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# A STATISTICAL ANALYSIS OF THE 10-YEAR CYCLE IN CANADA

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## INTRODUCTION

Despite the great interest of the 10-year wildlife cycle and the abundance of data, little effort has been made to analyse it by statistical methods; this is particularly surprising in view of the doubts about the reality of cycles expressed by Cole (1951, 1954). The best statistical treatment is that of Moran (1953), who considered the trapping records of the lynx\* in the Mackenzie River district of north-west Canada over the period 1821–1934; the data were obtained from records of the Hudson's Bay Company by Elton & Nicholson (1942). Fig. 1 shows the logarithm of the number trapped in each year. The reasons for using a logarithmic transformation are discussed by Moran (1949, 1953) and Williamson (1972).

It will be seen from Fig. 1 that there is an oscillation of considerable regularity with a period of about 10 years, but that the amplitude of the oscillations is rather irregular. The effect of the logarithmic transformation is to make the oscillations more symmetrical than in the arithmetic plot which is usually presented. Similar features are seen in data for other periods and other species.

In view of the regularity of the oscillations, the most obvious model to fit to the data is a sine function with a superimposed error term:

$$x_t = \mu + \alpha \sin 2\pi\omega(t - \phi) + e_t. \quad (1)$$

In this representation  $x_t$  is the logarithm (to the base 10) of the population size (or the number of animals caught) in the biological year  $t$ ,  $\alpha$  is the amplitude of the oscillations,  $1/\omega$  their period (in years) and  $\phi$  the phase lag (also in years). As Moran (1953) points out however, this model is inadequate since it fails to take into account the irregularity in the amplitude of the oscillations. As an alternative model Moran (1953) has proposed the second-order autoregressive scheme:

$$x_t = \mu + \beta_1 x_{t-1} + \beta_2 x_{t-2} + e_t. \quad (2)$$

This model gives rise to oscillations when  $\beta_1^2 + 4\beta_2 < 0$ , but these oscillations will be rather irregular both in period and amplitude; thus this model fails to account adequately for the regularity of the period of the oscillations.

In this paper I shall therefore use a mixed model containing both a sine function and a first-order autoregressive term:

$$x_t = \mu + \alpha \sin 2\pi\omega(t - \phi) + \beta x_{t-1} + e_t. \quad (3)$$

The sine function accounts for the regularity of the period of the oscillations and the autoregressive term for the irregularity in their amplitude since the error term,  $e_t$ , due to environmental factors, is incorporated into the process. It seems biologically reasonable to include a first-order autoregressive term in any model since it seems likely that

\* All scientific names are given in the Appendix.

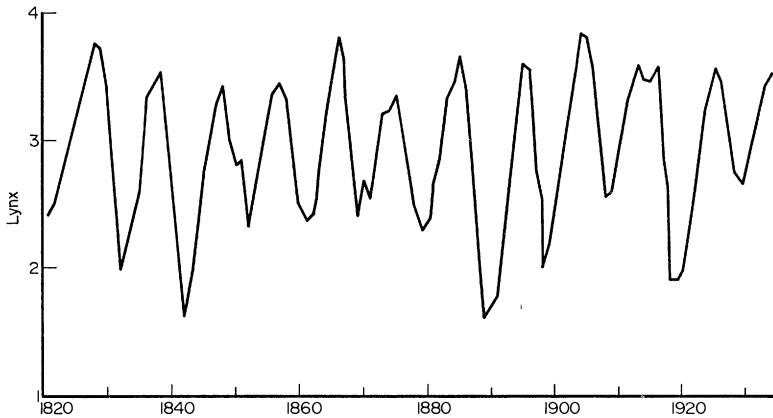


FIG. 1. Logarithmic plot of numbers of lynx trapped in the Mackenzie River region (Elton & Nicholson 1942).

the factors causing the oscillations must act through the birth and death rates of the population, and since the population size in any year depends on the population size in the previous year as well as on the birth and death rates.

The adequacy of the model (3) is justified more fully in the next section, and the method of estimating the parameters is described in the Statistical Appendix. Throughout this paper the period of the oscillations is taken as 9.63 years, the estimate obtained by Elton & Nicholson (1942) from lynx data for the whole of Canada between 1752 and 1935. The Statistical Appendix also shows how the estimated parameters  $\alpha$ ,  $\phi$  and  $\beta$  can be used to find estimates of the phase,  $\phi^*$ , and the amplitude,  $\alpha^*$ , after eliminating the effect of the autoregressive term  $\beta$ ; these can be regarded as estimates of the phase and of the average amplitude of the oscillations, and are the natural parameters to use in describing the cycle, and in comparing the cycle between different species, geographical areas or periods of time. The main part of this paper is concerned with estimating these parameters from the extensive data which exist on the fur-bearing mammals of Canada.

### VALIDATION OF THE MODEL

Two statistical tools have been used in analysing the data of Fig. 1, the correlogram and the periodogram. The correlogram is the graph of the serial correlation coefficients,  $r_s$ , plotted against the time lag,  $s$ . It has been computed by Moran (1953) for lags up to 27 years; the values given in his paper are shown graphically in Fig. 2. It is a smooth, oscillating curve with a period of about 10 years, corresponding to the period of the original data, and with little, if any, tendency to decrease in amplitude. It will be seen that the first serial correlation,  $r_1$ , is larger than any of the others; as Moran (1953) points out this is incompatible with a pure sine wave as in eqn 1. On the other hand a second-order autoregressive scheme as in eqn 2 should produce a correlogram which is quite heavily damped. Moran (1953) attributes the failure of the observed correlogram to show appreciable damping to a statistical artefact, but this explanation does not seem altogether convincing. A mixed model, as in eqn 3, is expected to produce a correlogram of the observed type in which the first serial correlation is the largest but which does not show appreciable damping thereafter.

The periodogram can be regarded as a decomposition of the variance, as in an analysis

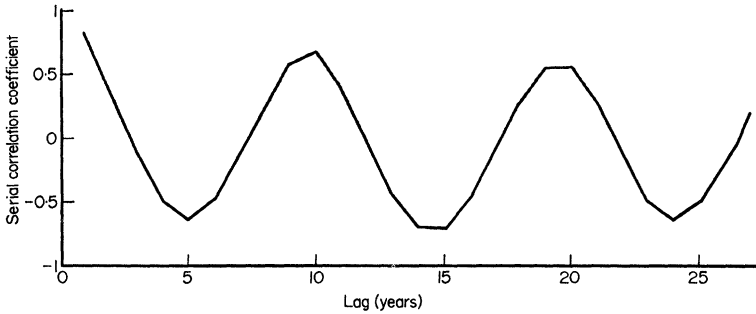


FIG. 2. Correlogram of the data in Fig. 1 (Moran 1953).

of variance, into components due to different frequencies. It has been computed by Bartlett (1954) for the data of Fig. 1; the values given by him are shown in condensed form in Table 1. There is a sharp peak, confined to a single component, at a frequency of 12/114 cycles per year (that is to say, at a period of about 10 years), which corresponds to the period of the original data. There is also a tendency for the components to decrease as the frequency decreases. A pure sine wave should produce a periodogram with a sharp peak confined to a single component, as observed, but should be flat everywhere else rather than decreasing with frequency. On the other hand, a second-order autoregressive scheme should produce a periodogram with a smooth peak occupying several components rather than the observed abrupt peak at a single component. The postulated mixed model (eqn 3) can, however, account for both features of the observed periodogram. The sine function accounts for the presence of an abrupt peak confined to a single component and the autoregressive term for the decline of the periodogram with increasing frequency elsewhere.

