

A spatial analysis of wildlife's ten-year cycle

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ABSTRACT. The population cycles that occur in several species of Canadian wildlife have been the subject of numerous studies in the twentieth century. To date, however, the emphasis of attention has been at the biological level. This paper introduces a rationale for a strictly geographic approach to the matter and presents the results of an initial statistical analysis of a spatially grouped time series: Canada lynx furs traded in the nineteenth and twentieth centuries. It is argued that the 10-year cycle represents a potential subject for study by geographers for two reasons. First, excellent sources of temporally and spatially-organized data exist. Second, causal theories now entertained include a strong geographic emphasis which has been poorly explored. In an effort to initiate spatial-temporal analysis of the problem, bivariate spectral time series analysis is applied to the lynx fur data to elicit information on regional and provincial lags in the spread of the population fluctuations across Canada. Earlier results reported in the literature are confirmed: a nodal region exists in west central Canada with the extremes of the country lagging 2–4 years behind. In addition, the results suggest that this nodal region has shifted some 500 or 600 miles to the southeast over the span of the last 100 years. This fact is interpreted as a lead favouring an approach to the study of 10-year cycles emphasizing macro-scale events.

Introduction

The population cycles that occur in several species of Canadian wildlife have been the subject of numerous studies in the twentieth century. Virtually all research before 1950 went into field-based examinations of the animals involved, especially the snowshoe hare (*Lepus americanus*) and the Canada lynx (*Lynx canadensis*), these being the species most strongly affected. The hope behind this strategy was that some direct causal influence, such as a disease, might be uncovered. Although no such mechanism was identified, these investigations resulted in the publication of a wealth of information on intra- and inter-species demography and ecology. For representative work, the reader should see Cross

(1940), Dymond (1947), Elton (1933), Elton & Nicholson (1942), Erickson (1944), Green & Evans (1940), MacLulich (1937) and Seton (1909).

In the late 1940s the question arose as to whether it could be proven statistically that the cycles did in fact exist. Cole (1951, 1954) suggested that the Hudson's Bay Company's yearly summary records of furs traded, often exhibited as proof of the existence of regular fluctuations, might have been incorrectly interpreted series of random values. Earlier, Palmgren (1949) had come to a similar conclusion. This idea was challenged by Butler (1953) and others, who pointed out that the regularity of the periods and the magnitude of the amplitudes involved seemed to preclude such an interpretation. Moran (1953) was the

first to subject some of the better series of data to formal analysis. He found that when tested against a model employing a second order autoregressive scheme, the records emerged as significantly cyclic. More recently, Bulmer (1974), using a more advanced model adding a first order autoregressive term to a sine function, retested both the Hudson's Bay Company records and a series of twentieth-century fur records kept by the Dominion Bureau of Statistics, and came to the same conclusions.

On the basis of these findings and numerous short- and long-term field studies, there can no longer be any doubt as to the existence of the 10-year cycle phenomenon. For the past 25 years the general feeling has been that the route to developing an understanding of the matter lies in improving our knowledge of the field habits of the organisms involved. Especially instrumental in this direction has been the work of Lloyd Keith and his students (see, for example, Keith, 1974; Keith, Rongstad & Meslow, 1966; Keith, Meslow & Rongstad, 1968; Meslow & Keith, 1968; Windberg & Keith, 1978). Years of demographic studies have led Keith to formulate a snowshoe hare population cycle model based on interaction between growing hare populations and their overwinter food supplies (Keith, 1974).

A second approach has been followed by population biologists, who have attempted in recent years to apply the rapidly growing body of mathematical ecology to the problem. This work has largely focused on hypothetical models of predator-prey interaction that might be relevant to the question. Such attempts as that by Gilpin (1973) have dealt primarily with time-dimensional considerations devoid of spatial context. To our knowledge, only Bulmer (1974, 1975) has made a serious attempt to draw statistically-based inferences from the spatial data available, and his results were applied to the derivation of an improved demographic model based on food chain relationships among cycling species.

