



Intrinsically generated coloured noise in laboratory insect populations

Octavio Miramontes¹ and Pejman Rohani²

¹*Departamento de Sistemas Complejos, Instituto de Física, Universidad Nacional Autónoma de México, México 01000, D.F. México (miro@servidor.unam.mx)*

²*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK (pej@zoo.cam.ac.uk)*

What are the mechanisms responsible for generating the erratic fluctuations observed in natural populations? This question has been at the centre of a long debate in contemporary ecology. The irregularities in the patterns of population abundance were initially mostly attributed to environmental factors. In the mid-1970s, however, it was proposed that these fluctuations may be generated intrinsically, by the underlying nonlinearities inherent in population processes. More recently, the focus of this argument has turned increasingly towards the statistical properties of population fluctuations, with many studies showing that ecological systems tend to be dominated by low-frequency or long-term dynamics, termed ‘red’ noise. Currently, the source of the ‘redness’ in ecological time-series is hotly debated, with the general consensus being that environmental variables are the major driving force. Here we show that three classic laboratory populations known to display irregular fluctuations also have reddened spectra. Furthermore, the dynamics of these populations show very well-defined generic scaling properties in the form of power laws. These results imply that long-term influences in ecological systems can be the product of intrinsic dynamics.

Keywords: coloured noise; laboratory populations; $1/f$ scaling; population dynamics; demographic stochasticity

1. INTRODUCTION

Laboratory insect populations have traditionally yielded valuable data for the study of fundamental aspects of ecological processes (e.g. Crombie 1945, 1946; Park 1948; Lloyd 1968). This is because in the laboratory, important environmental variables can be carefully controlled, thus minimizing the impact of external factors (‘noise’). Under such conditions, the dynamics observed in laboratory populations should, therefore, arise from intrinsic population processes under the specified conditions. There are many well-known instances of controlled laboratory populations that display irregular temporal fluctuations. Of special interest are cultured populations that have yielded relatively long data sets spanning many generations, because they allow a more precise analysis of their dynamics. Here, we examine two classic laboratory population experiments with time-series that are among the longest available in the literature.

2. THE LABORATORY POPULATIONS

The first time-series comes from the extensive study of the Australian sheep blowfly, *Lucilia cuprina*, by Nicholson in the mid-1950s. Nicholson carried out a series of laboratory experiments in which blowflies were maintained under precise conditions with a constant food supply (Nicholson 1957). The data set we examined contained 360 data points corresponding to measurements of population density taken every other day (Brillinger *et al.* 1980) (figure 1a). This relatively long data set has attracted much

theoretical interest, because it was historically considered as one of the very few recorded instances of possible chaotic dynamics in real populations (Hassell *et al.* 1976). The second and third examples correspond to the host–parasitoid system of the wasp parasitoid *Heterospilus prosopidis* (figure 1b) and its host, the bean weevil, *Callosobruchus chinensis* (figure 1c), cultured by Utida (1957). These data sets all contain the number of adults measured over 112 generations.

When analysing time-series data, ecologists are often limited by the fact that the available series are typically very short. This is an important drawback when the analysis involves nonlinear techniques for detecting complex dynamical behaviour such as measuring the rate of exponential divergence of trajectories or estimating the dimension of fractal sets; for high precision, these approaches typically require thousands of observations (Eckmann & Ruelle 1992). However, short time-series, containing hundreds of observations, are typically adequate for the identification of specific scaling behaviours that are characteristic of complex systems. During the last decade, it has been established firmly that a large number of natural systems containing several interacting individual components have statistically similar dynamical properties, independent of the particular details of the system. Examples include earthquakes (Bak & Tang 1989; Sornette 1992; Crisanti *et al.* 1992; Paczuski & Boettcher 1996), long-term climatic fluctuations (Grieger 1992), gaps in tropical forests (Solé & Manrubia, 1995), fossil records (Solé *et al.* 1996), bird extinction records (Keitt & Marquet 1996), and epidemic outbreaks

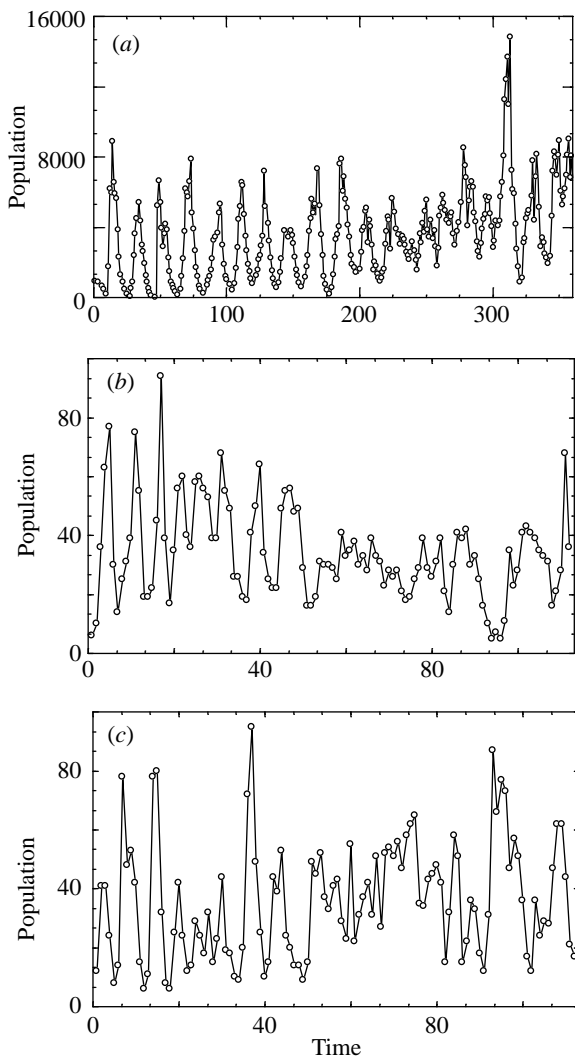


Figure 1. Three classic laboratory population time-series that show irregular temporal fluctuations: (a) the sheep blowfly, *Lucilia cuprina*, cultured by Nicholson; (b) the wasp parasitoid *Heterospilus prosopidis* (Hymenoptera Braconidae), and its host (c) the bean weevil, *Callosobruchus chinensis*, cultured by Utida.

