

Basic Properties of Mathematical Population Models

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Abstract

Mathematical population models are constructed based on plausible explicit and implicit biological assumptions. While it is easy to incorporate explicit assumptions correctly in the models, those implicit ones are often ill treated or forgotten. Indeed, this happens to some well known models in the literature and examples of such will be mentioned and discussed. For a model to be logically credible, we must do our best to ensure that all assumptions are incorporated correctly and consistently. To this end, we exam a simple set of criteria proposed by Arditi and Michalski in 1996. For patchy models, we add an additional criterion to their list. We also add some important criteria in other specific situations and comment on modelling of single species growths. Following criteria of Arditi and Michalski and other well accepted biological assumptions, we introduce some interesting three dimensional predator-dependent (ratio-dependent) population models. We also discuss various aspects of modelling population fluctuations.

Key words: Logical consistence, predator-prey models, ratio-dependent predator-prey model, logistic equation, time delay, patchy model.

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Running head: Properties of population models

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1 Introduction

The most important aspect of model design is to make sure that the perspective models can exhibit well known properties of the system. These properties may be explicit or implicit. The mathematical analysis of early stage models can reveal hidden properties of such models that may or may not agree with these well known properties. A discrepancy can often point out ways for the modification of such models. In other word, modelling is frequently an evolving process. Systematic mathematical analysis can often lead to better understanding of the plausible models. The exposed discrepancies in turn lead to the necessary modifications. The final model should, ideally, free of any significant discrepancies. The analysis of the final model can thus be expected to reveal important and nontrivial insights of the system.

In the last few decades, interest has been growing steadily in the designing and studying of mathematical models of population interactions. There is a tendency among mathematicians to rush into the analysis of a existing model without knowing the background or motivation of such model, or rush into the final models and indulge in the analysis of certain mathematical properties of such models. On the other hand, biologists may take pain to design and justify their models but give no or very limited analysis of their models. In the former case, if the motivation of the model is not appreciated, the analysis may not contribute to the understanding of the desired aspects of the model. If the model is not well posed, then analysis may not gain any real understanding of the system, indeed it can often lead to misleading findings. In the case that not enough analysis is carried out for a well motivated and plausible model, the results is no or minimum insights gained. This can leave readers wonder what is the purpose of introducing those models in the first place.

Mathematical population models can take many forms. Depending on the time scale and space structure of the problem, it can be modeled by difference equations, ordinary differential equations, delay differential equations, or partial differential equations, or the combination of these equations. When necessary, random effects can be considered in all those equations. A hallmark of mathematical modelling process is that for each specific motivation, there can often be several plausible models to chose. The final selection often depends on the nature of the problem to be modeled and the researchers's expertise of the various forms of differential equation models, computational skills and other backgrounds. In situations when no obvious choices can be made, it is important to consider as many plausible models as possible to distinguish model specific properties from model independent ones.

Clearly, to gain a deep understanding of the mathematical aspects of the problem and to yield nontrivial biological insights, we must take pain to construct biologically meaningful and mathematically tractable models. Clearly, this requires the expertise of both mathematics and biology. Ideally, this should be carried out as collaboration of mathematicians and biologists. However, this is not always the case. Often mathematicians are working alone or working with mathematicians. Ditto for biologists.

The purpose of this paper is to provide some practical and important criteria (new

and old) that should be met by any plausible population models. These criteria can guide model designers away from many common pitfalls. However, it should be stressed here that ultimately, it is the deep appreciation of the background and motivation of the system that yield good mathematical models and provide guidance to good mathematical questions and solutions.

This paper is organized as follows. In the next section, we provide some simple and effective criteria to ensure logical consistence in the models (with explicit and implicit assumptions). The third section provides a set of criteria to be observed by most models involving predator-prey type interactions. The fourth section presents some new and plausible three dimensional population models that satisfy the criteria contained in the previous sections. These models are expected to provide rich dynamics of population interactions that often observed in the field. In the last section, we briefly discuss the various aspects of modelling population fluctuations. Specifically, we provide a heuristic ordering of importance of the many deterministic factors whose presence may cause population to fluctuate.

2 Logical Consistence

Consider the problem of modelling the interaction of two competing preys and one common predator. The following model is introduced in Leon and Tumpson (1975) appears to be plausible:

$$\begin{cases} N'_1 &= r_1 N_1 \left(1 - \frac{N_1 + c_{12} N_2}{K_1}\right) - \frac{a_1 N_1 P}{1 + b_1 N_1} \\ N'_2 &= r_2 N_2 \left(1 - \frac{N_2 + c_{21} N_1}{K_2}\right) - \frac{a_2 N_2 P}{1 + b_2 N_2} \\ P' &= \frac{e_1 a_1 N_1 P}{1 + b_1 N_1} + \frac{e_2 a_2 N_2 P}{1 + b_2 N_2} - dP. \end{cases} \quad (2.1)$$

The initial values are assumed to be nonnegative. The above model has appeared also in Vandermeer (1993).