It is concluded that the mixed model (3) is more likely to provide a satisfactory representation of the data than either of the other two models. This conclusion is largely based on visual inspection of the correlogram and periodogram. To justify it more objectively, the residual sums of squares after fitting these three models are compared in Table 2. (See Bartlett (1954) and Moran (1953) for models (1) and (2) respectively; the method of fitting model (3) is described in the Statistical Appendix.) It will be seen that model (3)

Table 1. *Periodogram of the data in Fig. 1 (Bartlett 1954)*

Frequency (cycles per year)	(1-10)	11	12	13	(14-24)	(25-35)	(36-46)	(47-57)
	114	114	114	114	144	114	114	114
Intensity (sum of squares)	0.99*	0.91	21.02	0.58	0.17*	0.06*	0.03*	0.01*

\* Mean of ten or eleven values.

Table 2. *Residual variance after fitting different models to the data in Fig. 1*

Model fitted	Sum of squares	d.f.	Mean square
None	35.230	113	0.3118
Sine function (1)	14.205	111	0.1280
Second-order autoregressive (2)	5.788	109	0.0531
Sine function + first-order autoregressive (3)	5.067	109	0.0465

gives the best fit, although model (2) is also reasonably satisfactory. As a further check on its validity, the residuals from model (3) were calculated; no obvious pattern could be detected.

RESULTS

Canada, 1848–1909

Data on the fur sales of the Hudson’s Bay Company have been given by several authors. The reliability of the data and the method of converting the dates given into biological years (or outfit years) have been discussed by Elton & Nicholson (1942). All dates given here have been converted to biological years; for example, animals trapped in the winter of 1872/3 and sold on the London market in 1874 are referred to the biological year 1872. The most reliable source is Jones (1914) who tabulates data for many species for the period 1848–1909. The following obvious misprints were corrected.

Species	Biological year	Misprint
Fisher	1892	38631 should read 3863
Lynx	1889	1152 should read 11520
Lynx	1906	The price and the number are transposed. Number should read 38501
Raccoon	1878	15 should read 715

Confirmation of these corrections was obtained from the graphs in Seton (1912).

Data on five species (bobcat, musk-ox, sea-otter, fur seal, common seal) were too sparse or subject to too marked a trend to justify analysis. The periodogram was calculated for all the other species. In all cases where any peak was obvious it was confined to a single component which was the same for all these species and which corresponded to a period slightly less than 10 years. The data were therefore analyzed by the method just described, taking the period as 9·63 years and removing a linear or quadratic trend if necessary.

No evidence of a 10-year cycle was found in the following species: bear (mostly black bear), ermine (stoat), Arctic fox, otter, raccoon. The results for the remaining ten species are shown in Table 3 and Fig. 3. In the case of the wolf and coyote (which are not separated), the periods 1848–78 and 1879–1909 were analyzed separately since it appears from the graphs of the data that oscillations are confined to the latter period (Hewitt 1921; Elton 1927); this is confirmed by the analysis. MacFarlane (1908) considers that more than half of the furs were coyote in the first period, and the proportion was probably greater in the second period since wolf numbers fell markedly after the extermination of the plains bison (Hewitt 1921). Data for the snowshoe rabbit (varying hare) are not given by Jones (1914); they have been taken from Poland (1892) for the years 1848–89 and from the graph in Seton (1912) for 1890–1907. These data are not as reliable as the rest; furthermore they relate only to the Hudson’s Bay watershed since snowshoe rabbit was not traded from the interior of Canada (MacFarlane 1908).

It can be concluded that all the species in Table 3 (with the exception of the coyote and the wolf) were cyclic in the last half of the nineteenth century. The coyote was probably cyclic after 1879; nothing can be said about the wolf in this period. Before 1879 there is no evidence that either the coyote or the wolf were cyclic. The estimates of

Table 3. *The 10-year cycle in Canada, 1848–1909*

Species	Significance level of cycle (%)	$\hat{\alpha} \pm \text{S.E.}$	$10^{2\hat{\alpha}^*}$	Phase $\pm$ S.E. (relative to lynx)
Fisher	0.1	$0.09 \pm 0.02$	1.5	$1.9 \pm 0.3$
Red fox	0.1	$0.19 \pm 0.04$	2.4	$0.1 \pm 0.3$
Lynx	0.1	$0.50 \pm 0.04$	10.1	$(1904.7 \pm 0.1)^\dagger$
Marten	0.1	$0.11 \pm 0.03$	1.7	$-2.0 \pm 0.4$
Mink	0.1	$0.15 \pm 0.04$	2.1	$-1.7 \pm 0.3$
Muskrat	0.1	$0.18 \pm 0.04$	2.3	$-4.0 \pm 0.3$
Skunk	0.1	$0.19 \pm 0.06$	2.4	$0.2 \pm 0.5$
Wolf and coyote, 1848–78	NS	0	1.0	
Wolf and coyote, 1879–1909	0.1	$0.21 \pm 0.08$	2.6	$1.7 \pm 0.3$
Wolverine	0.1	$0.11 \pm 0.03$	1.7	$3.0 \pm 0.4$
Snowshoe rabbit $^\ddagger$	1	$0.37 \pm 0.15$	5.4	$-1.1 \pm 0.6$

$^\dagger$  Peak year nearest 1900.

$^\ddagger$  Phase relative to lynx in the Hudson's Bay watershed (average of North Central and James Bay areas in Table 6).

