

Population variability in space and time

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At the dawn of modern ecology, Charles S. Elton¹ was struck by the regularity by which some northern mammal populations fluctuate. The 'lemming cycle' soon became a favorite topic for population ecologists and Elton himself argued that the study of fluctuating (cyclic) populations should be the cornerstone of animal ecology. Since this time, population cycles have occupied a great deal of both theoretical and empirical ecology². Elton also noted that the regular fluctuations of Canada lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) were synchronized over large distances. Eventually, this led the Australian statistician Pat Moran³ to suggest that the synchronization of population fluctuations is possible if the local populations share the same density-dependent structure and the same environmental variability (Moran's theorem; Box 1). Hence, an interesting interplay should exist between population demography and random fluctuations in the environment, thus affecting vital rates of the population. There is now increasing empirical evidence, with a strong theoretical underpinning, of such an interplay⁴⁻⁹. Traditionally, theoretical population ecology has rested on deterministic models of populations and communities. However, in 1972, Robert May¹⁰ introduced ecologists to a modern account of stochastic processes. It was not until fast and inexpensive computers, allowing numerical simulations, were on everybody's desk that the interest for random processes took off. This development was fostered further by the growing interest in conservation biology (especially the extinction process) in the 1980s. Now, the time has come to review this development; recent overviews also show the interest to do so¹¹⁻¹⁴. In this paper, we briefly review how mathematical statistical tools have been used to elucidate how biological and stochastic environmental processes are intertwined.

Population regulation

At the core of understanding population variability lies the concept of population regulation. A commonly used definition¹⁵ is that a population is regulated if there is negative density-dependent feedback on population growth. At sufficiently high densities, per capita deaths exceed per capita births and the population declines; at lower densities the reverse is true. This might seem trivial because no

One of the most ubiquitous phenomena of all natural populations is their variability in numbers in space and time. However, there are notable differences among populations in the way the population size fluctuates. One of the major challenges in population and community ecology is to explain and understand this variety and to find possible underlying rules that might be modified from case-to-case. Population variability also has a spatial component because fluctuations are often synchronized over relatively large distances. Recently, this has led to growing interest in how 'internal' (density-dependent) processes interact with 'external' factors such as environmental variability.

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population grows without bounds. Nevertheless, this idea has been challenged mainly, but not exclusively, on empirical grounds¹⁶. The argument is that, although population growth cannot be boundless, factors other than density dependence come into play long before the regulatory process takes place. Such 'other factors' are usually random abiotic (e.g. weather) variations. Although this debate on population regulation might be outdated, it has highlighted the inevitable, but often forgotten, interplay between environmental stochasticity and endogenous density-dependent processes. Thus, the point of departure for understanding population variability is to acknowledge the mutual interaction of both factors.

Single-population dynamics

A simple and general way of representing the population renewal process, including internal feedback and external variability is:

$$N_t = f(N_{t-1}, \varepsilon_t)$$

Where N is the population density at time t , ε_t represents environmental stochasticity (a random deviate with zero mean), and f is a (usually nonlinear) function map-

ping the density and environmental stochasticity to a population size at time $t + 1$. The function f can be made a little more sophisticated and interesting by explicitly including density dependence and time lags greater than one. The usual approach of analysing such models in a general way is to study the linear approximation of the models (Box 2). Although most ecological processes are certainly strongly nonlinear, it is probable that the system spends most of its time near its steady state, where a linear approximation is usually sufficiently accurate¹⁷. In a discrete time model, such as Eqn 1, the parameters specifying function f can be adjusted so that all the main types of deterministic dynamics can be produced, ranging from asymptotically stable dynamics to cycles and chaos¹⁵. However, environmental stochasticity is never completely absent and it can cause several interesting problems. For example, it can mask deterministic dynamics completely, making it difficult to pick up the endogenous signal from a time series¹⁵, and it can also reinforce the underlying dynamics, making dampened oscillations persist as regular fluctuations (cycles)^{15,18-20}.

