GRAPHICAL ANALYSIS OF LAG IN POPULATION REACTION TO ENVIRONMENTAL CHANGE

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SUMMARY: A method of graphical analysis which accounts for cause/effect lag between biological populations and environmental factors is presented. The method involves analysis of ellipsoid curves generated by delayed population responses to cyclic environmental variables. Six ellipse types are distinguished which determine the type of relationship involved and provide a key to equations for calculating the lag interval. The equations are based on the formula $\tau = L\theta/360$, where θ = either arcsin x' /x" or 90+ arccos x' /x", x' and x" are measurements taken from the ellipse, τ = lag and L = independent cycle length.

The method is constrained to populations where generation time is small relative to duration of the independent cycle (L), and where lag is no greater than half L. Sampling interval should be short relative to L.

Examples are cited to demonstrate application of the method, and interpretation of biological relationships from it is discussed.

INTRODUCTION

Interpretation of relationships between biological populations and their environment is usually made from simultaneously recorded data. However, few populations respond immediately to fluctuations in environmental influences; more often a delay occurs between environmental change and population response. Because of delays or lag effects, descriptions of biological/environmental relationships which depend on coincident data are frequently inadequate.

Although consideration has been given to the effect of lag in population equations (Wangersky and Cunningham, 1956; May *et al.,* 1974; Wangersky, 1978) simple methods of estimating lag intervals and relating them to biological events are not available. In this paper we present a simple method of graphical analysis of the relationships between populations and environmental factors. The method involves analysis of ellipsoid curves which occur when dependent variables with lag are plotted against their independent influencing variables. Similar methods are commonly used in electronics to measure phase shift (Terman and Pettit, 1952).

A key is provided for broad interpretation of ellipse type and formulae are given for more precise measurement of lag. Several examples are presented to illustrate application of the method.

DEVELOPMENT OF THE METHOD

In nature, regularly cycling variables tend to approximate sine waves when their cycles remain relatively constant in magnitude. Biological populations which respond to these variables often do so with a lag determined by some function of generation time. Populations of organisms with a generation time which is small relative to cycle length of the influencing variable tend to mimic the wave form of that variable. For example, populations of many micro-organisms, nematodes, insects and small vertebrates fluctuate in response to cyclic variables such as temperature, moisture, light, and nutriment.

Figure 1 A illustrates the relationships between an independent variable (I) with cycle length (L) and dependent variables (a to j which mimic I, but which are of increasing distance (time) behind I. At a distance of half the cycle length of I the dependence relationship may be either positive or negative, the former having a lag of L/2 greater than the latter. However, as discussed in constraints below, lags of greater than L/2 cannot be measured using this method. Thus variables a to e represent positive dependents with lag (τ) starting at zero (a) and increasing by steps of L/10 from b to e; whilst f to j represent negative dependents with no lag (f) and progressively increasing lag (g to j. Plots between independent variable (I) and the ten dependent variables are presented individually in Figures I Ba-j, using data from sample times 1 to 11 in Figure I A and connecting the data points sequentially. Whilst a and f produce the expected straight regression lines, the lagging dependents all produce ellipsoid curves. Lagging positive dependents. have anti clockwise rotating ellipses whereas lagging negative dependents have clockwise rotating ellipses.