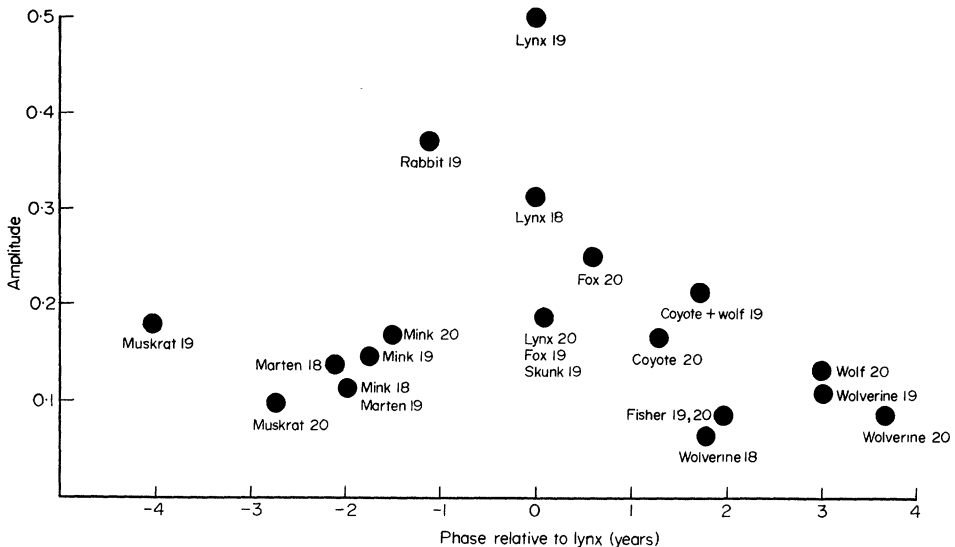


FIG. 3. The 10-year cycle in Canada. Numbers indicate the century.

the amplitude and phase for the snowshoe rabbit must therefore be treated with caution. (The claim by Gilpin (1973) that the rabbit cycle was one year *behind* the lynx cycle at the end of the nineteenth century has been rebutted by Williamson (1974).)

#### *Canada, 1920–1969*

The numbers of pelts of different species taken in Canada in the period 1920–69 have been extracted from the Canada Yearbook and analysed in the same way. For the red fox and the mink, which are extensively farmed, the numbers of wild animals are not given separately before 1960; for these two species the data of Butler (1953), obtained from Hudson's Bay Company records, have been used. For those species which did not show a significant cycle over the whole period, the periods 1920–44 and 1945–69 have been analysed separately. The results are shown in Table 4 and Fig. 3. (The data for

Table 4. *The 10-year cycle in Canada, 1920–1969*

Species	Significance level of cycle (%)	$\hat{\alpha}^* \pm \text{S.E.}$	$10^{2\hat{\alpha}^*}$	Phase $\pm$ S.E. (relative to lynx)
Coyote, 1920–44	1	$0.17 \pm 0.07$	2.2	$1.3 \pm 0.6$
Coyote, 1945–69	NS	0	1.0	
Fisher, 1920–69	1	$0.08 \pm 0.03$	1.4	$2.0 \pm 0.6$
Red fox, 1919–50	0.1	$0.25 \pm 0.04$	3.1	$0.6 \pm 0.5$
Lynx, 1920–69	0.1	$0.19 \pm 0.04$	2.4	$(1933.6 \pm 0.3)^\dagger$
Marten, 1920–44	NS	0	1.0	
Marten, 1945–69	NS	0	1.0	
Mink, 1919–51	0.1	$0.17 \pm 0.06$	2.2	$-1.5 \pm 0.5$
Muskrat, 1920–44	1	$0.10 \pm 0.04$	1.6	$-2.7 \pm 0.5$
Muskrat, 1945–69	NS	$0.02 \pm 0.11$	1.1	
Skunk, 1920–44	NS	0	1.0	
Skunk, 1945–69	NS	0	1.0	
Wolf <sup>‡</sup> , 1920–44	1	$0.13 \pm 0.05$	1.8	$3.0 \pm 0.5$
Wolf, 1945–69	NS	0	1.0	
Wolverine, 1920–69	0.1	$0.09 \pm 0.03$	1.5	$3.7 \pm 0.5$

<sup>†</sup> Peak year nearest 1930.

<sup>‡</sup> The figures for 1925–43 have been corrected by adding the coyote numbers for Manitoba given by Keith (1963) to coyote and subtracting them from wolf.

ermine were also analysed but showed no significant evidence of a cycle.) The Canada Yearbook data for wild mink and red fox for 1960–69 were examined visually. The mink is clearly still cyclic in this period but there is no clear pattern in the red fox except an upward trend.

It can be concluded that the fisher, lynx, mink and wolverine continue to be cyclic now, that the coyote and muskrat ceased to be cyclic about 1945 and that the marten and skunk ceased to be cyclic before 1920. The red fox was certainly cyclic until 1950, and may still be so today. The wolf was probably cyclic in 1920–44, but its status before then is uncertain. The phase relationships agree well with those found in the nineteenth century. No numerical data on the snowshoe rabbit for this period are available. However, by comparing indices of snowshoe rabbit abundance based on questionnaires with lynx catches for the same area, it appears that the snowshoe rabbit cycle is about 2 years ahead of the lynx cycle (MacLulich 1937; Butler 1953; Keith 1963). This estimate is probably to be preferred to the figure of 1 year ahead shown in Table 3 and Fig. 3 because of doubts about the accuracy and the geographical origin of the nineteenth century rabbit data; the rather high standard error of the estimate in Table 3 shows that these data are consistent with a cycle 2 years ahead of the lynx. The amplitude of the cycle, when it persists, is similar to the amplitude in the nineteenth century. The exception is the lynx, whose cycle has become much weaker.

#### *Canada, 1751–1847*

Poland (1892) gives data based on Hudson's Bay Company sales for the biological years 1751–1889. These data are not as reliable as those previously considered, but it seemed worthwhile analysing the years before 1848 since they are the only data available for this period. Only the following years have been used in the analysis: 1751–77, 1791–1807, 1821–32, 1838–47; for the fisher, mink and muskrat data are only given for a few years before 1777 and the period up to this year was also excluded. The reasons for not using the remaining years are as follows: (a) the years 1778–90 are distorted by a serious



epidemic of smallpox among the Indian trappers (Elton & Nicholson 1942); (b) the pairs of years 1808–09, 1833–34 and 1836–37 are distorted, the numbers in the first year being too low and those in the second too high, probably due to a delay in the shipment of furs to London (Elton & Nicholson 1942; Poland, 1892); (c) the numbers for some species in the years 1812–20, just prior to the amalgamation of the Hudson's Bay Company with the North-West Company, are very low, possibly due to competition between the two companies (Elton & Nicholson 1942).

