THE STATISTICAL ANALYSIS OF THE CANADIAN LYNX CYCLE

II. SYNCHRONIZATION AND METEOROLOGY

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Summary

It is shown that trapping figures for the lynx are definitely related to weather conditions. The significance of this for the various theories of the origin and synchronization of the cycle is discussed.

I. INTRODUCTION

In a previous paper (Moran 1953) an attempt was made to analyse the Canadian lynx cycle as a stochastic process. The series of logarithms, x_t, of the number of lynx caught in the Mackenzie River district were shown to be fairly well represented by a random process generated by the relationship

$$x_t - 2.9036 = 1.4101(x_{t-1} - 2.9036) - 0.7734(x_{t-2} - 2.9036) + \epsilon_t, \quad \ldots (1)$$

where ϵ_t is a completely random sequence with zero means and standard deviation 0.2143. This suggests, but does not prove, that some such random oscillatory process is causing the oscillations. Such a process can plausibly be assumed to be due to the intrinsic biological system. The lynx feeds almost exclusively on the snowshoe rabbit, and well-known investigations, e.g. those of Volterra (1931), suggest that in such circumstances oscillations in population density may be expected.

However, this does not explain why the oscillations are so clearly and strongly synchronized over the whole of Canada. We therefore inquire whether meteorological phenomena, for which we would expect a considerable degree of correlation over the whole area, could so influence the population densities as to synchronize the cycles. The random element ϵ_t in (1) may well be supposed to have a component due to the effect of meteorological conditions on the birth and death rates. It can easily be shown mathematically that if we have two processes, $\{x_t\}$, $\{y_t\}$, generated by the same relationship of form (1) with random elements ϵ_t and η_t, the expected correlation between x_t and y_t will be equal to the correlation between ϵ_t and η_t. Although the author has not calculated the correlations between x_t and the logarithms of the numbers of lynx caught in other regions it is obvious that they must be very high (Elton and Nicholson 1942, Table IV). It follows that if meteorological phenomena cause the synchronization, they must be closely correlated with ϵ_t and there must be a strong correlation between different parts of Canada. However, we do not know in what way such phenomena would affect the population.

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For a complete examination we should presumably have to calculate the multiple correlation coefficients of ϵ_t with both average and extreme temperatures and rainfalls for each month of the year. This is clearly impracticable and we therefore consider only certain selected variables. Hence we cannot expect to find very high correlations.

II. Correlation of Catch Records with Meteorological Data

The above remarks assume that the underlying process is at least approximately of the type generated by equation (**1**). This implies that if the external shock term, ϵ_t, were removed (i.e. the environment were kept uniform) the oscillations, being damped, would gradually die away. It is quite possible that the relationship between the lynx and the rabbit is of this kind. On the other hand it is quite possible that oscillations would occur even in a constant environment. Such oscillations would have to be represented by non-linear equations and the amplitude of the cycle would be determined by the non-linear terms. This fact has important implications for the synchronization problem.

The correlation coefficients of the residuals calculated from the fitted regression (**1**) with some of the available meteorological data were therefore found. These residuals were given in a previous paper (Moran 1953). It is important to notice that a test of the significance of these coefficients is quite independent of whether or not the process underlying the observations is of type (**1**). The effect of calculating correlation coefficients with residuals rather than with the original terms is to remove, as far as possible, the effect of population size in the two previous years and we would hence expect the effect, if any, of the meteorological phenomena to show up more clearly. This is, however, not quite the same as calculating a partial correlation coefficient.

It is well known that the ordinary test of significance for a correlation coefficient between two series does not hold if *both* series are serially dependent. In the present study the meteorological series are almost certainly not serially dependent although the author has not actually tested this. In any case the series of residuals should behave sufficiently as a series of completely independent terms to validate the test.

The meteorological series used were taken from the "World Weather Records" (Smithson. Misc. Coll., vols. 79 (1927) and 90 (1934)). Three stations were chosen:

Edmonton, lat. 53° 35′ N., long. 113° 30′ W.
Barkerville, lat. 53° 2′ N., long. 121° 35′ W.
Winnipeg, lat. 49° 53′ N., long. 97° 7′ W.