(Rhodes & Anderson 1996, 1997; Rhodes *et al.* 1997) among others. One generic property that these systems share is the existence of power laws governing several of their observables, and in particular the distributions of spatiotemporal fluctuations (Bak *et al.* 1988). When the exponent of the spectrum power law is *ca.* -1.0 , it is said that the given temporal phenomenon scales as the inverse of the frequency (f) or as '1/ f noise'. This is a very particular form of scaling because it means that fluctuations occur in the same proportion at all scales, i.e. the process is self-similar. In the following sections, we use three distinct approaches to demonstrate that these laboratory populations are dominated by low frequencies. In fact, their dynamics are 1/ f , and a great deal of fine structure can be found in the data.

3. POWER LAWS AND SCALING BEHAVIOUR

All three laboratory populations studied here have power spectra, $P(f)$, that fit a power law distribution well, highly reminiscent of 1/ f noise. The power spectrum for *L. cuprina*

scales as $P(f) \propto f^{-\alpha}$ with an exponent $\alpha \simeq 1.30$ (figure 2a, top). The parasitoid power spectrum scales with an exponent $\alpha \simeq 1.01$ (figure 2b, top), while the bean weevil power spectrum scales with $\alpha \simeq 0.83$ (figure 2c, top).

Each of the three populations also has a distribution of population fluctuation lifetimes that scales as a power law (figure 2, middle). We express the scaling relationship as $D(L) \propto L^{-\tau}$, where $D(L)$ is the distribution of fluctuations in lifetimes, L is the lifetime and τ is the scaling exponent. Blowflies have an average value of $\tau \simeq 1.07$ (figure 2a, middle) while the average values for the parasitoid (figure 2b, middle), and bean weevil (figure 2c, middle) are $\tau \simeq 0.95$ and $\tau \simeq 1.23$, respectively.

It is well known that the superposition of pulses of a given physical observable with a distribution of lifetimes $D(L) \propto L^{-\tau}$ leads to the power spectrum (Bak *et al.* 1988):

$$P(f) = \int \frac{LD(L)}{1 + (fL)^2} dL \simeq f^{-2+\tau} = f^{-\alpha}.$$

Thus, a 1/ f power spectrum is equivalent to a power law in the distribution of fluctuation lifetimes, and it is interesting to note that this relationship is remarkably well-satisfied by the numerical values we obtained for the scaling exponents α and τ in the three populations.

Moreover, the distribution of the absolute population changes in these populations also follows well-defined power laws. The absolute population change is defined as the magnitude of the difference between successive population numbers, summarizing all deaths and recruitments in the interval. When it follows a power law, it is expressed as $D(S) \propto S^{-\beta}$, where S is the size of absolute population change and $D(S)$ is the number of the absolute population changes of size S . Absolute population changes in Nicholson's blowflies are well-described by a power law with a scaling exponent $\beta \simeq 2.79$ (figure 2a, bottom). The scaling exponent for Utida's bean weevil and parasitoid populations are $\beta \simeq 1.75$ (figure 2b, bottom) and $\beta \simeq 1.70$ (figure 2c, bottom), respectively.

Some care must be taken when analysing Nicholson's data since it has been suggested that, during this experiment, an evolutionary change in the demographic parameters may have occurred (Stokes *et al.* 1988); the first half of the data shows a different dynamical behaviour compared with the second half. In the early part of the experiment, the population dynamics is characterized by large-amplitude fluctuations of a markedly cyclical nature. In the second half, the amplitude of the fluctuations becomes reduced, perhaps reflecting lower reproductive rates and greater tolerance to overcrowding (Stokes *et al.* 1988). In order to investigate whether this change in the dynamical behaviour of the population may give a wrong picture of the general scaling properties of the entire population, we carried out a separate examination of the two halves of the series.

Both the first and second parts of the series have power spectra that clearly scale as 1/ f (figure 2d,e, top). The estimated exponents are $\alpha = 1.19$ and $\alpha = 1.34$ for the first and second halves, respectively. Regarding the fluctuation lifetimes, the picture is slightly different (figure 2d,e, middle). As expected, the first part of the data does not exhibit a power law distribution in the fluctuation lifetimes (due to the regularity of the fluctuations), while the second clearly scales,

with an exponent of 0.87. Finally, both halves have absolute population changes that scale as power laws, with exponents 2.29 and 2.47 for the first and second parts, respectively (figure 2*d,e*, bottom). Therefore, the proposed evolutionary changes to demographic parameters appear to have little qualitative effect on the observed scaling behaviour.

4. THE IFS TEST

The self-similar nature of the population fluctuations can be highlighted further using an iterated function system (IFS) clumpiness test (Jeffrey 1992; Peak & Frame 1994; Spratt & Rowlands 1995; Mata-Toledo & Willis 1997). This technique is a novel way to visualize the fine structure of time-series; it can reveal correlations in the data, thus helping to characterize their 'colour'. Consider figure 3. In the top row, the plots correspond to white noise (figure 3*a*, top), $1/f$ noise (figure 3*b*, top) and Brownian ($1/f^2$) noise (figure 3*c*, top). White noise ($\alpha \simeq 0.0$) is a space-filling uncorrelated process that uniformly fills its space of representation. At the other extreme, Brownian noise ($\alpha \simeq 2.0$) tends to accumulate closely over the diagonals and some of the sides of the square, leaving most of the representation space empty. $1/f$ noise ($\alpha \simeq 1.0$) has the peculiarity of producing self-similar repeating triangular structures of different sizes and a tendency to accumulate, albeit in a somewhat dispersed way, near the diagonals. The middle row of figure 3 shows the IFS test for the Nicholson data. The complete series (figure 3*a*, middle) shows a $1/f$ -like pattern where some self-similar triangular structures are quite noticeable. The first (figure 3*b*, middle) and second halves (figure 3*c*, middle) of the data also clearly show $1/f$ scaling behaviour, despite their apparently different temporal nature, and despite the possible evolutionary change of demographic parameters. In fact, it is obvious that both halves belong to the same dynamical process. Finally, the wasp (figure 3*a*, bottom) and bean weevil (figure 3*b*, bottom) systems are depicted in the bottom row. Here, despite a faint tendency to accumulate near the diagonals, the nature of the fluctuations is inconclusive: this is likely to be due to the length of the time-series.