The results are shown in Table 5 and Fig. 3. There is definite evidence of a cycle in

Table 5. *The 10-year cycle in Canada, 1751–1847*

Species	Significance level of cycle (%)	$\hat{\alpha}^* \pm \text{S.E.}$	$10^{2\hat{\alpha}^*}$	Phase $\pm$ S.E. (relative to lynx)
Arctic and red fox	NS	$0.10 \pm 0.11$	1.6	
Fisher	NS	0	1.0	
Lynx	0.1	$0.31 \pm 0.06$	4.2	$(1799.5 \pm 0.3)^\ddagger$
Marten	0.1	$0.14 \pm 0.05$	1.9	$-2.1 \pm 0.5$
Mink	1	$0.12 \pm 0.05$	1.7	$-2.0 \pm 0.6$
Muskrat	NS	0	1.0	
Wolf and coyote	NS	0	1.0	
Wolverine	10	$0.07 \pm 0.04$	1.4	$1.8 \pm 1.0$

$^\ddagger$  Peak year nearest 1800.

the lynx, marten and mink and the phase relationships are the same as in subsequent years. The wolverine is not quite significant at the 5% level, but the result is consistent with the existence of a cycle of about the same magnitude and phase as in subsequent years. There is no evidence of a cycle in the fisher, Arctic and red fox (combined), muskrat or wolf and coyote (combined). The absence of a cycle in the fisher is rather surprising since a cycle is present in the whole of the period 1848–1969. The presence of a cycle in the red fox may have been obscured by the non-cyclic Arctic fox; in the 10-year period 1848–57 23% of the foxes caught were Arctic fox (Jones 1914). In view of the unreliability of the data it is felt that failure to demonstrate a cycle carries less weight than success in doing so.

#### *Geographical variation in Canada*

Elton & Nicholson (1942) present data on lynx returns of the Hudson's Bay Company for ten regions of Canada for the period 1821–1939, although there are some gaps in the data and some changes in the boundaries of the regions. There seems to be a decline in the amplitude of the cycle after the first world war, so that only data up to 1913 are analysed here. The results are shown in Table 6 and Fig. 4. The reader is referred to Elton & Nicholson (1942) for the boundaries of the regions. As they point out, the cycle is strongest and earliest in the Athabasca Basin region (covering much of the province of Alberta), and there is a tendency for it to become weaker and later as one moves away from there.

Keith (1963) has collected data of the returns of several species by province for the period 1919–57, which have been analysed as before. The results for the lynx, red fox and fisher are shown in Tables 7–9 and Fig. 4. In all three species the cycle is about 2 years earlier in the Prairie Provinces of Alberta, Saskatchewan and Manitoba than in the Eastern Provinces of Ontario and Quebec; it is also later in the lynx in British Columbia



Table 6. *The 10-year cycle in the lynx in different regions of Canada, 1821–1913*

Region	Significance level of cycle (%)	$\hat{\alpha}^* \pm \text{S.E.}$	$10^{2\hat{\alpha}^*}$	Phase $\pm$ S.E. (relative to lynx for all Canada)
West	0.1	$0.54 \pm 0.09$	12.3	$0.2 \pm 0.3$
MacKenzie River	0.1	$0.63 \pm 0.05$	18.5	$-0.4 \pm 0.1$
Athabasca Basin	0.1	$0.81 \pm 0.09$	40.9	$-0.5 \pm 0.2$
West Central	0.1	$0.66 \pm 0.06$	21.3	$-0.1 \pm 0.1$
Upper Saskatchewan	0.1	$0.79 \pm 0.08$	38.4	$0.5 \pm 0.2$
Winnipeg Basin	0.1	$0.53 \pm 0.05$	11.5	$0.6 \pm 0.1$
North Central	0.1	$0.53 \pm 0.11$	11.7	$1.1 \pm 0.2$
James Bay	0.1	$0.43 \pm 0.04$	7.2	$0.5 \pm 0.2$
Lakes	0.1	$0.22 \pm 0.05$	2.8	$0.7 \pm 0.4$
Gulf	NS	$0.10 \pm 0.13$	1.6	

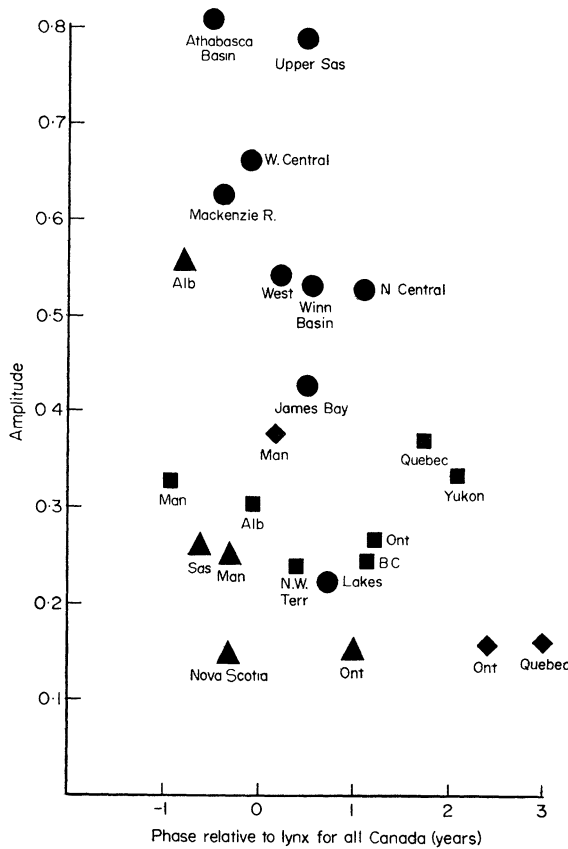


FIG. 4. Geographical variation in Canada. ●, Lynx, nineteenth century; ■, lynx, twentieth century; ▲, red fox, twentieth century; ◆, fisher, twentieth century.

in the west, but it does not persist here in the red fox or the fisher. In the last two species there is also a tendency for the amplitude to decrease as one moves away from the Prairie Provinces, but this is not true for the lynx in this period.

In view of this geographical variation we must consider whether the estimates of the phase in Table 3–5 and Fig. 3 may have been biased by differences between species in the

Table 7. *The 10-year cycle in the lynx in different provinces of Canada, 1919–57*

Province	Significance level of cycle (%)	$\hat{\alpha} \pm \text{S.E.}^*$	$10^{2\hat{\alpha}^*}$	Phase $\pm$ S.E. (relative to lynx for all Canada)
British Columbia	0.1	$0.25 \pm 0.08$	3.1	$1.1 \pm 0.2$
Alberta	0.1	$0.30 \pm 0.10$	4.0	$-0.1 \pm 0.4$
Saskatchewan†	NS	$0.10 \pm 0.20$	1.6	
Manitoba	0.1	$0.33 \pm 0.09$	4.6	$-0.9 \pm 0.4$
Ontario	0.1	$0.26 \pm 0.07$	3.2	$1.2 \pm 0.4$
Quebec	0.1	$0.37 \pm 0.07$	5.6	$1.7 \pm 0.2$
Northwest Territories	1	$0.24 \pm 0.08$	3.0	$0.4 \pm 0.5$
Yukon	0.1	$0.33 \pm 0.10$	4.5	$2.1 \pm 0.3$

† Visual inspection of the data suggests a marked cycle in the first half of the period with a phase of about  $-0.5$ , but no cycle in the second half of the period.

