

The Nicholson blowfly experiments: some history and EDA

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The renowned Australian entomologist Alexander J. Nicholson carried out a series of experiments in the 1950s with the intent of learning more about a sheep pest, the blowfly. The results presented here are driven by analyses of the data that Nicholson collected. The situation is of special interest because it involves a system that is nonlinear, has time lags and might be described as non-stationary. There are other complicating aspects including that: the data are aggregate referring to a sum of interacting cohorts, age effects exist, the data are measured at discrete times yet the phenomenon exists in continuous time and a structural change may be taking place. In the work, the spectrogram and complex demodulation prove to be useful tools since the phenomenon is varying, depending on both time and period (or frequency). These tools have in common the notion of an evolutionary spectrum. The goals are to explore some of Nicholson's data and to illustrate how the tools of complex demodulation and the spectrogram and subject matter can elicit information from time-series data.

Keywords: Blowfly (*Lucilia cuprina*); density dependence; evolutionary spectrum; insect biology; Nicholson's equation; nonlinearity; population dynamics; time lags.

JEL classifications: C02; C13; C22; C32.

1. INTRODUCTION

'... you ain't no better'n a blowfly.' Lucinda Bryant

Experimental data collected by the Australian entomologist A. J. Nicholson have motivated the development of novel mathematical and statistical tools. The richness of these data and the analyses is surprising. This article describes the work of Nicholson and then presents some exploratory data analyses highlighting analytically some aspects not directly apparent from time traces. Thereby its features, that Nicholson described verbally, are more formalized.

Alexander J. Nicholson was one of the important historical figures of the field of entomology in the 20th century. His research with sheep blowflies has stimulated much entomological, mathematical and statistical research. What has become known as Nicholson's (blowfly) equation has led to basic research in dynamical systems. Nicholson was Chief of the Division of Entomology at the Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO). In that position, he was able to have carried out an extensive series of laboratory experiments meant to learn the development of insect populations in density dependent situations. In the course of his work, he made basic contributions to the fields of evolutionary biology and nonlinear systems modelling. He wrote a series of papers that have become classics including Nicholson (1954a, 1954b), and (1957). His life and work are memorialized in Mackerras (1970).

1.1. Some history of the data and its modelling

There are many articles recounting this story; see, for example Hassell *et al.* (1976) and Renshaw (1994). I will focus on the parts that I have followed most closely. To begin, Robert May was a seminal researcher in the modern study of insect populations with density dependence. He vitalized the study of Nicholson's data. May's early papers include May (1974, 1975, 1976). The 1976 paper with George Oster is a key one. It focused on the dynamic complexity of simple ecological models. The level of complexity was astonishing. May's review papers include May (1986, 1989).

Oster and a student Ipaktchi (1978) set down the now ubiquitous model for the development of an insect population

$$\frac{dN(t)}{dt} = \beta N(t - \tau) \exp\left\{\frac{-N(t - \tau)}{\kappa}\right\} - \delta N(t)$$

now commonly known as Nicholson's equation. They discussed it in the context of the first 175 observations in the cage I data in Figure 8 in Nicholson (1957). They matched the discrete form of Nicholson's equation to the time series in that figure with a choice of parameter values. They digitized the figure by hand. The graph went off the top of the page in its later stages, leading to some missing values. Ipaktchi's (1979) doctoral thesis discussed and analysed that data. In particular, they examined spectra, as do Reuman

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et al. (2006). See also Gurney *et al.* (1980) who make use of the data in a figure in Nicholson (1954b) and also set down Nicholson's equation.

The parameters of the equation have been described as follows: β the birth rate, δ the death rate, τ the age at which adult flies emerge from their pupal cases and κ the population's carrying capacity. Towards interpretations of the parameters appearing rewrite Nicholson's equation as

$$\beta M \exp\left\{\frac{-M}{\kappa}\right\} - \delta N$$

The partial derivatives with respect to M and N are $\beta \exp\{-M/\kappa\} [1 - M/\kappa]$ and $-\delta$ respectively. The former shows, for fixed N , the population growth rate to be proportional to β for $M < \kappa$ and decline at for $M > \kappa$. The latter shows, for fixed M , δ to be the rate at which the population is falling.