Barkerville appeared to be the closest station with a sufficiently long series of observations. The area implied by the term 'Mackenzie River District' changed somewhat during the period considered (1821-1934), as is shown in the maps given by Elton and Nicholson (1942), but it is thought that this had little effect on the series. Edmonton was chosen because it was fairly near the area studied and had a somewhat longer series of observations than Barkerville. Winnipeg, on the other hand, was chosen because it was very distant. The seven series used are as follows and relate to temperature alone:

A_t.—The minima of the average monthly temperatures at Edmonton for December, January, and February of the winter $(t-1, t)$. 48 observations, 1883-1930.

B_t.—The sum of the average monthly temperatures at Edmonton for July, August, and September of the year t. 48 observations, 1883-1930.

C_t.—The minima of the average monthly temperatures at Winnipeg for December, January, and February of the winter $(t-1, t)$. 48 observations, 1883-1930.

TABLE 1

CORRELATION COEFFICIENTS OF TEMPERATURE SERIES ($A_t, \ldots, G_t$) WITH RESIDUALS OF ANNUAL LYNX CATCHES IN YEARS $t-1$, t, AND $t+1$

Temperature Series		R_{t-1}	R_t	R_{t+1}
Edmonton	A_t (48)	$-0\cdot151$	$-0\cdot087$	$+0\cdot394$**
	B_t (48)		$-0\cdot077$	$+0\cdot174$
Winnipeg	C_t (48)	$-0\cdot050$	$+0\cdot044$	$+0\cdot338$*
	D_t (48)		$+0\cdot001$	$+0\cdot027$
Barkerville	E_t (41)	$-0\cdot120$	$-0\cdot234$	$+0\cdot247$
	F_t (40)		$-0\cdot162$	$+0\cdot068$
	G_t (40)		$-0\cdot386$*	$+0\cdot063$

* Significant at 5 per cent. level.
** Significant at 1 per cent. level.

D_t.—The sum of the average monthly temperatures at Winnipeg for July, August, and September of the year t. 48 observations, 1883-1930.

E_t.—The minima of the average monthly temperatures at Barkerville for December, January, and February of the winter $(t-1, t)$. 41 observations, 1888-1906, and 1908-1929.

F_t.—The sum of the average monthly temperatures at Barkerville for May and June of the year t. 40 observations, 1888-1906 and 1908-1928.

G_t.—The sum of the average monthly temperatures at Barkerville for July, August, and September of the year t. 40 observations, 1888-1906 and 1907-1928.

The series of residuals used, which we denote by R_t, are given in the previous paper (Moran 1953) and are equal to

$$x_t - 2.9036 - 1.4101(x_{t-1} - 2.9036) + 0.7734(x_{t-2} - 2.9036),$$

where x_t is the logarithm of the number of lynx caught in the 'outfit' of the year t, i.e. caught during the period July 1 of year t to June 30 of year $t+1$. R_t thus represents in some degree the amount of the increase in population density in the trapping period $(t, t+1)$ when the effects of the population size in the two previous periods have been removed. The correlation coefficients of the series $A_t, \ldots, G_t$ were found with R_t and R_{t-1} and also the correlation of R_{t-1} with A_t, C_t, and E_t. These are shown in Table 1. The numbers of observations are shown in brackets.

The meaning of these coefficients may be illustrated by considering the first line; -0.151 is the correlation between the residuals corresponding to outfit t and the minimum winter temperature at Edmonton during the period corresponding to t, i.e. July 1 of year t to June 30 of year $t+1$. This is the period during which trapping took place. Similarly -0.087 is the correlation of R_t with the minimum winter temperature of the *previous* outfit and 0.394 is the correlation with the minimum temperature of the outfit before that.

It is clear that we can apply the ordinary tests of significance to these coefficients. The 5 and 1 per cent. two-sided significance levels for a single r and 48, 41, and 40 pairs of observations are shown in Table 2.

TABLE 2

SIGNIFICANCE LEVELS OF $r(\rho = 0)$

n	5%	1%
48	0·284	0·368
41	0·308	0·398
40	0·312	0·403

The coefficients in Table 1 which are individually significant at the 5 and 1 per cent. levels are indicated. We have to be careful in ascribing reality to significant coefficients where, as at present, we have calculated a number of coefficients. However, it seems clear that the sequence of residuals is not independent of the meteorological series. The implications of this fact require careful consideration.

