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978-0-521-83220-5 - Branching Processes: Variation, Growth, and Extinction of Populations
Patsy Haccou, Peter Jagers, and Vladimir A. Vatutin
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# 1

# Generalities

Why should a biologist read a book about branching processes in biology, and why should a mathematician?

This book is aimed primarily at biologists, so let us start with the mathematicians. *You* should read this book because it places a beautiful mathematical theory in a proper context. This is not to say that branching processes cannot be viewed in contexts other than those of population biology. On the contrary, branching processes occur in particle physics, in chemistry, and in computer science. However, mathematics can lose its direction in the jungle of problems that are syntactically well formed and mathematically intriguing, but that have no clear bearing on the outside world. Too many mathematicians, in our view, work on intellectual riddles, while important scientific problems escape their attention. You should read this book to see that branching processes are not only a fascinating mathematical structure, but also can help us to understand fundamental questions of nature.

This applies whatever your field of mathematics happens to be. If your expertise is in parts of mathematics other than probability or statistics, such as traditional applied mathematics oriented on differential equations or physics, there is a further point: this book suggests an alternative, largely discrete approach to population dynamics. It also emphasizes the need to model the complete spectrum from the behavior of individuals up to population phenomena. This is characteristic of modern stochastics and brings modeling a step forward from classic (deterministic) applied mathematics, in which equations are typically derived by intuitive, non-rigorous arguments, and then analyzed in a strict mathematical manner.

And now to those whose attention we really want to catch: biologists. *You* should read this book because many phenomena in areas like population biology, cell kinetics, bacterial growth, or DNA replication are general; they follow logically from the fundamental properties of populations. They are mathematical (i.e., logically inherent) properties of sets of individuals that change because the members generate new individuals. Why is extinction (of families, local populations, or species) so frequent? Is it a consequence of catastrophes or environmental changes external to populations? Or is it rather (or also) an intrinsic property of populations that they tend to die out? If so, how can frequent extinction be compatible with the famous Malthusian law of exponential increase, until resources become scarce? Is there a dichotomy between exponential growth and extinction, or are there other, slower forms of population growth? Can population size stabilize? What happens to the composition of populations if their multiplication persists for a long time? Does it stabilize? And what can be said about the history of surviving or extinct

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populations? How gradual or abrupt is natural extinction? What can be said about mutational history? Or about the time between now and the most recent common ancestors?

Such broad population dynamics questions are addressed in the second part of this book. Before that we introduce models of varying generality. These sharpen our vague intuitive notions about population development into mathematical concepts that build up strict theories. With the help of these we can understand what must or may happen. However, even if a problem eschews our efforts to provide a mathematical solution, its formulation in mathematical terms makes it possible to simulate the model, and thus learn about reality from what has aptly been termed “experiments in the model.” A mathematical model makes it possible to calculate explicitly the values of important population parameters, such as the doubling time or the growth rate, from parameters that describe individual behavior. Finally, it renders it possible to use population data to estimate parameters (e.g., the expected offspring size per individual) and test hypotheses about them, using the appropriate statistical distributions involved.

We emphasize here that branching processes have a role in general population dynamics. However, specific phenomena can (and should) also be analyzed through specific, tailor-made models. Such models are presented in the last part of the book, on topics that range across the spectrum from the smallest living entities to ecosystems and the evolution of life on earth.

Finally, it is one thing to wish to address biologists, but quite another to what extent biologists are prepared to receive our message. We certainly feel that biology is ripe for mathematical analysis, and the increasing role of mathematical formulation in all of biology, from algorithms for DNA sequencing and gene search to modeling of evolution and ecological systems, clearly bears witness to this. Unfortunately, many biologists may feel that they do not have the mathematical prerequisites for a text like ours.

We believe that our book can be read, in full, by an interested biologist with a basic command of calculus, linear algebra, and probability theory, and we dare hope that many others can capture the important ideas, and may even be intrigued enough to pursue a more thorough reading, with an elementary text book at their side. For your benefit we have collected text-book style facts of basic probability into a mathematical Appendix.