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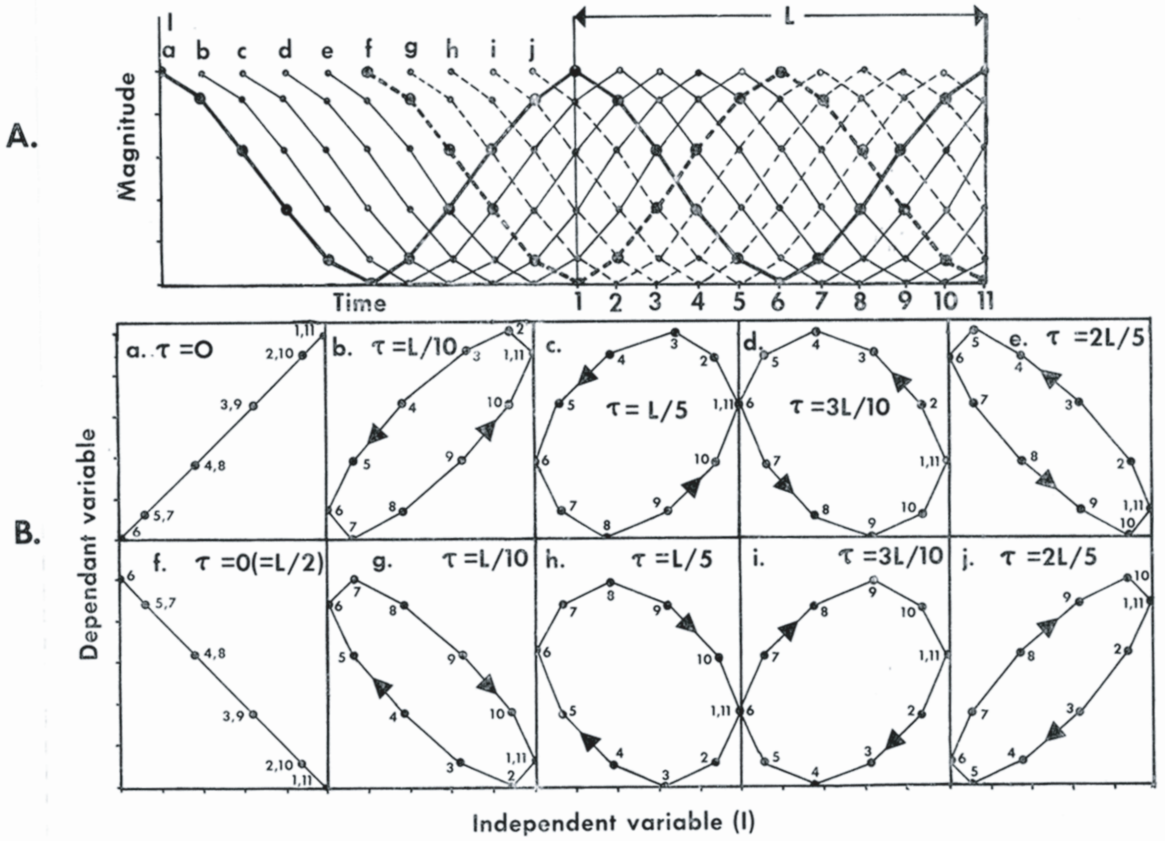

FIGURE 1. *Graphical representation of the relationship between a regularly cycling independent variable and dependent variables of increasing response delay,* τ.

(A) *Plots of independent and dependent variables over time. Magnitudes of all variables made equal for ease of presentation. I, independent variable of cycle length L; a–j, dependent variables sequentially increasing in distance from I by steps of L/10, solid-line curves a to e are positively dependent on I, broken-line curves f to j are negatively dependent.*

(B) *Plots of the dependent variables a–j (diagrams a–j respectively) against I, taking data sets from times 1–11 in A and connecting the points sequentially. Lag of the dependent variable indicated in each diagram.*

Inclination of the major axis of the ellipse corresponds with the dependence relationship when $\tau < \frac{1}{4}L$ (i.e. positive for positive dependence and negative for negative dependence); the ellipse becomes a circle when $\tau = \frac{1}{4}L$; and the ellipse assumes an inclination opposite to the dependence relationship when $\frac{1}{4}L < \tau < \frac{1}{2}L$. Phase difference or lag between two sine waves can be measured by the formula:

$$\tau = L\,\theta\,/\,360 \qquad (1)$$

where $\theta = \arcsin x'/x''$ (Terman and Pettit, 1952)

x' = the vertical distance of separation between independent and dependent curves at the point of inflexion (= half magnitude) of independent variable.

x'' = half magnitude of independent variable. (see Fig. 2).

This restricts measurement to a lag of no greater than quarter the independent wave length. It may be extended to measure lag intervals up to half L by substituting as follows:

when $0 < \tau < \frac{1}{4}L$, $\quad \theta = \arcsin x'/x''$ (2)

when $\frac{1}{4}L < \tau < \frac{1}{2}L$ $\quad \theta = 90 + \arccos x'/x''$ (3)

Phase ellipses can thus be categorised into six types; Table 1 provides a key to interpretation of each ellipse type and summarises the formulae for calculation of lag. Figure 2 illustrates the method, taking positive dependents band e from Figure 1, having defined lags of 1/10 and 4/10L respectively. Phase ellipses are type I (Fig. 2B) and type 3 (Fig. 2C).