The environmental 'noise' itself might also have properties that affect the resulting dynamics. In recent years, temporally autocorrelated ('coloured') noise has received a lot of attention because it is believed to be a better description of the actual environmental variability^{21,22}. There is an intricate and important interplay between the properties of the environmental stochasticity and the resulting population time series²³. The population subjected to noise is a filter of the noise signal²⁴. For example, white environmental noise usually results in a red population time series²⁵ (the 'out signal'), but the details depend on which part of the community is affected most by the stochasticity, as well as the feedback (density-dependent) structure of the community in which the population is embedded²⁶⁻³⁰. The problem with the interaction between environmental variability and the density-dependent structure of the population is further illustrated when one attempts to reconstruct the basic population features from the time series. Roughgarden²⁴, and later Royama³¹, showed that a time series from a population with a lagged density-dependent structure (i.e. the density at time t is dependent on the density both at time $t - 1$ and $t - 2$) and subject to white noise, is statistically identical to a population without lagged density dependence and subject to an environment with lag structure. A recent debate^{32,33} has shown that this problem is still unsolved. Recently, Ranta *et al.*³⁴ also showed how this ambiguity is manifested in different stability regimes in simple single-species models.

The exact nature of the environmental noise can also be crucial for population persistence³⁵⁻³⁷. Halley³⁶ suggested that autocorrelated environmental noise should increase the extinction risk compared with the hitherto default white noise. Before the 'noise industry' took off with Halley's seminal review, Strelben³⁸ had already shown for a continuous time model that the extinction risk increases when the product of ' r ' (per capita rate of population growth) and the environmental 'correlation time' (a measure of autocorrelation) are close to unity. Ripa and Lundberg³⁷, and others subsequently³⁹⁻⁴¹, showed that the extinction risk is a subtle interplay between the nature of the noise, the density-dependent structure of the population and the spatial structure of the environment. The nature of the environmental variability might also have community effects. Caswell and Cohen⁴² showed that species coexistence in competitive communities is less likely in red environments (with spatial structure).

Spatial extension

Population fluctuations can occur at various spatial scales. The fluctuations in a given location also translate into landscape-, region- or even continent-wide patterns of dynamics^{3,43}. One of the most striking large-scale phenomena is that geographically separate populations tend to fluctuate hand-in-hand and that synchronous dynamics seem to weaken the further apart the populations are. The catalogue of synchronous population fluctuations is increasing, including not only birds, mammals and insects, but also plants, invertebrates, fish, protists and viruses^{2,7}. A related phenomenon is the recent observation of possible travelling waves across larger geographical regions^{11,44}. It was first discussed in relation to theoretical models of the spread of infectious diseases^{45,46}, and later to multispecies interactions in local populations coupled by migration⁴⁷. Travelling waves indicate temporal and spatial fluctuations of high and low population density regions in an apparently organized way. Population waves are generated as a consequence of common density-dependent processes being

Box 1. Moran's theorem

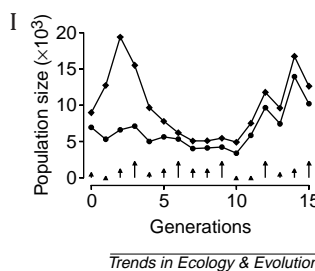
Consider two spatially separate populations, both governed by an identical renewal process. Let the two populations also share identical stochastic environments, such that they are perfectly temporally correlated with each other. We then have:

$$N_1(t + 1) = f[N_1(t)] + \varepsilon_1(t)$$

$$N_2(t + 1) = f[N_2(t)] + \varepsilon_2(t)$$

where N_i is the population size at location i , f is the linear renewal function mapping the population density from time t to $t + 1$, and ε_i is the environmental variability at the two locations. Moran's theorem³ states that if the two populations share the same f , then the correlation (ρ) between the two population sizes will be identical to the correlation between the environmental variabilities, $\rho(N_1, N_2) = \rho(\varepsilon_1, \varepsilon_2)$. Should the renewal function not be identical or nonlinear, Moran's theorem would only hold approximately^{3,4,10}. This more general association between the correlation among populations and the correlation among environmental variabilities is sometimes called the Moran effect^{5,9}.

