it is still a too complex ecosystem to be modeled intelligibly (15). By focusing on those species directly connected with the hare, a smaller and more tightly interlinked food web emerges (Fig. 1A). This is even more so when focusing on the species directly connected to the lynx (Fig. 2A).

To estimate the number of key interactions determining the dynamics of the snowshoe hare and the lynx, we have analyzed time series data on these species (Figs. 1B and 2B) and interpreted the results on the basis of recent ecological data [primarily from the Kluane Ecosystem Project (4, 16)]. The main statistical result of our investigation is that the embedding dimension for the lynx series is roughly two, whereas that of the hare series is closer to three. We discuss these statistical results from the point of view of ecological interactions: in spite of the apparent complexity of the underlying food web, the dynamics of the hare and the lynx seem to be rather simple (low dimensional). On the basis of the documented pattern, we propose two ecological models—one for the lynx and one for the snowshoe hare.

<table>
<thead>
<tr>
<th>The Data</th>
</tr>
</thead>
<tbody>
<tr>
<td>The time series data derive from the compilation of fur records on hares (17) and lynx (2) carried out by Charles Elton, Helen Chitty, and others of the <strong>Canadian Snowshoe Rabbit Enquiry</strong> (ref. 18; see also ref. 19). It was partly through this inquiry that ecologists were convinced that the vertebrate cycles of the boreal forest were not just an artifact of the trapping or smoothing of random numbers (20).</td>
</tr>
</tbody>
</table>

The snowshoe hare data derive from the main drainage of Hudson Bay, whereas the lynx data are from 10 different regions across boreal Canada (the two hare series correspond regionwise to the combined James Bay and Lakes lynx series; L13 in Table 1). Although benchmark data on the abundance of cyclic species, they have some drawbacks. (i) The hare data presented by MacLulich (17) as one time series are really two different sets of data (1844–1904 represents fur records, whereas 1905–1935 derives from questionnaires; Fig. 1B); they thus ought to be analyzed as two series. (ii) The data on the different regions of the lynx are of variable lengths (extending between 1821 and 1939; most end in 1934) and contain occasional missing values (for most series, data are lacking for 1892–1896 and 1914). (iii) The regions to which the lynx series refer vary somewhat in demarcation over time (2). Among the lynx series, the one from northwestern Canada (the Mackenzie River district adjacent to the area studied in the Kluane Ecosystem Project) is the one most commonly quoted (L3 in Table 1).

<table>
<thead>
<tr>
<th>The Structure of the Time Series</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Statistical Modeling.</strong> Data were log-transformed to stabilize the variance (25). This transformation is biologically suitable due to the multiplicative nature of the population dynamics process involving birth and death processes (26). The log-transformed series ( {X_t} ) were scaled to have zero mean and variance equal to one.</td>
</tr>
</tbody>
</table>

In our search for parsimonious models for the time series under study, we start with a general model and simplify it as far as statistically permissible. Throughout we rely on recent developments in time series analysis (refs. 21, 23, 27–32; see references therein for details).

We follow the long standing conjecture (24, 33–37) that the transformed series may adequately be modeled in delay coordinates as a general autoregressive model of order \( [or dimension; sensu Royama (38)] d \); that is, \( X_t = F_d(X_{t-1}, X_{t-2}, \ldots , X_{t-\mu}) + \epsilon_t \). We assume that \( \{\epsilon\} \) is time- and state-independent white noise (30). As suggested by Cheng and Tong (27), the function \( F_d \) determining the laws of the population dynamics can be estimated for a given choice of \( d \) with minimal assumptions, using nonparametric regression. Provided \( F_d \) is continuous, Cheng and Tong (28, 29) showed

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0027-8424/97/0945147-6$2.00/0

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Table 1. Nonlinear autoregressive structure of time series on snowshoe hare and lynx in the Canadian boreal forest: Dimension and complexity