CONSTRAINTS

This method is suitable for measuring lag in population reaction to environment change. Popula tion reaction is most often recorded as a change in numerical density, or in breeding potential of the individuals comprising the population. Such changes are intimately associated with events in the life cycle of the species, and lag can be considered to represent some function of generation time. The method cannot be used where lag is greater than generation time, that is where reaction to the environmental influence 'skips' one or more generations, as population fluctuations no longer mimic the cycle of the influencing variable in a simple manner. Similarly, unless generation time (and therefore lag) is small relative to the independent cycle length, the population reacts to or 'samples' the influencing variable too infrequently (for populations with discrete generations) or in too complex a manner (for continuously breeding populations) to produce a simple mimic of the independent variable.

Lags which can be measured by this method are thus constrained to be less than half the duration of the independent cycle length, that is $\tau < L/2$. A lag of greater than half is possible mathematically (see Fig. I), and no doubt also biologically, such as in physiological reactions to environmental change. However, the equations and key presented in Table 1 would no longer be applicable.

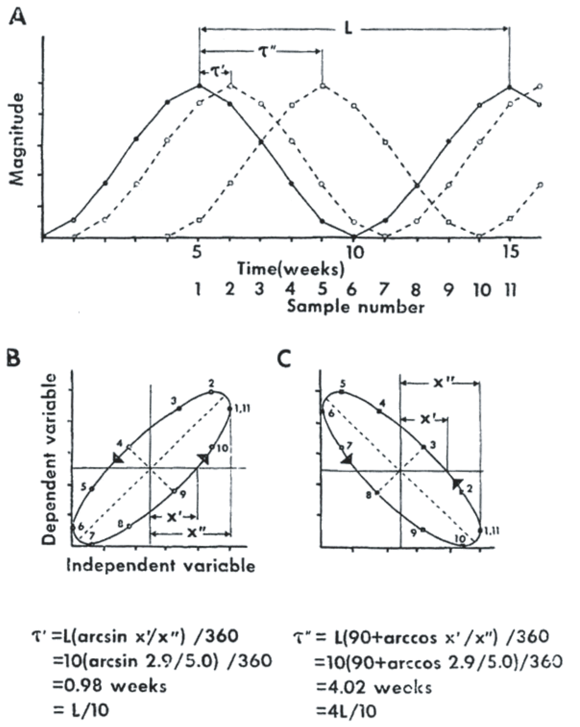

FIGURE 2. *Illustration of the method for calculating lag.*

(A) *Graph of independent variable I (solid line), and dependent variables b and e (broken lines) with lags of* τ' *(= L/10) and* τ'' *(= 4L/ 10) respectively, taken from Figure 1A.*

(B & C) *Correlation ellipses for b and e in relation to L constructed from sample data 1-11 in A; and calculation of* τ' *and* τ'' *from the ellipses.*

TABLE 1. *Key to interpretation of phase ellipse for estimation of lag.*

Ellipse characters					
Rotation	Inclination (major axis)	Ellipse Type	Correlation	Approximate lag	Lag equation
anticlockwise	positive	1	positive	$0<\tau<\frac{1}{4}L$	$\tau = L(\arcsin x'/x'')/360$
anticlockwise	nil*	2	positive	$\tau = \frac{1}{4}L$	$\tau = \frac{1}{4}L$
anticlockwise	negative	3	positive	$\frac{1}{4}L<\tau<\frac{1}{2}L$	$\tau = L(90 + \arccos x'/x'')/360$
clockwise	negative	4	negative	$0<\tau<\frac{1}{4}L$	$\tau = L(\arcsin x'/x'')/360$
clockwise	nil*	5	negative	$\tau = \frac{1}{4}L$	$\tau = \frac{1}{4}L$
clockwise	positive	6	negative	$\frac{1}{4}L<\tau<\frac{1}{2}L$	$\tau = L(90 + \arccos x'/x'')/360$

Note: *ellipse becomes a circle.

APPLICATION

A simple example of processed field data exhibiting a typical lagged relationship is given in Figure 3. Plots of total nematodes (Nematoda) in a sub-alpine tussock soil, and of corresponding soil temperature, both in relation to time, show that nematode density 'shadows' the temperature curve (Fig. 3A). The relationship between nematode numbers and temperature demonstrates a type I phase ellipse of anticlockwise rotation and positive inclination (Fig. 3B); that is, the correlation was positive and lag was less than $\frac{1}{4}$ independent cycle length (L). L in this case was 395 days, although the average L for temperature over a number of years would follow a yearly (365 day) cycle. The calculated lag was 78.4 days or approximately It sampling intervals (s.i. = 56 days). Adjustment of the data by moving nematode counts back in time by one and two sampling intervals relative to temperature measurements increased the correlation coefficient from 0.066 to 0.497 and 0.621 respectively. Thus, with compensation for lag, temperature was shown to account for approximately 38 % of the variation in total nematode numbers (Fig. 3C)