This writer visited the CSIRO Division of Entomology in Canberra in August 1977. After asking about the Nicholson data, he was taken to a filing cabinet containing many index cards in the basement of the building. The cards were full of data and DRB copied those relating to Nicholson's cage I experiment. Professor Don McNeil later obtained the data and had some keypunched. These are the values that appeared and were analysed in Brillinger *et al.* (1980). Since the data include eggs laid and flies emerged, the model of that paper was able to include age classes directly. Those data provided the basis for two theses. The Guttorp (1980) and Ipaktchi (1979) theses also included theoretical developments. Sadly a technician not realizing the value of Nicholson's data threw out the filing cabinet. This was a tragedy.

Oscillations are an obvious feature of many such data sets. Why are the data evidencing periodicity? Where do the oscillations come from? Why is the population persisting? An answer is to be found in Nicholson's basic postulate,

'no intrinsically variable phenomenon can continue to exist in the absence of a feed-back mechanism to limit its variability', Makerras (1970)

See also Kendall *et al.* (1999). Nicholson's cage I experiment persists without extinction or explosion because food was provided in a specifically selected amount. Briefly one can argue as follows. Suppose there are a lot of eggs. Then, many adults will arrive. Since the amount of food is limited. The female adults would not find enough to lay many eggs; hence there will be fewer eggs. The adults of these will have lots of food and many eggs will be laid, and so on. The square roots of the population's bidaily totals are graphed in Figure 1.

2. METHODS

2.1. Complex demodulation

Complex demodulation is a numerical technique motivated by analogue signal processing. Important uses include estimating inherent periods/frequencies of time-series data and characterizing non-stationarities and strength of signal. It can prove a sensitive tool for frequency and period detection and estimation.

Given time-series data $\{X_t, t = 1, \dots, T\}$ and the frequency ω_0 the steps include: compute the stretch of complex values

$$\{X_t \exp\{i\omega_0 t\}\}.$$

This vector is smoothed over t and then plots against t . The computations may be carried out using an FFT. An example is given in Figure 2. References include Tukey (1961), Bingham *et al.* (1967), Brillinger (1975), Hasan (1983) and Bloomfield (2000).

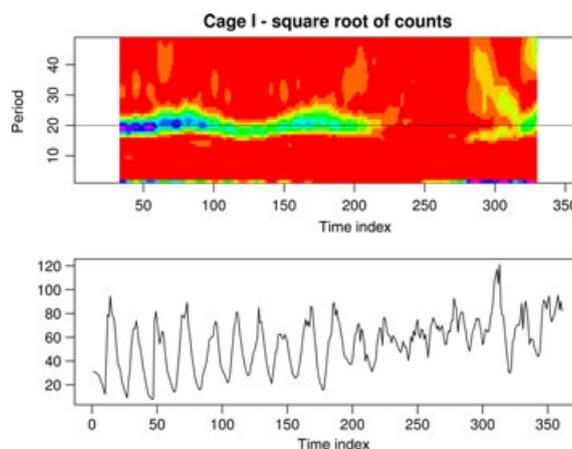


Figure 1. The bottom graph provides the square roots of the bidaily numbers of adults in Cage I. The top graph is the spectrogram of those data, with the y-axis period. The horizontal line is at period 20

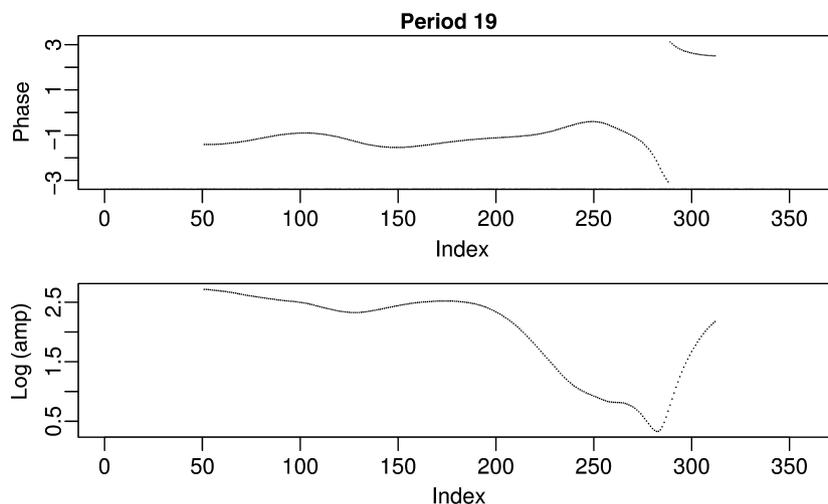


Figure 2. The results of complex demodulating the counts for cage I at period 19 (38 days)