## 1.1 The Role of Models

The most important function of models is to order our thoughts. With models we formulate what we know (or think we know) about the world, and we perform thought experiments through “what if” scenarios. Every scientist makes models of the system that he or she studies. In many instances, initial models are verbal rather than mathematical. There is nothing wrong with verbal models, and they may suffice. As the scenarios become more complicated, however, it becomes increasingly difficult to keep track of verbal arguments and to check their consistency. Verbal models therefore involve the risk that they may overlook important

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factors and/or introduce logical inconsistencies. Here, mathematics provides a powerful language that forces us to be logically consistent and helps provide an explicitness about assumptions. Although a set of equations may seem daunting and complex, in most instances it is much easier to check the logic of an argument from such a list than when it is formulated in ordinary language. (The latter also takes up much more space!)

Another important use of models is their function as an idealization of the world. Whenever we formulate a model, we are forced to make a choice concerning which aspects of "the real world" we include in our description and which we choose to ignore (for the moment). This is true for verbal and mathematical models alike, but is more easily noted in the latter: mathematical formulations reveal contradictions and implicit assumptions. (This lack of gullibility may be one of the reasons for the unwarranted aversion toward formulation in mathematical terms.)

We cannot simply put everything we know about a system into a model because it soon becomes intractable. Computers help in this respect. They can accommodate many factors, but it is often difficult to determine which of these affect the predictions of the model and in what way. Modeling always involves a compromise between realism and the tractability of mathematics (or verbal arguments), and the inherent conflict between the two becomes more pronounced the more complex the system under study is.

The choice of what is put into a model and what is left out depends not only on the perceived importance of various factors, but also on the purpose of the model: is it to gain insight into a specific question or to address general issues and detect general patterns? Or is it to control a process, as in many engineering applications, rather than to understand it?

When we seek the answer to a specific question in a specific system, we might put in more detailed knowledge about the system. Such models have been called "tactical," since the results often have limited relevance. If we are interested in general patterns and conclusions, we need more of a "strategic" model, alternatively termed "conceptual." In such a model, we want to make assumptions that apply in a large class of systems and we want to draw very general conclusions (e.g., what were the most important factors in the evolution of sexual reproduction?). A strategic model cannot readily be used for any specific system, but it might indicate which general pattern to expect. Finally, if the purpose is prediction, management, control, or even purely descriptive, "black box" models, with a simplistic structure, but with many parameters so that they can be fitted to many data sets, have proved useful, even though their explanatory scientific value seems limited. Examples of such models are time series, such as autoregressive processes or moving averages, or artificial neural networks. Here we do not consider such descriptive models, even though they have been used in population biology, for instance to describe periodicity in the famous Hudson Bay Company data set on lynx and hare [cf. Diggle (1990), which also gives further references].

The models we consider are individual-based. They start from descriptions of, or assumptions about, individual life and reproduction, and deduce the behavior of populations. Such models are sometimes called mechanistic, and the whole approach reductionist, since properties of populations are brought back to the underlying mechanisms of individual life. Population models can also be based directly on phenomena that appear at the population level; these are called phenomenological. For instance, the effects of population density may be hard to describe at the individual level but established much more easily at the population level; an example is the well known phenomenon of "logistic growth."

Still, a word of warning is required here. Phenomenological population models carry tacit assumptions about the individual level. These should be pondered and made explicit, so that they are first of all not self-contradictory, but also so that they do not imply assumptions we are not willing to make.

As an illustration of this, many simple classic formulations of population dynamics, in terms of differential equations, can be shown to imply that individuals have exponentially distributed life spans. Other models, often otherwise quite sophisticated, have a basic Markov structure, which again means the same. However, a property that characterizes exponential distributions is that the conditional distribution of surviving another time period, given that you have survived up to a certain age, is independent of the latter. The biological meaning of this is that individuals do not age. This may actually be acceptable in models, say, of populations of small birds for which the hardships of life mean individuals do not die of old age itself (though the risk of dying is often higher for chicks than for adults). But it certainly matters in demography, or in cell kinetics, in which cells have to perform various tasks, like doubling their DNA, before splitting. For such cases, we demonstrate that one can do without the dubious and often simply false assumption of exponentially distributed life spans.