Table 8. *The 10-year cycle in the red fox in different provinces of Canada, 1919–57*

Province	Significance level of cycle (%)	$\hat{\alpha}^* \pm \text{S.E.}$	$10^{2\hat{\alpha}^*}$	Phase $\pm$ S.E. (relative to lynx for all Canada)
British Columbia	NS	$0.10 \pm 0.28$	1.6	
Alberta	0.1	$0.55 \pm 0.09$	12.5	$-0.8 \pm 0.3$
Saskatchewan	0.1	$0.26 \pm 0.07$	3.4	$-0.6 \pm 0.4$
Manitoba	1	$0.25 \pm 0.10$	3.1	$-0.3 \pm 0.5$
Ontario	5	$0.15 \pm 0.07$	2.0	$1.0 \pm 0.8$
New Brunswick	NS	0	1.0	
Nova Scotia	1	$0.15 \pm 0.07$	2.0	$-0.3 \pm 0.6$

Table 9. *The 10-year cycle in the fisher in different provinces of Canada, 1919–57*

Province	Significance level of cycle (%)	$\hat{\alpha}^* \pm \text{S.E.}$	$10^{2\hat{\alpha}^*}$	Phase $\pm$ S.E. (relative to lynx for all Canada)
British Columbia	NS	$0.03 \pm 0.04$	1.2	
Manitoba	0.1	$0.37 \pm 0.13$	5.4	$0.2 \pm 0.5$
Ontario	1	$0.15 \pm 0.06$	2.0	$2.4 \pm 0.5$
Quebec	0.1	$0.16 \pm 0.05$	2.0	$3.0 \pm 0.4$

amplitude of the cycle or in the numbers of animals trapped in different parts of Canada. Comparison of the results in Tables 7 and 8 indicates that the red fox is in phase with the lynx, in agreement with the results in Tables 3 and 4. On the other hand, comparison of Tables 7 and 9 suggests that the fisher cycle is only 1 year behind the lynx cycle, rather than 2 years behind as indicated by the data for the whole of Canada. Thus the phase estimates in Tables 3–5 must be interpreted with some caution. In the case of the coyote there is probably a bias in the other direction since 95% of the catch since 1919 has been from the three Prairie Provinces (Keith 1963) whose lynx cycle is half a year ahead of the cycle for all Canada (Table 7); the figure of 1.3 years in Table 4 should therefore be increased to 1.8 years. Keith (1963) also gives data for mink in Saskatchewan and Manitoba; analysis of these data indicates that the figure for the phase given in Table 4 is probably correct.

*Other species in Canada*

Phelps & Belding (1931) have published records of salmon fishing on the Restigouche River, New Brunswick from 1879 to 1930 and have suggested that they show a 10-year cycle. Their data have been analysed by the present method, eliminating a quadratic trend with time, and the results are shown in Table 10. The existence of a 10-year cycle

Table 10. *The 10-year cycle in the Atlantic salmon in New Brunswick, 1879–1930*

Weight class	Significance level of cycle (%)	$\hat{\alpha}^* \pm \text{S.E.}$	$10^{2\hat{\alpha}^*}$	Peak year $\pm$ S.E. (nearest 1900)
6–16 lb (2 years at sea)	1	$0.13 \pm 0.05$	1.8	$1904.2 \pm 0.4$
17–28 lb (3 years at sea)	1	$0.12 \pm 0.04$	1.7	$1905.0 \pm 0.4$
All weights	0.1	$0.11 \pm 0.03$	1.7	$1904.5 \pm 0.3$

is confirmed. It will also be observed that the cycle is about one year later in the heavier than in the lighter fish. Phelps & Belding (1931) suggest that these weight classes correspond to fish which have spent 3 and 2 years at sea respectively, and they conclude that the cycle is due to a cyclic factor acting on mortality of the young fish (parr) in the river before they go to sea for the first time.

The data on bird populations are not good enough to justify statistical analysis, but there is quite strong evidence of a 10-year cycle in Canada in the horned owl and the goshawk (Lack 1954) and also in several gallinaceous species, of which the ruffed grouse is the best-documented (Lack 1954; Keith 1963).

*Population cycles in Russia*

There is good evidence of a cycle similar to the Canadian cycle throughout the taiga zone of Russia, the snowshoe rabbit being replaced by the mountain hare. The data are not available in a suitable form or over a long enough period for statistical analysis and are presented here graphically. Fig. 5 (taken from Naumov 1972) shows data for the mountain hare and the European lynx in the republic of Komi in the north-eastern corner of European Russia. There is a definite suggestion of a cycle in both species, though the

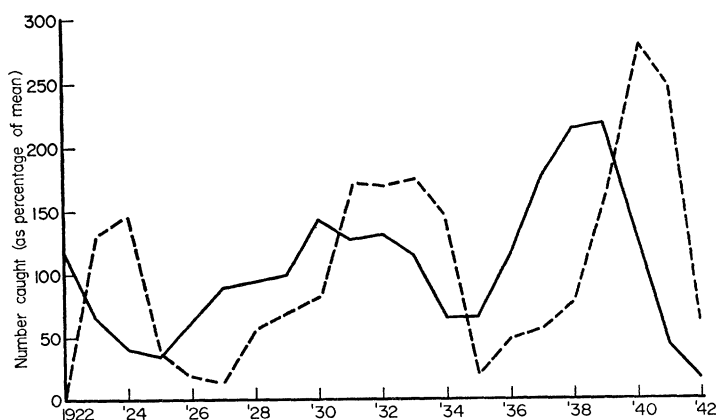


FIG. 5. Population changes in the mountain hare (—), and the European lynx (---) in the Komi region of Russia (Naumov 1972).

period seems to be nearer 8 than 10 years; the lynx cycle lags 1–2 years behind the hare cycle. Fig. 6 shows data for the mountain hare, lynx, red fox and wolf in Yakutia in Eastern Siberia. The data for these four species for 1932–54 have been calculated by averaging the data shown graphically by Labutin (1960) for five regions of Yakutia; the data for the mountain hare for 1924–31 and 1955–58 are taken from the graph in Kolosov, Lavrov & Naumov (1965). There is a strong suggestion of a cycle in all four species,