George Leslie proposed a matrix-modelling approach to the Moran effect⁶³. He assumed two nonconnected populations (both with four age groups) living in limited environments, proximate enough to share the effect of some external



random and density-independent factors. Leslie⁶³ showed that iterating such a system of two independent populations [represented here (Fig. 1) as closed diamonds and closed circles, respectively] initially fluctuating out of phase will soon lead to synchronous dynamics as a result of external disturbances. The length of the arrows in Fig. 1 indicates the strength of the Moran effect. The data are taken from Refs 2,63.

locally in differing phases. This might be due to spatial linkage between the local units, biotic interactions, global and local noise affecting the subunits differently or a joint effect of all components. There is an important difference between true travelling waves and a single wave front crossing the landscape. A single wave front is often found in the initial spread of a disease or after exotics have been introduced to new areas, whereas true travelling waves are a long-term phenomenon⁴⁸⁻⁵⁰. Recently, much emphasis has been put on the problem of parsing out the relative

Box 2. Linearization

Generally, population dynamics is a nonlinear stochastic process. Nonlinearities tend to be complicated to deal with, both when we want to do analytic stochastic modelling and when analysing data. The way around the problem is to approximate the nonlinear model with a linear one, for which the mathematical and statistical theories are more developed and tractable. Let us assume that the population process is described as:

$$N_t = f(N_{t-1}, \varepsilon_t) \tag{1}$$

where N_t is population density at time t and ε_t is a series of random variables with identical distributions (mean and variance). Function f specifies how the population density one time step back, plus the stochastic environment ε_t , is mapped into the current time step. Let us assume that the (deterministic) stationary (equilibrium) value of the population is N^* and that ε has mean ε^* . The linear approximation of Eqn 1 close to N^* is then:

$$x_t = ax_{t-1} + b\phi_t \tag{2}$$

where $x_t = N_t - N^*$, $a = ff(N^*, \varepsilon^*)/fN$, $b = ff(N^*, \varepsilon^*)/f\varepsilon$, and $\phi_t = \varepsilon_t - \varepsilon^*$

Equation 2 is the Taylor expansion of Eqn 1 where second order terms and higher are omitted. The statistical properties of this equation are well known⁶⁴ and can now be used for model fitting or analytical investigations. The parameters a and b also have immediate biological interpretations; a is the slope of the recruitment function (f) at equilibrium (determining the deterministic dynamics of the population) and b is the sensitivity of the population to the environmental variability (ε).

Box 3. Spectral analysis

Spectral analysis of a time series is the decomposition of the series into its frequency components. The meaning of this can be understood by comparing a time series with visible light. White light is a mixture of all colours, each colour representing a particular wavelength. The inverse of the wavelength is frequency. Blue light has a relatively short wavelength – it is light of high frequency. A time series from natural populations is usually a mixture of many frequencies, but if it is dominated by long wavelengths (low frequency) it is said to be ‘red’ and if it is dominated by short wavelengths it is ‘blue’. If there is a strong cyclic component in the time series, a certain wavelength, corresponding to the cycle period, is dominating.

A discrete time series $x(t)$, $t = 0, 1, 2, \dots, L - 1$ (L is the length of the series) has the periodogram P_x , which serves as an estimate of the power spectrum of the underlying stochastic process:

$$P_x(f) = 1/L |X(f)|^2$$

where f is frequency, $X(f)$ is the discrete Fourier transform of the time series, and $|\dots|^2$ indicates the squared modulus of the transform. The periodogram, or power spectrum, indicates how much each frequency contributes to the variance of the time series. Note that a periodogram is calculated from a sample time series and a power spectrum is a statistical property of a stochastic process. The power spectrum describes the expected periodogram, but any single periodogram usually deviates substantially from the power spectrum, irrespective of the length of the time series. The noisiness of periodograms is the reason why they are often smoothed in some way to give a more realistic estimate of the underlying power spectrum. In the ecological literature, the terms power spectrum and periodogram are often mixed.