Finally, a word about the very concept of a *model*. It derives its meaning from scale models, simplified but yet replicas of larger structures, such as buildings or ships. Among the connotations of the concept is therefore a structural similarity between the model and the original, albeit simplified, sometimes even to the extent of caricature, but still there. In phenomenological modeling there is less of this similarity, and in what we have called "black box" modeling above it is almost always absent. Affinity between model and reality, as in the type of models considered here, certainly makes us more confident about our conclusions than mere curve fitting, which may cease to work around the next corner.

## 1.2 The Role of Randomness

The fate of individuals is stochastic. There is nothing mysterious in such an assertion, simply a recognition that it would be impossible to record all the conditions that have repercussions on the life career of an individual, even if this were possible in principle (a matter over which honorable people can disagree). Thus, life spans are influenced by predation risks, food access, weather, and other processes that can only be described as stochastic. As a result, life span is a random variable and different individuals usually have different life spans.

It is often argued that stochasticity at the individual level can be ignored in the study of large groups of individuals, and so deterministic models can be used to study their fate. However, such models are always approximations, since (obviously) if individuals evolve in a stochastic manner, so do finite populations. The best approach is always to perform this approximation explicitly, that is to use the fully fledged stochastic model and show that by some law-of-large-numbers effect it is well approximated by a deterministic simplification. Thus we may have a chance to estimate the magnitude of the errors involved, and also to discover aspects for which the approximation is unfeasible. We discuss such approximations further in this book, and often come back to the possible existence of stationary – i.e., possibly fluctuating locally, but in the long run stable – populations, for which disregard of stochasticity leads to radically different phenomena. Indeed, the place of extinction in population dynamics, and evolution even, and concepts like viability cannot be understood within the framework of stationary or deterministic population theory.

Population randomness through individual variability is called “demographic stochasticity.” Another source of randomness is environmental stochasticity, caused by spatial and/or temporal variation in environmental factors, that affects the population as a whole or their members individually. The environment in its turn can be influenced by the population (e.g., by its size). Thus, it may be interesting to study feedback loops like environment → individual reproductive behavior → population size → environment.

Whereas the impact of demographic stochasticity can diminish for large population sizes, the effects of environmental stochasticity remain important for larger populations and should be included in model formulations, if relevant to the real biological system.

Additional sources of randomness to be incorporated may be the effects of measurement errors or factors not explicitly included in a model, but lumped together into an unspecified random effect (incomplete description).

Mainly, we are concerned here with modeling demographic stochasticity, sometimes in combination with environmental stochasticity. Branching process models were developed originally to account for inter-individual variation in offspring numbers and life spans (i.e., forms of demographic stochasticity). More recently, environmental stochasticity was added to these models. The latter may drastically change predictions about population size or structure, and also what is sometimes called “post-diction,” attempts to reconstruct history from data about the present (e.g., the time back to the last common ancestor of those presently alive in the branching process). Other recent developments in branching processes of interest to biologists are the introduction of processes whereby individuals may interact, compete or collaborate, and the above-mentioned feedback scheme, whereby population size or other properties of a population, say mirroring the availability of resources, may influence individual reproduction.

There are several reasons why demographic stochasticity may remain important in populations. Populations may be prevented from growing to relatively large sizes (e.g., because of resource limitations or repeated environmental disturbances). Furthermore, even for large populations care should be taken with deterministic approximations. For instance, when the effects of environmental factors are non-linear, the effects on expected population size are not identical to the expected effects on population size. Therefore, in general it is advisable to formulate an individual-based stochastic model first and then, if possible, derive stochastic or deterministic approximations, rather than to start at higher levels. We illustrate this point in Section 1.4. Other contexts in which demographic stochasticity is important involve the fate of (initially) small subgroups of populations, as in models of evolutionary processes.