5. THE HURST EXPONENT

The calculation of the Hurst exponent provides yet another approach that can be used to characterize the colour of noise and measure the predictability of population time-series. It is given by the so-called Hurst law (Mandelbrot 1983; Feder 1988; Peitgen *et al.* 1993):

$$R/S = (p/2)^H.$$

The calculation of the parameters of this relationship (known as rescaled range analysis) is as follows. Consider a time-series containing n points. This series can be subdivided into n/p segments, each of length p ($10 \leq p < n/2$ for convenience). For each segment, the maximum range (R) and the standard deviation (S) are calculated, and then the term R/S is averaged for all segments. The fraction R/S is related to the Hurst exponent (H) by the above formula. Usually, the Hurst exponent is calculated by estimating the value of R/S for all possible values of p , the

pairs obtained are log-transformed and a linear regression is performed on them. The slope of the regression line is the Hurst exponent.

Hurst exponents fall in the range 0–1 and have intuitive interpretations. A value $0.5 < H \leq 1$ indicates what is commonly termed 'statistically persistent behaviour'; that is, whatever the past trend in the series, it is likely to continue in the future, implying a strong degree of predictability. The most extreme case is $H = 1$ which represents a straight line with a non-zero slope. Here there are no changes along the line when passing from the past to the future; there is absolute predictability in the process. A value $0 \leq H < 0.5$ represents 'anti-persistent behaviour': it is expected that whatever the current direction of change, it is unlikely to continue in the future and so predictability decreases. In the limit of $H = 0$, successive changes in the time-series are totally uncorrelated and prediction is not possible. In summary, white noise is characterized by $H = 0$, a value of $H = 0.5$ indicates Brownian motion, and $1/f$ noise is located in the range $0 < H < 0.5$.

The Hurst exponents calculated for Nicholson and Utida's laboratory populations all lie in the range $0 \leq H < 0.5$. For Nicholson's blowflies, $H \simeq 0.22$ (the first and second halves of the data showed $H \simeq 0.46$ and $H \simeq 0.37$, respectively). The bean weevil had $H \simeq 0.15$, while its parasitoid had $H \simeq 0.14$. These values lie well within the range expected for a $1/f$ process. The estimates of H obtained for Utida's populations are, however, quite low. Could these time-series be governed by a white noise process? To address this question, we used a property of the so-called fractional Brownian motion, generated after performing integration (successive addition) on the time-series generated by uncorrelated Gaussian processes. The integration of a Gaussian uncorrelated signal (with $H \simeq 0$) produces a random fractal with $H = 0.5$ (Spratt & Rowlands 1995). We have integrated Utida's data and have found that the Hurst exponents of the two integrated signals are $H \simeq 1$, leading us to conclude that Utida's time-series are extremely unlikely to be Gaussian uncorrelated processes.

There is an important relationship between the value of the Hurst exponent of a time-series and its fractal dimension, D (Feder 1988; Peitgen *et al.* 1993): $D = 2 - H$. A straight line with $H = 1$ has a fractal dimension equal to 1. White noise with $H = 0$ has a fractal dimension of 2, as expected for a process that is space filling. On the other hand, all the Hurst exponents found for the populations above signal that their fractal dimensions are non-integers, as is expected for a dynamical behaviour that has properties of self-similarity.

6. DISCUSSION

The foregoing results provide strong evidence that populations free from the influences of environmental forcing can produce fluctuations characterized by well-defined scaling laws. These findings relate to a recent debate regarding the importance of the dominance of high and low frequencies in the power spectra of ecological time-series (Steele 1985; Pimm & Redfearn 1988; Halley 1996; Caswell & Cohen 1995; Cohen 1995; Sugihara 1995, 1996; White *et al.* 1996*a,b*; Kaitala & Ranta 1996; Ripa & Lundberg 1996; Sumi *et al.* 1997;