2.2. Dynamic spectrum/spectrogram

The sound spectrograph is a wave analyser, which produces a permanent visual record showing the distribution of energy in both frequency and time (Koenig *et al.* 1946). A bank of digital bandpass filters may be used to break a time series down into frequency components and a spectrogram obtained by the plotting running mean squares in a contour or image plot. Narrow band components appear as ridges. Pure frequency components appear as horizontal straight lines as do changes in frequency. One can look for harmonics and subharmonics of a given frequency and changes in these. In the case of the data of this article, and in particular given the stimulations that Nicholson employed, it appears more useful to plot the periodogram statistic vs. period rather than frequency. This may be viewed as an estimate of an evolutionary spectrum (Priestley, 1961).

The periodogram may be computed via complex demodulating at a sequence of frequencies or periods as follows.

Given the segment, $Y_u, u = 1, \dots, U$, of the time-series data, $\{X_t, t = 1, \dots, T\}$, one computes the periodogram.

$$\left| \sum_u Y_u \exp \left\{ \frac{-i2\pi u}{p} \right\} \right|^2 \quad p = 1, \dots, P.$$

One then slides this computation along $\{X_t\}$. The results may be displayed in contour or image form. There are examples in the Figures 4 and 5.

2.3. Exploratory data analysis

Exploratory data analysis (EDA) as a collection of techniques is one of John Tukey's creations (see Tukey, 1977). Quoting him '... three of the main strategies of data analysis are: 1. graphical presentation. 2. provision of flexibility in viewpoint and in facilities, 3. intensive search for parsimony and simplicity ...' There is an 'emphasis on the discovery of the unexpected'. Spectrogram analysis and complex demodulation have each lead to unexpected discoveries.

Exploratory data analyses of the data from three of Nicholson's experiments are presented. The series studied are those of cages C, H and I whose plots appear in Figure 8 in Nicholson (1957).

3. EXPLORATORY DATA ANALYSIS OF NICHOLSON'S CAGES C, H AND I

3.1. Constant food input case, cage I

There have been many analyses of the population size data of cage I. See Figure 1 for a plot of the square root, M_t , of the adult counts, N_t . A complication is that change may be taking place and in many of the analyses that have appeared have employed only the first 200 or so data points only. A goal of the work here is to study the whole data record highlighting oscillations and changes.

Cage I was a control experiment. The culture was supplied with a constant supply of food, at the level of .4 mg/day. Also the larvae were provided with ample food to survive on their own and to not be competing for food with the adults. For the record, the stages of blowfly development are egg (12–24 hours), larva (5–10 days), pupa (6–8 days), and with this experiment there was a major oscillatory period of 45 days; see Oster (1981). With other conditions it may vary.

To begin the data analyses, a choice was made to work with M_t the square root of the population count at time index t , N_t , and to work with period p , rather than frequency. Here, t indexes every other day, which is how the data were collected. The square root is

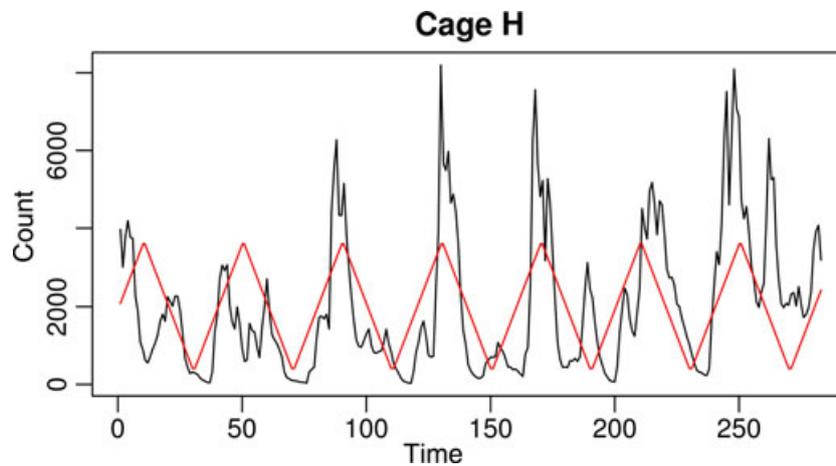


Figure 3. The square roots of the cage H data are plotted, as is a representation of the saw tooth manner in which the food was delivered to the cage