If N_1 and N_2 are identical species, then $r_1 = r_2 = r$, $c_{12} = c_{21} = c$, $a_1 = a_2 = a$, $K_1 = K_2 = K$, $b_1 = b_2 = b$, $e_1 = e_2 = e$. Let $N = N_1 + N_2$, then the model that consistent with (1.1) should take the form

$$\begin{cases} N' &= rN \left(1 - \frac{N}{K}\right) - \frac{aN P}{1 + bN} \\ P' &= \frac{eaN P}{1 + bN} - dP. \end{cases} \quad (2.2)$$

If model (1.1) is a logically sound one, it should reduce itself to (1.2) in this situation. However, this is not the case, instead, it becomes

$$\begin{cases} N' &= rN \left(1 - \frac{N}{K}\right) - \frac{aN_1 P}{1 + bN_1} - \frac{aN_2 P}{1 + bN_2} \\ P' &= \frac{eaN_1 P}{1 + bN_1} + \frac{eaN_2 P}{1 + bN_2} - dP. \end{cases} \quad (2.3)$$

Arditi and Michalski (1996) thus point out that internal consistence of a theory of trophic interactions requires that model equations of such systems obey some basic logical

conditions.

- **Criterion 1.** The equations must be invariant under identification of identical species.
- **Criterion 2.** The system of equations for a food web must separate into independent subsystems if the community splits into disconnected sub-webs.

While these two criteria seem to easy to be satisfied, many models in the literature failed to do so. The previous model is just one of many such models. A logically consistent model of the two prey-one predator interaction may take the form

$$\begin{cases} N_1' &= r_1 N_1 \left(1 - \frac{N_1 + c_{12} N_2}{K_1}\right) - \frac{a_1 N_1 P}{1 + b_1 N_1 + b_2 N_2} \\ N_2' &= r_2 N_2 \left(1 - \frac{N_2 + c_{21} N_1}{K_2}\right) - \frac{a_2 N_2 P}{1 + b_1 N_1 + b_2 N_2} \\ P' &= \frac{e_1 a_1 N_1 P}{1 + b_1 N_1 + b_2 N_2} + \frac{e_2 a_2 N_2 P}{1 + b_1 N_1 + b_2 N_2} - dP. \end{cases} \quad (2.4)$$

Well, is this a good model now? It appears to be so if model (2.2) is sound. So, the question becomes: is model (2.2) a good predator-prey model? Unfortunately, there is no definite answer to this question. Indeed, such question brought a somewhat emotionally charged debate among theoretical biologists in the last several years and the debate is still lingering (see Abrams and Ginzburg (2000), Berryman et al.(1995) and the references cited). We will return to this in the next section.

We now turn our attention to patchy models. The following predator-prey system in a two-patch environment was introduced and investigated by Kuang and Takeuchi (1993):

$$\begin{cases} x_1' &= x_1 g_1(x_1) - y p_1(x_1) + \varepsilon(x_2 - x_1) \\ x_2' &= x_2 g_2(x_2) - y p_2(x_2) + \varepsilon(x_1 - x_2) \\ y' &= y[-s(y) + c_1 p_1(x_1) + c_2 p_2(x_2)]. \end{cases} \quad (2.5)$$

where $g_i(x_i)$, $p_i(x_i)$ and $s(y)$ are continuously differentiable functions. Here $x_i(t)$ represents the prey population in the i -th patch, $i = 1, 2$ at time $t \geq 0$. We think of patches with a barrier only as far as the prey population is concerned, whereas the predator population has no barriers between patches. Thus $y(t)$ stands for the total predator population for both patches. The following are assumptions for the involved functions.

(H1): $g_i(0) > 0$; $g_i'(x_i) < 0$; there is a $K_i > 0$ such that $g_i(K_i) = 0$, $i = 1, 2$.

(H2): $p_i(0) = 0$; $p_i'(x_i) > 0$, $i = 1, 2$.

ε is a positive constant that can be viewed as the dispersal rate or inverse barrier strength. It is assumed here that the net exchange from the j -th patch to i -th patch is proportional to the difference $x_j - x_i$ of population densities in each patch.

(H3): $s(0) > 0$; $s'(y) \geq 0$.

$c_i > 0$ is the conversion ratio of prey into predator.