Fitting of ellipses to data is most accurately done by computer. A programme was developed by J. Maindonald (Applied Mathematics Division, DSIR, Auckland). The method used was to fit the general equation of the second degree f (x, y) = 1, where $f(x, y) = ax^2 + by^2 + 2fx + 2gy + 2hxy$ by minimising the sum of squares $\sum[f(x, y) - 1]^2$ taken over all points (x, y). The fitting can be handled by using a standard multiple regression programme to regress the variable $z \equiv 1$ upon the variables x^2, y^2, x, y, xy.

However, closely comparable estimates of lag have been achieved by first fitting ellipses to the same data by eye. To ensure optimum graphical interpretation, the ranges of each variable in a relationship are best scaled to equal magnitude using the transformation:

$$X_i = k(x_i - x_{min} / (x_{max} - x_{min})) \quad (4)$$

where Xi = scaled value
xi = data point at sample date i
x_{min} = lowest value of x
x_{max} = highest value of x
k = desired maximum magnitude (e.g., 10)

With a larger number of data points the fit of the ellipse is more precise and a better estimate of lag is possible. It also reduces the chance of aliasing, where spurious dependence cycles may be generated by too few sample points; e.g., a sampling frequency of 3L/4 would produce a dependence cycle of length 3L, and a frequency of L/2 could generate a

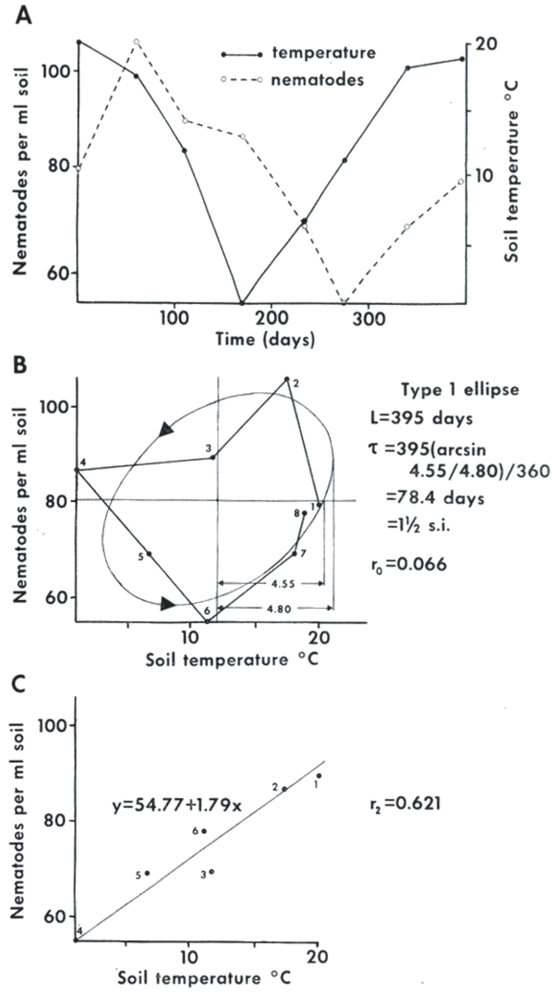

FIGURE 3. *A biological example demonstrating lag and its calculation.*

(A) *Fluctuation* in *total nematode numbers* in *a soil under sub-alpine tussock grassland, and in corresponding soil temperature* (15 *cm deep), over one year*.

(8) *Phase ellipse of nematode numbers versus soil temperature, and calculation of lag; s.i., sampling interval;* r_o, *correlation coefficient disregarding lag effect*.

(C) *Relationship of nematode numbers and soil temperature after adjustment of data by two sample intervals (112 days) to compensate for lag in nematode numbers;* r_2, *correlation coefficient of data after adjustment by two s.i.*

