

# Interlinking hare and lynx dynamics using a century's worth of annual data

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Received: 30 June 2007 / Accepted: 10 March 2008 / Published online: 29 April 2008  
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**Abstract** The classic fur trade records on Canadian lynx (*Lynx canadensis*) have rarely been analysed in direct conjunction with data on its principal prey, the snowshoe hare (*Lepus americanus*). Comparable long-term data for hare exist only for a region south of Hudson Bay. We fitted a bivariate log-linear time-series model to this hare and lynx data to disentangle the within- and between-population interactions of these species. To reduce problems with fur returns being non-normal and non-linearly related to abundance, we transformed the fur returns to a normal distribution based on sample quantiles. The estimated

effect on next year's lynx abundance of a 1% increase in current hare abundance was a 0.23% (SE = 0.05) increase in lynx. Conversely, a 1% increase in current lynx abundance corresponded to a 0.46% (SE = 0.12) decrease in next year's hare abundance. This contrasts with some earlier studies. However, these studies mixed hare data from south of Hudson Bay with lynx totals for all of Canada. Despite this asymmetry of interaction strengths, coefficients of determination were similar for hare versus lynx and lynx versus hare, because hare abundance varies more than lynx. Both species showed clear intraspecific density-dependence of about equal strength. A 1% increase in current abundance increased next year's abundance by about 0.75%.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10144-008-0088-2) contains supplementary material, which is available to authorized users.

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**Keywords** Linear model · Population cycles ·  
Population dynamics · Predator–prey models

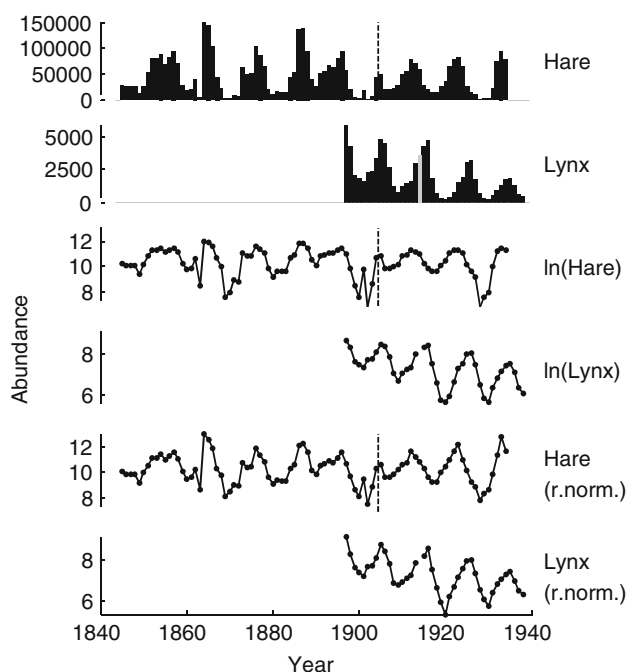
## Introduction

Long time-series of abundance are often limited to one or very few species. Although most species are part of a food web (Pimm 1982), single-species analyses can provide much insight into ecological interactions (Stenseth et al. 1998), viewing the system through the eyes of whatever species is available. Here, we evaluate the consistency between single-species analyses, fitting a full two-species model for comparison and added insight.

The snowshoe hare (*Lepus americanus*) and Canadian lynx (*Lynx canadensis*) are a tightly coupled predator–prey pair whose dynamics are relatively independent of that of other species in the ecosystem (Stenseth 1995; Stenseth et al. 1997; Krebs et al. 2001). Previous work has mostly viewed these dynamics through time-series data on lynx,

for which long fur-trapping records are available throughout its range in North America. Such single-species models suffice to diagnose several dynamical features of a system, such as stability properties, damping ratio and power spectrum (e.g., Royama 1992), but cannot disentangle within- and between-population interactions. Here, we extend earlier results by fitting a two-species model based on the available long-term hare data, which originate from the main drainage of Hudson Bay, Canada (Fig. 1). This analysis allows identification of the strengths of intra- and inter-specific interactions.

A similar analysis on mink and muskrat (Erb et al. 2001) fitted univariate autoregressive models to each species, using the abundance of the other species as a covariate. This works well when there are no missing values, but the incomplete temporal overlap (Fig. 1) of the hare and lynx data necessitates a fully bivariate time-series model.