Even given the dubious assumption that an adequate biological/demographic model of the 10-year cycle phenomenon now exists, there still remains the problem of how to interpret the spatial/temporal coordination between population highs and lows and their sequential

spread across Canada. It is possible to view this matter somewhat apart from existing biological considerations, as the traditional division of hypotheses implemented to explain 10-year cycles involves both biological and geographic elements. In the 'free vibration' model, it is assumed that elements peculiar to the boreal forest biome and inherent to the populations concerned have generated the population fluctuations. In the 'forced vibration' model it is assumed that some climatological or cosmic force extrinsic to the populations concerned has exerted a periodic stress upon them and in so doing has co-ordinated their interactions spatially. The first notion has the advantage of being accessible to all manner of biological study, but is utterly incapable of suggesting modes of understanding regional or continental level patterns. The second notion, while potentially easier to model spatially/temporally, is more difficult to interpret biologically.

It is the authors' feeling that exhaustive investigation of the forced vibration model has been stalled by an insufficient basis upon which to construct and test hypotheses. Historically, no one has been able to uncover an extrinsic agent that cycles in periods comparable to those of the wildlife population fluctuations, and the matter has been left alone. Perhaps, however, the causal agent is not obviously cyclic or might be understood as linked to extrinsic forces that are not cyclic themselves. If the agent should be biological, perhaps it is of a systemic nature that better lends itself to study at a greater spatial/temporal scale than is now being attempted. Whatever the case may be, there appears to be a gap in our understanding of the phenomenon at the geographic level that should be filled before further productive analysis can be applied. Data pertaining to the matter should be scrutinized with an awareness of their possible relevance to large-scale spatial relationships between the change of population levels over time and space and relevant extrinsic and intrinsic forces. This could save us much time, as explicit hypotheses might be derived that would admit of test at the biological level.

In the present study, fur records of the Canada lynx kept by the Dominion Bureau of Statistics and the Hudson's Bay Company are

subjected to bivariate spectral time series analysis. The purpose here is to help lay the foundation for a geographic study of the 10-year cycle phenomenon. The results presented also provide a reliability test for a means of grouping the qualitative spatial data of 'The Canadian Snowshoe Rabbit Enquiry' (Elton, 1933) to be reported in the near future.

The data

One of the remarkable things about the 10-year cycle phenomenon is the plentitude of information about it available. Investigators, both professional and casual, have reported formal findings and subjective impressions of the last 100 years in hundreds of publications. In addition to biological studies, there exist published records (some of which extend back to the early eighteenth century) of furs traded and regional to continental-wide questionnaire studies of population trends. A good starting point in tracking down this information is the bibliography of *Wildlife's ten-year cycle*, by Lloyd Keith (1963). In addition to published reports,

considerable unpublished information still lies buried in the archives of the Hudson's Bay Company in Winnipeg.

Two series of fur data have contributed to this pre-study. Hudson's Bay Company post by post records of lynx pelts traded in the nineteenth and early twentieth centuries were grouped by Elton & Nicholson (1942) into ten 'regions'. Although the exact relative boundaries of these regions did not remain the same over this period, we feel, as did Bulmer (1974), that the changes involved, especially during the period 1821-91, are not of great significance. It was not possible, however, to use all the regions created by Elton & Nicholson due to the fact that some of them lacked data for parts of this period. Six regions were eventually chosen, all in the west and midwest of Canada (see Figs. 1 and 2). Readers are referred to Elton & Nicholson (1942, pp. 228-229) for the exact values of the relevant data.