Finally, a point that may seem less important: in reality, populations are usually measured by counting their numbers, although there are exceptions when the relevant entity may be something like total body mass. Deterministic theories treat these discrete numbers as continuous and even differentiable functions. This results in assertions such as those in the Ricker model of Section 1.4 (see Figure 1.1), for which the population number might even be irrational. Depending upon ideology, you may feel this to be a mere nuisance or a major epistemological problem, as when certain models claim that an epidemic goes on forever in a cyclic manner, but actually the minimum of each epidemic cycle, though strictly positive, is much less than the one carrier needed to prolong the epidemic. Anyhow, it is certainly an advantage in population modeling that branching processes are integer valued.

## 1.3 Branching Processes: Some First Words

As pointed out, branching processes are individual-based models for the growth of populations. This property they share with the more advanced deterministic models, in particular those of structured population dynamics (cf. Metz and Diekmann 1986; Diekmann *et al.* 1998, 2001), in which the course of individual lives is described by differential equations, at least in the most prominent cases. In branching processes we content ourselves with probabilistic descriptions of life careers: the basic purpose is thus to deduce properties of the processes (i.e., of populations) from the probability laws of individual childbearing and life spans.

Many methods and techniques used in population biology have a branching process background or interpretation. For example, the Leslie matrices of classic demography are nothing but descriptions of the expected reproductive behavior of individuals of various age groups. Populations in discrete time for which age matters for reproduction are but a special form of multi-type branching processes, which are discussed in Sections 2.3 and 2.4.

An individual is understood in a broad sense: it might be an animal or a plant, but also a cell or an elementary particle – the defining property is that it gives birth, splits into, or somehow generates new individuals. It could even be a whole population that gives rise to new populations through mutation (speciation), or if it lives in one patch by colonization of other patches. The name “branching process” alludes to the family trees thus arising. However, more often the name refers to the simpler stochastic process that records the population sizes at various times only, or records the sizes of subsequent generations, rather than to the complete population tree. Historically, the first question tackled with the help of branching processes was that of population extinction: what is the probability that a population dies out? Other classic topics are the possible stabilization of population sizes, growth rates, and age distributions or other aspects of population composition.

The theory started with (Bienaymé–)Galton–Watson processes (discrete-time models) and Markov branching processes (their continuous-time equivalents). For overviews of its fascinating history, see Kendall (1966), Jagers (1975), and Heyde and Seneta (1977).

The Galton–Watson processes just count generation sizes. In real life, generations and physical time can have quite diverse relationships. Whatever these are, the problem of ultimate extinction is unaffected: if there is a time when the population is extinct, there must also be an empty generation, and vice versa – even if generations can overlap and be shifted drastically in time.

In the simplest case, Galton–Watson processes can also be viewed as real-time processes, provided all the individuals can be assumed to have the same life span of length one (year or season). In such cases, we assume that individuals are born at the beginning of the season.

Somewhat more general discrete-time processes allow individuals to live over several discrete seasons, during which they may give birth repeatedly. Still more general processes allow arbitrary life spans, and arbitrary reproduction during life.

In all traditional models, however, independence in reproduction and survival among different individuals is assumed. The rationale for this is that the models are meant for small populations, in which resource limitations, for example, can be assumed not to play an important role. Obviously, the latter is not true for many biological systems. As pointed out, recent research has concerned these restrictions and analyzed setups in which, for example, reproduction may depend on resources, population size, or density. We report some findings in Sections 2.6, 5.8, and 6.5.

