

Skeletons, noise and population growth: the end of an old debate?

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Population dynamics models remain largely deterministic, although the presence of random fluctuations in nature is well recognized. This deterministic approach is based on the implicit assumption that systems can be separated into a deterministic part that captures the essential features of the system and a random part that can be neglected. But is it possible, in general, to understand population dynamics without the explicit consideration of random fluctuations? Here, we suggest perhaps not, and argue that the dynamics of many systems are a result of interactions between the deterministic nonlinear skeleton and noise.

Ever since the pioneering work of Lotka [1], Volterra [2] and Elton [3] during the 1920s, there has been a recurring debate about the relative importance of exogenous (environmental) variables versus endogenous (density-dependent) factors in determining observed fluctuations in population size. During the 1950s, the debate reached fever pitch with two main protagonists: Nicholson championed density-dependent (deterministic) processes [4] and Andrewartha and Birch defended the density-independent (stochastic) school. Following the publication of his 1957 paper, Nicholson is generally considered to have won the debate [4], and much work during the following decades concentrated on what is often referred to as the ‘dogma of density-dependent factors’. The discovery, by May [5], during the 1970s, that simple discrete-time models of density dependence could generate chaotic dynamics suggested that the observed erratic fluctuations in population size are generated by relatively simple deterministic rules; his findings further reinforced the view that we need not necessarily resort to stochastic factors to explain empirical patterns. Over the past decade or so, there has been a concentrated effort to evaluate critically model predictions against observed empirical patterns, which has led to researchers revisiting the deterministic–stochastic dichotomy and a realization that, in many instances, deterministic model frameworks should incorporate stochasticity [6,7].

The deterministic–stochastic debate can be distilled as follows: if our understanding of population dynamics is to be caricatured by a mathematical model, do we consider only

the intrinsic non-linear factors known to influence mortality and fecundity (e.g. density dependence) or should we also incorporate stochasticity (both demographic and environmental)? In recent years, it has become increasingly apparent that noise and non-linearity are both important and, more crucially, that they can interact to give rise to dynamics that would not have been predicted by rigidly deterministic models [6,8–12]. Here, we consider the treatment of stochastic processes (noise) in population dynamics models. We argue that, in many circumstances, stochasticity cannot be considered independently of the non-linear component of the model; hence, the choice of ‘deterministic skeleton’ and the treatment of noise can have a substantial impact on the interpretation of factors underlying the dynamics of populations. We briefly consider the types of stochastic model that have recently proven popular, before addressing issues concerning the construction of the deterministic skeleton and the treatment of noise.

Modelling approaches

Recent stochastic population models can be classified into two categories [13]: the first, known as inductive models, are concerned with fitting models to time-series data [14]. The second category, classified as deductive models, do not explicitly use the patterns in the time-series data to construct and parameterize a model, but instead use data on the mechanistic processes thought to have generated the observed time series [15]. These models are then used to simulate time series, which are then compared to empirical observation. Most recently published stochastic population models are inductive [11,16–18]. This raises the question of how complex should a model be?

How complex should a model be?

Both deductive and inductive models must strike the correct balance between biological realism (model complexity) and statistical rigour. Given that most ecological time series are comparatively short, models (especially inductive ones) are often simple because, in general, there should be many data points per parameter estimated [19]. This issue has recently been raised by Ginsberg and Jensen [20], who criticized many complex inductive models because they involved estimating more parameters than is justified given the quantity of data. Ginsberg and Jensen argue for parsimony by suggesting that all population cycles can be explained with one three-parameter