**Fig. 1** Fur-trapping records of snowshoe hare (*Lepus americanus*) and Canadian lynx (*Lynx canadensis*) from south of Hudson Bay, Canada. *Top* Original data (for the hare, data from 1905 onwards are from questionnaires; MacLulich 1937). *Middle* In-transformed series. *Bottom* Rank-normalized series, where the values in each series are transformed into quantiles of a log-normal distribution corresponding to their rank in the original data set. This was done to prevent the statistical estimation from being dominated by the occasional deep lows of the hare series, which are believed to result from a nonlinear relationship between abundance and trapping when hare abundance is low. Note that the lynx value for 1914 is missing; the grey bar shows a linearly interpolated value. Vertical line shows the divide between fur returns and questionnaire estimates of hare

## Materials and methods

### A discrete-time model for a predator–prey system

Let  $X^1$  and  $X^2$  be a measure of the abundance of hare and lynx, respectively, and assume that this measure is monotonically related to actual abundance. We model the two-species system as a first-order vector autoregressive process (Ives et al. 2003):

$$\begin{aligned} X_t^1 - X_{t-1}^1 &= b_1 + a_{11}X_{t-1}^1 + a_{12}X_{t-1}^2 + \varepsilon_t^1 \\ X_t^2 - X_{t-1}^2 &= b_2 + a_{21}X_{t-1}^1 + a_{22}X_{t-1}^2 + \varepsilon_t^2 \end{aligned} \quad (1)$$

or in matrix form

$$X_t = b + (I + A)X_{t-1} + \varepsilon_t \quad (2)$$

where  $X_t$ ,  $b$  and  $\varepsilon_t$  are  $2 \times 1$  vectors,  $A$  is a  $2 \times 2$  matrix, and  $I$  is the  $2 \times 2$  identity matrix. Furthermore,  $\varepsilon_t$  is bivariate white noise; that is,  $\{\varepsilon_t\}$  is joint normal, with  $\varepsilon_t^i$  and  $\varepsilon_s^j$  independent if  $s \neq t$ , and  $E(\varepsilon_t \varepsilon_t') = \Sigma$ . Conditioning on the starting values  $\{X_1\}$ , Eq. 2 provides a complete description of the distribution of  $\{X_t\}$ , which is joint normal with expectation  $\mu$  and variance–covariance matrix  $\Omega$ , both of which are known functions of  $A$ ,  $b$  and  $\Sigma$ . The influence of current hare abundance on future lynx abundance is estimated by considering the distribution of the lynx time-series conditional on the observed hare series. If the model is stationary, so that its mean and variance do not change over time (equivalently, that all eigenvalues of  $(I + A)$  have absolute value less than one), Eq. 2 specifies the full unconditional distribution of  $\{X_t\}$ . In the following, we assume that the model is stationary, which is validated by the empirical results. However, this assumption is not crucial.

Below, we describe how this model can be applied even when the data are not linearly related to actual abundance. However, it is helpful to consider the straightforward ecological interpretation that the elements of  $(I + A)$  have in the case where  $X$  is the logarithm of abundance  $N$  (e.g., Royama 1992), namely that a  $p$  percent change in  $N_{t-1}^j$  will cause an  $(I + A)_{ij} \times p$  percent change in  $N_t^i$ , provided  $p$  is small. In technical terms,  $(I + A)_{ij}$  is the elasticity of  $N_t^i$  with respect to  $N_{t-1}^j$  (Case and Fair 1999) (see S1 in Electronic supplementary material (ESM) for derivation).

The full model implies an autoregressive-moving average (ARMA(2,1)) process for each of the state variables, providing a useful comparison with previous single-species studies (see below).

### The data

The only long fur-trade records of snowshoe hare are from the main drainage of Hudson Bay, Canada. MacLulich

(1937) and Elton and Nicholson (1942) discuss in detail how to align fur returns with the years of their biological production. However, Elton and Nicholson (1942: p. 219) argued that MacLulich's figures for 1844–1906 should be moved to 1845–1907, and we have followed this advice. Up to 1904, hare numbers were based on fur returns, and thereafter on questionnaires. We allowed for this difference in measurement units by centering each log-transformed hare series at zero, thus expressing observations relative to the geometric mean for each hare series. The choice to center at zero was arbitrary and has no effect on the parameters of interest, because all parameters except  $b$  are invariant under a multiplicative change of measurement unit. For the lynx, we used the sum of the Lakes and James Bay regions of Elton and Nicholson (1942). The time-series of both hare and lynx exhibit approximately 10-year cycles (Fig. 1).