The second source of pelt data is the twentieth century record of the Dominion Bureau of Statistics. This has been compiled on an annual basis since 1921 by animal and

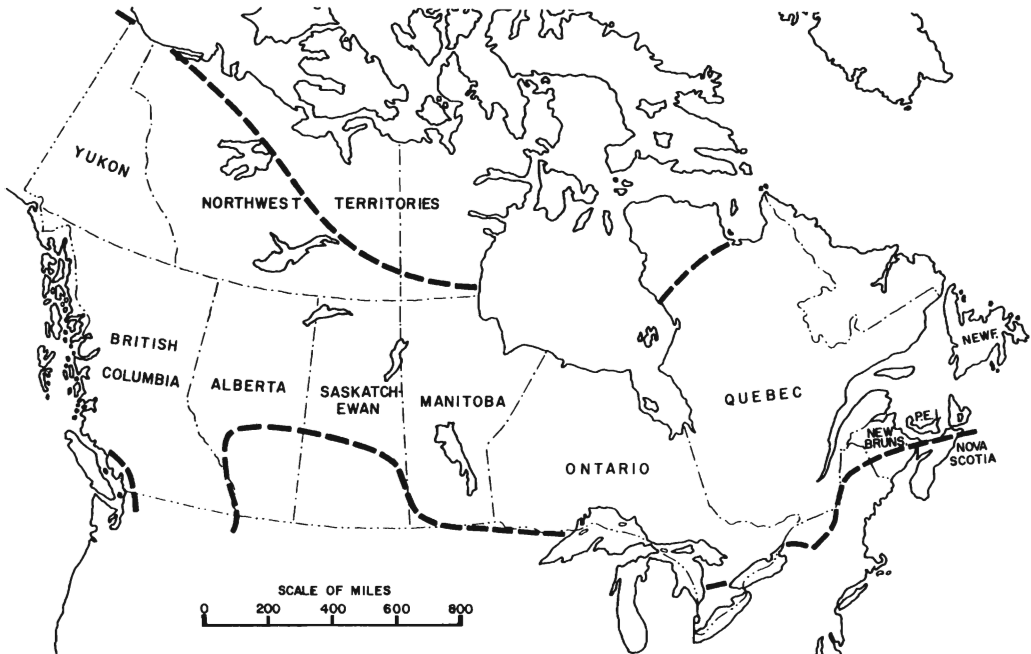


FIG. 1. Canada, with limits of the Canadian range of the lynx (*Lynx canadensis*) added.

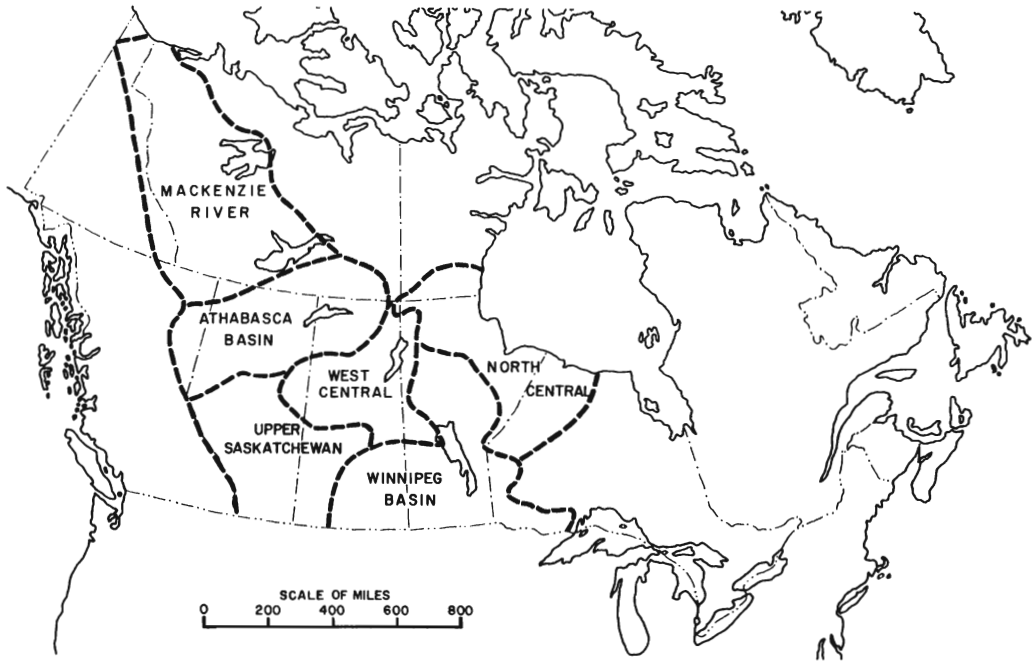


FIG. 2. Location of six of the 'regions' into which nineteenth-century lynx fur data were grouped by Elton & Nicholson (after Elton & Nicholson, 1942).

province (Dominion Bureau of Statistics, 1921–77). These records proved difficult to obtain, as it seems that only the library of the Dominion Bureau of Statistics itself contains a full series of these short yearly reports.