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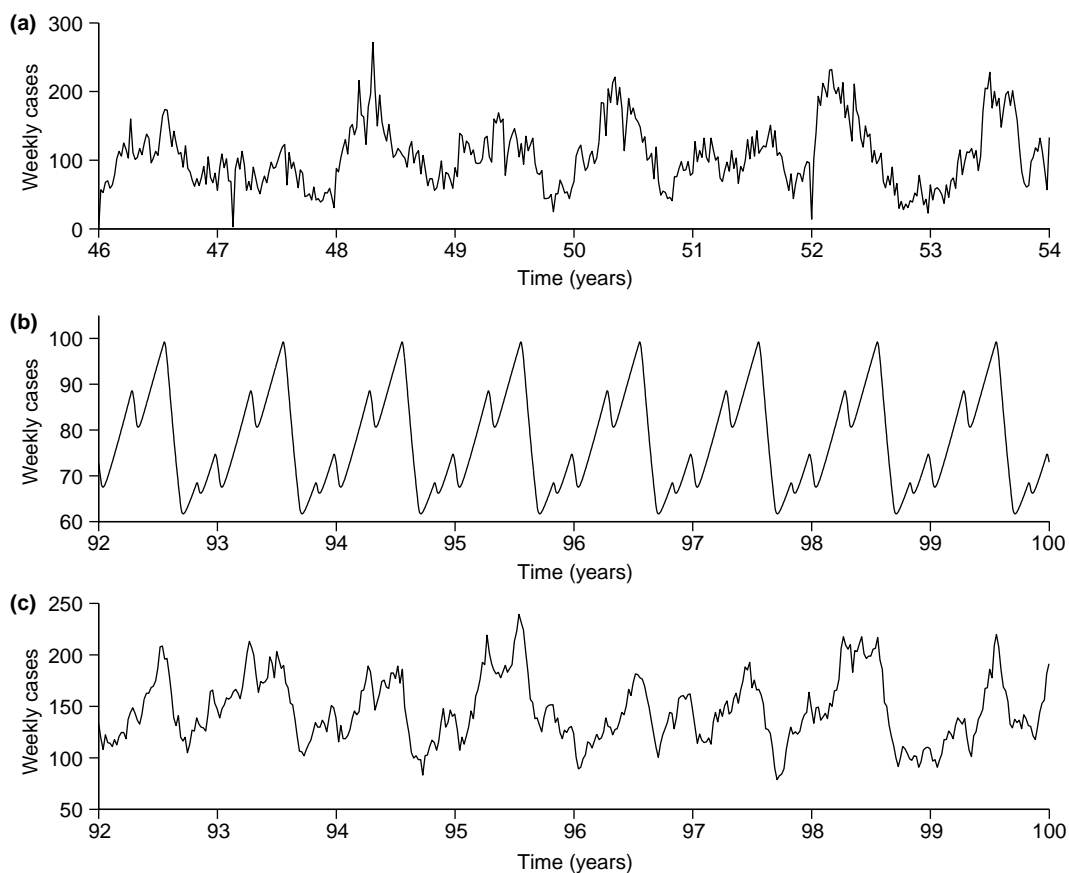
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Box 1. Model complexity and the dynamics of childhood diseases

Rohani and colleagues have explored the epidemics of measles and whooping cough in England and Wales [39]. They have demonstrated that for both diseases the simple Susceptible–Exposed–Infected–Recovered (SEIR) demographic models with seasonal forcing (to mimic the aggregation of children in schools) represent a biologically appropriate ‘deterministic skeleton’. For measles, this fully deterministic model provided a good framework for explaining the observed dynamical transitions resulting from either systematic trends in the population birth rate or mass-vaccination [36]. By contrast, the same deterministic framework is spectacularly unsuccessful at capturing, however qualitatively, whooping cough epidemics (Figure 1). The

reason appears to be the fragility of the deterministic whooping cough skeleton; it is surprisingly prone to the effects of stochasticity and the overall dynamics might be explained as being the result of an interaction between stochasticity and unstable periodic orbits [40].

As well as providing an example of issues concerning model complexity, this case study also highlights the importance of studying comparative population dynamics because measles has been extensively studied as a ‘prototypical’ childhood infection. The lessons learnt from understanding its epidemics are not, it would seem, universally applicable. There is no reason to suppose that the absence of generality from this comparison is limited to childhood diseases.



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Figure 1. Noise and non-linearity in epidemics. (a) Weekly whooping cough cases in Birmingham; (b) predictions from a deterministic so-called SEIR skeleton; (c) addition of stochasticity into the model. The stochastic model captures the observed dynamics substantially better than the deterministic version [40].

model. At one level (the observation that cycles occur because of a largely deterministic build-up of individuals that are susceptible to disease, starvation, predation or resource competition) they are correct, but understanding which limiting factor is responsible for the dynamics is necessary for generality, as this determines the types of cycle observed. Recent demonstrations of the interplay between non-linear skeletons and noise [21–26] suggest that there is a place for more complex inductive and deductive models where data permit their construction.