#### Normalization by ranks

The deep troughs in the hare data (Fig. 1) suggest that a log-transformation is not sufficient to satisfy the normality assumption of Eq. 2. Hare or lynx may not be trapped in proportion to abundance when they are rare (e.g., because trappers may invest less effort when expected catches are low; see chapter 13 of Turchin 2003 for discussion). To reduce artifacts caused by this non-normality, at little cost in terms of bias and precision (see below), we molded each time-series into normality by replacing the observations  $x$  with quantiles of a normal distribution having the same mean and standard deviation as the original data. The quantiles were the sample quantiles as used in Q-Q plots (Johnson and Wichern 1992), i.e.,  $p_{(j)} = (j - \frac{1}{2})/n$  corresponding to the sorted  $x_{(j)}$ . Thus, we need neither assume that fur returns are proportional to abundance, nor that the dynamics is linear in log-transformed abundance. All we assume is that the dynamics are linear (with constant noise variance) for some monotonous transformation of actual abundance, and that fur returns are monotonously related to actual abundance. For brevity, we sometimes use “abundance” to describe this proxy below, while keeping in mind the reservations mentioned above.

This normalization might result in some bias and loss of precision. We estimated these errors using 1,000 time-series simulated from the fitted model (Eq. 2), estimating parameters both after rank-normalization and without it. The redundant rank-normalization caused the self-effects  $a_{11}$  and  $a_{22}$  to be overestimated (i.e., more negative) by about 15%, compared to estimates from the non-transformed, simulated data. Other parameters changed by 5–10%, while standard errors changed little.

#### Statistical analysis

We also fitted a model allowing for additive Gaussian (i.e., normally distributed) observation error in a so-called state-space model (e.g., Chatfield 1996).

$$Y_t^i = X_t^i + \eta_t^i, \quad i = 1, 2$$

where  $\eta_t^1$  and  $\eta_t^2$  are independent normal distributed error terms with expectation 0 and variances  $\sigma_{\eta^1}^2$  and  $\sigma_{\eta^2}^2$ , respectively. As detailed below, adding measurement error did not significantly improve the model, so the main emphasis of the paper will be on a model without measurement error.

We estimated parameters by maximum likelihood, finding the values of  $A$ ,  $b$ ,  $\Sigma$ ,  $\sigma_{\eta^1}^2$  and  $\sigma_{\eta^2}^2$  that maximize the joint probability density of the observed data (i.e., the transformed time-series of fur returns, corresponding to  $Y$  when including measurement error, and to  $X$  when excluding measurement error), using standard quasi-Newton algorithms for nonlinear optimization (Nocedal and Wright 1999). Missing observations are easily handled in such a framework. The model implies that the full data series follows a multivariate normal distribution whose means, variances and covariances are known functions of the parameters. The marginal distribution of the data that are not missing is then also normal with the same element-wise expectations, variances and co-variances. We can calculate  $R^2$ -like statistics as the proportion of variation in current hare abundance explained by last year's lynx abundance (denoted lynx  $\rightarrow$  hare), and so on for each combination of species (hare  $\rightarrow$  hare, lynx  $\rightarrow$  lynx, and hare  $\rightarrow$  lynx). These values do not sum to 100% because the hare and lynx series are correlated. Nevertheless, they represent a useful supplement to the ecological interaction coefficients  $a_{ij}$ .

We compared the power spectral density of the fitted model (Brockwell and Davis 1996) to the observed time series for each species, smoothing the latter using a Parzen window with the default bandwidth suggested by Chatfield (1996). For a given frequency interval  $\lambda_1 \leq \lambda \leq \lambda_2$ , the area under the power spectral density curve  $f(\lambda)$  is the variance accounted for by that frequency band, i.e.,  $\int_{\lambda_1}^{\lambda_2} f(\lambda) d\lambda$ . For ease of interpretation, we also show power spectral densities with respect to the period,  $1/\lambda$ . To preserve areas under the power spectral density curve, we plotted  $\lambda^2 f(\lambda)$  against  $1/\lambda$  (Freund 1992:266). Hence, the shape of the spectral density function depends on whether the horizontal axis shows frequency or period, as in Figs. 3 and 4, respectively; see S1 in ESM for details. Consequently, the period of maximal power density may not be exactly equal to the inverse of the frequency of maximal power density.

Comparing food-web interactions as viewed through the eyes of hare, lynx, and both species

Because missing values are readily accommodated in our maximum likelihood approach, Eq. 2 can be used to view the predator–prey dynamics through the eyes of the lynx, the hare, or the full predator–prey system. Agreement between the three sets of conclusions should be grounds for optimism in trusting conclusions drawn from other, single-species analyses. Conversely, inconsistency would suggest skepticism.

Technically, a situation with data on only one species is a special case of missing data, as described above. Then, the model (without measurement errors) describes the process of the observed species as an autoregressive moving average (ARMA(2,1)) process (see S1 in ESM). (The moving average term, ignored in traditional, purely AR models of the lynx, e.g., Moran 1953a, arises from the indirect effect on lynx of the noise that affected hare dynamics in the previous year.)