Pretesting indicated that it would be impossible to elicit significant results at the province level for most species without implementing an involved trend removal strategy first. A future report is planned based on such analysis. The main problems encountered included missing and intermittent data, weak 10-year periodicities, and marked trend of a non-linear variety. In the end, we tested only the 57-year record of the lynx. Because of the constraints on spectral series analysis, short series were not examined. Readers interested in an analysis of provincial and regional fur series data of shorter length should consult Bulmer (1974).

The reliability of the fur data themselves deserves some comment at this point. To the authors' knowledge, no one has ever mounted a lasting challenge to their reliability as an indicator of the period of cycling populations.

It is clear, however, that one should not consider them literally representative of the actual amplitudes of the cycles. Several factors (among these: (1) differing rates of human predation within the cycles; (2) the fluctuating fur market; (3) the effect of varying hunting and trapping regulations; and (4) long-term population trends and/or fluctuations within the populations concerned) surely complicate unbiased assessment, and it is probably better to rely on field-based reports on population levels in this regard. None the less, only when the cyclic response is rather slight (a situation not obtaining in the Canada lynx population) should fur data be seriously questioned as an indicator of period.

Methods

Spectral analysis procedures provide an effective means for studying the relationship between data sets arranged in time series. The technique centres on the decomposition of a stationary time series (or a non-stationary time series which has been transformed into a

stationary time series) into an infinite number of frequency bands representing cyclical components in the data. A single time series is stationary when the mean and covariance function do not vary significantly from one portion of the time series to the next. The variance spectrum of the time series data shows how the variance of the time series is distributed over frequency; i.e. the variance spectrum shows that portion of the variance contributed by each frequency band. A peak in the variance spectrum at a certain frequency usually indicates that some important generating process within the data is operating at that wavelength.

As Mitchell *et al.* (1966) point out, if the first lag autocorrelation coefficient (r_1) of a time series does not differ significantly from zero, it can be assumed that the time series is persistence free. When this is the case, 'white noise' is taken as the null hypothesis. However, as is often the case, r_1 will differ from zero by a statistically significant amount. If this occurs, and if

$$r_2 = r_1^2 \text{ and } r_3 = r_1^3, \text{ etc.},$$

then the null hypothesis that should be used is based on Markov 'red noise'. From the equation given above, it is apparent that the shape of the 'red noise' null hypothesis will depend on the value of r_1 . On the other hand, the 'white noise' hypothesis consists of a horizontal straight line which has a constant value at all points and is equal to the average value of all the raw spectral estimates.

The decision between the 'white noise' or 'red noise' hypothesis is based on statistical tests outline in Mitchell *et al.* (1966). The choice of the proper test depends on how closely the frequency distribution of the series is given by the normal distribution. Based on tests involving skewness and kurtosis in data sets, it was determined that the lynx time series were near normal in nature. Under such circumstances, Mitchell *et al.* (1966) suggest using the von Neumann ratio to test for the validity of the 'red noise' hypothesis. Once it has been decided that the 'red noise' hypothesis is to be used, it can be constructed from the following equation:

$$H_k = \bar{s} \left[\frac{1 - r_1^2}{1 + r_1^2 - 2r_1 \cos(\pi k/m)} \right],$$

where r_1 is the first lag autocorrelation coefficient, k is the lag number between $k = 0$ and $k = m$, and \bar{s} is the average of the $m + 1$ raw spectral estimates. The null hypothesis along with its confidence bands and the spectral estimates can be plotted on the same graph for comparison purposes (see Fig. 3).