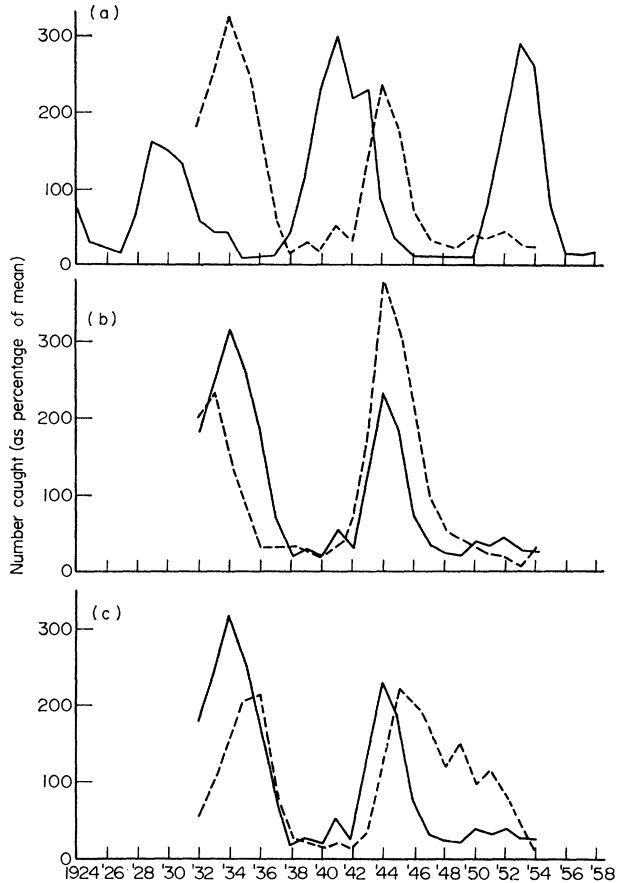


FIG. 6. Population changes in the mountain hare and its predators in Yakutia. (From Labutin (1960) for 1932–54; Kolosov, Lavrov & Naumov (1965) for other years.) (a) mountain hare (—) and lynx (---); (b) lynx (—) and fox (---); (c) lynx (—) and wolf (---).

though the period seems to be slightly longer than ten years, with the lynx and the fox about 3 years after the mountain hare and the wolf 1–2 years after the lynx and the fox. The graphs for the five regions of Yakutia given by Labutin (1960) also show that the cycle is about 2 years later in the Verkhoyanskoy district in the east of Yakutia than in the rest of the republic.

## DISCUSSION

The 10-year cycle affects a large number of species in much of the Boreal forest zone of the Holarctic region. Theories about the cause of the cycle have been reviewed by Lack

(1954) and Keith (1963). The simplest theory is that the snowshoe rabbit cycle is the cause of the cycle in all other species through their relation with it in the food chain; thus Lack (1954) suggests that birds of prey such as the horned owl are cyclic because they eat snowshoe rabbits, whereas gallinaceous birds such as the ruffed grouse are cyclic because they are eaten by predators which are themselves cyclic because they eat snowshoe rabbits. (Keith (1963) criticizes Lack's theory of the grouse cycle on the grounds that the grouse should follow the rabbit peak whereas it is in fact either simultaneous with or slightly before it. However, it seems difficult to predict what the relationship between the rabbit and the grouse cycles should be without studying specific models of this complex situation. For evidence of predation of horned owls on snowshoe rabbits, see Bird (1929), Errington, Hamerstrom & Hamerstrom (1940) and Rusch *et al.* (1972); for predation of horned owls, red foxes and lynxes on ruffed grouse see Darrow (1947) and Nellis, Wetmore & Keith (1972).) The rabbit cycle may, as Lack (1954) suggests, be due to a plant-herbivore interaction. We shall here take the rabbit cycle as given and consider only whether it can account for the other cycles which have been found in the previous section.

The snowshoe rabbit is a dominant item in the food of four of the cyclic predators in northern North America, lynx, coyote, red fox and fisher. (For the lynx, see Nellis *et al.* (1972); for the coyote, Cowan & MacKay (1950), Dearborn (1932), Murie (1945), Sperry (1941); for the red fox, Darborn (1932), Dodds (1955), Johnson (1970); for the fisher, De Vos (1952), Hamilton & Cook (1955).) There is no difficulty in attributing the cycles in these species to the snowshoe rabbit. The only problem is why the cycle should be later by 1 (or possibly 2) years in the coyote and the fisher than in the lynx and the red fox. Butler (1953) attributes the lag in the fisher to delayed implantation (the young born in any year were conceived the previous year); it is not clear, however, without further analysis what effect this will have on the phase lag. There are several other factors which might affect the phase lag between the prey cycle and the predator cycle, such as age at first breeding, the changing age structure of the population, switching to alternative food and density-dependent factors whereby the predator population is influenced by its own abundance as well as by the abundance of prey. This problem requires a more detailed investigation than is possible here.

Mech (1970) has reviewed the literature on the wolf; he concludes that it mainly depends on large ungulates for food and that snowshoe rabbits form only a small part of its diet. He suggests, however, that they may become more important to the wolf in certain areas or during high rabbit populations. Stebles (1944) has found a high proportion of snowshoe rabbits in a small sample of wolf scats and stomach contents in Michigan. Murie (1944) found snowshoe rabbit in only 3 out of 1174 wolf scats in Alaska, but he attributed this to the scarcity of rabbits at the time and he cites two reports of their importance to wolves, the first of a pack which lived largely on rabbits in the Athabasca-MacKenzie region and the second of wolves hunting rabbits in British Columbia. Hewitt (1921) attributes the appearance of a cycle in the last quarter of the nineteenth century (Table 3) to the extermination of the plains bison which forced wolves to become dependent on other prey, but the position is complicated by the inclusion of coyote in these data. The existence of a cycle in the wolf is confirmed by the Russian data.

The habits of the wolverine are not well known, but Rausch & Pearson (1972) found that snowshoe rabbit formed an appreciable proportion of their diet in Alaska.

The skunk is mainly insectivorous, though its diet is more varied in winter, but it is not known to eat snowshoe rabbits (Dearborn 1932; Wood 1954). The skunk is a minor

predator on some cyclic birds such as the ruffed grouse (Darrow 1947), and it is possible that this factor was of more importance in the nineteenth century when the skunk was cyclic. Another possibility is that the skunk cycle was due to a cyclic predator. Seton (1910) cites the horned owl as the main enemy of the skunk, and he also suggests that predation on the young by coyotes, foxes and owls may be very high.

We turn finally to three species whose cycle is ahead of the lynx—the marten, the mink and the muskrat. The muskrat cycle is often attributed to a cyclic climatic factor, but it seems simpler to implicate the mink cycle, since mink is an important predator of muskrat (Dearborn (1932), Errington (1943), Hamilton (1959)) and since the muskrat cycle is about 2 years ahead of the mink cycle. We must postulate that the mink cycle causes the muskrat cycle and not the other way round since it has persisted from the middle of the eighteenth century until today whereas the muskrat cycle can only be demonstrated in the middle of that period. It is possible that the cycle in the Atlantic salmon is also due to predation by mink.