For reasons of symmetry, single-species ARMA(2,1) models based on either hare or lynx will produce identical autoregressive coefficients (see S1 in ESM and Akaike 1974). We tested whether the data agreed with this prediction, using a standard likelihood ratio test comparing the joint maximum likelihood of the ARMA(2,1) models under the restriction that the autoregressive coefficients be equal, with the maximum likelihood of the unrestricted ARMA(2,1) models. This constitutes a test of the hypothesis that Eq. 2 accounts for the dynamics of the two species, versus the hypothesis that the dynamics of one or both species depends strongly on factors other than those included in the model.

When measurement error is taken into account, the full model implies that single-species data follow ARMA(2,2) processes, although only a subset of ARMA(2,2) models are consistent with the model.

## Results

Parameter estimates for the full two-species analysis

The estimated interaction matrix ( $A \pm \text{SE}$ ) for the full model with measurement errors was

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} -0.25 & -0.52 \\ 0.26 & -0.26 \end{bmatrix} \pm \begin{bmatrix} 0.09 & 0.12 \\ 0.07 & 0.07 \end{bmatrix}. \quad (3)$$

The process noise variances for hare and lynx were estimated to  $\sigma_{11} = 0.37 \pm 0.17$ ,  $\sigma_{22} = 0.19 \pm 0.05$ , with a correlation of  $\rho = 0.29 \pm 0.14$ . The measurement error

variances were estimated to  $\sigma_{\eta_1}^2 = 0.12 \pm 0.11$  and  $\sigma_{\eta_2}^2 = 0$ .

Thus, the likelihood of the model was not improved by allowing for observation error on lynx. The point estimate of zero complicates formal significance testing. However, observation error on the hare was not significant ( $P = 0.14$ , one-sided likelihood ratio test), and a joint test for observation error on both species would thus have  $P > 0.14$ . Similarly, the AIC model selection criterion (Akaike 1974) favors the model without measurement errors, rather than one with observation error on one or both species. Even for hare, measurement error is only estimated to account for about 5% of the total standard deviation. Hence, we proceed with analyses based on a model without measurement error.

The estimated interaction matrix ( $A \pm \text{SE}$ ) for Eq. 1 was

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} -0.31 & -0.46 \\ 0.23 & -0.25 \end{bmatrix} \pm \begin{bmatrix} 0.08 & 0.12 \\ 0.05 & 0.07 \end{bmatrix}. \quad (4)$$

The noise parameters for hare and lynx were estimated to  $\sigma_{11} = 0.57 \pm 0.10$ ,  $\sigma_{22} = 0.20 \pm 0.04$ , with a correlation of  $\rho = 0.25 \pm 0.13$ .

Thus, the full two-species analysis showed clear within-species density-dependence in both hare and lynx. The density-dependence is about equally strong in the two species, and can be spelled out biologically under the assumption that  $X$  is approximately the logarithm of actual abundance. Other things being equal, a 1% increase in the current abundance of a species would only increase next year's abundance of that species by about 0.7% ( $1 + a_{11} = 0.67 \pm 0.08$ ,  $1 + a_{22} = 0.75 \pm 0.07$ ).

The predator–prey interaction is highly significant, but asymmetric, with hare being almost twice as strongly affected by a unit change in lynx abundance as vice versa. For each 1% increase in current lynx abundance, next year's hare abundance would drop by about 0.5% ( $a_{12} = -0.46 \pm 0.12$ ). On the other hand, a 1% increase in current hare abundance would increase next year's lynx abundance by only 0.25% ( $a_{21} = 0.23 \pm 0.05$ ).

Coefficients of determination ( $R^2$ ) for hare were 0.48 with respect to previous hare abundance, 0.11 with respect to previous lynx abundance, and 0.55 with respect to both (the  $R^2$  values with respect to each species do not add up to that for both, because the hare and lynx series are correlated). The  $R^2$  for lynx were 0.10 with respect to hare, 0.56 with respect to lynx, and 0.70 overall. Thus, although Eq. 3 shows the effect coefficient of lynx on hare to be stronger than that of hare on lynx ( $-0.44$  vs.  $0.23$ ), variation in lynx explains only about as much of the actual variation in hare, as what hare explains of lynx (0.10). The reason for this

apparent paradox is that the abundance of hare varies much more than that of the lynx.

Furthermore, population growth showed greater random variation in hare than lynx ( $\sigma_{11} = 0.62 \pm 0.10$  vs.  $\sigma_{22} = 0.19 \pm 0.04$ , with correlation  $\rho = 0.23 \pm 0.14$ ).