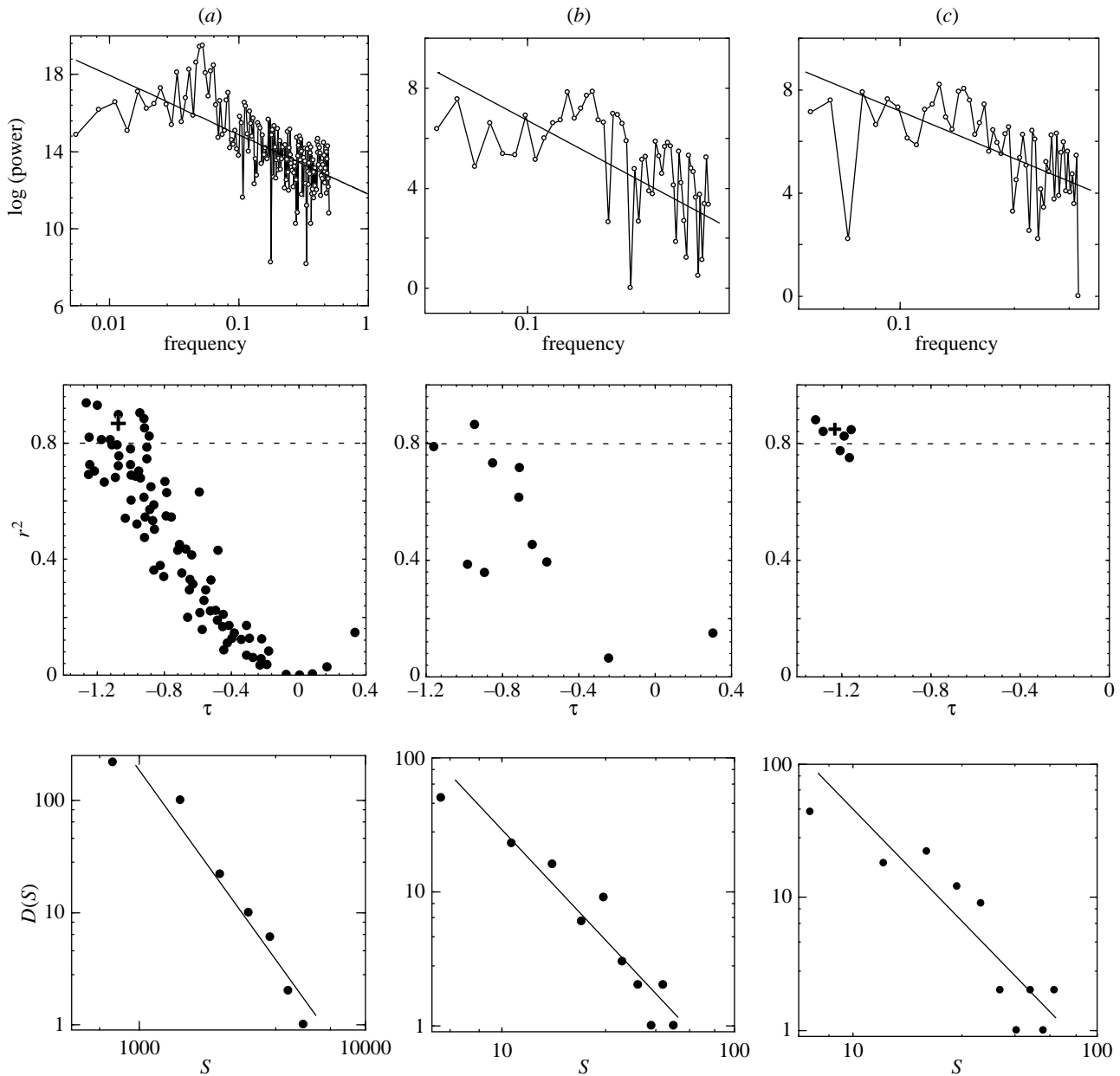


Figure 2. Scaling relationships for the data presented in figure 1 were calculated as follows. Power spectra are estimated with a discrete Fourier transform (the data are previously detrended and the mean subtracted), then a linear fitting is applied on the log-log-transformed spectra. The slope of the linear fitting is the value of the exponent, α . The distribution of fluctuation lifetimes was estimated in the following way: lifetimes are, in short, the width of the population fluctuations at a given baseline. Due to the finite nature of the data sets $\{X_1, \dots, X_n\}$, not any arbitrary baseline would easily reveal the power law nature of the lifetimes distribution. To overcome this, we used several baselines, subdividing regularly the interval $[X_{\min}, X_{\max}]$ in a number totalling, at least, twice the number of data points in the time-series. Each baseline gives a distribution that is used to build a histogram of ten frequency classes that, in turn, is log-log-transformed and linearly fitted. In this case, we apply the constraint that only those baselines giving at least six non-zero frequency classes would be considered, in order to increase the significance of the method. The resulting set of slopes (the τ exponent) and the regression of the fit (r^2) are shown, but only those fittings having an $r^2 \geq 0.80$ (above the dotted line) are considered for the estimation of an average scaling exponent and its regression (the average values are represented by the cross). In the case of the blowflies (a, middle), the mean exponent and regression were found to be ≈ 1.07 ($r^2 = 0.87$, $n = 13$), for the parasitoid (b, middle) the value was ≈ 0.95 ($r^2 = 0.864$, $n = 1$), and for the bean weevil (c, middle) the value was ≈ 1.23 ($r^2 = 0.85$, $n = 4$). Despite the relatively short nature of the data sets, there is a clearly identifiable trend in the graphs that relate the exponent τ with the regression of the fitting in a non-arbitrary manner. The trend is evident in the blowflies and wasps, but is less obvious in the bean weevils. The distribution of the absolute population changes are calculated as follows: the data set $\{X_1, \dots, X_n\}$ is transformed into the data set $\{Y_1, \dots, Y_{n-1}\}$ where $Y_i = \|X_i - X_{i+1}\|$. A histogram of ten frequency classes is constructed in the interval $[Y_{\min}, Y_{\max}]$. The frequency value, together with the left value of each frequency class, are log-log-transformed and a linear fitting is applied. The value of the slope is the value of the β exponent that for the blowflies (a, bottom) was found to be ≈ 2.79 ($r^2 = 0.95$), for the parasitoid (b, bottom) ≈ 1.75 ($r^2 = 0.91$), and for the weevil (c, bottom) ≈ 1.70 ($r^2 = 0.82$). Departure from the fitted line at large values of S is due to the discrete nature of the time-series. The blowflies data can be separated into two halves in order to find out whether these are $1/f$ processes themselves. The first half (d) is analysed and we estimated the following values: $\alpha \approx 1.19$ and $\beta \approx 2.29$ ($r^2 = 0.94$). For the second half (e), the values found are $\alpha \approx 1.34$, $\beta \approx 2.4$ ($r^2 = 0.93$) and $\tau \approx 0.87$ ($r^2 = 0.8$, $n = 1$).