Imagine that these two are identical patches, then $x_1 = x_2, c_1 = c_2, p_1 = p_2, g_1 = g_2$. Letting $x = x_1, g = g_1, p = p_1, c = c_1$, then the above model is reduce to

$$\begin{cases} x' &= xg(x) - yp(x) \\ y' &= y[-s(y) + 2cp(x)] \end{cases} \quad (2.6)$$

However, this is not what we expected. The expected model in such case is

$$\begin{cases} x' &= xg(x) - yp(x) \\ y' &= y[-s(y) + cp(x)]. \end{cases} \quad (2.7)$$

A more plausible model may take such form:

$$\begin{cases} x'_1 &= x_1g_1(x_1) - yx_1p_1(x_1, x_2) + \varepsilon(x_2 - x_1) \\ x'_2 &= x_2g_2(x_2) - yx_2p_2(x_1, x_2) + \varepsilon(x_1 - x_2) \\ y' &= y[-s(y) + c_1x_1p_1(x_1, x_2) + c_2x_2p_2(x_1, x_2)], \end{cases} \quad (2.8)$$

where $p_i(x_1, x_2) = P(x_1 + c_ix_2)$ for some function P and some constant c_i . For example, $p_i(x_1, x_2) = a_i/(1 + x_1 + x_2)$.

The above example lead us to propose the following criterion:

- **Criterion 3. The equations must be invariant under identification of identical patches.**

There are many situations where one need to subdivide a population into classes, such as juvenile and adult classes, infective and susceptible classes, normal cells and tumor cells, plasmid-bearing and plasmid-free classes or microorganism, etc. For such kind models, it is often assumed that these classes share a common growth limiting resource. In such situation, it is often necessary for the model equations to satisfy the following criterion.

- **Criterion 4. When a species is divided into classes, the crowding effect should be a function of the total species population density or weighted sum of these classes.**

Simple as it appears, the above criterion is often violated in the models appeared in the literature.

For example, the following model of a host-phage system is proposed by H.J. Bremermann (Bremermann (1983)).

$$\begin{aligned} \frac{dS(t)}{dt} &= \alpha S(t) \left(1 - \frac{S(t)}{C}\right) - KS(t)P(t) \\ \frac{dI(t)}{dt} &= KS(t)P(t) - \lambda I(t) \\ \frac{dP(t)}{dt} &= b\lambda I(t) - \mu P(t). \end{aligned} \quad (2.9)$$

Here S is the density of healthy bacteria and I is the density of infected bacteria and P the density of viruses. One can see that since the infected bacteria are competing with the

healthy bacteria for resource, the growth function for S should be $\alpha S(t)(1 - (S(t) + I(t))/C)$, instead of $\alpha S(t)(1 - S(t))/C$. A similar but more plausible model is introduced and studied in Beretta and Kuang (1998a). An even more realistic model of such system is proposed and investigated in Beretta and Kuang(2001).

To end this section, we want to point out that caution need to be exercised when using logistic equation to model a resource or a single species growth. The logistic equation, in its common form

$$x' = rx(1 - x/K) = rx - (r/K)x^2 \quad (2.10)$$

can be highly misleading (Ginzburg (1992)). For example, some researchers mistake r as the birth rate (for a example, see the deterministic parasite-host model in Ebert et al. (2000)). In reality, it is the birth rate minus natural death rate. In order to avoid such error, a prudent way to formulate the growth of a population is to identify its birth and death mechanisms (see Turchin (2001)). Simply put, the model in general takes the form

$$x' = B(x) - D(x), \quad (2.11)$$

where $B(x)$ describes the birth term and $D(x)$ describes the death term. In general, this (birth and death) approach should be adopted when formulating multi-species models.

3 Predator-Dependence vs. Prey-Dependence

Predator-prey interaction and competition are often viewed as the two main building blocks in mathematical population models. When species compete, they often compete for growth limited resources. When these resources are explicitly modelled (this is often necessary if we are to understand the more delicate dynamics of population interactions), a simple competition interaction maybe expanded as a multiple species predator-prey interactions. This suggests that predator-prey interaction is in fact almost the only and thus the dominant interaction in population dynamics. Naturally, the modelling of predator-prey interaction entails much care and indeed endured much debates (Abrams and Ginzburg (2000), Skalski and Gilliam (2001)).

According to Berryman et al.(1995), credible and simple predator-prey should in general possess some minimum biological and ecological properties. In brief terms, they are:

- **A: there is negative effect of predators on prey;**
- **B: there is positive effect of prey on predators;**
- **C: predators must have finite appetites and finite per-capita reproductive rates;**
- **D: when resources are low RELATIVE to population density, the predator per-capita growth rate should decline with its density.**

We may also add the following obvious property (positivity and dissipativity) to the above list.

- **E: solutions of positive initial conditions should stay positive and eventually uniformly bounded.**

Property B, while intuitive, fails if we also model the physiology make ups of the prey and predator and keep track of nutrient elements (such as Phosphorous and Nitrogen). Such stoichiometry based predator-prey model (Loladze, Kuang and Elser (2000)) can exhibit negative effect of prey on predators when a shared element is in short supply. For such models, several predator can coexist on a single prey (Loladze, Kuang, Elser and Fagan (2002)) in the form of stable steady state. Property B also fails when prey can form group defense (Freedman and Wolkowicz (1986)).