We assessed the relative contributions of “independent noise” on hare and lynx (the independent components of  $\varepsilon_t^1$  and  $\varepsilon_t^2$ ; see Methods in S1 in ESM) in generating the variation in hare and lynx abundance ( $X_t^1$  and  $X_t^2$ ). (Note that these variance components do not add up to 100% because the noise terms are correlated.) The variation in hare was explained 24% by independent noise in the lynx equation, and 76% by independent noise in the hare equation. Variation in lynx was explained 54 and 32%, respectively, by independent noise in the lynx and hare equation. This suggests that the independent variation happening at a lower level of the trophic system affects the system more strongly than the independent variation higher up in the system, though noise at both levels have substantial effects on the dynamics of the system.

#### Comparing stories: consistency between AR coefficients

There was good agreement (Fig. 2) between the AR coefficients implied by estimates from data on both species combined, those from single-species ARMA(2,1) models estimated independently, and those from separate ARMA(2,1) models estimated under the restriction of equal AR coefficients. As seen in Fig. 2, the AR coefficients based on lynx data only are very similar to those based on hare data only (likelihood ratio test for equal coefficients,  $P = 0.77$ ). Although the point estimates from the full model imply slightly longer period than suggested by the single-species analyses, the difference is not statistically significant (Fig. 2).

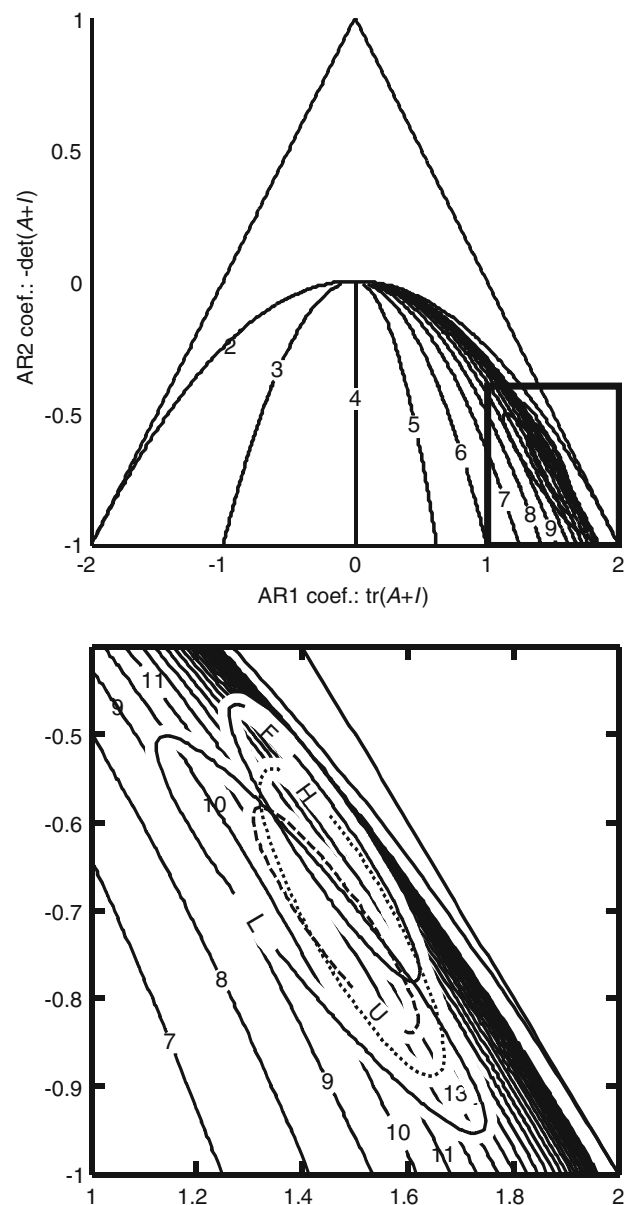
#### Spectral analysis of ARMA(2,1) processes

The ARMA(2,1) models for hare and lynx derived from the full model (Eq. 3) were, respectively,

$$\begin{aligned} X_t^1 &= 1.44X_{t-1}^1 - 0.62X_{t-2}^1 + \varepsilon_t^1 - 0.70\varepsilon_{t-1}^1, \\ \{\varepsilon_t^1\} &\sim \text{WN}(0, 0.66) \quad \text{for hare} \\ X_t^2 &= 1.44X_{t-1}^2 - 0.62X_{t-2}^2 + \varepsilon_t^2 - 0.50\varepsilon_{t-1}^2, \\ \{\varepsilon_t^2\} &\sim \text{WN}(0, 0.23) \quad \text{for lynx} \end{aligned} \quad (5)$$