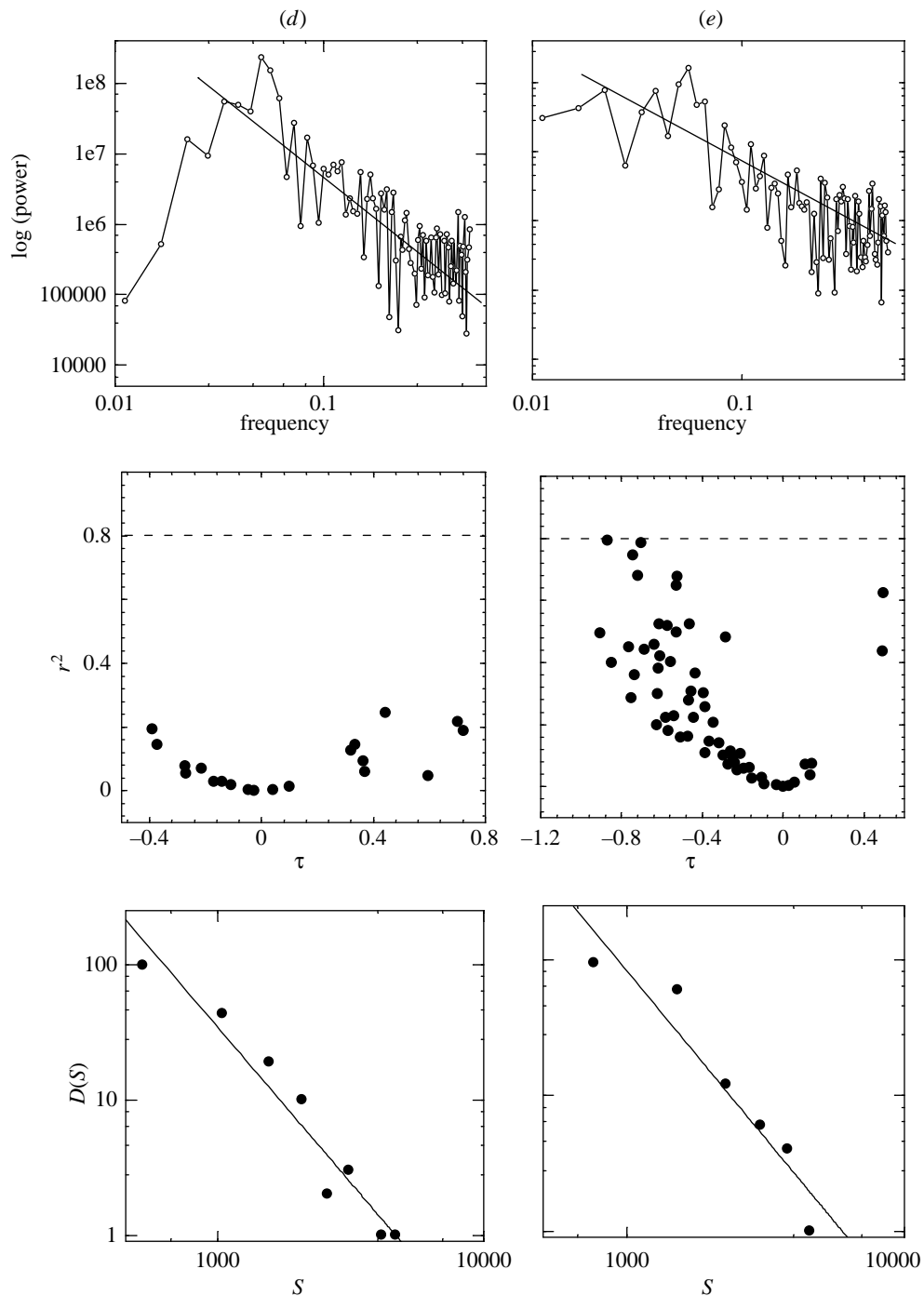


Figure 2. (d) and (e).

Petchey *et al.* 1997). Clearly, our results support the generally accepted fact that many natural population fluctuations show ‘reddened’ spectra, with low frequencies dominant. Traditionally, the dominance of low frequencies in ecological systems has been attributed to external environmental forcing (Steele 1985; Pimm & Redfern 1988; Halley 1996; Sugihara 1996). In contrast, however, we have shown that red noise may arise in laboratory systems, generated by internal population processes in the absence of environmental noise.

What intrinsic ecological mechanisms could be generating these patterns? It has been shown that simple single-species models exhibiting chaos as a result of strong density dependence may give rise to red noise (Blarer &

Doebeli 1996; White *et al.* 1996*b*). Whether the demographic parameters required for this are sufficiently realistic as to be expected in nature is a moot point. We propose what we believe to be a more generic mechanism. We suggest that these dynamics may simply arise naturally from the interaction between (demographic) stochasticity and density dependence. Consider a very simple, though ecologically defensible, model of a population with non-overlapping generations, where population size is integer-valued and birth and death events are stochastic processes (with a Poisson distribution) such that

$$\mathcal{N}_s(t) = \text{Poisson}[\mathcal{N}(t)e^{-\lambda\mathcal{N}(t)/K}] \quad (1)$$