Errington (1943) has suggested that mink predation has little effect on muskrat population dynamics since mink only take old or sick prey which would die shortly in any case. This theory can be tested by considering the residuals from the fitted model,  $e_t$ , which represent changes in population size due to environmental factors which vary from year to year. The correlations between the residuals for mink and muskrat in the same year and in the previous year are shown below.

Area and period	Mink with muskrat the year before	Mink with muskrat the same year	Muskrat with mink the year before
Canada, 1848–1909 (Jones 1914)	+0.40**	+0.43***	–0.42***
Saskatchewan, 1914–57 (Keith 1963)	+0.40**	+0.36*	–0.20
Manitoba, 1924–57 (Keith 1963)	+0.23	+0.21	–0.35*

(One, two or three asterisks indicate significance at the 5%, 1% or 0.1% levels respectively.) An increase in muskrat is followed by an increase in mink a year later and an increase in mink is followed by a decrease in muskrat a year later. This strongly suggests that the prey–predator relationship between the two species directly affects the population dynamics of both of them. There is also a positive correlation between the residuals of the two species in the same year, which may be attributed either to a climatic factor which affects them both or to an immediate effect of the number of prey on the mortality of the predator.

The snowshoe rabbit is sometimes eaten by both marten and mink but it forms only a small part of the diet of either species. (For the marten see Cowan & Mackay (1950); Quick (1955); Lensink, Skoog & Buckley (1955); Marshall (1946); Murie (1961); for the mink, Dearborn (1932), Hamilton (1959), Sealander (1943).) In any case, the cycle in both species is either just before or simultaneous with the rabbit cycle, which rules out a direct causal relationship. This fact suggests that the marten and mink cycles may be due to cycles in their predators. The horned owl is known to be a predator of both species (Errington, Hamerstrom & Hamerstrom (1940); Grinnell, Dixon & Linsdale (1937); Seton (1910)). There may also be competition between the marten and the fisher for denning sites (De Vos 1952). There are also reports that martens are killed by fishers and by lynxes (De Vos (1952); Grinnell, Dixon & Linsdale (1937); Seton (1910)).

In conclusion, it must be admitted that the evidence linking some of the cyclic predators

(particularly wolf, skunk, marten and mink) directly or indirectly with the snowshoe rabbit is rather weak. Nevertheless, this still seems to be the most plausible explanation since no cyclic meteorological factor has been discovered. Fig. 7 shows the ecological links between the snowshoe hare and the other cyclic species which are suggested here, though it must be emphasized that some of them are very tentative.

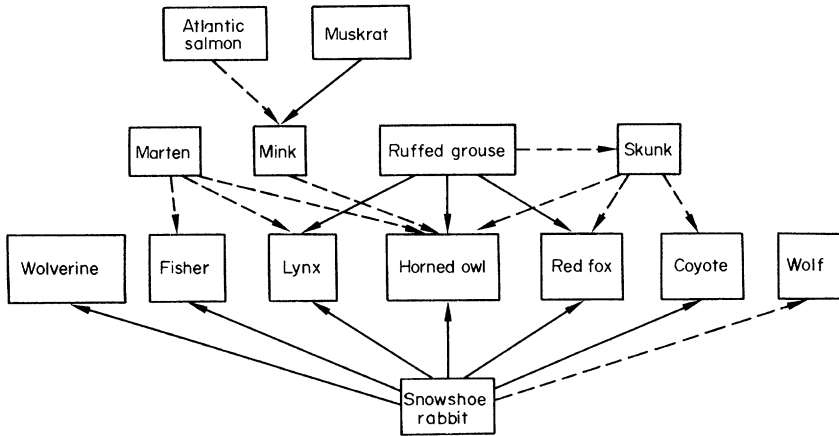


FIG. 7. Probable and possible links in the food chain between the snowshoe rabbit and other cyclic species.

## SUMMARY

(1) The main features of the ten-year cycle are the regularity of the period and the irregularity of the amplitude of the oscillations; these features are obvious in data on the lynx cycle, and in the correlogram and periodogram calculated from the data.

(2) A statistical model is proposed for the analysis of the 10-year cycle which takes these features into account by including both a strictly periodic term and an autoregressive term depending on the size of the population in the previous year; it is shown that this model fits the data better than the second-order autoregressive model used by Moran (1953).

(3) All data on the ten-year cycle in Canada have the same period of about 9.63 years. The other parameters in the model can be estimated by the method of least squares, and estimates of the phase and the average amplitude of the oscillations can then be obtained.

(4) This method is used to analyse data on the fur-bearing mammals of Canada between 1751 and 1969. A 10-year cycle exists during at least part of this time in the following species: coyote, fisher, red fox, lynx, marten, mink, muskrat, skunk, wolf, wolverine and snowshoe rabbit. A cycle has also been confirmed in the Atlantic salmon. There is a tendency for the cycle to be most pronounced in the midwest of Canada and to become weaker and later as one moves away from this region. A similar cycle exists in the taiga zone of Russia.

(5) The simplest theory is that the cycle in all other species is caused, directly or indirectly, by the cycle in the snowshoe rabbit. The food habits of all the cyclic species



are reviewed with this theory in mind. There is considerable difficulty in linking some of the cyclic species convincingly with the snowshoe rabbit, but this is nevertheless still thought to be the most likely explanation since no cyclic meteorological factor has been discovered.

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## APPENDIX

### Scientific names of animals

Vernacular name	Scientific name	Vernacular name	Scientific name
Bear, black	<i>Ursus americanus</i> Pallas	Musk-ox	<i>Ovibos moschatus</i> (Zimmermann)
Bison	<i>Bison bison</i> (L.)	Muskrat	<i>Ondatra zibethicus</i> (L.)
Bobcat	<i>Lynx rufus</i> (Schreber)	Otter	<i>Lutra canadensis</i> (Schreber)
Coyote	<i>Canis latrans</i> Say	Otter, sea	<i>Enhydra lutris</i> (L.)
Ermine (stoat)	<i>Mustela erminea</i> L.	Rabbit, snowshoe (varying hare)	<i>L. americanus</i> Erxleben
Fisher	<i>Martes pennanti</i> (Erxleben)	Raccoon	<i>Procyon lotor</i> (L.)
Fox, Arctic	<i>Alopex lagopus</i> (L.)	Seal, fur	<i>Callorhinus ursinus</i> (L.)
Fox, red	<i>Vulpes vulpes</i> (L.)	Seal, common (harbour)	<i>Phoca vitulina</i> L.
Hare, Arctic	<i>Lepus arcticus</i> Ross	Skunk	<i>Mephitis mephitis</i> (Schreber)
Hare, mountain (blue)	<i>L. timidus</i> L.	Wolf	<i>Canis lupus</i> L.
Lynx, Canadian	<i>Lynx canadensis</i> Kerr	Wolverine	<i>Gulo gulo</i> L.
Lynx, European	<i>L. lynx</i> L.	Goshawk	<i>Accipiter gentilis</i> (L.)
Marten	<i>Martes americana</i> (Turton)	Grouse, ruffed	<i>Bonasa umbellus</i> (L.)
Mink	<i>Mustela vison</i> Schreber	Owl, horned	<i>Bubo virginianus</i> (Gmelin)
		Salmon, Atlantic	<i>Salmo salar</i> L.