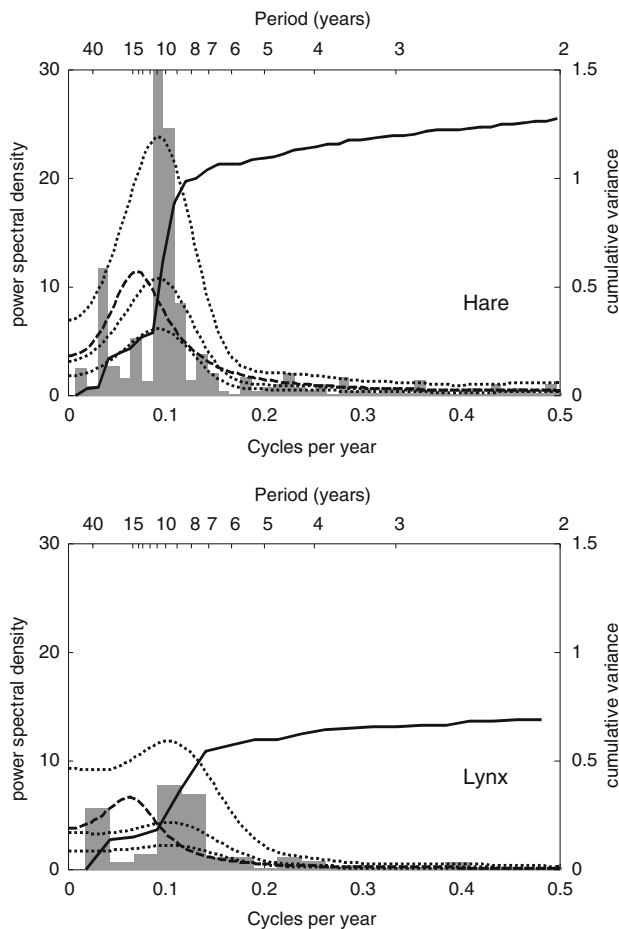
where WN denotes white noise.

The power spectral density of the ARMA(2,1) processes peak at frequencies of  $1/(14.2 \text{ years})$  and  $1/(16.0 \text{ years})$  for hare and lynx, respectively (Fig. 3). The corresponding period lengths are similar to that of the deterministic



**Fig. 2** Comparison of estimated autoregressive coefficients from four models of the hare–lynx dynamics. *Ellipses* Wald-based 95% confidence regions. The label *F* denotes the full two-species model  $X_t = b + (I + A)X_{t-1} + \varepsilon_t$ , which can be rewritten as an ARMA(2,1) process (in terms of either hare or lynx abundance), whose autoregressive parameters are the trace, and minus the determinant, respectively, of the  $2 \times 2$  matrix  $(A + I)$ . These AR coefficients are invariant to the choice of hare or lynx for the state variable in the ARMA(2,1) process. Labels *H* and *L* denote single-species ARMA(2,1) models based only on observations of hare and lynx, respectively. Label *U* denotes the unconstrained simultaneous estimation of two ARMA(2,1) processes for the hare and the lynx, used to test for the equality in AR coefficients implied by the two-species model. *Numbered contours* indicate the period (in years) of the deterministic skeleton of the model (see Royama 1992 for details); the *triangle* encloses the parameter combinations which produce stationary dynamics (i.e., where all eigenvalues of  $(I + A)$  have modulus less than one)