<table>
<thead>
<tr>
<th>No.</th>
<th>Time series</th>
<th>Years</th>
<th>Dimension</th>
<th>Linearity (P value)</th>
<th>Additivity (P value)</th>
<th>The General Additive Model: $X_t = f_1(X_{t-1}) + f_2(X_{t-2}) + \cdots + f_d(X_{t-d}) + \xi_t$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>N-W*</td>
<td>LL reg*</td>
<td>H-T</td>
<td>Slope at equilibrium of the GAM (linear coefficients ± 2 SEM)</td>
</tr>
<tr>
<td>H1</td>
<td>Snowshoe hare</td>
<td>1844–1904</td>
<td>3 (0.39)</td>
<td>3 (0.33)</td>
<td>1 (0.18)</td>
<td>4 (0.35;0.39)</td>
</tr>
<tr>
<td>H2</td>
<td>Snowshoe hare</td>
<td>1905–1935</td>
<td>3 (0.39)</td>
<td>3 (0.33)</td>
<td>1 (0.18)</td>
<td>4 (0.35;0.39)</td>
</tr>
<tr>
<td>L1</td>
<td>West</td>
<td>1825–1856</td>
<td>2 (0.28)</td>
<td>2 (0.25)</td>
<td>0 (0.01)</td>
<td>4 (0.17;0.18)</td>
</tr>
<tr>
<td>L2</td>
<td>West</td>
<td>1897–1934</td>
<td>2 (0.28)</td>
<td>2 (0.25)</td>
<td>0 (0.01)</td>
<td>4 (0.17;0.18)</td>
</tr>
<tr>
<td>L3</td>
<td>MacKenzie River</td>
<td>1821–1934</td>
<td>2 (0.19)</td>
<td>2 (0.15;0.16)</td>
<td>0 (0.01)</td>
<td>4 (0.17;0.18)</td>
</tr>
<tr>
<td>L4</td>
<td>Athabasca Basin</td>
<td>1821–1891</td>
<td>2 (0.31)</td>
<td>2 (0.24)</td>
<td>0 (0.05)</td>
<td>3 (0.35;0.41)</td>
</tr>
<tr>
<td>L5</td>
<td>Athabasca Basin</td>
<td>1897–1934</td>
<td>2 (0.47;0.50)</td>
<td>2 (0.20)</td>
<td>0 (0.00)</td>
<td>3 (0.35;0.41)</td>
</tr>
<tr>
<td>L6</td>
<td>West Central</td>
<td>1821–1891</td>
<td>2 (0.15)</td>
<td>2 (0.09)</td>
<td>0 (0.08)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L7</td>
<td>West Central</td>
<td>1897–1934</td>
<td>4 (0.38;0.48)</td>
<td>4 (0.23;0.30)</td>
<td>0 (0.01)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L8</td>
<td>Upper Saskatchewan</td>
<td>1821–1891</td>
<td>2 (0.21)</td>
<td>2 (0.17;0.20)</td>
<td>0 (0.00)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L9</td>
<td>Winnipeg Basin</td>
<td>1821–1891</td>
<td>3 (0.19;0.21)</td>
<td>3 (0.14;0.16)</td>
<td>0 (0.01)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L10</td>
<td>North Central</td>
<td>1821–1891</td>
<td>2 (0.35)</td>
<td>2 (0.35)</td>
<td>0 (0.01)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L11</td>
<td>James Bay</td>
<td>1895–1939</td>
<td>2 (0.20)</td>
<td>2 (0.11)</td>
<td>0 (0.01)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L12</td>
<td>Lakes</td>
<td>1897–1939</td>
<td>2 (0.26)</td>
<td>2 (0.20)</td>
<td>0 (0.01)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L13</td>
<td>James B. + Lakes</td>
<td>1897–1939</td>
<td>2 (0.20)</td>
<td>2 (0.13)</td>
<td>0 (0.01)</td>
<td>2 (0.10)</td>
</tr>
<tr>
<td>L14</td>
<td>Gulf</td>
<td>1897–1939</td>
<td>2 (0.55)</td>
<td>2 (0.39)</td>
<td>0 (0.01)</td>
<td>2 (0.10)</td>
</tr>
</tbody>
</table>

Dimension refers to the optimal order using CV, adopting the Nadaraya–Watson kernel (N-W), the locally linear model (LL-reg), the additive model (GAM), or the linear autoregression model (Linear). The corresponding CV value is given in parentheses. The CV value for dimension two (and three) for all lynx (and hare) series are given as the second number in the parentheses whenever not optimal (not boldface). Two methods were used for testing nonlinearity [H-T (21); Tsay (22)]. For both methods, $P$ values are given in parentheses. Additivity gives $P$ values from a Lagrange multiplier test for additivity (23). The estimated partial derivatives of the various functions (see text) at equilibrium of the skeleton model is given under lag1, lag2, and lag3. The corresponding linear autoregressive parameters (±2 SEM) are given in parentheses. No detrending has been carried out in spite of possible trends in some of the time series. Check marks indicate tests for which the null hypothesis was not rejected. Boldface indicates order estimates corresponding to the structure and complexity hypothesized in the main text of the paper.