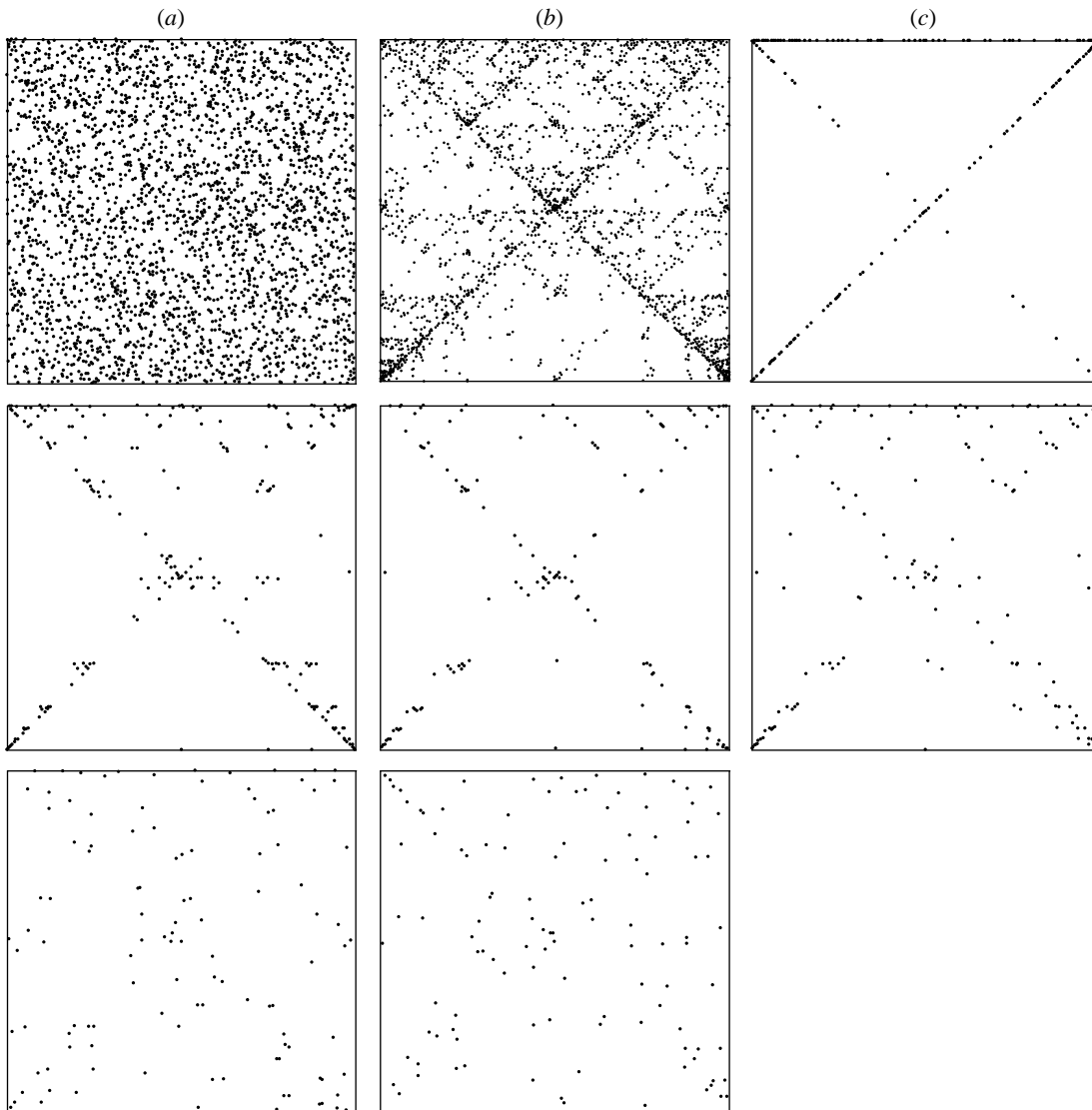


Figure 3. An IFS clumpiness test is applied to the population series. This technique is used to create a pattern that helps to visually characterize the colour of the noise since it produces clumped patterns for coloured noise while producing homogeneously filled spaces when the data are uncorrelated. The technique works in the following way. The data set is sorted from the minimum to the maximum value and then subdivided into four segments such that each segment contains the same number of points (notice that the segments could be of different lengths). The original unsorted data set is then normalized and coarse-grained into four values, say 1,2,3 and 4, representing the quartile to where the data belong. The representation space is a square where the four corners are labelled 1,3,2,4 in a clockwise direction (starting in the lower left corner). Each value of the coarse-grained series is associated with the corner having the same number. A point is plotted half the way between the center of the square and the first point of the series. A second point is plotted half way between the first plotted point and the second point in the series, and so on. We applied this test to artificially generated data using the following iterative map $\gamma_{t+1} = \eta\gamma_t + (1 - \eta)\epsilon_t$, where γ_{t+1} and γ_t represent successive elements in the time-series, η denotes the strength (and the sign) of the correlation between successive terms, and ϵ_t is a normally distributed random variable with zero mean and unit variance. By manipulating η , it is possible to generate noise with different colours (η is negative, zero or positive for blue, white or red noise, respectively). The results of the IFS test on these data are depicted for white noise ($\eta = 0.01$) (a, top), $1/f$ noise ($\eta = 0.69$) (b, top) and Brownian noise ($\eta = 0.99$) (c, top) series containing 3×10^3 points each.

$$\mathcal{N}(t+1) = \text{Poisson}[\mathcal{N}_s(t)e^{\lambda}]. \quad (2)$$

Here, $\mathcal{N}_s(t)$ denotes the number of individuals in generation t that survived to reproduce, $\text{Poisson}[\]$ represents a random number generated from a Poisson distribution with the mean given in square brackets, λ represents the intrinsic rate of growth, and K is the environmental carrying capacity. Given a small rate of increase (figure 4a), the dynamics of this system exhibit a $1/f$ scaling in the power spectrum (figure 4b), and power laws in the

fluctuation lifetimes (figure 4c) and in the absolute population changes (figure 4c). The IFS test is highly reminiscent of $1/f$ noise (figure 4d) and the Hurst exponent was found to be $H \simeq 0.29$ that is typical of $1/f$ dynamics. In this instance, therefore, the simple interplay between weak levels of density-dependent population self-regulation and demographic stochasticity can very easily generate similar dynamics to those observed in these laboratory populations. While it is encouraging that such a simple ecological model can generate a reddened