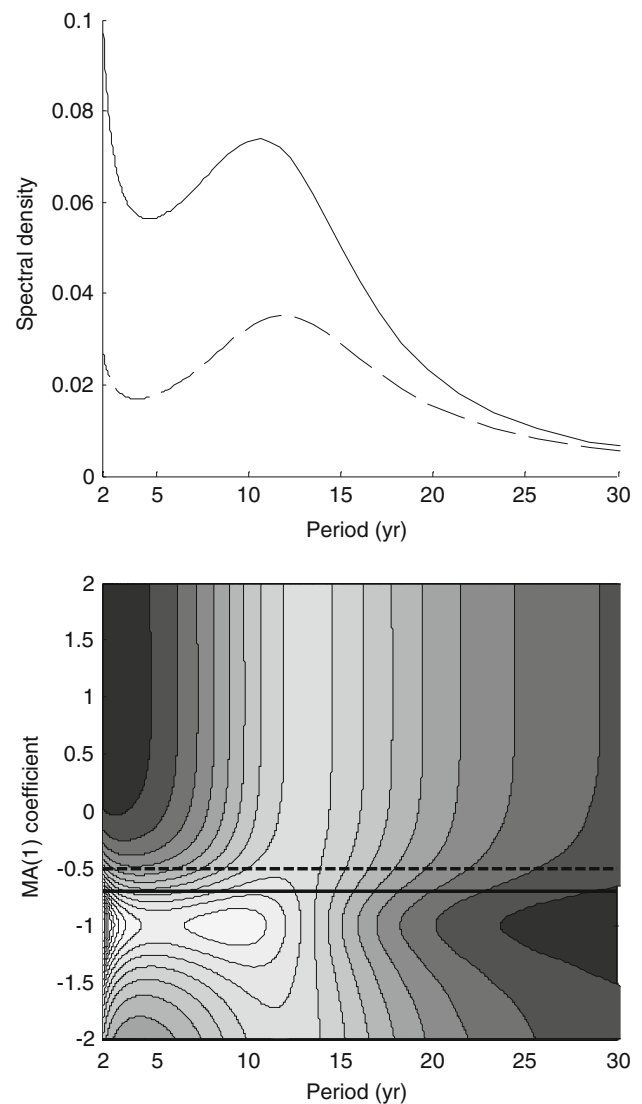




**Fig. 3** Spectral analysis of hare and lynx data and the fitted predator-prey model. The power spectral density (PSD) shows the contribution to the variance in each frequency interval. *Dashed line* Model PSD, *grey histogram* unsmoothed sample PSD, *dotted lines* smoothed sample PSD with 95% confidence intervals, *solid line* cumulative sample spectral distribution

skeleton for the full model (15.1 years; 95% CI 12.3–20.8 years), although somewhat longer than that of the ones based on hare only, lynx only, or unconstrained ARMA(2,1) processes (hare only: 12.9 years, 95% CI 10.7–18.2; lynx only: 11.0 years, 95% CI 9.1–14.8; both, unconstrained: 12.0 years, 95% CI 10.6–14.0; see Fig. 2). The full model also has a rather longer period than the 9- to 11-year peak of the sample spectral density (Fig. 3). However, agreement is better for power density with respect to period, which for the fitted ARMA(2,1) models peaks at 10.7 years for hare and 11.6 years for lynx (Fig. 4). The peak is perhaps also more narrow for the sample than the model spectrum, although it is within the 95% CI for the smoothed spectrum.

The negative MA term makes the spectral density peak at a shorter period than the corresponding pure AR process (peak period 12.7 years; Fig. 4). Generally, a large



**Fig. 4** Moving-average terms modify the spectral density of a stochastic process. Spectral density of ARMA(2,1) processes with varying MA coefficients and AR coefficients equal to those fitted for the two-species hare-lynx model. *Top* Spectral densities corresponding to the MA terms implied for the two-species model fitted to hare and lynx. *Bottom* Contours showing the effect of the MA term on the location of the spectral peak. *Solid and dashed lines* indicate MA coefficients implied for hare and lynx by the fitted two-species model

proportion of the variance is due to periodicities shorter than those of the deterministic skeleton (14.5 years). Thus, the stochastic processes are somewhat more in accordance with the sample spectral density than what the periodic skeleton shows (contours in Fig. 2).

## Discussion

The estimates from the full model (Eq. 3) showed that the population growth of hares is negatively affected, not only

by lynx abundance ( $a_{12} < 0$ ), but also by hare abundance ( $a_{11} < 0$ ). The former effect describes how the hare population is affected by the relatively slow process of year-to-year changes in lynx abundance (its numerical response). The latter is a negative “self-effect” of hare, which in the context of this model means short-term mechanisms which are not mediated through changes in lynx abundance and which cannot be identified from annual observations alone. Food limitation has been proposed as such a mechanism, although the experimental evidence for this is weak. Survival rates of adult hares and number of young produced per female begin to decline from maximum levels well before hares reach peak densities (Krebs et al. 2001). Food supplementation experiments reduce but fail to eliminate this pattern (Krebs et al. 2001). An apparent self-effect of hare might also arise from short-term changes in predation by lynx. However, the food intake of lynx saturates well below peak densities of hares (O’Donoghue et al. 2001), so any predation-mediated effect of hare on itself must be indirect, through the reproductive response of the lynx, and on a time-scale of years.

Indeed, a combination of food supplementation and predator exclusion did strongly attenuate the snowshoe hare cycle in a large-scale study (Krebs et al. 2001). However, predator exclusion falls beyond the scope of our current model, which is an approximation around some long-term average lynx abundance. Moreover, keeping lynx abundance constant reduces our model to an AR(1) process, which can only have cyclicity at a period of about 2 years. It is likely that other processes are allowed to dominate in regulating hare dynamics in the absence of lynx. Earlier studies (Stenseth et al. 1997; Krebs et al. 2001) have suggested that the hare is also regulated from below, in the sense that its food supply varies in a way which affects hare dynamics. A dynamic food supply for hares can easily be incorporated into our current modeling framework, but the analysis and its interpretation becomes rather complicated, and is thus not included here. Furthermore, residuals from the model show no relationship to previous hare density, suggesting that any dynamic effect of food on hare density is relatively small, in accordance with earlier conclusions (Stenseth 1995; Stenseth et al. 1997).