The answer to the question of how complex a model should be depends on the question at hand, the system under investigation, the required scale of resolution and the data available [12,19,27]. System dependence is

illustrated by recent studies of childhood disease. In **Box 1**, we give an example of how models of substantially different complexity are required to provide an equivalent level of understanding for two apparently similar disease systems, where the scale of resolution is the infection status of the host and the fundamental processes equivalent to birth, death and dispersal in animal or plant systems are susceptibility, immunity and infectivity. This comparison demonstrates how a deterministic model works well for one system, whilst a stochastic model is needed to provide an equivalent level of understanding for another, qualitatively similar system.

The scale dependence of model complexity is illustrated by spatial models in which discrete individuals interact

according to the local densities that they experience. At one extreme, we expect small-scale population dynamics to be trivially dominated by noise; at the other extreme, we might expect large-scale dynamics to be accurately approximated by fully deterministic equations. Examples of such approximations in ecology have been developed for individual-based models of plant growth and competition [28] and for a variety of lattice and network-based models of disease [29]. Interestingly, however, noise can play an essential role at intermediate spatial scales, as has been illustrated with individual-based predator-prey models [30]. Population cycles display cycles of fairly regular periods but varied amplitudes, termed 'quasi-cycles' [31]. This behavior arises from the interplay of the nonlinear interactions between individuals, which are local in the spatial case, and the noise from either environmental fluctuations or individual uncertainty.

As well as the issues of model complexity discussed above, modelers must decide on the form that the skeleton will take. One important issue is whether the skeleton should be either discrete or continuous.

Deterministic skeletons: discrete or continuous?

The size of any real population, at any point in time, has to be an integer value, because all populations consist of individuals: fractions of individuals do not exist [12]. Consequently, it makes logical sense that models should be integer based unless we are interested in variables such as biomass and concentration. Most models, however, are not integer based, mainly because the mathematical theory underpinning integer-valued deterministic models is under-developed and complex. Until recently, it had been assumed there would be few consequences of working with mathematically tractable continuous-state models; however, recent research has challenged this view by demonstrating the importance of recognizing the discrete nature of ecological populations [32,33].

Part of the confusion is due to the fact that, when modelers make deterministic models probabilistic by incorporating demographic stochasticity into a non-integer-based (continuous) deterministic model, they in fact add two new ingredients: (i) a probabilistic component; and (ii) integer-valued population sizes. When models with demographic stochasticity exhibit radically different properties compared to their continuous deterministic counterparts, it is inevitably attributed solely to the importance of demographic stochasticity. For example, at the 2003 Ecological Society of America (ESA) meeting in Savannah, Aaron King (University of Tennessee at Knoxville, USA) used a host-parasitoid model to demonstrate convincingly that making population size discrete valued in a deterministic model (i.e. no demographic stochasticity) can have dramatic consequences on population size and variation in population growth. Until the mathematics of discrete-valued models is better developed, most researchers are likely to continue to use continuous-value models. However, integer-value models are biologically more realistic and results (and, consequently, interpretation) can differ markedly between the two approaches.

Which form of noise?

In the mathematical literature, 'noise' is the term applied to whatever obscures or reduces the clarity of a signal. In population ecology, it can be loosely thought of as whatever we do not understand in population dynamics [16]. Environmental noise can be generated by a range of factors, such as climatic effects, natural enemies, inter-specific competition or anthropogenic change, that are not included in the deterministic skeleton. Another form of noise is demographic, which is introduced by the uncertainty in the fate of individuals. Here, we do not consider measurement error explicitly although it is a type of noise (but see [14]). If the deterministic skeleton is structurally inappropriate or only captures some of several important processes, noise might, in fact, be deterministic in origin. There are now various examples where substantial amounts of presumed noise have been explained by the incorporation of additional processes into models [34]. In spite of its unknown origins and the fact these origins are almost certainly system specific, there are various generalized noise 'treatments' that have been proposed [35], with different treatments generating contrasting population dynamics.

Noise treatments

The first treatment is the 'deterministic' one. This considers noise to be completely divorced from the deterministic skeleton; noise is unimportant and can, therefore, be discarded. This treatment is considered sensible if a population is large and its dynamics are governed entirely by the deterministic skeleton, with, at most, only a small amount of measurement error contributing the only noise. In reality, we are yet to discover such a system, and population size is not always a reliable indicator of the importance of noise. Simple nonlinear models of disease formulated at the individual level have shown, for example, that noise can sustain oscillations that would otherwise decay in the fully deterministic case.