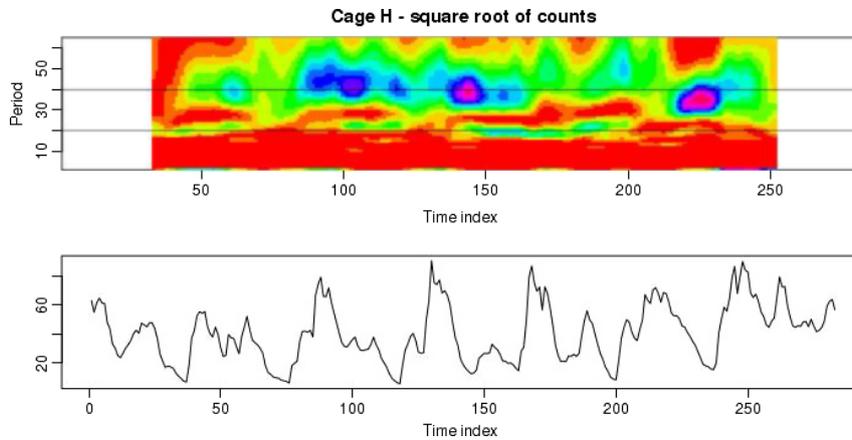


Figure 4. The data are from a study of the effect of adding food in a stylized manner with a period of 40 time steps (80 minutes). Horizontal lines are drawn at levels of 40 and 20 for reference.

taken to symmetrize the distribution of the counts and to moderate the influences of the extra-large values. Period is used because that is how Nicholson selected the food input forms for cages C and H.

The bottom trace in Figure 1 is the time series, M_t , of present interest. One sees regular oscillations deteriorating to irregular movement around time index $t = 200$.

The spectrogram is the top image. The time index t runs horizontally and the period, p , vertically.

The horizontal ridge, which has noticeable width, is centred about a period of about 20 time index steps. (Half of Oster's 45 days corresponds to 22.5 time index steps. Complex demodulation will provide more information about an appropriate value.) One sees the ridge decaying away at about time step 225. Then, it reappears around time step 275. There is also a decreasing chirp signal running down from time step 275 to 325. A horizontal line at level 20 has been added as a reference.

In Figure 1, the time series has been aligned below the spectrogram allowing one to line up behaviours. The horizontal line in the image plot is at period 20. That the natural frequency value decays away after $t = 200$ is apparent in both plots. Also apparent is the unusual behaviour around time 300. That the series is trending upward after time 250 shows in the power to the right and bottom of the spectrogram.

Figure 2 provides the results of a complex demodulation analysis. Were a narrow band sine wave demodulated at the 'correct' frequency the phase plot should be horizontal. Some experimentation with different period values suggested $t = 19$, corresponding to 38 days. The phase plot does wander some. This behaviour is consistent with that evidenced in the spectrogram. The amplitude plot also follows the shape of the ridge in the spectrogram.

3.2. Fluctuating environmental factors

The above is the title of the seventh section, in Nicholson (1957). In that section, he describes an attempt to study in the laboratory the outside world's complications. He does this by manipulating the food supply.