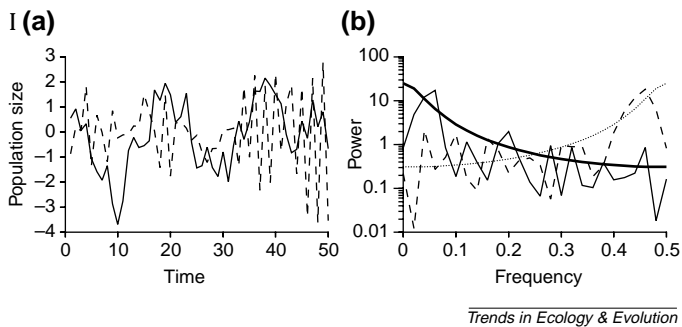


Fig. 1a shows two time series: one red, dominated by low frequencies and long wavelengths (unbroken line); and one blue, dominated by high frequency oscillations and short wavelengths (broken line). Fig. 1b shows the periodograms of the time series in Fig. 1a. The exact power spectra of the stochastic processes that were used to generate the time series are also indicated (thick unbroken line and dotted line).

importance of migration and the Moran effect (spatially autocorrelated noise; Box 1), for the production of synchronous population dynamics and travelling waves.

The dispersal of individuals among local populations (arbitrarily delimited and located) has two important and immediate consequences for both local and global dynamics. At the global scale, migration can enhance synchrony, and there is both theoretical and empirical support for this effect^{11,15,44,51–53}. One interesting example of this is the recent experimental finding by Holyoak and Lawler⁵⁴, when synchronous dynamics were generated by letting protists and bacteria disperse between connected jars. At the local scale, migration can be viewed as an additional disturbance event that might destabilize otherwise stable dynamics. Thus far, the direct effect of migration on local population fluctuations has mainly been of interest to theoreticians. Although most natural populations are linked by migration, there are certainly exceptions. Recently, it was shown that two isolated, but geographically adjacent, populations of Soay sheep (*Ovis aries*) were synchronized by the Moran effect (correlated environments) alone⁴. The interplay between migration and shared noisy environments is further illustrated by the common observation of

more or less clear synchrony versus distance patterns. As the distance between populations increases, the correlation of population densities decreases. This is readily explained by distance-dependent dispersal⁵¹ or spatially autocorrelated environmental variability^{6,15}. Although the theory of distance-dependent synchrony is well developed, the tests are far from trivial^{11,44}.

Measuring variability

Measuring population variability usually requires long-term estimates of population density or abundance. However, this is a rather trivial problem compared with the challenge of determining appropriate temporal and spatial scales. When it comes to population synchrony over larger geographical regions, an interesting invariant property seems to emerge. For example, the classic Canada lynx data set appears to retain basic properties regardless of how Canada is divided into different regions. Choosing the biologically arbitrary Canadian provinces and their equally arbitrary geometric midpoints generates the same synchrony versus distance pattern as more strictly developed simulation models⁵¹. Far from trivial is the choice of statistics beyond means and variances to describe observed population time series. For example, finding the periodic components of the time series by autocorrelation functions (ACF) and partial autocorrelation functions (PACF) is aggravated by the fact that the samples are not independent through time because of the time lags in the population we want to reveal. Analyses in the frequency domain [for example, by spectral analysis (Box 3)] might be less afflicted by that problem, but are problematic because of the rather qualitative interpretation of them. For example, the recently suggested ‘colour index’²⁸ is not a rigorous test of the autocorrelation structure of the time series³.

The whole problem of measuring population variability also inevitably relates to the somewhat philosophical question of what exactly is measured. The conventional attitude is that behind the noisy time series lies the ‘true’ biotic process of (density-dependent) births and deaths, and that this can be revealed once the noise has been peeled off. Generally, this is what time-series analysis is all about. The question is whether it is possible to simply disentangle the biotic signal from the noise. One could actually argue that the manifestation of the population through its time series is only possible because of the combined and inseparable birth, death and ‘disturbance’ processes. The only thing to parse out is then measurement (observation) error, because stochasticity is a built-in property of all biological systems. This view opens up new avenues for studying stochastic systems in ecology, and it highlights the fact that deterministic and stochastic modelling must merge even deeper when it comes to data analysis⁵⁵.