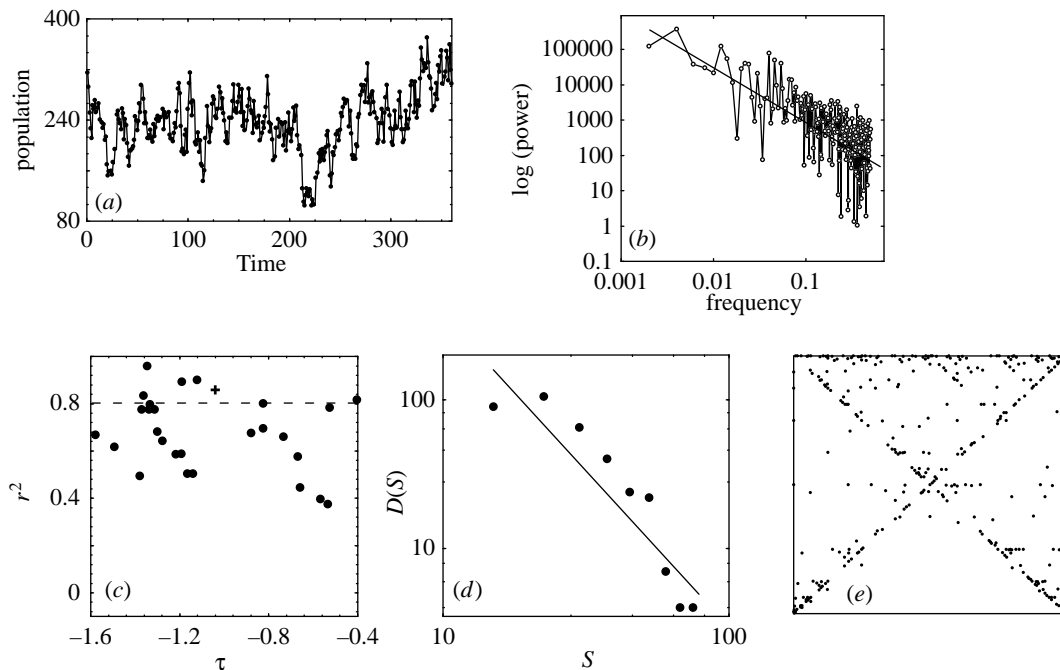


Figure 4. The dynamics of the stochastic one-dimensional map given by equations (2) and (3) for $\lambda = 0.1$ and $K = 250$. We have (a) the time-series, (b) the power spectrum with $\alpha = 1.362$, (c) the distribution of fluctuation lifetimes ($\tau = 1.04$, $r^2 = 0.86$, $n = 6$), (d) the distribution of the absolute population changes ($\beta = 1.61$, $r^2 = 0.8$) and (e) the results of the IFS test. The dynamics are very much consistent both with that of the laboratory populations and with artificially generated $1/f$ noise.

spectrum, it may not represent the precise mechanisms at work in Nicholson and Utida's populations. The system defined by equations (2) and (3) is meant to demonstrate that producing self-similar ecological dynamics does not necessarily rely on highly complex or unrealistic processes.

The ubiquity of $1/f$ dynamics is one of the major puzzles in contemporary physical science. It is well known that many diverse phenomena generate $1/f$ noise in their observables (e.g. Dutta & Horn 1981; Handel & Chung 1993; Hooge 1994; Milotti 1995), and many theories have been advanced to attempt an identification of the underlying processes responsible. These include 'self-organized criticality' (Bak *et al.* 1988), 'extremal dynamics' (Miller *et al.* 1993) and 'extremized physical information' (Frieden & Hughes 1994), among others. Currently, none of these theories is generally accepted as the ultimate explanation for power law scaling. Perhaps it is unlikely that such a universal explanation exists. We will not make any attempt to force any general conclusions regarding the examined population fluctuations as evidence to support any of the above proposed explanations. The most important conclusions to emerge from our analyses are that populations which are protected from external forcing (i) may generate a red-shifted spectrum, and (ii) can exhibit fluctuations with a great deal of intricate structure. We have also proposed a simple ecological mechanism which can realistically generate similar dynamics. These findings suggest that there is perhaps more scope for 'intrinsic' explanations for the observation of reddened spectra in natural populations.

We are grateful to P. Miramontes, R. V. Solé, C. Sprott and T. Kawai for stimulating discussion. It is a pleasure to thank

Bryan Grenfell, David Earn, Matt Keeling and two anonymous reviewers for their perceptive comments on this paper. O.M. was partly supported by a DGAPA-UNAM fellowship (IN 108496) and a CONACYT grant (3280P-E9607). P.R. was supported by a NERC postdoctoral research fellowship.

REFERENCES

- Bak, P. & Tang, C. 1989 Earthquakes as a self-organized critical phenomenon. *J. Geophys. Res.—Sol. Earth Planet.* **94**, 15 635–15 637.
- Bak, P., Tang, C. & Wiesenfeld, K. 1988 Self-organized criticality. *Phys. Rev. A* **38**, 364–374.
- Blarer, A. & Doebeli, M. 1996 In the red zone. *Nature*, **380**, 589–590.
- Brillinger, D. R., Guckenheimer, J., Guttorp, P. & Oster, G. F. 1980 Empirical modelling of population time series data: the case of age and density dependent vital rates. *Lect. Math. Life Sci.* **13**, 65–90.
- Caswell, H. & Cohen, J. E. 1995 Red, white and blue: environmental variance spectra and coexistence in metapopulations. *J. Theor. Biol.* **176**, 301–316.
- Cohen J. E. 1995 Unexpected dominance of high frequencies in chaotic nonlinear population models. *Nature* **378**, 610–612.
- Crisanti, A., Jensen, M. H., Vulpiani A. & Paladin, G. 1992 Strongly intermittent chaos and scaling in an earthquake model. *Phys. Rev. A* **46**, R7363–R736.
- Crombie, A. C. 1945 On competition between different species of graminivorous insects. *Proc. R. Soc. Lond.* **B132**, 362–395.
- Crombie, A. C. 1946 Further experiments on insect competition. *Proc. R. Soc. Lond.* **B133**, 76–109.
- Dutta, P. & Horn, P. M. 1981 Low-frequency fluctuations in solids: $1/f$ noise. *Rev. Modern Phys.* **53**, 497–516.
- Eckmann, J. P. & Ruelle, D. 1992 Fundamental limitations for estimating dimensions and lyapunov exponents in dynamical systems. *Physica D* **56**, 185–187.
- Feder, J. 1988 *Fractals*. Plenum Press.