The 95% and 5% points of the χ^2/ν distribution are used to calculate the confidence bands for the null hypothesis. For a complete discussion of the backing theoretical principles see Mitchell *et al.* (1966). The two values obtained from the χ^2/ν distribution for the time series degrees of freedom are the same for all the spectral estimates. Thus, the null hypothesis confidence envelope is obtained by multiplying the null hypothesis values at each lag by the 95% and 5% points of the χ^2/ν distribution. In the present case, the 95% confidence limit for the null hypothesis was obtained by multiplying each value of the null hypothesis by 2.15. The 5% confidence limit was obtained by multiplication by 0.25 (for a graphic representation, see Fig. 3).

The most important aspect of the use of the null hypothesis centres on its relationship to the spectral estimates. If a comparison of the spectral estimates and the null hypothesis demonstrates that none of the spectral estimates lies above the 95% confidence limit or below the 5% confidence limit, then it is safe to conclude that the calculated sample spectrum comes from a population whose spectrum is specified by the null hypothesis — the Markov 'red noise' process in the present case.

However, if one of the spectral estimates were found to lie outside the confidence envelope, the meaning of this event would have to be evaluated. In the present case, the only spectral estimate which consistently lies outside the envelope has a dominant period of 9.33 years (for the regional data) or 9.5 years (for the provincial data), and it lies above the 95% confidence limit. If there is *a priori* reason for the occurrence of a particular period, as there is here, the interpretation of the results is straightforward. The estimate at the period between 9 and 10 years is significant at (or above) the 95% confidence level. If no *a priori* information is available, Mitchell *et al.* (1966) suggest testing a particular spectral estimate at a level of significance

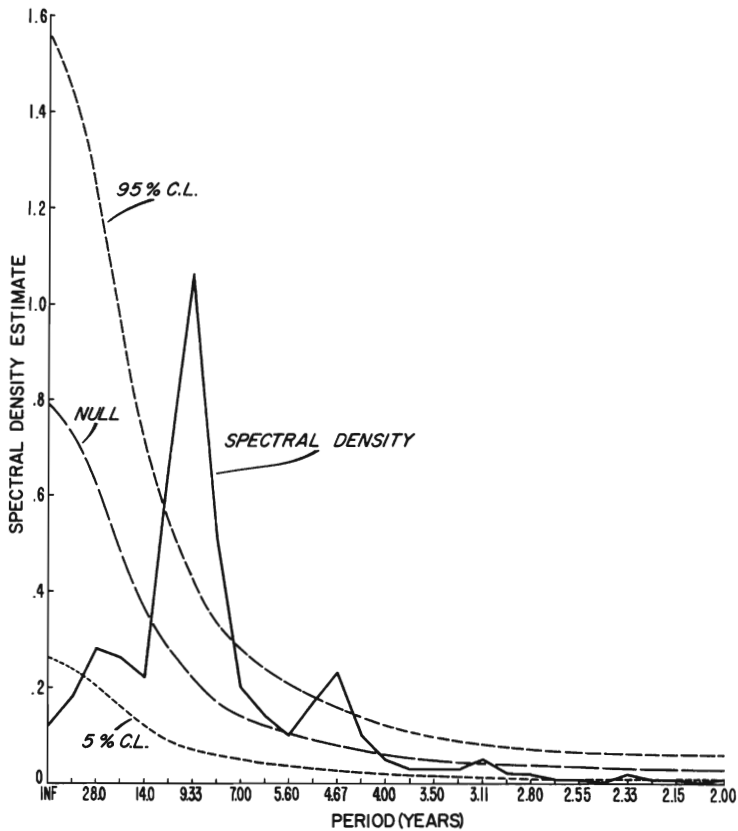


FIG. 3. Sample univariate spectrum (Upper Saskatchewan Region) with null hypothesis and 5% and 95% confidence bands added.

obtained from

$$P_d = \frac{100m + 95\%}{m + 1}$$

In the present case, P_d would equal 99.75% for the provincial data ($m = 19$ lags) or 99.83% for the regional data ($m = 28$ lags). This procedure can be used to show that the period between 9 and 10 years is still significant.

