A SIMPLE MATHEMATICAL MODEL
FOR BATESIAN MIMICRY

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A simple mathematical model is presented for Batesian mimicry, which occurs when a harmless species (mimic) is morphologically similar to another species (model) that is noxious or distasteful to predators, thus gaining a measure of protection. Although mathematical models for species interaction, such as predator-prey or competition, are well known, there is no similar literature on mimicry. The mathematical model developed here is a one-dimensional iterated map which has the full range of dynamic behavior present in the logistic map, depending on the values of its parameters. The dynamics ranges from a stable fixed point and stable cycles through chaotic dynamics achieved through a sequence of period doubling bifurcations.

1. Introduction

The use of mathematical models to predict the dynamics of interacting species dates back to Lotka and Volterra in the 1920s. Despite some severe limitations, the predator-prey and competition models of Lotka-Volterra are featured widely in both calculus and differential equations texts, and these models are generalized for consideration of symbiosis, commensalism, and amensalism. See, for example, Begon et al. (1996). More realistic models have appeared in the literature, for example, Holling's (1959) approach to predator-prey interactions in which a functional response term replaces the insatiable predators of Lotka-Volterra. Discrete-time models have also been applied to most forms of multispecies interactions; the host-parasitoid model of Nicholson-Bailey (1935) atypically being more than simply a discrete-time counterpart of a continuous model. However, the notion of *mimicry* seems to have escaped mathematical analysis. The purpose of this paper is to build and then analyze a simple model of Batesian mimicry.

Batesian mimicry occurs when a harmless species (or *mimic*) is morphologically similar to another species (or *model*) that is noxious or distasteful to predators. In addition, the mimic may behave in similar ways to the model. The mimic uses these physical and behavioral similarities to gain a measure of protection from its potential predators. Perhaps the best-known example is that of the monarch butterfly, which is poisonous to many birds, and the similar viceroy butterfly that is not. Holling [2] conjectured that there

is a limit to the number of mimics that can exist within a given population of models. That is, there is a maximum ratio of mimics to models; this ratio is therefore *optimal* in the sense that it provides the maximum benefit for the mimic. Heuristically, if there are too many mimics, predators will find palatable prey within the model-mimic system and will sample freely from this, thus providing the mimic with little benefit. On the other hand, if the system is almost exclusively model, the few mimics present are likely to go undetected, and will gain full protection from their similarity to the unpalatable model. The question is whether there is a balancing point between these two extremes: Is there a model: mimic ratio at which the system is stable, so that predation leaves this ratio more or less unchanged?

In the next section, we propose a simple mathematical model for Batesian mimicry that takes the form of a one-dimensional iterated map. In the final section, we analyze this model and show that it exhibits a range of dynamic behavior similar to that of the well-known logistic map.

2. The mathematical model

In this section, we propose a simple model for Batesian mimicry. We begin with a number of assumptions for our model. Whether these apply to a given model-mimic system in nature will of course depend on the life histories of the particular species involved.

We assume that predators have a variety of preys available to them that includes the model and mimic species. The models are unpalatable, and although the predator may eat some models, generally models will prove themselves noxious to their predators and will escape if sampled. Predators are assumed to have short-term memories, so that although they will for a time remember the bad experience from eating, or attempting to eat a model, they will later sample again from the model-mimic system.

We assume that the level of predation on the model-mimic system depends only on the model: mimic ratio, and not on the actual numbers of models and mimics. Predation on other species is ignored, deemed to have no effect in light of the above assumption since the model: mimic ratio is unaffected by the sampling of prey outside of the system.

We will work with discrete-time steps, and define X_n to be the number of models in the population at time n and Y_n to be the number of mimics in the population at time n. Of interest is the ratio $X_n : Y_n$ and how this changes over time n. To measure this, we define the related variable

$$Z_n = \frac{X_n}{X_n + Y_n} \tag{2.1}$$

which measures the model proportion of the total model-mimic population. Clearly, $0 \leq Z_n \leq 1$. We propose to model the system using an iterated map $Z_{n+1} = f(Z_n)$ and will determine a number of properties of the function f. We will assume this function is continuous.