The correlations which we therefore take as significant are those of R_t with:

(1) The mean temperature for July, August, and September at Barkerville during the period of the previous outfit (-0.386). The values for Edmonton (-0.077) and Winnipeg (-0.001) are very small.

(2) The minimum temperatures in December, January, and February of the outfit $t-2$ (0.394 at Edmonton, 0.338 at Winnipeg, and 0.247 at Barkerville).

Lynx apparently mate in January and February and the young are born in March or April, the gestation period being about 60 days, and there are four or five young in a litter (Burt 1946; Rand 1948). These figures are worth considering in relation to the trapping numbers given in Elton and Nicholson (1942, Table IV). If there is only one litter and no deaths at all during the year the population's maximum rate of increase will be given by a ratio $1 + \frac{1}{2}(4) = 3$, or $1 + \frac{1}{2}(5) = 3.5$, of one year's population to the previous one. If the trapping figures in Table IV of Elton and Nicholson's paper really are proportional to the actual population size it would seem that those ratios are occasionally attained or even exceeded. We can neglect the figures for small catches, but for values over 1000 statistical errors should not be large. Consider as an example the figures in Table 3.

Taking into account the fact that some animals must die even in the best years, the observed ratios in Table 3 are remarkably high. Three possible explanations suggest themselves:

(1) The trapping figures are not good estimates of the true population densities because of sampling or other random errors. If this is true we must have a considerable error term superimposed on the underlying random process and this will deflate the serial correlations of x_t. This does not seem consistent with the very high values observed, e.g. $r_1 = 0.795$.

(2) The trapping figures are closely related to the actual population density, but in a non-linear fashion, so that trapping efficiency increases for large population densities. While this may be true for very small densities it seems unlikely for densities of size corresponding to the trapping figures of Table 3.

(3) More than one litter is produced during a year when conditions are exceptionally favourable. From the figures alone this looks the most plausible explanation but Elton states (personal communication) that it is biologically very unlikely. He suggests that migration from one district to another may be important but examination of figures for neighbouring districts such as those given in Table 3 seems to make this unlikely.

TABLE 3

INCREASE OF LYNX POPULATIONS IN SUCCESSIVE YEARS

Region	1865	1866	Ratio	1883	1884	Ratio
Mackenzie River	3311	6721	2·03	2042	2811	1·38
Athabasca Basin	3511	1756	0·50	5736	12882	2·24
West Central	6138	12584	2·05	3015	9580	3·18
Upper Saskatchewan	4185	14671	3·50	1161	6336	5·45
Winnipeg Basin	9743	21096	2·17	3587	10331	2·87

III. DISCUSSION

Now consider in what ways the weather might affect the population size. It might act directly by affecting the death rate. Thus we might expect R_t to be positively correlated with the minimum winter temperature during the outfit t or perhaps $t-1$. This is not observed. Alternatively it might be the birth rate which is affected. It is not known at what age the lynx begin to be trapped but if it is the birth rate which is affected we would expect R_t to be positively correlated with the minimum winter temperature during the outfit $t-1$ or $t-2$. In fact it is only with $t-2$ that significant values are observed. Alternatively the weather may act directly on the rabbit population or indirectly by affecting the vegetation. This would also imply a lag like the one observed and would also suggest that summer weather plays a part. Under normal circumstances the sole food of the lynx is the snowshoe rabbit, which feeds on vegetation and is therefore presumably very dependent on weather.

We have, however, to consider the important question as to whether the observed correlations might be due to the effect of weather on the trappers and the trapping efficiency rather than on the animal population. Elton states (personal communication) that some such effect may be expected and that, for example, very heavy snowfalls must hinder trapping. In the present and previous paper we have assumed that the number trapped, y_t, can be regarded as a fairly accurate estimate either of the actual population multiplied by a constant or, if trapping efficiency varies with population density, of some definite function of the total population, so that we can write

$$y_t = a f(N_t),$$

where N_t is the total population. If a varies from year to year so that we write it a_t we have

$$x_t = \log a_t + \log f(N_t).$$

If we now suppose a_t not to be serially correlated, since it is presumably dependent only on the weather and other serially random influences, the quantity $\log a_t$ plays the part of a random error superimposed on the random process $\{\log f(N_t)\}$. Thus if it is the trapping efficiency rather than the population which is influenced by weather two conclusions may be drawn:

(1) There will be a strong positive correlation between the residuals for each outfit and the minimum temperature in December, January, and February of the same outfit. This is not observed, the correlations being small and negative (-0.151 for Edmonton, -0.05 for Winnipeg, and -0.12 for Barkerville). Thus the effect of heavy snowfalls mentioned by Elton does not show up in these figures.