On the basis of the above procedure, the statistical significance of the period between 9 and 10 years is clearly established. Those familiar with the 10-year cycle literature and data might consider these results to be somewhat trivial; however, the procedures outlined above clear the way for the use of the more elegant procedures associated with cross spectral analysis. In addition, the spectrum analysis has established the fact that there

are no other significant short-term periodicities in the lynx data (apart from a barely significant harmonic that occasionally appears at 4.67 or 4.75 years: these have no apparent biological interpretation and are seemingly due to a statistical artefact related to the symmetry of the cycle).

Cross spectral analysis makes it possible to examine in the frequency domain the relationship between two time series; in this case, spatially related pelt data. The squared coherency, which is analogous to a squared correlation coefficient, provides a means of determining (again in the frequency domain) the strength of the relationship between the two time series at a given frequency. The squared coherency spectrum may indicate that the two series are correlated at a particular frequency, but that one series may lead or lag behind the other series in time. The

phase spectrum provides a means to examine this lead or lag.

The spectra of primary interest in this study were the squared coherency and phase spectra. Following the work of Bloomfield (1976), observed values of the squared coherency less than or equal to $\sigma(0.95)^2$ were regarded as not significantly different from zero. The value of $\sigma(0.95)^2$ is given by:

$$\sigma(0.95)^2 = 1 - 20^{-g^2/(1-g^2)} \quad (1)$$

$$g^2 = \frac{2}{\text{degrees of freedom}},$$

where $\sigma(0.95)^2$ is the 95% point of the distribution of the observed squared coherency when the theoretical squared coherency is equal to zero. Tests using the lynx data indicate the coherence for the peak between 9 and 10 years is statistically significant. Rayner (1971) provides a thorough discussion on calculating cross spectral estimates.

Bloomfield (1976) has also stated that the phase spectra are not well determined at any frequency for which the squared coherency value is less than or equal to $\sigma(0.95)^2$. According to Rayner (1971), phase lag is indeterminate insofar as multiples of the period under investigation may be added; however, in our case, independent field evidence supports the phase lags reported in Tables 1 and 2. The phase spectra values were considered only in those frequency bands that were statistically significant on the basis of the test given by Equation (1).

The spectra used in this study were calculated using the computer program from the *Statistical package for the social sciences* (Nie *et al.*, 1975). The Hamming window function was utilized in all calculations. Ku,

Telford & Lin (1971) found that in their work in geophysics, the Hanning and Hamming windows provided the best compromise between resolution and stability in the calculation of the spectra. This conclusion was found to be valid in pre-tests of the present data sets.

Results and Discussion

Results of the bivariate analyses are given in Tables 1 and 2. In these tables are listed phase lags between particular pairs of regions or provinces.

A short examination of the set of phase lags in Tables 1 and 2 reconfirms what has been thought about the spatial/temporal aspects of the 10-year cycle phenomenon for many years; that is, that the 'wave' of population change appears first in the west central part of Canada and spreads from there to the extremes of the country. This curious fact is what has led many observers into believing that some general synchronizing agent might exist. Any theory purporting to explain the entire matter must deal with the fact that almost the whole of Canada is synchronized with respect to this nodal area.

Closer examination of Tables 1 and 2 leads to the discovery of an interesting difference between them. In the nineteenth century it would appear that the nodal region existed in extreme northern Alberta; this at least is the best guess we can make given the coarseness of the network under examination. Generally speaking, reversals of population trends occurred first in the Athabasca Basin region (northern Alberta) and spread out rapidly to appear shortly thereafter in the

TABLE 1. Phase lags (in years) between sets of regionally grouped Canada lynx fur data (1821-91) at period of 9.33 years. Table should be read 'Row leads column by x years'.