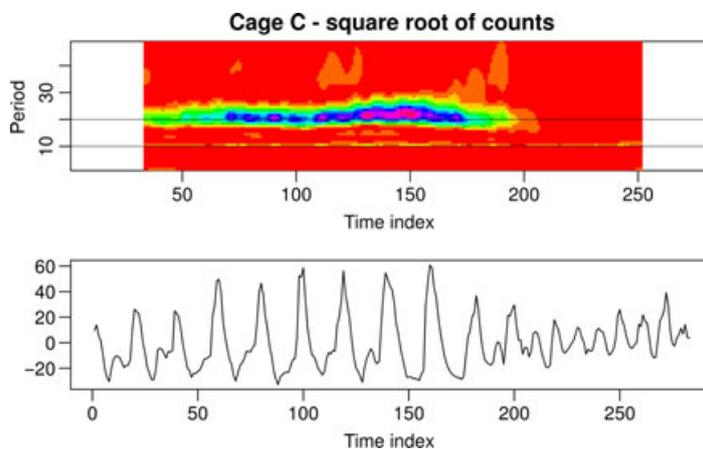


Figure 5. The spectrogram and square root plots of the cage C data. In this case, the food is applied with period 10. Horizontal lines have been added at levels 10 and 20

In cage I the food inserted, ground liver, was kept at a constant level. In cages C and H, to be studied next, food is provided at regular time intervals in a saw tooth fashion. One question is whether this input can be recognized in the C and H population series. In the case of cages C and H, the periods Nicholson chose were 10 and 40 respectively with the food level progressing between 0.05 and 0.50 and then 0.50 and 0.05 gm/day in regular fashion. To illustrate this fashion, Figure 3 shows the saw tooth form superposed on the graph of the square roots of the cage H counts. The amplitude of the saw tooth has been selected here to make things clearer. The crosscovariance function was employed to align the time stretches, the precise alignment being unclear in Figure 8 in Nicholson (1957).

Nicholson (1957) wrote the following about the data collected for cage H.

‘Near the beginning of this experiment two population peaks fitted within one period of food change; but the population changed progressively to a condition in which there was only one major population peak within this period of food change accompanied by one or more minor peaks. ... the period of intrinsic oscillation becomes completely dominated by the period of food change.’

One notices that the alignment does shift.

The spectrogram for the H data is provided in Figure 4. The bottom plot is the square root of the data series itself. The top is the spectrogram. Horizontal lines have been added at period 40 and at period 20. The first is the period with which the food was delivered. The latter appears close to the natural frequency, which Nicholson above calls the period of intrinsic oscillation.

There is some evidence for the presence of the natural period of oscillation near level 20. One can infer that the food level variability is having an impact from the ridge and peaks near level 40 in the spectrogram of Figure 4.

Nicholson (1957) remarks of the cage C data plot, ‘It will be noticed that the period of the population oscillation in C is slightly longer than the natural period in the control (I) and that the oscillations up to about the 500th day correspond regularly to alternate periods of food fluctuation. At about this time there is a sudden change, after which the period of population oscillations halved so that each population peak corresponds to each period of food change.’

It is worth remarking that a comparison of Figures 1 and 5 does provide evidence for Nicholson’s ‘slightly longer’ remark. (His 500th day corresponds to a longer data set. Here one might say $t = 200$.) He sees oscillations thereafter at the period halved. The spectrogram provides evidence for period 10 oscillations the whole time. This was a surprise.

3. SUMMARY AND CONCLUSIONS

Contributions of the work include the following:

- There are new data and new data analyses and some surprises, e.g. the lurking of period of 10 in Figure 5.
- The figures provide formal support for some of Nicholson’s remarks in Nicholson (1957).
- The approach separated out multiple frequency components that were decaying. Bifurcations, as occur for a variety of dynamical systems, were given a chance to appear, but did not.

The importance of the age structure to describing the behaviour of insect systems is often commented on. Age structure is made use of in Oster and Ikatchi (1978), Ipakatchi (1979), Brillinger *et al.* (1980) and Guttorp (1980).

Future work will address other data sets and dynamical systems aspects, but Oster (1981) warns of the futility that can arise in model fitting due to the sensitivity of some models to initial conditions.

P. A. P. Pat Moran (personal communication) warned of the large gap in drawing conclusions between the laboratory and the field results. He also remarked concerning the lab work that Nicholson was using the flies as a computer.

In summary, the methods of complex demodulation and spectrogram analysis have been highlighted and their power to decompose a non-stationary series into interpretable components shown.

Acknowledgements

This research was supported in part by the NSF Grant DMS-1007553. I thank John Guckenheimer, Peter Guttorp and George Oster for all they did to get me educated with this topic. I also thank the very helpful editor David Stoffer. Ryan Lovett helped substantially with the preparation of the images of the paper.

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