The second is the 'equilibrium' treatment, where noise provides some 'fuzziness' around the deterministic skeleton. In other words, the underlying source of the noise is completely independent from the deterministic factors in the model. The deterministic skeleton is considered effectively correct but perhaps overlooks, for example, fluctuations introduced by demographic stochasticity. This is the most common perception and treatment of noise. The third is the passive treatment, where noise is considered to influence the transition from one deterministic system state to another. For example, consider a population that is subject to strong Allee effects (below a threshold population size, the rate of population growth is positively related to density, whereas, above the threshold, population growth is negatively related to density) with a fixed carrying capacity (the maximum sustainable population size). The deterministic model predicts terminal population decline below the population threshold and density-dependent growth above it. There are two possible equilibria (extinction and the carrying capacity), with population size the only determinant of eventual dynamics. The skeleton explains the dynamics well, and noise is unimportant except in causing the transition

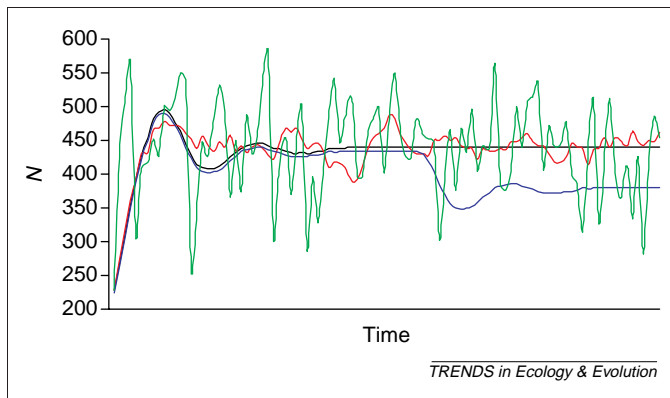


Figure 1. Examples of the consequences of different noise treatments around an age- and sex-structured deterministic skeleton (see [35] for model details). The deterministic treatment does not consider noise; the equilibrium treatment considers only demographic stochasticity in survival and recruitment; the passive treatment considers a change in mean weather conditions occurring at the arrow; and the active treatment incorporates interactions between density and climate that influence survival and recruitment rates. The passive treatment line has been moved down slightly to distinguish it from the deterministic treatment line.

from one equilibrium to another. Examples also include transitions between attractors other than equilibria, such as cycles of different periods in a model for childhood epidemics [36], and transitions leading to spatial pattern formation through diffusive instabilities [37].

The final treatment is the most interesting and is termed ‘active’. Here, noise interacts with the nonlinearity in the deterministic skeleton, and population patterns cannot be fully captured from either component alone [21–26]. In particular, under the active treatment, knowledge of the stable, long-term properties (attractors) of the deterministic skeleton is insufficient to understand the dynamics of the population. The standard analyses based on bifurcation diagrams, that describe how long-term population dynamics change with the values of model parameters, neither predict, nor explain, the dynamics produced when noise is added. Examples of the active treatment of noise include those given in [21–26].

In Figure 1, we demonstrate how the different noise treatments can influence the type of population dynamics that a model predicts. The system is described in Box 2 and the model is described in detail in [38]. Below, we discuss the active treatment in further detail.

Active noise

The epidemics of whooping cough represent one example of the interaction between noise and nonlinearity (Box 1, [39,40]). Another disease example comes from cholera: a nonlinear time series model can only generate the multiple coexisting cyclic frequencies observed in historical data once noise is added to the deterministic skeleton [41]. A non-disease example comes from Soay sheep *Ovis aries* living on the St Kilda archipelago, UK and is described in Box 2. Another non-disease example is given by the phenomenon of noise amplification in population models [26] near the bifurcation point of the nonlinear deterministic system at which an equilibrium loses stability. Noise sustains the otherwise decaying oscillations in a behavior similar to the quasi-cycles described above [31]. One exciting possibility is that the

Box 2. Inductive and deductive models of Soay sheep

The population of Soay sheep (*Ovis aries*) on the St Kilda Archipelago, UK exhibits periodic ‘crashes’ when up to 60% of animals can die. The population has been studied in detail for nearly 20 years, with complete life histories known for many hundreds of individuals. The best inductive population model yet identified for this population proposed that climatic effects (specifically the frequency of storms in late winter) on population growth rate are strongest when the sheep population is large [10]; the model, however, explains only 20% of the observed variance in population growth.