	North Central Region	Winnipeg Basin Region	Upper Saskatchewan Region	West Central Region	MacKenzie River Region
Athabasca Basin Region	1.429	1.237	0.874	0.596	0.212
MacKenzie River Region	1.104	0.864	0.579	0.336	
West Central Region	0.878	0.631	0.327		
Upper Saskatchewan Region	0.578	0.304			
Winnipeg Basin Region	0.312				

TABLE 2. Phase lags (in years) between sets of provincially grouped Canada lynx fur data (1920-76) at period of 9.50 years. Table should be read 'Row leads column by x years'.

	Quebec	Yukon Terr.	British Columbia	Ontario	Alberta	North- west Terrs.	Manitoba	Saskat- chewan
Nova Scotia	4.423	4.462	3.584	3.010	2.471	2.154	1.551	1.514
Saskatchewan	3.366	3.126	2.175	1.187	1.004	0.434	0.025	
Manitoba	3.033	2.848	2.055	1.277	0.949	0.504		
Northwest Terrs.	1.859	1.933	1.329	0.699	0.484			
Alberta	2.300	2.001	1.172	0.361				
Ontario	1.017	1.024	0.505					
British Columbia	1.005	0.920						
Yukon Territory	-0.053							

MacKenzie River region. The trend reversal wave moved a bit more slowly in the southerly and south-easterly direction, reaching the West Central region (central Saskatchewan) next. The other regions to the east and far west trailed still further.

In the twentieth century, however, a somewhat different pattern seems to have evolved. Population trend reversals appear first in a nodal region situated in northeastern Saskatchewan or even western Manitoba. From there the wave has usually moved fastest to the east and south into Manitoba. In this century, therefore, trend reversals begin in northern Alberta relatively later than they did in the nineteenth century. In fact, the entire nodal district seems to have shifted 500 or 600 miles to the southeast over the span of the last 100 years.

This peculiarity has apparently not been noted before. It is interesting in that it suggests the unlikelihood that a simple 'free vibration' model of the phenomenon can be adequate. While it is possible to conceptualize a set of biological interactions generating population fluctuations of 10 years' period, it is quite another matter to use such reasoning to explain spatial shifts of the whole system over a 150-year period in the same manner. One approach might be to introduce the possibility of long-term shifts in the gene pools of the populations involved, but this is untestable. Another is to suppose relative changes in the ranges and/or densities of the populations. This idea is again untestable, and does not seem to lead anywhere anyway. A third interpretation is that

the whole system is responding to some at least partially external set of factors whose spatial nature changes over time. This may even constitute the causal agent we have been looking for. We feel that this lead is exploitable, but first depends on a better reconstruction of the spatial/temporal pattern of wave movement itself over a period of time (against which hypotheses might be tested). Such work is now in progress.

A final point that should be raised here concerns the place of geographic research within the framework of 10-year cycle studies. It has been assumed since the beginning of critical investigation that the matter is a biological problem. While it is true that the transfer agents of the cyclic wave are living things, it is short-sighted to assume that all work relevant to the matter must focus on individual creatures, food chains, or populations. Despite the fact that an overall solution must eventually be constructed at the biological level, there is no *a priori* reason why geographers cannot construct their own spatially-orientated models that are, at least initially, independent of the biological context. Should the main causal force be an extrinsic agent, it may be most efficient to take this approach. Naturally, it will be incumbent upon the investigator to identify a plausible link between the spatial model developed and what is going on at the biological (and in the end more definitely testable) level. There is a clear super-population element to this system that displays its own spatial/temporal characteristics, and we should make use of it.

Acknowledgments

The authors would like to express their thanks to David Lambert of Indiana University for assistance in tailoring the SPSS program to our needs, and to John Dickson of The Dominion Bureau of Statistics, Ottawa, Canada, for providing us with copies of *Fur production*.