*CV value in parenthesis. First number gives the CV for the optimal dimension; second number (if present) gives the CV for dimension three for hare, and dimension two for lynx. The degrees of freedom for each lag is restricted to be 0 (the lag is not present), 1 (linear), 2 (nonlinear), or 4 (strongly nonlinear).

†Series has been interpolated for the missing observations in year 1914.

‡The L3 series in the linear case is selected to have dimension 11 based on the AIC (24) criterion when there is no upper limit for the possible dimensions to be selected. This is exceptional compared with the other lynx series.
that the sample size requirement is exponential in $d$ for estimation of the functional form of $F_d$ but is at most quadratic in $d$ for the estimation of the dimension. To find the appropriate dimension for the series (and their underlying process), we employ cross-validation (39–42). That is, for each $d$ considered ($d = 1, \ldots, 4$), we estimate $F_d$ based on all but one data point, which is subsequently predicted. This is repeated for each data point. The sum of squared out-of-sample prediction errors [the cross-validation (CV) value; a rough estimate of the percentage noise is used as a measure of the model suitability] of the $d$ corresponding to the autoregressive model minimizing the CV value provide a consistent estimate of $d$, under minimal assumptions (25–28). To estimate the functions $F_d$, we employ two different nonparametric regression methods: (i) the Nadaraya–Watson kernel regression (21, 27, 28) and (ii) a locally linear regression (31, 32, 43). We employ a Gaussian product kernel for both. The consensus arising (Table 1) is that the snowshoe hare may parsimoniously be described by a model of dimension three (note that H2 appears cleaner in terms of predictability, based on its CV value, than H1), whereas the series for the lynx is more likely to be governed by a process of dimension two. The advantage of employing flexible models for $F_d$ is that conclusions reached are not biased by any parametric prejudices. The disadvantage is that such general models have a high number of degrees of freedom (ref. 44, chapter 3) causing loss in precision (high statistical variance). These models may also be victims of the curse of dimensionality (45). Indeed, the statistical uncertainty associated with any estimate may be paramount when the number of data points is relatively low. The high degree of consistency across the different data sets (Table 1) is, however, encouraging.

To increase precision we investigate the possibilities of imposing some restrictive assumptions. One such simplifying assumption involve assuming that there is no interaction, on the logarithmic scale, between years (44, 46):

$$X_t = F_d(x) = f_1(X_t-1) + \cdots + f_d(X_{t-d}) + e_t. \quad [1]$$

On the basis of the test for additivity by Chen et al. (23), this restrictive assumption appears permissible for 15 of 16 time series (Table 1); the rejection level of the deviating series (L12) is not far from the nominal 0.05 level. Additivity may, of course, be an artifact of low power due to the small sample size. However, the conclusion is biologically reasonable (see below) and the sample size is, after all, not particularly low. Estimating the optimal dimension by using CV of the additive model (Table 1) yields conclusions consistent with the analyses based on the more general models. Note, specifically that the additive models are usually as good as the more complicated models for prediction (see CV values in Table 1).

Since we have demonstrated approximate additivity, a linear model (on the logarithmic scale) represents the next level of simplification:

$$X_t = \alpha_1X_{t-1} + \alpha_2X_{t-2} + \alpha_3X_{t-3} + \cdots + \alpha_dX_{t-d} + e_t. \quad [2]$$

Two tests of nonlinearity were employed: (i) The nonparametric test by Hjellvik and Tjøstheim (21) and (ii) the Tukey one-degree-of-freedom test by Tsay (22). The null hypothesis of linearity is rejected in 5 of the 14 lynx series and is close to a nominal 0.05 level for one of the hare series (H1). This (31%) at a nominal 0.05 level and 50% at a 0.1 level) is more than expected under linearity (assuming the different series to be independent).
However, it is less than one may expect under extreme nonlinearity (see ref. 47). The estimates of \( d \) based on cross-validation of the linear models are generally higher than that based on the nonlinear models, as expected for nonlinear systems (48). Thus, it appears that the hare series may be represented an additive process on a logarithmic scale of order around three, while the order for the lynx series is around two. The lynx is certainly a nonlinear process (as previously concluded for series L3; see, for example, refs. 24 and 49). The same seems to be the case for the hare. Note, however, that the nonlinear function appear monotonic and not highly curved (Fig. 3).

Despite significant nonlinearities, the monotonity of the \( f_i \) functions justifies the linear autoregressive model (Eq. 2) as a useful average of the state dependent (functional) autoregressive coefficients of the dynamics, because these may be interpreted as coefficients of statistical density dependence (13, 47, 51).