It is easy to see that model (2.2) satisfies properties A-C, and E. However, it fails to satisfy property D. This is because that the predator per-capita growth rate takes the form of $eaN/(1 + bN) - d$, which is independent of the density of P . Hence, the predator per-capita growth rate will NOT decline with its density even if resource is low RELATIVE to the predator population density.

Arditi and Ginzburg (1989) have suggested that, in situations characterized by strong space and time heterogeneities, the functional response can be approximated by a function of the prey (x)-to-predator (y) ratio (x/y). This function can be approximated by Michaelis-Menten-Holling form(so-called ratio-dependent form)

$$\frac{as}{b + s} = \frac{ax}{by + x}.$$

However, through formal mechanistic derivations, one often arrive at the more general and realistic Beddington functional response of the form (Beddington (1975), Huisman and De Boer (1997), Cosner et al. (1998))

$$\frac{ax}{by + x + c} = \frac{ax/y}{b + x/y + c/y}$$

or the so-called Hassell-Varley functional response of the form (Cosner et al. (1998), Skalski and Gilliam (2001))

$$\frac{ax}{bx + y^m}, \quad m \in (0, 1].$$

Following Huisman and De Boer (1997), I shall call models employing predator-depending predator functional response(s) as predator-dependent models.

Generally, a **predator-dependent** predator-prey model takes the form of

$$\begin{cases} x' = xg(x/K) - yP(x, y), x(0) > 0, \\ y' = cyP(x, y) - dy, y(0) > 0. \end{cases} \quad (3.1)$$

When $P(x, y) = p(x/y)$, we call model (1.4) (strictly)**ratio-dependent**.

The traditional (or **prey-dependent**) model takes the form

$$\begin{cases} x' = xg(x/K) - yp(x), x(0) > 0, \\ y' = cyp(x) - dy, y(0) > 0. \end{cases} \quad (3.2)$$

One can see that predator-dependent models do possess properties A-E while the prey-dependent ones lack property D.

Mathematically, we may think both the traditional prey-dependent and ratio-dependent models as limiting cases of the general predator-dependent ones (Beddington type or Hassell-Varley type functional responses).

It turns out that, in many aspects, the ratio-dependent models actually provide the richest dynamics, while the prey-dependent ones provide the least in dynamical behavior. Since the ratio-dependent form use one less parameter than the general Beddington or Hassell-Varley type functional responses, it is viewed by many biologists as a viable and sometimes preferred alternative to the traditional Holling type II functional response. However, as to be expected, when confronted with real data sets, both Holling type II and ratio-dependent functional responses do not fare well compare to those more general functional responses (Skalski and Gilliam (2001)).

Until very recently, both ecologists and mathematicians chose to ignore the rich dynamics provided by the strict ratio-dependent models, especially that on the boundary and close to the origin (the origin is a singular equilibrium, which renders direct local stability analysis impossible). Some researchers regard such interesting dynamics as “pathological behavior”. This is, however, a serious mistake. Emerging empirical and theoretical evidence (e.g., Akcakaya et al.(1995)) suggests that such “pathological behavior” is not only realistic, but the *lack of such dynamics in prey-predator models actually makes them pathological in a biological sense.* Recent efforts (Kuang and Beretta(1998), Kuang(1999), Hsu et al. (2001), (2001a), Xiao and Ruan (2001)) show that the presupposed “pathological behavior” of solutions are not pathological at all. To see this point more clearly, consider the following example of “pathological behavior”. For ratio-dependent model, even if there is a positive steady state, both prey and predator can still go extinct (Kuang (1999)). The extinction (i.e., the collapse of the system) may occur in two distinct ways. In one way, both species become extinct regardless of the initial densities. In the other case, both species will die out only if the initial prey/predator ratio is too low. In the first case, extinction often occurs as a result of high predator efficiency in catching and/or converting prey biomass. The second way has many subtle and interesting applications. For example, it indicates that altering the ratio of prey to predators through over-harvesting of prey species, or over-stocking of predators may lead to the collapse of the whole system and the extinction of both species.

According to Arditi and Michalski(1996), a possible generalization of this response to an arbitrary food web is

$$x'_i = f_1(X_{basal})x_i + \frac{a_i \sum_{k \in R(i)} e_{ki} x_k^{r(i)}}{x_i + \sum_{k \in R(i)} b_{ki} x_k^{r(i)}} x_i - \sum_{j \in C(i)} \frac{a_j x_i^{r(j)}}{x_j + \sum_{k \in R(j)} b_{kj} x_k^{r(j)}} x_j^{c(i)} - \mu_i x_i. \quad (3.3)$$