Firstly, it is clear that $f(0) = 0$ and $f(1) = 1$. That is, 0 and 1 are fixed points of the iterated map. The condition simply says that if the system ever consists entirely of one species or the other, then it will continue to do so. Next, we consider what happens close to $Z = 0$. Here, the system is predominately mimic, and so predators will sample more
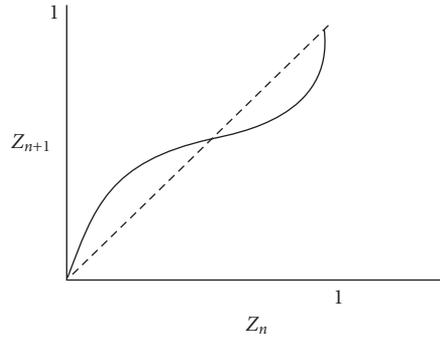
Figure 2.1. The graph of f in the simplest case. The model: mimic ratio will tend to an optimal value.

or less freely from the system. Because some models will be sampled but not eaten, the model: mimic ratio will change in favor of the models. This implies that for ε small, $\varepsilon < f(\varepsilon)$. Consequently, the fixed point $Z = 0$ is unstable.

Next, we consider what happens close to $Z = 1$. If for ε small, $f(1 - \varepsilon) < 1 - \varepsilon$, then by the continuity of f, the iterated map has at least one fixed point between 0 and 1. If the fixed point is unique, and since 0 and 1 are unstable fixed points, it is reasonable to think that this fixed point would be stable (although this is not necessarily true). This would then be the "optimal" model: mimic ratio conjectured in [2] (see Figure 2.1).

However, it is hard to justify the fact that $f(1 - \varepsilon) < 1 - \varepsilon$. In this case, the population is almost exclusively model and there will be little predation on the system. Thus, the ratio will be affected by factors other than predation and the shape of the graph of f near $Z = 1$ is therefore determined by life history factors external to the mathematical model. It is clear however that it cannot be the case that $f(Z) > Z$ for all $0 < Z < 1$, since then $Z = 1$ is a global attractor. The model-mimic system would not evolve in these circumstances.

The possibility that $1 - \varepsilon < f(1 - \varepsilon)$ requires that f has more than one fixed point between 0 and 1. The simplest case with two fixed points is illustrated in Figure 2.2. Note that the rightmost fixed point Z_R is unstable. The model: mimic ratios beyond this value lead to the extinction of the mimic. The interesting part of the dynamics lies to the left of this fixed point. In this case, the graph of f over $[0, Z_R]$ has the same shape of the graph of f over $[0,1]$ in Figure 2.1.

In general, f may have many fixed points, but we may assume that f has the shape given in Figure 2.1, since otherwise we may restrict f to a domain $[Z_1, Z_2]$ (where $0 \leq Z_1 \leq Z_2 \leq 1$) on which the graph has this shape. If the graph of f is steeper than shown at the unique fixed point between 0 and 1, then this fixed point may be unstable and the dynamics more complex. This is further discussed in the next section.

3. Analysis of the mathematical model

In order to determine the possible dynamics of the system, we will make some adjustments to the function whose graph is shown in Figure 2.1. Rather than work with the domain $[0,1]$, we will use $[-1,1]$ and we will further rescale Z so that the fixed points
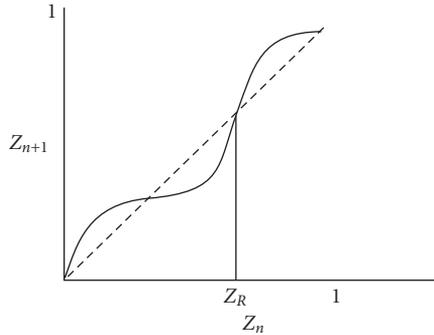
Figure 2.2. The simplest graph of f if the fixed point at $Z = 1$ is stable. The model: mimic ratio will tend to one of two values depending on the initial conditions.

lie at $Z = -1$, 0, and 1. Such a rescaling has no effect on the dynamics; it merely gives us different points of reference. We choose to use the family of functions

$$f(Z) = aZ^3 + (1-a)Z \qquad (3.1)$$

for our study of the dynamics of the mimicry system under $Z_{n+1} = f(Z_n)$, noting cautiously that this choice introduces a symmetry that is unlikely to be present in the function f of Figure 2.1. For more general functions, we would certainly expect more general results. But, as we will show, the above family of functions shows the full richness of dynamics present in the logistic map.