Population growth in lynx also showed a direct, negative density-dependence, in addition to the expected positive effect of hare abundance. Again, shorter-term data is required to identify underlying mechanisms, and intensive field studies suggest that competition may shift from interference to exploitation as yearling females stop recruiting young at peak hare densities and home ranges break down during the decline of hares (Mowat et al. 1996).

The estimated interaction coefficients for hare and lynx are within the variation found in a similar analysis of mink–muskrat interactions (Erb et al. 2001), which show similar fluctuations and periodicity as the hare and lynx.

The predator–prey interaction coefficients between hare and lynx ( $a_{12}$  and  $a_{21}$ ) are asymmetric: a given relative change in lynx abundance causes a strong relative change in hare abundance, whereas a change in hare abundance has less effect on next year’s lynx abundance. However, the hare is also subject to greater random variation, and hence shows greater relative variability than the lynx. A consequence of this is that, statistically speaking, the current abundance of lynx and hare both explain about 10% of each other’s variance in the next year.

There was reasonably good agreement between the full model and the two models based on single-species data (see Fig. 2 for details). However, the derivation of single-species ARMA(2,1) models from the two-species model (see S1 in ESM for details) forces a reinterpretation of the AR(1) and AR(2) coefficients, which were previously described as direct and delayed density dependence, respectively (Stenseth et al. 1997, 1998). In terms of the two-species model of Eq. 2, the first AR parameter is the trace of the matrix ( $A + I$ ), containing the sum of direct effects of each species on itself. The second AR parameter, the negative of determinant of ( $A + I$ ), importantly represents the predator–prey feedback loop, as represented by the product of interspecific effects. However, this is modified by the product of intraspecific effects. Furthermore, there will in general be moving-average terms in single-species models derived from purely autoregressive, multi-species models (cf. Eq. 2 and S1 in ESM). In the hare–lynx system, however, the MA term appears not to make much difference for the dynamics (numerical analyses, not shown). Our estimates of AR parameters for the area south of Hudson Bay are rather similar to Moran’s (1953b) (1.47 and  $-0.67$ , well inside the confidence ellipses in Fig. 2). Although better goodness-of-fit could be achieved with more complex statistical models, we found it more helpful at this stage to interpret a simple model with a mechanistic underpinning.

Previous two-species analyses of hare–lynx data have given puzzling results. “Do hares eat lynx?” asked Gilpin (1973), because lynx seemed to decrease when hares were most abundant. However, this paradoxical conclusion was obtained by combining lynx totals for all of Canada with hare data from just south of Hudson Bay (data from Leigh 1968). As the cycles are often out of phase in different regions (Stenseth et al. 2004), such spurious results may easily arise (Finerty 1979). By contrast, our analysis using hare and lynx data from the same region shows the cycle going entirely in the expected direction.

Many ecologists tend to be skeptical of linearity, pointing to the prevalence of non-linear interactions in ecology (May 1986), and indeed a number of non-linear features have been identified in the lynx dynamics (Tong 1990; Royama 1992; Stenseth et al. 1997, 1998). For instance, the narrow peak of the sample spectrum reflects the regularity of the cycles, which is greater than what a linear system can exhibit. However, a linear approximation, while simple, often captures essential features of a system's dynamics in a fairly wide neighborhood of the point of linearization. For instance, the AR coefficients of lynx differ between the increase and decrease phases (Stenseth et al. 1998). Our present estimate of the first AR coefficient is about midway between those for the two phases; the second AR coefficient is slightly more negative in our present estimate, but on the other hand the earlier model did not include an MA term. The availability of a host of techniques for the analysis and interpretation of linear models (Caswell 2001) may well outweigh the usefulness of constructing non-linear models which are less tractable. Furthermore, linear models allow us to diagnose deviation from linearity. If, for instance, the direct density-dependence of lynx was stronger at high levels of lynx abundance than suggested by our linear models, the residuals of the lynx equation plotted against lagged lynx abundance should give something like an inverted U-shape. Thus, from our analysis, we could informally have inferred that a linear model was not appropriate for the system at hand, and our residual plots would suggest what kind of non-linearity we would have to introduce into the model. However, our residual plots (not shown) do not indicate any such non-linearities, corroborating the bivariate model given by Eq. 2. In summary, the linear model in this study has proved useful in identifying the interaction coefficients between hare and lynx.

**Acknowledgments** This work was funded through grants from the Nordic Ministry (to NCoE-EcoClim) and from the University of Oslo (to CEES). Helpful comments on earlier versions of the paper were provided by Øistein Holen, Charley J. Krebs, and two anonymous referees.

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