Deductive construction of a more complex deterministic skeleton, which includes density-dependent age- and sex-specific survival and recruitment functions, and the incorporation of state-specific stochastic climatic factors, enabled (90% of the variation in population growth to be explored [38]. The predominant reason for the impressive performance of this model was that it captured important, persistent differences in the contribution of different cohorts to the population dynamics. These cohort differences are generated by the effects of interactions between density and climate on survival rates throughout the life of the cohort, which generate substantial fluctuations in the age- and sex-structure of the population and, consequently, the susceptibility of the population to both stochastic and deterministic processes. This model was a deductive model involving the analysis of survival and reproductive histories of several thousand animals. Combination of these functions into a model of the time series predicted the time series well [38].

weak sensitivity to initial conditions observed in many real time series [42] can result, in part, from these quasi-cyclic dynamics [26,43].

The literature about the role of noise in population models is large and increasing. It would currently be rash to claim any widely supported generalizations, but both the theoretical and empirical literature about the active treatment of noise is rapidly expanding. What is clear is that, in all studied empirical systems, both nonlinear feedbacks and noise influence population dynamics. Traditionally, modelers have concentrated on ‘stable’ dynamics to explain patterns in data. It is also increasingly apparent that we also need to understand ‘unstable’ structures that interact with noise to give rise to unpredictable dynamics [21,22,40]. From this new perspective, we can often develop a good understanding of the consequences of stochasticity by a comprehensive examination of the properties of the deterministic skeleton. Within this context, the distinction between passive and active noise treatments becomes somewhat blurred. Whether this is the rule rather than the exception remains to be determined.

It is also apparent that the identification of interactions between deterministic and stochastic processes can require both considerable data and a solid understanding of the biology of the system. A detailed understanding of the active treatment of noise can only come from a three-pronged approach involving the development of theory, the development of statistical approaches to fit complex models to data, and the collection of data that enable competing theoretical hypotheses to be disentangled.

Model selection

There might often be multiple, competing hypotheses proposed to explain a specific pattern in population

dynamics. For example, multiple deterministic and stochastic processes have been proposed to explain the cyclic fluctuations of pine looper moth [44]. Many decades of fieldwork have identified a list of mechanisms operating in the system that could be invoked to explain the data qualitatively, but could not determine which mechanisms were causal. Identifying approaches for model selection in nonlinear systems with measurement and process error, when knowledge about system variables is incomplete, is an active area of research [19]. Recent developments in this area might even reverse our perception of the respective roles of models and experimental data, as proposed by Steve Ellner (Cornell University, USA) at the last 2003 ESA meeting. He presented an approach to select among competing mechanistic models as a way to test different hypotheses for the origin of population cycles, with an application to the population cycles in the pine looper moth. He concluded by reminding us that usually, we think ‘Models tell us what is possible, but Experiments reveal what is actual’ whereas, in this case, ‘Experiments tell us what is possible, but Models reveal what is actual’.

Conclusions

Recent research has demonstrated that an understanding of population dynamics (across multiple levels of abstraction) requires consideration of the interaction between nonlinear feedbacks and noise. One conclusion arising from this realization has been that the naïve dichotomy between whether density-dependent or density-independent processes determine population fluctuations is neither relevant to, nor informative [45]. The death of the debate has, however, raised several important new questions. How should a deterministic skeleton be chosen? Should it be discrete or continuous? How should noise be incorporated? How does noise interact with the nonlinearity of the skeleton? Which dynamical properties of the deterministic system, if any, fully explain this interaction?

It could be argued that the classic, purely deterministic and purely stochastic syntheses of population biology have failed to identify many, if any, of the generalities that underpin observed patterns of fluctuations in population size. It is too early to determine whether the new deterministic–stochastic synthesis will deliver generalities, but if it stimulates as much debate as the old dichotomy our understanding of population dynamics can only be substantially enhanced. A crucial first step is a better understanding of the exciting mathematics behind the interaction between non-linear skeletons and noise.

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