Both the log-linear and the log-additive model indicate negative direct density dependence for the hare (\( \alpha_1 \); see refs. 13 and 51) ranging from \(-0.38\) to \(-0.05\) with a mean of \(-0.23\). There is essentially no dependency on the second lag (\( \alpha_2 \) ranging from 0.06 to 0.11 with a mean of 0.09), but a strong negative dependency on the third lag is observed (\( \alpha_3 \) ranging from \(-0.52\) to \(-0.24\) with a mean of \(-0.38\) (Table 1 and Fig. 3A). The three-dimensional structure of the hare system is consistent with earlier theoretical arguments (17, 52, 53) and with experimental results (4). For the lynx, the direct density dependency is positive (\( \alpha_1 \) ranging from 0.01 to 0.48 with a mean of 0.26); the lagged dependency is strongly negative (\( \alpha_2 \) ranging from \(-0.84\) to \(-0.27\) with a mean of \(-0.63\)) (Table 1 and Fig. 3B). The two-dimensional structure for the lynx (L3) has been deduced in several earlier studies including Moran’s (ref. 33; but see §).

All additive skeleton models (with \( e_i = 0 \) for all values of \( i \)) shown in Table 1 give rise to dampened oscillations (as judged by the Schur-Cohn stability criterion for linear difference equations; refs. 54 and 55). Thus, we do not observe limit cycles as reported by Tong (36) [based on the SETAR(2;2,2) model for the L3 lynx series]. The dampened oscillations will, however, be sustained in the presence of environmental stochastics. The difference between limit cycles and weakly damp-
ened cycles are, therefore, not so conspicuous in stochastic systems (see, e.g., ref. 47).

**Ecological Interpretations.** Recent studies have shown that the hares feed on a variety of food plants and are eaten by an array of predators (Fig. 1A) (56–59). The lynx is a specialist on hares but may utilize other prey species (Fig. 2A) (60, 61). When prey are scarce some predators may act as top predators on the lynx (62).

The present statistical results are consistent with the three-level trophic model for the hare (4, 56, 58). Other models involving spatial structure or age-structure are also possible. Due to recent field experiments and observations (e.g., ref. 4), we emphasis the trophic hypothesis as the more plausible scenario. In contrast to the more complex regulation of the hare, the lynx dynamics are thought to be food-driven (60, 61). The vegetation appear to segregate into palatable and non-palatable species (primarily Betula glandulosa, Salix glauca, and Picea glauca), the hare has a mixed diet (66). Preferred foods are typically reduced during the peak of the hare cycle, whereas less preferred (but still palatable) species remain common (59). The impact of hares on their food plants is transient (58) and the recovery of the preferred food plants is substantial even before the decline is complete. At Kluane essentially no effect on the herbaceous vegetation of excluding hares from a 4-ha plot for 8 years has been found (R. Turkington, personal communication).

**A Vegetation–Hare Predator Model.** Let \( H_t \) be the abundance of hares at time \( t \), \( V_t \) be the abundance of the vegetation at time \( t \), and \( P_t \) be the abundance of predators at time \( t \); notice that \( P_t \) does not consist of lynx only but the combination of a variety of predator species preying upon the hare. The functions \( F_b \), \( F_v \), and \( F_p \) describe per capita ecological interactions such that

\[
V_{t+1} = V'_t F_v(V'_p, H_t, e_v), \quad [3a]
\]

\[
H_{t+1} = H'_t F_h(V'_p, H'_v, P_t, e_h), \quad [3b]
\]

\[
P_{t+1} = P'_t F_p(H'_p, P'_v, e_p), \quad [3c]
\]

where \( e_v, e_h \), and \( e_p \) represent stochastic influences. There is no general agreement about the impact of hares on edible vegetation (see also above): Wolff (56) and Keith (57) have measured stronger impacts on vegetation at the peak of the cycle than measured in the Kluane Ecosystem Project (R. Turkington, unpublished results). However, rapid vegetation recovery after the cyclic peak have been observed in all studies (56–58). The effect of the hare on the vegetation seems by large negligible, thus allowing us to assume \( \partial F_v / \partial h \approx 0 \) (\( h = \ln H \)). The total predator community is strongly affected by the hare cycle, and the abundance of all the major hare predators—lynx, coyote, great-horned owl, and northern goshawk—follow the hare cycle closely (58, 70), suggesting \( \partial F_p / \partial h > 0 \) and \( \partial F_p / \partial p < 0 \) (where \( p = \ln P \)). Approximating the \( F \) functions in Eq. 3 by the first terms in a Taylor expansion in log-transformed abundances, we may, under minimal additional assumptions, write the log-linear model in delay coordinates (see Eq. 2):

\[
h_t = \alpha_1 h_{t-1} + \alpha_2 h_{t-2} + \alpha_3 h_{t-3} + e_t, \quad [4]
\]

where \( \alpha_1, \alpha_2 \), and \( \alpha_3 \) are statistical parameters that may be written as functionals of the ecological system portrayed by Eq. 3.