Model testing

Ecological theory provides us with a suite of possible explanations for population variability under various circumstances. The real challenge lies in the confrontation with data. Historically, two principal approaches emerge from the literature. The statistical analysis of population time series is one commonly used method. Standard linear time-series models [autoregressive (AR) models¹⁵] are commonly used to reveal population cycles and possible time lags owing to density-dependent regulation in the time series. Recently, various nonlinear models have also become more popular; for example, the response surface technique⁵⁶ used by Turchin^{57,58}. Recently, more sophisticated tools have been developed. The piecewise linear

models [SETAR (Refs 4,55,59,60)], similar to both linear and nonlinear standard methods, have been used to handle putative underlying nonlinearities in the biological process. However, the mechanistic modelling approach does not begin with a statistical description of data. Instead, theories of explicit population processes, such as per capita births and deaths, are used to generate the population dynamic phenomena (e.g. cycles) that we observe in nature. The parameters of the models are then estimated from (possibly independent) data and the resulting dynamics are compared with real time series. The recent review by Kendall *et al.*⁶¹ is an example of the synthesis of both approaches.

In both approaches discussed previously, there is an 'error' to be taken care of. The variance not explained by the models stems from measurement error, or environmental or demographic stochasticity not accounted for by the models. If environmental and demographic stochasticity become integral parts of the model itself, this problem can be partly reduced. But, there is a risk that this only gets us out of the frying pan and into the fire, because then we have to have reliable data on these processes and the mechanisms for how they interact with the biology of the organisms, which is far from trivial⁶².

To resolve such problems, which will necessarily be of fundamental importance in future work on population variability, we require a sophisticated combination of stochastic, statistical and mechanistic modelling approaches. This work has a long and successful history, and it will continue to be at the core of ecology.

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Behavioral endocrinology of mammalian fatherhood

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Upon first exposure to a newborn, male rats (*Rattus norvegicus*) attack and consume them. However, repeated exposure to young pups elicits parental behavior (e.g. licking, retrieval and a nursing posture over the pups) over a period of several days. During this transformation from killer to caregiver, hormones involved in maternal behavior do not change and endocrine manipulations, including castration, have little effect. Thus, initially, hormones did not appear to be involved in mammalian paternal behavior¹.

Instead, evidence supporting a role for hormones in both the onset and the maintenance of male parental behavior has come consistently, but slowly, from studies of naturally paternal species. Direct paternal care is rare in mammals but is found in some species; for example, callitrichid primates that bear twin offspring (*Callithrix* and *Saguinus* spp.), and rodents, including prairie voles (*Microtus ochrogaster*), California mice (*Peromyscus californicus*), Mongolian gerbils (*Meriones unguiculatus*) and Djungarian hamsters (*Phodopus campbelli*). In each case, both field and laboratory data support a reproductive payoff to the paternal male, in terms of increased female fertility

Mammalian fatherhood involves a muted version of the maternal experience. In spite of previous assumptions to the contrary, hormones influence mammalian paternal behavior. Naturally paternal males experience dynamic changes in the same hormones involved in maternal behavior and these hormones have access to the same brain pathways. Men becoming fathers for the first time are similar to their female partners too. These recent studies are still correlational, but promise to illuminate maternal behavior and to biologically validate the experiences of involved fathers.

and improved offspring survival and/or growth^{2,3}. Paternal behavior includes all aspects of maternal behavior except lactation (and at least one bat species is capable of lactation⁴) and can include midwifery during the birth⁵ (Fig. 1). It also appears to involve activating existing neural circuits leading to maternal behavior.

Sexual dimorphism?

Hormones, including estradiol, progesterone, testosterone, cortisol, prolactin, vasopressin and oxytocin, are involved in the onset and maintenance of mammalian maternal behavior (Table 1). Except for a small number of genes on the Y chromosome, male and female mammals have the same DNA. Sexual dimorphism in neuroendocrine and endocrine pathways is usually minimal⁶, except for neuroendocrine circuits leading to stereotypical sexual behavior.

Thus, rather than selecting for novel pathways to elicit paternal behavior, laws of parsimony suggest that natural selection should activate pre-existing maternal neural and endocrine circuits. Current hypotheses assume that this homology will extend to neuroendocrine circuits involved in paternal and maternal behavior^{6–8}.

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