## 1.4 Stochastic and Deterministic Modeling: An Illustration

Many deterministic models are simply expectation versions of branching processes. These we shall meet in the discussion of the corresponding branching processes. However, where there are non-linear dependences, difficulties may arise. We illustrate this with a well-known deterministic approach to population-size dependence, the so-called Ricker equation. It has the form

$$z_{n+1} = m z_n e^{-b z_n} , \tag{1.1}$$

which relates population size at time $n + 1$, $z_{n+1}$, to size during the preceding period, $z_n$. What happens if modeling is refined down to an individual stochastic level?

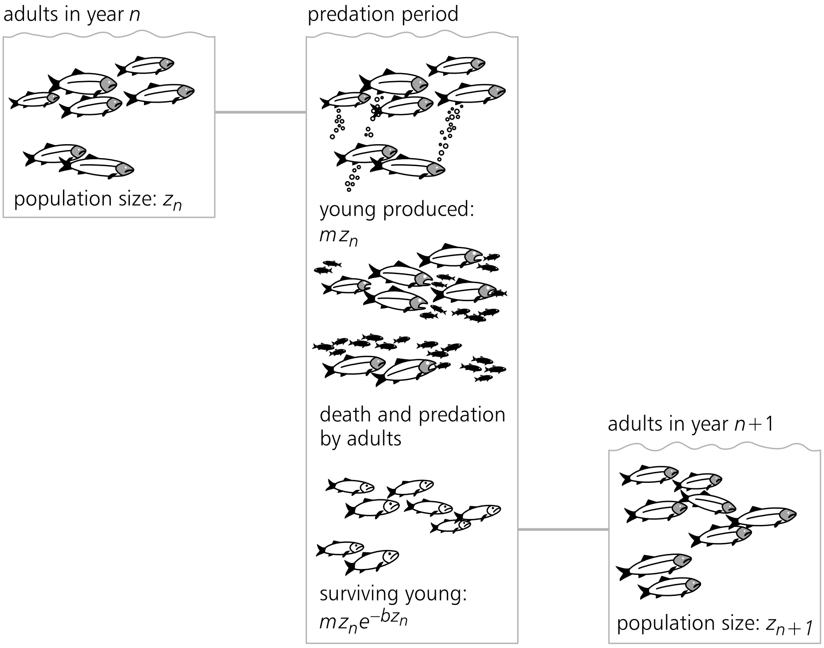

**Figure 1.1** The Ricker model: adults predate on juveniles. Those young that survive the vulnerable period form the next generation.

The Ricker equation purports to model predation on juveniles by adults, as happens in many fish species. The rationale behind it is (cf. also Figure 1.1): adults produce $m$ juveniles, on average, so the juvenile population consists of $m \times z_n$ individuals. There follows a period during which predation by adults occurs. The predation rate is assumed proportional to population density $z_n/A$, where $A$ is the area occupied by the population. By a differential equations argument, the proportion of juveniles that survive the predation period has the form claimed, $e^{-bz_n}$. Indeed, a conventional argument is as follows: let $j(t)$ denote the number of juveniles alive after a portion $t$ of the predation period has passed, $0 \le t \le 1$. Then, $j(0) = mz_n$, $j'(t) = -bz_n j(t)$ for some constant $b > 0$, and hence

$$z_{n+1} = j(1) = mz_ne^{-bz_n}\ , \tag{1.2}$$

in this deterministic framework.

A stochastic version of this is to say that each of the $Z_n$ individuals in the $n$th generation generates a random number of offspring, with expectation $m$. In total there are $j_{n+1}$ juveniles, and the expected offspring size in the $(n+1)$th period, given the number of adults, $Z_n$, is

$$\mathbb{E}[j_{n+1}|Z_n] = mZ_n\ . \tag{1.3}$$

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Each of the young fish is then subjected to a predation risk $1 - e^{-bZ_n}$ independently. As a consequence, the next generation, $Z_{n+1}$, is distributed binomially with parameters $j_{n+1}$ and $e^{-bZ_n}$, given $Z_n$ and $j_{n+1}$ (see the Appendix).