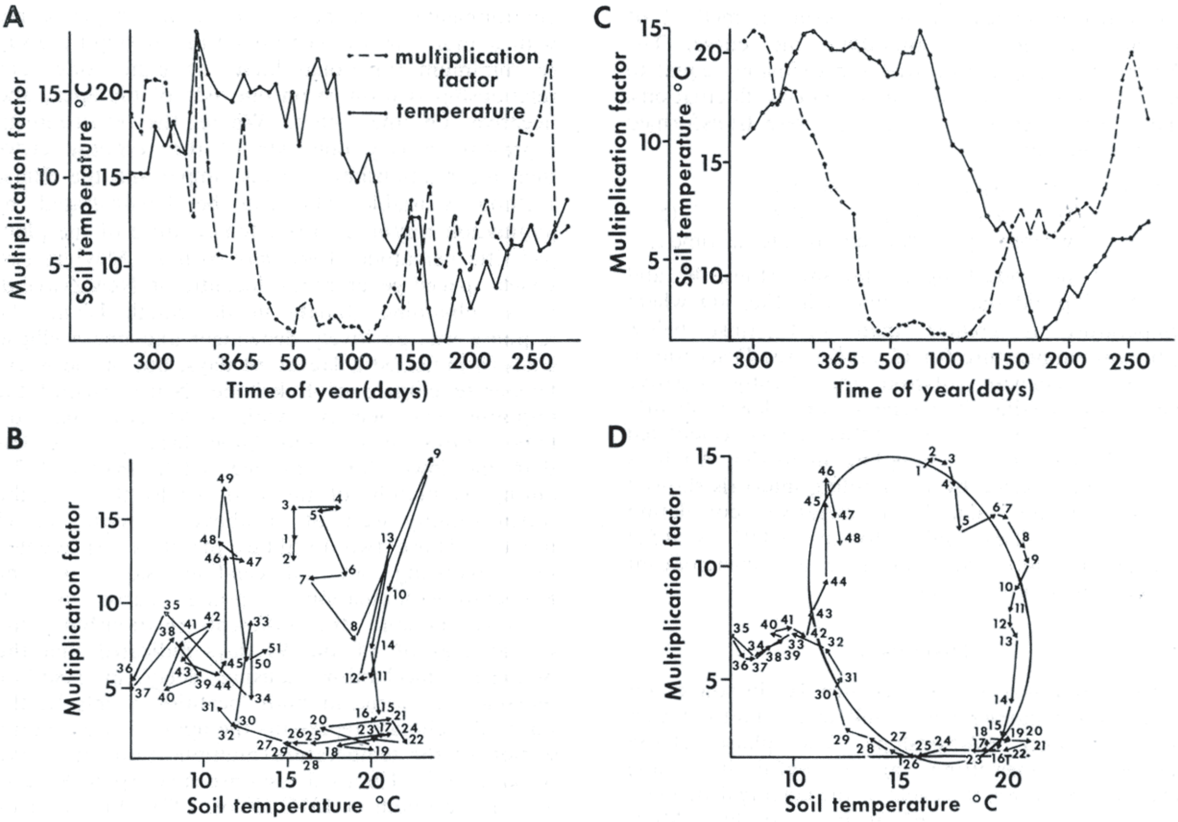

FIGURE 4. *Application of the correlation ellipse method where many data points are available.*

(A) *Fluctuations in multiplication factor of potato cyst nematode at Pukekohe and in corresponding soil temperature* (15 *cm deep, at planting date of host potato), over one year.*

(B) *Correlation plot of multiplication factor versus soil temperature, showing basic clockwise rotating ellipsoid, but with many secondary convolutions.*

(C) *Same plot as A, but using smoothed data.*

(D) *Correlation plot using smoothed data, with an ellipse fitted statistically to data coordinates above* 12 °C (*% variance accounted for in fit:* 99.6).

[straight line for the dependent. More data points also allow a closer match of data adjustment interval to the calculated lag during the final assessment of actual association (r) in the relationship. Data adjustment interval is restricted to multiples of sample interval, and if the latter is large in relation to lag, only a coarse compensation for lag effect is possible.

Figure 4 illustrates use of the method when many data points are available. The relationship concerns the response (multiplication factor) of a population of potato cyst nematode *(Globodera pallida* Mulvey & Stone) to varying soil temperatures at Pukekohe in the North Island of New Zealand. Weekly measurements were recorded throughout one year, and the plotted cycles indicated the presence of a dependence relationship (Fig. 4A). A correlation plot of the data produces a basic ellipsoid shape of clockwise rotation, but which is confused by many minor convolutions resulting from short-term secondary temperature cycling (Fig. 4B). The negative nature (clockwise rotation) of the relationship is upheld even in the secondary cycles (e.g., data points 8-13, 19-23, 39-43). To obtain a measure of lag in the primary relationship, however, it is desirable to minimise effects of secondary fluctuations and other biological 'noise' by using a method of moving averages for smoothing the curve. The chosen averaging period was approximately equal to the duration of most of the secondary fluctuations, that is four weeks, and the data were transformed by the equation