Here, two set of interrelated auxiliary variables are used:

$$x_i^{r(j)} = \frac{m_{ij} x_j^{c(i)}}{\sum_{k \in C(i)} m_{ik} x_k^{c(i)}} x_i, \quad x_j^{c(i)} = \frac{n_{ij} x_i^{r(j)}}{\sum_{k \in R(j)} n_{kj} x_k^{r(j)}} x_j, \quad (3.4)$$

where $R(i)$ is the set of all resources of species i ; $C(i)$ is the set of all consumers of species i . X_{basal} is the vector of abundances of all basal species (those that have no resources). n_{ij} is the relative preference of consumer x_j for resource x_i (among other resource species), and m_{ij} is the relative competition efficiency of consumer x_j (among other predator species) for resource x_i . Roughly speaking, $x_i^{r(j)}$ is the part of species x_i that is currently being accessed as a resource by species x_j , and $x_j^{c(i)}$ is the part of species x_j that is currently acting as a consumer on species x_i . Note that $x_i^{r(j)}$ and $x_j^{c(i)}$ are defined in a nested manner. These nesting equations actually describe the competition relations of predators compete by sharing their prey inter- and intraspecifically. The precise values of $x_i^{r(j)}$ and $x_j^{c(i)}$ can not, usually, be written as simple explicit functions of densities.

4 Some Ratio-Dependent Multiple-Species Population Models

It can be seen that the general model proposed by Arditi and Michalski(1996) is complicated in nature, and may not admit explicit expression when there are more than four species involved. However, in the case of simple food chain, this is straightforward. It takes the following general form.

$$\begin{cases} x'_i &= x_i[f_i(x_{i-1}/x_i) - g_i(x_i/x_{i+1})], \\ x'_n &= x_n f_n(x_{n-1}/x_n), \end{cases} \quad (4.1)$$

where $i = 1, \dots, n-1, n > 2, x_0 = K$.

More specifically, we can consider the specific case

$$\begin{cases} x'(t) &= rx \left(1 - \frac{x}{K}\right) - \frac{1}{\eta_1} \frac{m_1 xy}{a_1 y + x}, \\ y'(t) &= \frac{m_1 xy}{a_1 y + x} - d_1 y - \frac{1}{\eta_2} \frac{m_2 yz}{a_2 z + y}, \\ z'(t) &= \frac{m_2 yz}{a_2 z + y} - d_2 z, \end{cases} \quad (4.2)$$

where x, y, z stand for the population density of prey, predator and top predator, respectively. For $i = 1, 2, \eta_i, m_i, a_i, d_i$ are the yield constants, maximal predator growth rates, half-saturation constants and predator's death rates respectively. r and K , as before, are the prey intrinsic growth rate and carrying capacity respectively. Observe that the simple relation of these three species: z prey on y and only on y , and y prey on x and nutrient recycling is not accounted for. This simple relation produces the so-called simple food chain. A distinct feature of simple food chain is the so-called **domino effect**: if one species dies out, all the species at higher trophic levels die out as well. This model has been studied by Hsu et al. (2002). It turns out ratio-dependent food chain indeed possesses rich and novel dynamics. For example, it can have three coexistent attractors.

Other manageable cases (require careful computations) include two preys-one predator and one prey-two predators models.

One prey species shared by two predator species: The ratio-dependent model takes the form

$$\begin{cases} x' &= rx\left(1 - \frac{x}{K}\right) - \frac{c_1xu}{ax + u + mv} - \frac{c_2xmv}{bx + u + mv}, \\ u' &= u\left(-d_1 + \frac{e_1c_1x}{ax + u + mv}\right), \\ v' &= v\left(-d_2 + \frac{e_2c_2x}{bx + u + mv}\right). \end{cases} \quad (4.3)$$

Here the meanings of r, K are obvious and c_1, c_2 are catching efficiency constants. m is the relative efficiency of v with respect to u . $c_1/a, c_2m/b$ describes the maximum per-capita catching rate for u, v respectively. e_1, e_2 are conversion rates and d_1, d_2 are death rates. This model has been studied by Hsu et al. (2001a).

In the process of deriving the above model, we made use of the obvious fact that $u^{c(x)} = u, v^{c(x)} = v$. This leads to $x^{r(u)} = \frac{p_1u^{c(x)}x}{p_1u^{c(x)} + p_2v^{c(x)}} = \frac{p_1ux}{p_1u + p_2v}$, and $x^{r(v)} = \frac{p_2v^{c(x)}x}{p_1u^{c(x)} + p_2v^{c(x)}} = \frac{p_2vx}{p_1u + p_2v}$ for some positive constants p_1, p_2 .