## STATISTICAL APPENDIX

For the purpose of statistical analysis the model,

$$x_t = \mu + \alpha \sin 2\pi\omega(t - \phi) + \beta x_{t-1} + e_t \quad (A1)$$

is more conveniently expressed in the form

$$x_t = \mu + \alpha_1 \sin 2\pi\omega t + \alpha_2 \cos 2\pi\omega t + \beta x_{t-1} + e_t \quad (\text{A2})$$

where

$$\begin{aligned} \alpha_1 &= \alpha \cos 2\pi\omega\phi, \\ \alpha_2 &= -\alpha \sin 2\pi\omega\phi. \end{aligned} \quad (\text{A3})$$

(The equations giving  $\alpha$  and  $\phi$  in terms of  $\alpha_1$  and  $\alpha_2$  are

$$\begin{aligned} \alpha &= \sqrt{(\alpha_1^2 + \alpha_2^2)}, \\ \phi &= -\arctan(\alpha_2/\alpha_1)/2\pi\omega, \text{ when } \alpha_1 > 0. \end{aligned} \quad (\text{A4})$$

When  $\alpha_1$  is negative,  $1/2\omega$  must be subtracted from, or added to, the above expression for the phase according as  $\alpha_2$  is positive or negative.) The first step in the analysis is to estimate the frequency of the oscillation,  $\omega$  (or its period,  $1/\omega$ ). If the oscillations are well-defined this can usually be done to sufficient accuracy by inspection of the data or of the periodogram. It has been shown by Whittle (1954) that  $\omega$  can be estimated much more accurately than the other parameters of the model, so that a rather crude method of estimating it is adequate. From extensive data on lynx catches for the whole of Canada, Elton & Nicholson (1942) have shown that there were nineteen complete cycles between the peak years of 1752 and 1935, giving a period of 9.63 years. This figure has been used in the present paper.

If  $\omega$  is assumed to be known the model is linear in the remaining parameters, which can be estimated by least squares and their variances and covariances found in the usual way. (Durbin (1960) has justified the use of the standard method for an autoregressive model.) The method can be extended if necessary to include a linear or quadratic function of time in the model to eliminate trend. The presence of gaps in the data presents no problem, but the first observation after a gap cannot be used as a dependent variate; the number of degrees of freedom for the residual sum of squares is therefore  $n-4-b$ , where  $n$  is the number of observations and  $b$  is the number of blocks of data without gaps. A test for the significance of the cyclical component can be obtained by finding the residual sum of squares under the reduced model omitting  $\alpha_1$  and  $\alpha_2$ ; the resulting  $F$  ratio has 2 and  $(n-4-b)$  degrees of freedom.

The estimates of the parameters  $\alpha_1$  and  $\alpha_2$  cannot be used by themselves to provide information about the phase and amplitude of the cycle since they are also affected by the autoregressive term  $\beta$ . We shall therefore consider what the oscillations would be in the absence of the error term  $e_t$ . Under these circumstances there will be a strictly periodic oscillation which can be represented equivalently by

$$x_t = \mu + \alpha_1 \sin 2\pi\omega t + \alpha_2 \cos 2\pi\omega t + \beta x_{t-1}, \quad (\text{A5})$$

or by

$$x_t = \mu^* + \alpha_1^* \sin 2\pi\omega t + \alpha_2^* \cos 2\pi\omega t. \quad (\text{A6})$$

By the use of elementary trigonometrical identities we find that the equations giving  $\alpha_1^*$  and  $\alpha_2^*$  in terms of  $\alpha_1$ ,  $\alpha_2$  and  $\beta$  are

$$\begin{aligned} \alpha_1^* &= [(1 - \beta \cos 2\pi\omega)\alpha_1 + (\beta \sin 2\pi\omega)\alpha_2]/(1 - 2\beta \cos 2\pi\omega + \beta^2), \\ \alpha_2^* &= [-(\beta \sin 2\pi\omega)\alpha_1 + (1 - \beta \cos 2\pi\omega)\alpha_2]/(1 - 2\beta \cos 2\pi\omega + \beta^2). \end{aligned} \quad (\text{A7})$$

Hence

$$\alpha_1^{*2} + \alpha_2^{*2} = (\alpha_1^2 + \alpha_2^2) / (1 - 2\beta \cos 2\pi\omega + \beta^2)$$

$$\frac{\alpha_2^*}{\alpha_1^*} = \frac{-(\beta \sin 2\pi\omega)\alpha_1 + (1 - \beta \cos 2\pi\omega)\alpha_2}{(1 - \beta \cos 2\pi\omega)\alpha_1 + (\beta \sin 2\pi\omega)\alpha_2}. \quad (\text{A8})$$

The amplitude and phase of (A6) which are denoted by  $\alpha^*$  and  $\phi^*$  can now be obtained by substituting these expressions in the starred analogue of (A4). (In estimating the amplitude,  $\alpha_1^2$  has been estimated by  $\hat{\alpha}_1^2 - \text{Var}(\hat{\alpha}_1)$ , where  $\hat{\alpha}_1$  is the estimated value of  $\alpha_1$ , and likewise for  $\alpha_2^2$  and  $\beta^2$ . This procedure eliminates bias since  $E(\hat{\alpha}_1^2) = \alpha_1^2 + \text{Var}(\hat{\alpha}_1)$ .) The standard errors of the resulting estimates of the amplitude and phase have been found by the standard 'Delta technique' for functions of random variables (Kendall & Stuart, 1963, p. 232). The value for the amplitude means that there is a difference of  $2\alpha^*$  on average in the logarithms of the population size between the peak and the trough of the cycle; this implies that the peak population size is  $10^{2\alpha^*}$  times larger than the lowest population size. The value for the phase relates to the middle of the cycle; the peak of the cycle occurs 2.41 years later.

An alternative way of regarding (A6) is to say that it represents the best predictor of  $x_t$  if  $x_{t-1}$  is not known. A similar answer would be obtained if one fitted a periodic function without an autoregressive term to the data, but the standard errors of the estimates would be larger than under the method used here since relevant information would be ignored.