Interpreting the statistical results on the basis of Eqs. 3 and 4, the observed patterns of direct and delayed density dependence (\( \alpha_1 > 0, \alpha_2 \approx 0, \) and \( \alpha_3 < 0 \)) may be shown to be highly plausible: given internal regulation through intraguild predation within the predator guild, \( (\partial F_p / \partial p = 0) \), the condition \( \alpha_3 < 0 \) is satisfied by assuming fairly weak self-regulation in both the vegetation and the preferred food plants \( (\partial F_v / \partial v \) and \( \partial F_v / \partial h \) are slightly negative, as documented in refs. 71–74). If \( \partial F_p / \partial p \) is too negative, the relation \( \alpha_3 > 0 \) is violated: our statistical results, thus, introduces restrictions on the strength of the intraguild predator interaction—it must be strong, but not too strong. The relation \( \alpha_2 \approx 0 \) is fulfilled under a wide range of interaction strengths.

**A Hare–Lynx Model.** Let \( H_t \) be the abundance of hares (with the possible inclusion of other herbivores preyed upon by the lynx; \( H_t \) may be different from \( H_t \) used in the hare model) at time \( t \) and let \( L_t \) the abundance of lynx at time \( t \). The functions \( G_h \) and \( G_l \) describe the ecological interactions such that

\[
H'_{t+1} = H'_t G_h(H'_p, L_t, e_h), \quad [5a]
\]

\[
L_{t+1} = L'_t G_l(H'_h, L_t, e_l). \quad [5b]
\]

Lynx occupy discrete territories during most of the hare cycle (63, 65, 67, 68) and only at the low phase (when hares are

\[\]
scarcely) does the territorial system break down as many lynx go nomadic. A few lynx individuals survive the low phase by diversifying their diet with red squirrels and rodents. Hares represent the main food, however, even in the low phase (refs. 65, 67, and 68; M. O’Donoghue, personal communication; B. Slough, personal communication).

Approximating the $G$ functions in Eq. 5 by the first terms in a Taylor expansion in log-transformed abundances, we may write: $\ell = \beta_1 l_{-1} + \beta_2 l_{-2} + e$, where $\beta_1$ and $\beta_2$ are statistical parameters that may be written as functionals of the ecological system portrayed by Eq. 5.**

Due to the tight trophic interactions between the lynx and the hare (i.e., $\gamma G_0/\ell < 0$ and $\gamma G_0/\ell > 0$), the empirical patterns of statistical density dependence seen in the parsimonious time series model for the lynx (Table 1; $\beta_1 > 0$ and $\beta_2 < 0$), are easily fulfilled in the predator–prey system if self-regulation within both the lynx and the hare populations are not too strong (the hare model requiring similar weak self-regulation in the hare).

**The parameters in the autoregressive model for the lynx are given as follows: $\beta_1 = 2 + \alpha G_0/\ell + \alpha G_1/\ell$ and $\beta_2 = \alpha G_0/\ell \alpha G_1/\ell - (1 + \alpha G_0/\ell)(1 + \alpha G_1/\ell)$.

Conclusion

Despite the complexity of the boreal food web, the realized dynamics of the snowshoe hare and the Canadian lynx are found to be of low dimension. We have furthermore found an asymmetry in the way the lynx and the hare are positioned within the ecosystem: The snowshoe hare appear to be regulated from below and above (by a variety of predators including the lynx). The lynx, in contrast, seems to be regulated only from below, and primarily by the hare. Thus, from the hare’s point of view, the food chain is a vegetation–hare–predator chain, whereas from the lynx point of view, the hare–lynx interaction dominates. The snowshoe hare certainly plays an interesting role in the ecological theatre of the Canadian boreal forest ecosystem.

Comments by Rudy Boonstra, Robert M. May, George Sugihara, Howell Tong, and two anonymous referees on earlier versions of the paper were very helpful. Grants to N.C.S. and O.N.B. from the Norwegian Research Council and the University of Oslo and to C.J.K. from the Natural Sciences and Engineering Research Council of Canada are acknowledged.