Measuring Patterns in Population Fluctuations

E. Ranta et al. state (1) that Canadian lynx populations exhibit time-varying synchrony analogous to spatiotemporal patterns produced by their simulation model. Similarities between their model and the lynx data, however, appear to be superficial and exaggerated by their analytical methods.

First, a cross-correlation coefficient is a meaningful measure of synchrony only when the population data are stationary. Overall, the lynx data are stationary; however, there is a prominent upward trend for 1947 to 1961. Cross-correlations measured over a window as small as 15 years are sensitive to such long phases of nonstationarity. This causes a problem with the moving window analysis presented in figure 1D in the report (1): as the window is moved into and out of the nonstationary portion of the data, the cross-correlation swings high and then low. Thus, oscillatory patterns in this figure are an illusion created by the single transition from negative cross-correlations around year 28 to positive ones around year 34, and back to negative ones by year 40. The impression of oscillations is further enhanced by correlation coefficients being inherently positively autocorrelated as a result of the sharing of data points among successive windows. Also, clustering of correlograms in the 30- to 40-year window of figure 1D erroneously suggests that alleged shifts in synchrony are numerous, but this clustering is the result of nonstationarity being more pronounced in central populations (Manitoba, Saskatchewan, and Alberta) than in satellite populations (British Columbia, Yukon, Northwest Territories, Ontario, and Quebec). My reanalysis of the lynx data using four other techniques—differencing original data, splicing out nonstationary sections of data, using a window larger than 15 years, and moving the window in increments larger than 1 year—reveals that synchrony has not changed over time. What requires explanation are regional differences in nonstationarity of the pellet harvest reported for 1947 to 1961—and these could be a result of regional differences in trapping practices associated with changing post-war socioeconomic conditions.

Second, a cross-correlation coefficient seems an inaccurate measure of synchrony for populations that cycle in phase and then suddenly snap out of phase, as does the pair of populations shown in figure 1G of the report (1). In these data, the smooth transition from a high correlation around generation 600 to no correlation around generation 695 to a negative correlation around generation 730 is not indicative of the abruptness of the transition at generation 695. It is, in part, the artificial smoothness of oscillations in figure 1F that leads to the superficial resemblance with correlograms of lynx data in figure 1D. The resemblance disappears when cross-correlations are calculated on differenced data or over a series of nonzero temporal lags.

**Barry Cooke**
Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

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Response: Cooke suggests that changes in the cross-correlation coefficient over time, which we interpreted (1) as an indication of changing synchrony in the dynamics of Canadian lynx, are an artifact resulting from nonstationary data. Nonstationarity is certainly an aspect to be taken into account in analyses of population data. We agree with Cooke that the 1919 to 1968 lynx data from eight Canadian provinces are stationary; so are our simulation results. The concern is now whether nonstationarity in our time-window analysis is responsible for the observation of fluctuating synchrony.

Reanalyzing the data so that this linear trend is removed from each window shows that synchrony of fluctuation over time remains, although some details change (Fig. 1).

Differencing is another powerful statistical method for trend elimination [in biological terms log-transformed and differenced data are better known as data on population growth rate (2)]. An analysis by differencing the log-transformed lynx data confirms that synchrony (cross-correlation) in lynx population growth rate seems not to be time invariant either (Fig. 1C).

The maximum amplitude in the time-window analysis is 1.6 for the original data and 1.7 and 1.4 for the detrended and differenced data, respectively (15-year window). Increasing the time window length to 25 years yields maxima of amplitudes 1.2, 1.0, and 0.8. Thus, the pattern of fluctuating synchrony remains.

The use of a time window larger than 15 years, or moving the window in increments larger than 1 year, does not change our conclusion: the pattern of fluctuating synchrony remains. By increasing the time window, however, the fluctuations become tamer. When one increases the window size to ultimate, only one correlation coefficient remains for every pair of time series compared. We use a 15-year sliding window because it is well established that the lynx population cycle has a period of 9 or 10 years (in this data set), and 15 years is long enough to cover one full cycle in any sliding window.

Finally, making the subsequent time windows with less overlap has the following effects on the maxima of amplitudes (listed in same order as above). With a 5-year step: 1.6, 1.7, and 1.4 (n = 11 data points for each pair of provinces); 10-year step: 1.6, 1.7, and 1.4 (n = 6); 15-year step (totally nonoverlapping windows): 1.4, 1.6, and 1.4 (n = 4). Changing synchrony remains in the lynx data, and nonstationarity does not have a dominant effect on our results. Cooke’s “splicing out nonstationary sections of data” is a technique unknown to us.

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Figure 1. Example of fluctuating synchrony in pairs (measured with cross correlation, lag zero); data on Canadian lynx populations originating from eight provinces. In all graphs, a 15-year sliding window is used with step length one. (A) Original data, no detrending (1). (B) Linear trends removed for each window. (C) Data differenced for each window. Wide fluctuations in synchrony indicate that the system is not time invariant.
Cooke also states that “a cross-correlation coefficient seems an inaccurate measure of synchrony,” referring to abrupt changes in the synchrony in the simulated data (figure 1G in (1)). We agree, but the method is capable of pinpointing that such changes in synchrony between any two time series are taking place. For the two series, one first has perfect correlation, then negative correlation (the series are out of phase), and finally, again, high, positive correlation with returning synchrony. The window length used smoothens the pattern of such temporal change. The major point, however, is that dispersal of individuals among randomly located population subunits is capable of breaking down population renewal, obeying deterministic Moran-Ricker dynamics. This is an intriguing finding of the effects of linkage-caused nonlinearity on its own merits.

**Esa Ranta**  
**Veijo Kaitala**  
**Per Lundberg**  
Division of Population Biology,  
Department of Ecology and Systematics,  
University of Helsinki,  
Post Office Box 17,  
FIN-00014 Finland  
E-mail: esa.ranta@helsinki.fi

**References**

2. Population size and growth rate have different meanings in population ecology. Denoting $X = \log(N)$, where $N$ represents the original data, we get $R_t = X_{t+1} - X_t$, that is, the population growth rate.

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