(2) The serial correlation coefficients of the series x_t will be deflated below what they would otherwise have been. In fact $r_1 = 0.795$, which is large, and the general shape of the correlogram suggests that this is not so.

It therefore seems clear that the effect of the weather is directly or indirectly on the lynx population and not on the trapping efficiency. The correlation with the minimum winter temperatures of the outfit 2 yr before (0.394 for Edmonton, 0.338 for Winnipeg, and 0.247 for Barkerville) might be due either to the direct effect of the weather on the birth rate at that time, the young not being trapped until 21 months later; or to the effect on the rabbit population, thus reducing the future food supply of the lynx. The correlation with the mean summer temperature at Barkerville (-0.386) is not so easy to explain. Trapping does not take place at this time. It is possible that the effect, if real, is on the vegetation and thus on the rabbit.

If then we regard it as proven that the weather influences the lynx cycle, can this be the explanation of the synchronization of cycle over the whole of Canada? That such a synchronization exists is quite clear from an examination of the records (Elton and Nicholson 1942, Table IV). No attempt has been made to calculate the correlation coefficients between the series for different trapping regions but the close synchronization of the peaks and troughs shows that they must be high.

Suppose that the logarithms of the trapping numbers in two different regions can be represented by processes defined by the relations

$$x_t = ax_{t-1} + bx_{t-2} + \epsilon_t,$$
$$z_t = az_{t-1} + bz_{t-2} + \eta_t,$$

so that the structures of the processes are the same but the random elements, ϵ_t, η_t, are different but correlated, then it is easy to show that the correlation between x_t and z_t will be equal to that between ϵ_t and η_t. (If the autoregression coefficients are different in the two processes, this result no longer holds exactly.) Now if ϵ_t and η_t are closely correlated with the local meteorological conditions, and the latter in the two regions are correlated, we have a possible explanation for the correlation between the observed records.

As an illustration of the correlation between weather conditions at different places the correlation coefficient between the series A_t and C_t (minimum winter temperatures at Edmonton and Winnipeg) was calculated and found to be 0.681. This is fairly high and certainly significant, but from Table 1 it is clear that the observed correlations with the particular meteorological series chosen are not high enough to account for the correlation between the trapping records. This, however, is scarcely to be expected. What would be relevant is the multiple correlation coefficient between the residuals and *all* the meteorological factors affecting the population. The calculation of such a correlation coefficient would be a very large undertaking and would leave many fewer degrees of freedom for testing its significance. All we can say therefore is that the observed correlation coefficients are consistent with, and suggestive of, the idea that weather is the synchronizing agency, and that the populations concerned are definitely dependent on some of the meteorological factors. It should also be pointed out that we have omitted consideration of precipitation. Some authors believe (Rowan 1950) that this may be an important factor because of its effect on the river levels.

If on the other hand the underlying process is non-linear, and the cycles would occur in a uniform environment, it is possible that a lower correlation between the residuals in different places might still produce a high probability of synchronization, in much the same way as a weak regular electrical oscillation will synchronize a highly non-linear electrical oscillator such as a multivibrator. The mathematical implications of such a non-linear situation would be very much more difficult to investigate.

So far then our findings are consistent with the view that the cause of the cycle is the predator-prey relationship of the lynx and the rabbit and that the synchronization is due to weather. Some difficulties about this theory need stating. Firstly, it is known that other animals, including fish, cycle in unison with the lynx (see Rowan 1950). It is difficult to see how these animals are ecologically dependent on the lynx or rabbit. Moreover, Elton and Nicholson (1942) state that they have evidence that rabbits introduced onto Anticosti I. cycle with the mainland population although no lynx are present. If this is true, it is very hard to reconcile with the above theory (Hutchinson and Deevey 1949). Thus it is hard to study the whole series of trapping records without feeling that there is some very powerful external influence at work. On the other hand solar activity, as indicated by sunspot numbers, is definitely not related to the lynx cycle (Moran 1949) and no other natural phenomenon seems to provide an explanation.

IV. Acknowledgments

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