For f to map $[-1, 1]$ into $[-1, 1]$, interest lies in the parameter range $0 < a \leq 4$, and in all cases the fixed points at ± 1 are unstable. If $a \leq 1$, then f is an increasing function, and the fixed point $Z = 0$ has basin of attraction $(-1, 1)$. If $1 < a \leq 4$, then f is an N-shaped function; for $1 < a \leq 2$, the fixed point $Z = 0$ has basin of attraction $(-1, 1)$, but a period-doubling bifurcation takes place at $a = 2$ and this is the beginning of the more complex dynamics that takes place over the parameter range $2 < a \leq 4$.

It is easily shown that for $a > 1$, the iterated map $Z_{n+1} = aZ_n^3 - (1-a)Z_n$ has negative Schwarzian derivative. This has two well-known consequences (see, e.g., Guckenheimer and Holmes [1]). Firstly, all flip bifurcations are supercritical, and so we may expect a cascade of period-doubling bifurcations as seen in the logistic map (see, e.g., May [4]). Secondly, if the iterated map has a stable periodic orbit γ, then the trajectory that starts at the maximum or minimum points of f in $(-1, 1)$ will approach γ.

The given function has its maximum and minimum values at $Z^{\pm} = \pm\sqrt{(a-1)/a}$. It follows from the oddness of f that the trajectory through Z^+ differs throughout from that through Z^- only in sign. The bifurcation diagram starting at Z^+ is given in Figure 3.1. The bifurcation diagram starting at Z^- can be obtained from that of Z^+ by reflection across the a-axis. The full bifurcation diagram is obtained by combining these two diagrams and yields that given in Figure 3.2.

Figure 3.2 looks very similar to the bifurcation diagram of the logistic map (see [1] or [4]). Initially, trajectories tend to the stable fixed point at $Z = 0$, then to a stable 2-cycle, and so forth. However, there is one important difference. The bifurcation at $a = 3$
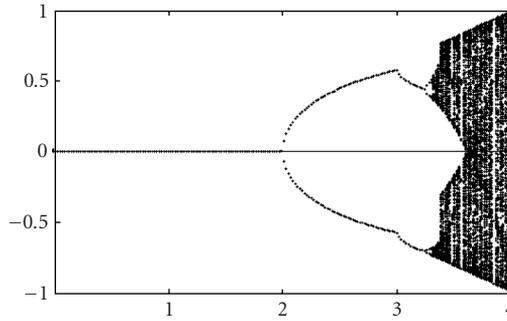
Figure 3.1. The bifurcation diagram of the iterated map $Z_{n+1} = aZ_n^3 + (1-a)Z_n$ over $0 < a < 4$ obtained from $Z_0 = Z^+$.
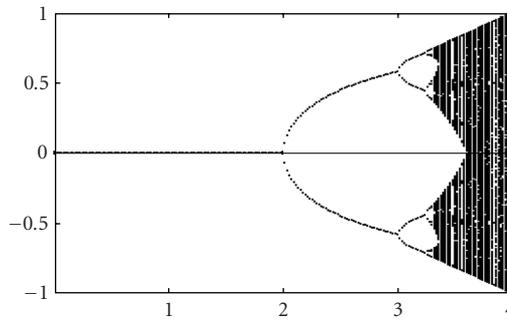

Figure 3.2. The complete bifurcation diagram of the iterated map $Z_{n+1} = aZ_n^3 + (1-a)Z_n$ over $0 < a < 4$ obtained using $Z_0 = Z^+$ and Z^-.

is not a flip bifurcation, but a pitchfork bifurcation. It is easy to see that $\pm\sqrt{(a-2)/a}$ is a 2-cycle of the iterated map. This is stable in the range $2 < a < 3$, and at $a = 3$, this *symmetric* 2-*cycle* loses its stability. At $a = 3$, we see the appearance of two *asymmetric* 2-*cycles* given by $\pm\sqrt{((a-1)\pm\sqrt{(a-3)(a+1)})/2a}$. These two 2-cycles are initially stable, losing their stability in a flip bifurcation at $a = 1 + \sqrt{5}$. This is the first in the cascade of such bifurcations. The dynamics after this point is very much like that of the logistic map.