References

- Bloomfield, P. (1976) *Fourier analysis of time series: an introduction*. John Wiley, New York.
- Bulmer, M.G. (1974) A statistical analysis of the 10-year cycle in Canada. *J. Anim. Ecol.* 43, 701–718.
- Bulmer, M.G. (1975) Phase relations in the ten-year cycle. *J. Anim. Ecol.* 44, 611–620.
- Butler, L. (1953) The nature of cycles in populations of Canadian mammals. *Can. J. Zool.* 31, 242–262.
- Cole, L.C. (1951) Population cycles and random oscillations. *J. Wildl. Mngmnt*, 15, 233–252.
- Cole, L.C. (1954) Some features of random population cycles. *J. Wildl. Mngmnt*, 18, 2–24.
- Cross, E.C. (1940) Periodic fluctuations in numbers of the red fox in Ontario. *J. Mammal.* 21, 294–306.
- Dominion Bureau of Statistics (1921–77) *Fur production*. Ottawa, Canada.
- Dymond, J.R. (1947) Fluctuations in animal populations with special reference to those of Canada. *Trans. Roy. Soc. Can.* 41, 1–34.
- Elton, C. (1933) The Canadian snowshoe rabbit enquiry, 1931–1932. *Can. Field-Nat.* 47, 63–69 and 84–86.
- Elton, C. & Nicholson, M. (1942) The ten-year cycle in numbers of the lynx in Canada. *J. Anim. Ecol.* 11, 215–244.
- Erickson, A.B. (1944) Helminth infections in relation to population fluctuations in snowshoe hares. *J. Wildl. Mngmnt*, 8, 134–153.
- Gilpin, M.E. (1973) Do hares eat lynx? *Am. Nat.* 107, 727–730.
- Green, R.G. & Evans, C.A. (1940) Studies on a population cycle of snowshoe hares on the Lake Alexander area. *J. Wildl. Mngmnt*, 4, 200–238, 267–278, and 247–258.
- Keith, L.B. (1963) *Wildlife's ten-year cycle*. The University of Wisconsin Press, Madison, Wisconsin.
- Keith, L.B. (1974) Some features of population dynamics in mammals. *Trans. 11th int. Congr. Game Biol. Stockholm, Sweden*, pp. 17–58.
- Keith, L.B., Meslow, E.C. & Rongstad, D.J. (1968) Techniques for snowshoe hare population studies. *J. Wildl. Mngmnt*, 32, 801–812.
- Keith, L.B., Rongstad, O.J. & Meslow, E.C. (1966) Regional differences in reproductive traits of the snowshoe hare. *Can. J. Zool.* 44, 953–961.
- Ku, C.C., Telford, W.M. & Lin, S.H. (1971) The use of linear filtering in gravity problems. *Geophysics*, 36, 1174–1203.
- MacLulich, D.A. (1937) Fluctuations in the numbers of the varying hare (*Lepus americanus*). *Univ. Toronto Studies, Biol. Ser.* No. 43.
- Meslow, E.C. & Keith, L.B. (1968) Demographic parameters of a snowshoe hare population. *J. Wildl. Mngmnt*, 32, 812–834.
- Mitchell, J.M., Dzerdzevskii, B., Flohn, H., Hofmeyr, W.L., Lamb, H.H., Rao, K.N. & Wallen, C.C. (1966) The power spectrum and general principles of its application to the evaluation of non-randomness in climatological series. In: *Climatic change*. World Meteorological Organization, Geneva, Switzerland.
- Moran, P.A.P. (1953) The statistical analysis of the Canadian lynx cycle. *Aust. J. Zool.* 1, 163–173 and 291–298.
- Nie, N.H., Hall, C.H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. (1975) *Statistical package for the social sciences*. McGraw-Hill, New York.
- Palmgren, P. (1949) Some remarks on the short term fluctuations in the numbers of northern birds and mammals. *Oikos*, 1, 114–121.
- Rayner, J. (1971) *An introduction to spectral analysis*. Pion Press, London.
- Seton, E.T. (1909) *Life histories of northern animals*, Vol. 1. Scribner's, New York.
- Windberg, L.A. & Keith, L.B. (1978) Snowshoe hare populations in woodlot habitat. *Can. J. Zool.* 56, 1071–1080.