If we are opt to use Beddington type functional response, than the above model may take the following more general form

$$\begin{cases} x' &= rx\left(1 - \frac{x}{K}\right) - \frac{c_1xu}{ax + u + mv + \alpha} - \frac{c_2xmv}{bx + u + mv + \beta}, \\ u' &= u\left(-d_1 + \frac{e_1c_1x}{ax + u + mv + \alpha}\right), \\ v' &= v\left(-d_2 + \frac{e_2c_2x}{bx + u + mv + \beta}\right). \end{cases} \quad (4.4)$$

The analysis on the ratio-dependent one prey-two predator model reveals some very interesting dynamics. While competitive exclusion principle still hold for most parameter values for the competing predators, it is very often that we see both can go extinct as either the result of the parameter values or the selection of initial data. For some parameter values, coexistence is indeed possible. Many other interesting dynamics can be shown through carefully designed computer simulations. These results are reported in Hsu et al. (2001a).

Two prey species competing for the same resource (implicitly) predated by one predator species: The strict ratio-dependent model takes the form

$$\begin{cases} u' &= r_1u\left(1 - \frac{u+v}{K}\right) - x\frac{c_1u^2}{(ax + u + mv)(u + mv)}, \\ v' &= r_2v\left(1 - \frac{u+v}{K}\right) - x\frac{c_2m^2v^2}{(ax + u + mv)(u + mv)}, \\ x' &= x\left(-d + \frac{e_1c_1u^2}{(ax + u + mv)(u + mv)} + \frac{e_2c_2m^2v^2}{(ax + u + mv)(u + mv)}\right). \end{cases} \quad (4.5)$$

Here the meanings of $r_1, r_2, K, c_1, c_2, e_1, e_2, d$ are obvious from the previous model. m is the relative preference of the predator on v with respect to u . This model is yet to be studied in detail. But it is expected that the predator may mediate the coexistence of the two competing prey species.

One can also use the Beddington functional response in the above model. This should result

$$\begin{cases} u' = r_1 u \left(1 - \frac{u+v}{K}\right) - x \frac{c_1 u^2}{(b+ax+u+mv)(u+mv)}, \\ v' = r_2 v \left(1 - \frac{u+v}{K}\right) - x \frac{c_2 m^2 v^2}{(b+ax+u+mv)(u+mv)}, \\ x' = x \left(-d + \frac{e_1 c_1 u^2}{(b+ax+u+mv)(u+mv)} + \frac{e_2 c_2 m^2 v^2}{(b+ax+u+mv)(u+mv)}\right). \end{cases} \quad (4.6)$$

One of the underlying fundamental biological question for the above models ((4.3)-(4.6)) is, how the invasion of a competing prey species or a predator species affect an existing predator-prey interaction? This is, of course, a very general question that can only be answered under more specific conditions. Mathematical analysis of proper models should enable us to pin down some of these conditions.

5 Modelling Population Fluctuations

Although about 90% population in nature do not exhibit sustainable oscillation (Krukonis and Schaffer (1991), Kendall et al (1998)), we tend to pay more attention to those do and often try to model such a behavior. There are four typical approaches for modelling such behavior: (i) introduce more species into the model, and consider the higher dimensional systems (like predator-prey interactions, May(1974)); (ii) assume that the per capita growth function is time dependent and periodic in time; (iii) take into account the time delay effect in the population dynamics (Smith and Kuang (1992), Zhao et al. (1997)); (iv) taking into account the random effect in the nature. Generally speaking, approach (i) is rather artificial, while (ii), (iii) and (iv) emphasize only one aspect of reality. Although all of them are good mechanisms of generating periodic solutions (and therefore offer some explanations to the often observed oscillatory behavior in population densities), it does not give us much insight as which is the real generating or dominating force behind the oscillatory behavior if only one of such mechanism is considered. Naturally, more realistic and interesting models of single species growth should take into account both the seasonality of the changing environment and the effects of time delays.

Existing results on the existence of periodic solutions in periodic differential equation population models suggests (Gopalsamy et al. (1990), Li (1999), Li and Kuang (2001), Kuang (1993), Tang and Kuang (1997) Zhang and Gopalsamy (1990)) that when strong seasonal force is in action, regardless the length of time delay and many other factors, it is often the primary factor causing notable population fluctuations. In addition, in such cases, the fluctuation is often quite robust and synchronizes with the season. When seasonal effect is weak or absent (this is often the case if the unit of time is long), but delay length is significant, then delay may be the primary source of destabilization. Indeed, significant delay can often lead to chaotic population behavior. In such cases, the stability of any fluctuation is often not clear. Indeed, there are often numerous periodic solution coexist.

If both the seasonal effect and time delay are significant, then seasonal behavior can still be observed (Li (1999), Li and Kuang (2001)). In this case, an important issue is whether or not cycles of multiple seasons exist and if they exist, what causes that. Time delay can well be a suspect. In cases both seasonal effect and time delay are insignificant, the cause of fluctuation may well be the result of predator-prey interactions of the system. Of course, to produce periodic solutions in such models, it is often necessary to assume that the predator functional responses are of Holling type II or III forms, or other more general predator-dependent forms. In these cases, the fluctuations are frequently robust.