- Frieden, B. R. & Hughes, R. J. 1994 Spectral $1/f$ noise derived from extremized physical information. *Phys. Rev. E* **49**, 2644–2649.
- Grieger, B. 1992 Quaternary climatic fluctuations as a consequence of self-organized criticality. *Physica A* **191**, 51–56.
- Halley, J. M. 1996 Ecology, evolution and $1/f$ noise. *Trends Ecol. Evol.* **11**, 33–37.
- Hassell, M. P., Lawton, J. H. & May, R. M. 1976 Patterns of dynamical behaviour in single-species populations. *J. Anim. Ecol.* **45**, 471–478.
- Handel, P. H. & Chung, A. L. (eds) 1993 *Noise in physical systems and $1/f$ fluctuations*. AIP Conference Proceedings 285, American Institute of Physics.
- Hooge, F. N. 1994 $1/f$ noise sources. *IEEE Trans. Elect. Dev.* **41**, 1926–1935.
- Jeffrey, H. J. 1992 Chaos game visualization of sequences. *Comput. Graphics* **16**, 25–33.
- Kaitala, V. & Ranta, E. 1996 Red/blue chaotic power spectra. *Nature* **381**, 198–199.
- Keitt, T. H. & Marquet P. A. 1996 The introduced Hawaiian avifauna reconsidered: evidence for self-organized criticality?. *J. Theor. Biol.* **182**, 161–167.
- Lloyd, M. 1968 Self regulation of adult numbers by cannibalism in two laboratory strains of flour beetles (*Tribolium castaneum*). *Ecology* **49**, 245–259.
- Mata-Toledo, R. A. & Willis, M. A. 1997 Visualization of random sequences using the Chaos Game algorithm. *J. Systems Software* **39**, 3.
- Mandelbrot, B. 1983 *The fractal geometry of nature*. W. H. Freeman and Co.
- Milotti, E. 1995 Linear processes that produce $1/f$ or flicker noise. *Phys. Rev. E* **51**, 3087–3103.
- Miller, S. L., Miller, W. M. & McWhorter, P. J. 1993 Extremal dynamics: a unifying physical explanation of fractals, $1/f$ noise and activated processes. *J. Appl. Phys.* **73**, 2617–2628.
- Nicholson, A. J. 1957 The self-adjustment of populations to change. *Cold Spring Harb. Symp. Quant. Biol.* **22**, 153–173.
- Paczuski, M. & Boettcher, S. 1996 Universality in sandpiles, interface depinning, and earthquake models. *Phys. Rev. Lett.* **77**, 111.
- Park, T. 1948 Experimental studies of interspecies competition. *Ecol. Monogr.* **18**, 265–308.
- Peak, D. & Frame, M. 1994 *Chaos under control*. W. H. Freeman & Co.
- Peitgen, H.-O., Jürgens, H. & Saupe, D. *Fractals for the classroom*. Springer.
- Petchey, O. L., Gonzalez, A. & Wilson, H. B. 1997 Effects on population persistence: the interaction between environmental noise colour, intraspecific and space. *Proc. R. Soc. Lond. B* **264**, 1841–1847.
- Pimm, S. L. & Redfearn, A. 1988 The variability of population densities. *Nature* **334**, 613–628.
- Ripa, J. & Lundberg, P. 1996 Noise colour and the risk of population extinctions. *Proc. R. Soc. Lond. B* **263**, 1751–1753.
- Rhodes, C. J. & Anderson, R. M. 1996 Power laws governing epidemics in isolated populations. *Nature* **381**, 600–602.
- Rhodes, C. J. & Anderson, R. M. 1997 Epidemic thresholds and vaccination in a lattice model of disease spread. *Theor. Popul. Biol.* **52**, 101.
- Rhodes, C. J., Jensen, H. J. & Anderson, R. M. 1997 On the statistical mechanics of simple epidemics. *Proc. R. Soc. Lond. B* **264**, 1639–1646.
- Schroeder, M. 1991 *Fractals, chaos, power laws*. W. H. Freeman & Co.
- Solé, R. V. & Manrubia, S. C. 1995 Are rain-forests self-organized in a critical state? *J. Theor. Biol.* **173**, 31–40.
- Solé, R. V., Bascompte, J. & Manrubia, S. C. 1996 Extinction: bad genes or weak chaos? *Proc. R. Soc. Lond. B* **263**, 161–168.
- Sornette, D. 1992 Self-organized criticality, earthquakes and plate-tectonics. *Phys. Rev. Lett.* **69**, 1287.
- Sprott, J. C. & Rowlands, G. 1995 *Chaos data analyzer*. Physics Academic Software (American Institute of Physics).
- Steele, J. H. 1985 A comparison of terrestrial and marine ecological systems. *Nature* **313**, 355–358.
- Stokes, T. K., Guernsey, W. S. C., Nisbet, R. M. & Blythe, S. P. 1988 Parameter evolution in a laboratory insect population. *Theor. Popul. Biol.* **34**, 248–265.
- Sugihara, G. 1995 From out of the blue. *Nature* **378**, 559.
- Sugihara, G. 1996 Red/blue chaotic power spectra. *Nature* **381**, 199.
- Sumi, A., Ohtomo, N., Tanaka, Y., Koyama, A. & Saito, K. 1997 Comprehensive spectral analysis of time series data of recurrent epidemics. *Jpn J. Appl. Phys.* **36**, 1303–1318.
- Utida, S. 1957 Cyclic fluctuations of population density intrinsic to the host–parasite system. *Ecology* **38**, 442–449.
- White, A., Bowers, R. G. & Begon, M. 1996a Red/blue chaotic power spectra. *Nature* **381**, 198.
- White, A., Begon, M. & Bowers, R. G. 1996b Explaining the colour of power spectra in chaotic ecological models. *Proc. R. Soc. Lond. B* **263**, 1731–1737.