Conditional distributions and expectations, as above, play a crucial role throughout this book. Typically, it is easier to see what the conditional expectation (e.g., given some crucial information) will be, than it is to determine the overall, unconditional expectation directly. However, the latter equals the expectation of the former (see the Appendix).

In the present case, properties of the binomial distribution imply that the expected population size in the next period, given both the number of juveniles, $j_{n+1}$, and the population size, $Z_n$, in the preceding period, is

$$\mathbb{E}[Z_{n+1}|j_{n+1}, Z_n] = j_{n+1}e^{-bZ_n} . \tag{1.4}$$

The expectation of this over all possible values of $j_{n+1}$, given only $Z_n$, is

$$\mathbb{E}[Z_{n+1}|Z_n] = mZ_n e^{-bZ_n} , \tag{1.5}$$

as given by the binomial distribution. Hence, unconditionally,

$$\mathbb{E}[Z_{n+1}] = m\mathbb{E}[Z_n e^{-bZ_n}] . \tag{1.6}$$

This illustrates well what happens to non-linear relationships, in which a deterministic derivation is replaced by expectations in a stochastic model. In the present terminology, the deterministic model we started from only considers $m_n = \mathbb{E}[Z_n]$; it cannot distinguish between the real population size and its expectation. Therefore, it claims that

$$m_{n+1} = mm_n e^{-bm_n} . \tag{1.7}$$

A more refined analysis, however, results in the recursion (1.6), and certainly

$$m\mathbb{E}[Z_n e^{-bZ_n}] \neq m\mathbb{E}[Z_n]e^{-b\mathbb{E}[Z_n]} = mm_n e^{-bm_n} , \tag{1.8}$$

except in degenerate cases. Actually, Jensen's inequality (see the Appendix) tells us that the expectation of a convex (concave) function is larger (smaller) than the function of the expectation. Since the function $Ze^{-bZ}$ is concave for small $z$ and convex for large, the deterministic model tends to fluctuate less than does the expectation of the stochastic model. In particular, if the population starts from a high level, deterministic theory underestimates its expected size and, conversely if it starts small, size is overestimated.

As is shown in Section 5.2, stochastic Ricker populations inevitably die out. Their so-called quasi-stationary behavior (i.e., what the population development looks like, given that the population is not yet extinct) was discussed for small $b$ by Högnäs (1997). He showed that short-term development follows the deterministic model, at least in a crude sense. We return to this later (Section 6.9).

The Ricker model is just one in a whole family of deterministic discrete-time models that have the mathematical form

$$x_{n+1} = f(x_n) , \tag{1.9}$$

where $x_n$ either equals the population size $Z_n$ or else the population density, $x_n = Z_n/K$; $K$ is the maximal population size in the deterministic model (or a typically approximate maximal level in stochastic cases) and is often referred to as the *carrying capacity*. Thus, in the Ricker approach, $f(x) = xe^{-bKx}$ in terms of density. Another classic, but somewhat ad hoc population model, Verhulst's so-called logistic model from 1845, has $f(x) = x(1-x), 0 \leq x \leq 1$, where $x$ stands for density again. In the logistic case, $f$ is concave along its whole interval of definition, so that by Jensen's inequality the deterministic relationship always overestimates the expected population density. The reason for this is simply that the model is not defined for population sizes larger than the carrying capacity.

In biomathematical literature the recursion above is usually formulated in terms of the individual reproduction function $R$, so that

$$x_{n+1} = x_n R(x_n) \ . \tag{1.10}$$

Mathematically, the two are, of course, equivalent, but the first is slightly more general and, from the point of interpretation, the second form has great advantages.

## 1.5 Structure of the Book

Chapters 2 and 3 give an overview of branching processes and their main characteristics, with an emphasis on biological interpretation. Chapter 4 is the most technical chapter of the book. It deals with relations between branching processes and other models of population dynamics, in particular diffusion processes and deterministic models. Chapters 5 and 6 describe how important characteristics of population dynamics can be studied with branching processes. Finally, Chapter 7 gives examples of recent applications of branching processes in various fields of biology.