In the case of discrete population models (modelled by difference equations), such kind of ordering of the cause of fluctuation is nonexistent. The reason is that in discrete models, both time delay and seasonal effect are often automatically built into the equations. This can explain why discrete models are so rich in dynamics (Kot (2001)).

To summarize these discussion, we may suggest the following statements as simple guidelines in selecting the more suitable model equations for oscillatory population dynamics.

Criteria for modelling population fluctuation:

- **Criterion 1.** When population fluctuation synchronizes with the season, a periodic differential equation model should be considered.
- **Criterion 2.** When the period of population fluctuation differs from the season period, and time delay is not negligible, then a delay differential equation model or difference equation model should be considered.
- **Criterion 3.** When seasonal effect and time delay effect are both negligible, then predator-prey interaction may be the catalyst of population fluctuation. In such cases, predation processes should be explicitly modelled.

References

- [1] P. A. Abrams and L. R. Ginzburg (2000): *The nature of predation: prey dependent, ratio-dependent or neither?* Trends in Ecology & Evolution, **15**, 337-341.
- [2] H. R. Akcakaya, R. Arditi and L. R. Ginzburg (1995): *Ratio-dependent prediction: an abstraction that works*, Ecology, **76**, 995-1004.
- [3] R. Arditi and J. Michalski (1996): *Nonlinear food web models and their response to increased basal productivity*, in *Food webs: Integration of Patterns and Dynamics*, eds. G. A. Polis and K. O. Winemiller, 122-133, Chapman and Hall, New York.
- [4] R. Arditi and L. R. Ginzburg (1989): *Coupling in predator-prey dynamics: ratio-dependence*, J. Theoretical Biology, **139**, 311-326.

- [5] J. R. Beddington (1975): *Mutual interference between parasites or predators and its effect on searching efficiency*, J. Anim. Ecol., **44**, 331-340.
- [6] E. Beretta and Y. Kuang (1998): *Global analyses in some delayed ratio-dependent predator-prey systems*, Nonlinear Analysis, T.M.A., **32**, 381-408.
- [7] E. Beretta and Y. Kuang (1998a): *Modeling and analysis of a marine bacteriophage infection*, Math. Biosc., **149**, 57-76.
- [8] E. Beretta and Y. Kuang (2001): *Modeling and analysis of a marine bacteriophage infection with latency period*, Nonlinear analysis: Real World Applications, **2**, 35-74.
- [9] H. J. Bremermann (1983): *Parasites at the origin of life*, J. Math. Biol., **16**, 165-180.
- [10] A. A. Berryman, A. P. Gutierrez and R. Arditi (1995): *Credible, realistic and useful predator-prey models*, Ecology, **76**, 1980-1985.
- [11] A. A. Berryman, J. Michalski, A. P. Gutierrez and R. Arditi (1995a): *Logistic theory of food web dynamics*, Ecology, **76**, 336-343.
- [12] C. Cosner, D. L. DeAngelis, J. S. Ault and D. B. Olson (1999): *Effects of spatial grouping on the functional response of predators*, Theor. Pop. Biol., **56**, 65-75.
- [13] D. L. DeAngelis, R. A. Goldstein and R. V. O'Neill (1975): *A model for trophic interaction*, Ecology, **56**, 881-892.
- [14] D. Ebert, M. Lipstich and K. L. Mangin (2000): *The effect of parasites on host population density and extinction: experimental epidemiology with Daphnia and six microparasites*, American Naturalist **156**, 459-477.
- [15] H. I. Freedman and G. S. K. Wolkowicz (1986): *Predator-prey systems with group defence: the paradox of enrichment revisited*, Bull. Math. Biol., **48**, 493-508.
- [16] R. E. Gaines and J. L. Mawhin (1977): *Coincidence Degree and Nonlinear Differential Equations*, Springer-Verlag, Berlin.
- [17] L. R. Ginzburg (1992): *Evolutionary consequences of basic growth equations*, Trends Ecol. Evol., **7**, 133-133.
- [18] L. R. Ginzburg and H. R. Akcakaya (1992): *Consequences of ratio-dependent predation for steady state properties of ecosystems*, Ecology, **73**, 1536-1543.
- [19] K. Gopalsamy, M. R. S. Kulenovic and G. Ladas (1990): *Environmental periodicity and time delays in a "food-limited" population model*, J. Math. Anal. Appl., **147**, 545-555.
- [20] S. B. Hsu, T. W. Hwang and Y. Kuang (2001): *Global Analysis of the Michaelis-Menten type ratio-dependence predator-prey system*, J. Math. Biol., **42**, 489-506.