$$X_i, Y_i = (x_i + x_{i+1} + x_{i+2} + x_{i+3})/4, \quad (y_i + y_{i+1} + y_{i+2} + y_{i+3})/4 \qquad (5)$$

where x_i, y_i = data coordinates at time t,

to reveal the underlying relationship (Figs. 4C and D). An ellipsoid shape is obvious in Fig. 4D where temperature is greater than 12°C (just below optimum temperature for G. *pallida*. see Discussion), and the clockwise rotation and slightly negative inclination classifies it as type 4 with a lag of slightly less than L/4 (365/4 = 91). Actual lag was calculated to be 77 days (= 11 sampling intervals). Analysis of the data adjusted by 11 sampling intervals showed a very highly significant negative correlation ($r = -0.88$, critical value for $p < 0.001$ is 0.52) whereas non-adjusted data gave a non-significant correlation of $r = -0.09$.

Discussion

Analyses which do not recognise lag in studies on population dynamics may result in misinterpretation of cause/effect relationships. The phase ellipse method for measuring lag is useful in simple relationships where the cycle of the lagging dependent mimics that of the influencing variable. More complex relationships cannot be solved graphically and require sophisticated analytical techniques. Such techniques can also be used on less complex relationships, but most researchers make an initial plot of the two variables to examine the possible relationship, and by taking this a step further to include the ellipse method the visual information is extended and a simple estimate of lag can be calculated.

The constraint of the method whereby lag can be measured only if it is less than L/2 is of little hindrance biologically, since in most instances where lag is greater than L/2, the dependent cycle no longer forms a simple mimic of the influencing variable, and the phase ellipse method of determining lag is no longer possible. An exception to this may be in physiological reactions where the influencing variable has a short cycle, and although reaction time may be greater than L/2 the relationship remains simple. Some modifications of the method may be possible to accommodate this.

The phase ellipse method, as do many others, assumes that the underlying response relationship is linear. In fact most biological responses to environmental influences form a bell-shaped curve with a more or less central optimum sloping away to minimum functional limits on either side. The relationship is positive on one side of the apex, and negative on the other. Where the environment represents largely one side of the response curve to en the relationship remains simple and the ellipse method is usable. This can be demonstrated by population response to soil temperature of the plant parasitic nematode *Aglenchus costatus* Meyl in two widely spaced geographical localities in New Zealand. In a sub-alpine climate in the South Island the response was positively dependent and phase ellipse analysis indicated a lag of 84 days, but in the warm temperate climate of Pukekohe (North Island) the response was negative with a 91 day lag. Soil temperatures in the sub-alpine locality were less than the lower limit for egg hatch (Wood, 1973) during 5f months of the year, whilst those of the warm locality were at or above optimum for 91< months. Those two localities therefore represented the ascending and descending sides of the temperature/population response curve of *A. costatus*. Despite the different relationships, the similar lags of 84 and 91 days indicated that the biological mechanism causing delay in response remained the same in both localities. Similarly, the Pukekohe climate represents the upper or descending section of the temperature/multiplication rate curve for G. *pallida*. The total response curve spans 8-22°C with an optimum at 15°C (Foot, 1978). For most of the year soil temperatures at Pukekohe are at or above optimum but for two to three months they drop below. During this time the negative relationship no longer holds (data points 34-41 in Fig. 4D), am! in fact a slight positive influence is evident.

In nature, organisms have evolved in close response to the demands of their environment. Problems which have presented difficult barriers have generally been overcome by 'escape' mechanisms such as migration, diapause, and restriction of breeding to specific seasons; most other responses to regularly recurring environmental changes may have developed as simple direct relationships with a cause/effect lag.

The phase ellipse method of measuring lag in simple relationships, therefore, has wide application in population biology. Whilst this paper has dealt entirely with nematode reaction to temperature, the method is equally applicable to a wide variety of organisms, especially those with rapid generation turnover such as micro-organisms, insects, nematodes, and some small vertebrates. Any influencing variable which has a cyclic pattern could evince a lagging cyclic response. Measurement of lag not only allows more accurate assessment of environmental effects but may also provide insight into the biological processes operating within the relationship. In many instances lag is a measure of mean generation time, but it could also, for example, pinpoint a sensitive stage within the life cycle by comparing lag time with known generation time.

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