The first 3-cycle appears when a equals the smallest positive root of the polynomial $F(a) = 4a^8 - 48a^7 + 189a^6 - 144a^5 - 828a^4 + 2052a^3 - 972a^2 - 2700a + 4644$ (approximately $a = 3.6995$). The consequences of the existence of a 3-cycle are well known (see, e.g., [3]).

We also note that for values of $a > 4$, the maximum and minimum values of the function f map outside of the interval $[-1, 1]$. If this interval does not represent the complete range of the model: mimic ratios, but only a part, $[Z_1, Z_2]$, this situation is still feasible (see Figure 3.3). The trajectories of many points map outside $[-1, 1]$ and are attracted elsewhere, but if we restrict the function f to those points whose trajectories remain in $[-1, 1]$, the dynamics may be represented by a bi-infinite sequence on three symbols L, M, R. It is well known that periodic orbits exist of all periods, and that there exists a dense aperiodic trajectory. [This situation also parallels a case in the logistic map.]
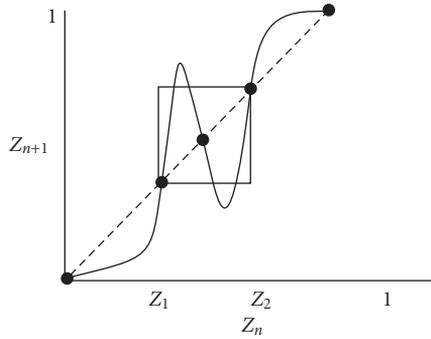
Figure 3.3. Example of a function in which the interval $[Z_1, Z_2]$ maps outside of itself but within $[0,1]$.

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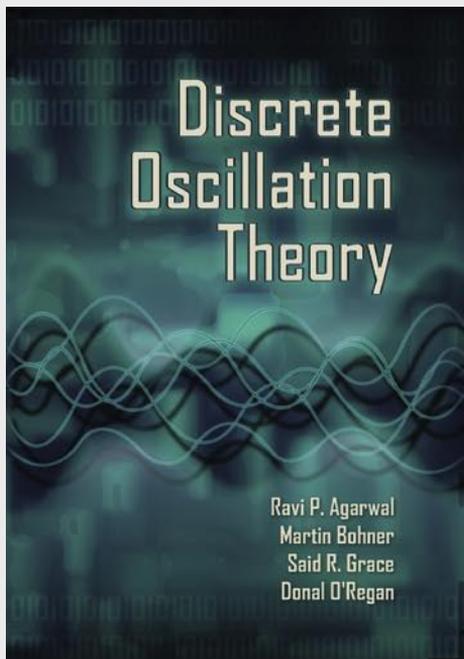
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DISCRETE OSCILLATION THEORY

Ravi P. Agarwal, Martin Bohner, Said R. Grace, and Donal O'Regan

This book is devoted to a rapidly developing branch of the qualitative theory of difference equations with or without delays. It presents the theory of oscillation of difference equations, exhibiting classical as well as very recent results in that area. While there are several books on difference equations and also on oscillation theory for ordinary differential equations, there is until now no book devoted solely to oscillation theory for difference equations. This book is filling the gap, and it can easily be used as an encyclopedia and reference tool for discrete oscillation theory.

In nine chapters, the book covers a wide range of subjects, including oscillation theory for second-order linear difference equations, systems of difference equations, half-linear difference equations, nonlinear difference equations, neutral difference equations, delay difference equations, and differential equations with piecewise constant arguments. This book summarizes almost 300 recent research papers and hence covers all aspects of discrete oscillation theory that have been discussed in recent journal articles. The presented theory is illustrated with 121 examples throughout the book. Each chapter concludes with a section that is devoted to notes and bibliographical and historical remarks.

The book is addressed to a wide audience of specialists such as mathematicians, engineers, biologists, and physicists. Besides serving as a reference tool for researchers in difference equations, this book can also be easily used as a textbook for undergraduate or graduate classes. It is written at a level easy to understand for college students who have had courses in calculus.

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