- [21] S. B. Hsu, T. W. Hwang and Y. Kuang (2001a): *Rich dynamics of a ratio-dependent one prey two predator model*, J. Math. Biol., **43**, 377-396.
- [22] S. B. Hsu, T. W. Hwang and Y. Kuang (2002): *A ratio-dependent food chain model and its applications to biological control*, preprint.
- [23] G. Huisman and R. J. DeBoer (1997): *A formal derivation of the 'Beddington' functional response*, J. theor. Biol. **185**, 389-400
- [24] C. Jost, O. Arino and R. Arditi (1999): *About deterministic extinction in ratio-dependent predator-prey models*. Bull. Math. Biol., **61**, 19-32.
- [25] B. E. Kendall, J. Prendergast and O. N. Bjornstad (1998): *The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles*, Ecol. Letters, **1**, 160-164.
- [26] B. E. Kendall, C. J. Briggs, W. W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet and S. N. Wood (1999): *Why do populations cycle? A synthesis of statistical and mechanistic modelling approaches*, Ecology **80**, 1789-1805.
- [27] M. Kot (2001): *Elements of Mathematical Ecology*, Univ. Cambridge Press, Cambridge.
- [28] G. Krukonis and W. M. Schaffer (1991): *Population cycles in mammals and birds: does periodicity scale with body size?* Journal of Theor. Biol., **148**, 469-493.
- [29] Y. Kuang (1993): *Delay Differential Equations with Applications in Population Dynamics*, Academic Press, Boston.
- [30] Y. Kuang (1999): *Rich dynamics of Gause-type ratio-dependent predator-prey system*, The Fields Institute Communications **21**, 325-337.
- [31] Y. Kuang and E. Beretta (1998): *Global qualitative analysis of a ratio-dependent predator-prey system*, J. Math. Biol. **36**, 389-406.
- [32] Y. Kuang and Takeuchi (1993): *Predator-prey dynamics in models of prey dispersal in two-patch environments*, Math. Biosci., **120**, 77-98.
- [33] J. A. Leon and D. B. Tumpson (1975): *Competition between two species for two complementary or substitutable resources*, J. Theor. Biol., **50**, 185-201.
- [34] Y. Li (1999): *Periodic solutions of a periodic delay predator-prey system*, Proc. Amer. Math. Soc., **127**, 1331-1335.
- [35] Y. Li and Y. Kuang (2001): *Periodic solutions in periodic delay Lotka-Volterra equations and systems*, J. Math. Anal. Appl., **255**, 260-280.
- [36] I. Loladze, Y. Kuang and J. J. Elser (2000): *Stoichiometry in producer-grazer systems: Linking energy flow with element cycling*, Bull.Math. Biol., **62**, 1137-1162.

- [37] I. Loladze, Y. Kuang, J. Elser and W. Fagan (2002): *A stoichiometric exception to the competitive exclusion principle*, preprint.
- [38] R. M. May (2001): *Stability and Complexity in Model Ecosystems (Princeton Landmarks in Biology)*, Princeton University Press, Princeton.
- [39] J. Michalski and R. Arditi (1995): *Food web structure at equilibrium and far from it: is it the same?*, Proc. R. Soc. Lond. B **185**, 459-474.
- [40] J. Michalski, J.-Ch. Poggiale, R. Arditi and P. M. Auger (1997): *Macroscopic dynamic effects of migrations in patchy predator-prey systems*, J. Theor. biol. **259**, 217-222.
- [41] M. L. Rosenzweig (1969): *Paradox of enrichment: destabilization of exploitation systems in ecological time*, Science, **171**, 385-387.
- [42] G. T. Skalski and J. F. Gilliam (2001): *Functional responses with predator interference: viable alternatives to the Holling type II model*, Ecology, **82**, 3083-3092.
- [43] H. L. Smith and Y. Kuang (1992): *Periodic solutions of delay differential equations of threshold-type delays*, in: Oscillation and Dynamics in Delay Equations, Graef and Hale ed. 153-176, Contemporary Mathematics **129**, AMS, Providence.
- [44] B. R. Tang and Y. Kuang (1997): *Existence, uniqueness and asymptotic stability of periodic solutions of periodic functional differential systems*, Tohoku Mathematical Journal, **49**, 217-239.
- [45] P. Turchin (2001): *Does population ecology have general laws?*, OIKOS, **94**, 17-26.
- [46] J. Vandermeer (1993): *Loose coupling of predator-prey cycles: Entrainment, chaos, and intermittency in the classic MacArthur consumer-resource equations*, American Naturalist, **141**, 687-716.
- [47] B. G. Zhang and K. Gopalsamy (1990): *Global attractivity and oscillations in a periodic delay-logistic equation*, J. Math. Anal. Appl., **150**, 274-283.
- [48] T. Zhao, Y. Kuang and H. L. Smith (1997): *Global existence of periodic solutions in a class of delayed Gause-type predator-prey systems*, Nonlinear Analysis, TMA, **28**, 1373-1394.
- [49] D. Xiao and S. Ruan (2001): *Global dynamics of a ratio-dependent predator-prey system*, J. Math. Biol., **43**, 268-290.